



Review article

Testing of behavioural asymmetries as markers for brain lateralization of emotional states in pet dogs: A critical review

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ABSTRACT

Domestic dogs (*Canis familiaris*) hold a unique position in human society, particularly in their role as social companions; as such, it is important to understand their emotional lives. There has been growing interest in studying behavioural biases in dogs as indirect markers (reflecting lateralized brain activity) of their emotional states. In this paper, we not only review the previous literature on emotion-related behavioural lateralization in dogs, but also propose and apply the concept of evidential weight to previous research. This allows us to examine different hypotheses about emotion-related brain asymmetries (i.e., Right-Hemisphere-, Valence-, Approach-Withdrawal-Hypothesis) on the basis of a “likelihood-ist” concept of evidence. We argue that previous studies have not been able to discriminate well between competing hypotheses and tended to focus on confirmation bias than critically assess different hypotheses; as such there is a strong case for more systematic investigation to pull these theories apart. We present the areas for future research and explain their importance for understanding the emotional lives of dogs.

1. Introduction

The assessment of emotional states in non-human animals (hereafter referred to as “animals”) is important for research in various academic disciplines, including those investigating animal behaviour, animal cognition, comparative psychology, neuroscience, animal welfare and animal ethics (Paul et al., 2005). Emotional states (or emotions) are relatively short-lasting states that can occur in response to external stimuli (e.g., changes in the environment) and/or internal (mental) representations that (i) involve appraisal processes which assess the stimuli/internal representations as salient to current goals (Adolphs, 2010; Ben, Ze’ev, 2010; Scherer et al., 2005), (ii) are typically associated with changes in different response systems (e.g., peripheral physiological, behavioural, experiential (Mendl et al., 2010; Moors, 2009; Scherer et al., 2005) (iii) involve the activation of distinct neuronal networks (Palomero-Gallagher and Amunts, 2021), and (iv) are distinguishable from other affective phenomena such as moods (e.g., cheerfulness) or affective traits (e.g., shyness) in that they are typically associated with particular, identifiable objects (e.g., external stimuli and/or internal representations) (Ben-Ze’ev, 2010). The study of emotional states in non-human animals presents a particular challenge, since, unlike

humans, animals cannot give linguistic reports to describe their emotions. Research therefore relies exclusively on non-linguistic measures to draw conclusions about their emotional processes. As such, various neurobiological, physiological, endocrinological and behavioural markers are used to investigate animal emotional states.

One approach to studying emotions in (both humans and) animals is provided by correlates of brain lateralization research. Brain lateralization refers to functional asymmetries between the right and the left side of the brain. Although emotions are accepted to involve lateralized brain activity, the precise contribution of each hemisphere and its manifestations are still much debated (Demaree et al., 2005; Gainotti, 2019; Leliveld et al., 2013; Ocklenburg and Güntürkün, 2018; Palomero-Gallagher and Amunts, 2021). Different hypotheses are proposed including, for instance, the Right-Hemisphere-Hypothesis claiming that emotional states predominantly involve networks within the right hemisphere (Gainotti, 1972, 2019). Compared to that, the Valence- and the Approach-Withdrawal-Hypothesis assume that both hemispheres can play a prevailing role depending on either the predominant emotional valence (positive vs. negative) at the time or emotionally driven action tendencies (approach vs. withdrawal motivation), respectively (Davidson, 1995; Silberman and Weingartner, 1986) (see

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Fig. 1).

In animals, most findings on brain lateralization in emotional states are not inferred from direct measurements of the animals' brain, but indirectly through observations of asymmetric behaviour reflecting brain lateralization; i.e. behavioural asymmetries serve as markers of lateralized brain activity. The vertebrate nervous system has a predominantly contralateral organisation: Nerves to and from one side of the body cross the midline of the body and are mainly connected to the opposite side of the brain. As a result, sensory input from one side of the body (e.g., from the right or left eye, or ear) is mainly processed by the opposite side of the brain (Rogers et al., 2013; see Fig. 2a + b). A notable exception is the olfactory system, where the nerve fibres connect ipsilaterally to the brain (Royet and Plailly, 2004; see Fig. 2c). Not only afferent but also efferent pathways cross the midline of the body. Consequently, movements of the left or right half of the body are controlled by networks of the respective contralateral brain hemisphere (see Fig. 3). Given this organisation of the vertebrate nervous system, lateralized brain activity in emotionally relevant contexts can be studied indirectly by examining behavioural biases. For example, if an animal assesses a stimulus as emotionally salient and inspects this stimulus predominantly with one eye/ear/nostril and/or shows emotionally motivated (expressive and/or other) asymmetric motor behaviour in response to the stimulus, conclusions may be drawn on this basis about the relative activity of the two brain hemispheres. Provided that lateralized brain activity is indirectly reflected in behavioural asymmetries, lateralization research is expected to provide a non-invasive, easy-to-use and cost-effective methodological approach to investigate animal emotions.

In this paper we begin by reviewing the hypothesised relationships between brain lateralization and emotions which provide the theoretical basis for empirical studies in animals. We then discuss the previous literature on behavioural markers of brain lateralization during emotional states in pet dogs. Unlike previous reviews on pet dogs and other animals (Leliveld et al., 2013; Siniscalchi et al., 2017, 2021), the current review provides a detailed discussion of the evidential weight of recent lateralization research with dogs on competing hypotheses by applying a “likelihood-ist” concept of evidence (Hájek and Joyce, 2008; Meester and Slooten, 2021; Royall, 1997). We argue that previous studies with dogs have not been able to effectively discriminate between competing hypotheses and suggest directions for future studies to systematically investigate the different hypotheses about lateralization and emotion in dogs (and other animals).

2. Brain lateralization and emotional states

Animal research mainly focuses three hypotheses on brain lateralization and emotional states: The Right Hemisphere Hypothesis, the Valence Hypothesis, and the Approach Withdrawal Hypothesis (see Fig. 1). All three hypotheses were originally introduced in the context of human research and later applied in research on (vertebrate) animals.

- (1) **Right Hemisphere Hypothesis (hereafter “RHH”)**: For any emotional state, the constituent brain processes predominantly

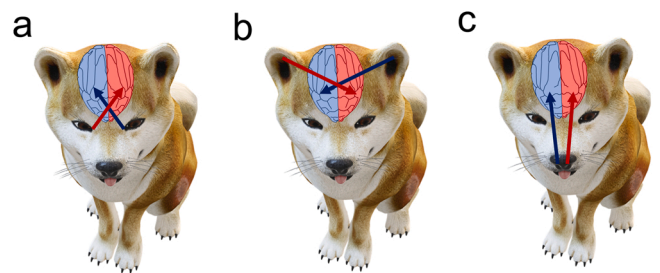


Fig. 2. Organisation of the vertebrate nervous system. (a) Visual and (b) auditory sensory input from one side of the body (i.e., from the right or left eye, or ear) is mainly processed by the opposite side of the brain; (c) olfactory information is mainly transmitted to the ipsilateral hemisphere.

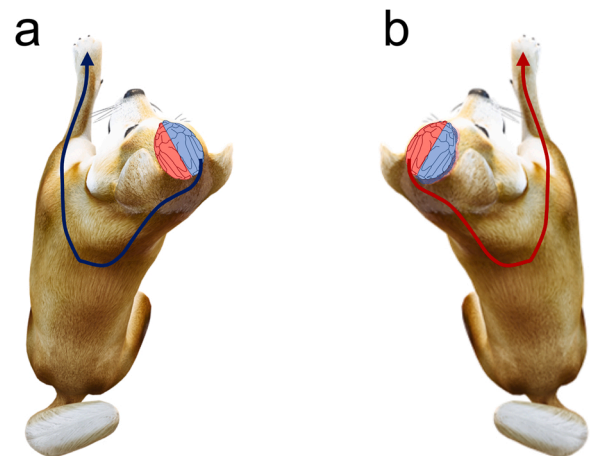


Fig. 3. Organisation of the vertebrate nervous system. Movements of (a) the left or (b) right half of the body are mainly controlled by networks of the respective contralateral brain hemisphere.

involve the activation of the right hemisphere (Gainotti, 1972, 2019).

- (2) **Valence Hypothesis (hereafter “VH”)**: For emotional states with a negative emotional valence, the constituent brain processes predominantly involve the activation of the right hemisphere, whereas the left hemisphere is relatively more involved in emotional states with a positive valence. (Silberman and Weingartner, 1986).
- (3) **Approach Withdrawal Hypothesis (hereafter “AWH”)**: For emotional states which are associated with approach and withdrawal motivations, brain processes that subserve these states are associated with a dominant activity of the left and right hemisphere, respectively (Davidson, 1995).

AWH only relates to lateralized brain processes insofar as emotionally relevant contexts motivate approach/withdrawal tendencies. In

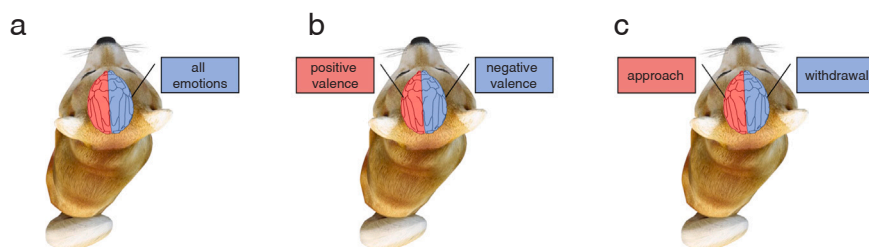


Fig. 1. Different hypotheses on emotion-related brain lateralization. (a) Right-Hemisphere-Hypothesis; (b) Valence-Hypothesis; (c) Approach-Withdrawal-Hypothesis.

contrast, the other two hypotheses generate predictions even if such tendencies are absent. To illustrate the potential inter-relationships and distinctions between these hypotheses, consider the following: If a stimulus is appraised as rewarding and positively valenced, it may induce an emotional state involving stimulus-directed approach motivation. Provided that stimulus-directed approach tendencies are a constituent part of this emotional state, all three hypotheses, i.e. RHH, VH and AWH, predict asymmetric brain activity. However, after the rewarding stimulus has been successfully approached, stimulus-related emotions might still be present (e.g., happiness, contentment). In such post-goal attainment emotional states, only RHH and VH generate predictions. Compared to that, AWH applies exclusively to pre-goal attainment emotional states, when there is still engagement in stimulus-directed approach (or withdrawal) behaviour. In contrast to RHH, VH and AWH claim that either hemisphere might play a dominant role depending on the emotionally relevant contexts. While VH assumes that the valence (positive vs. negative) of the emotionally relevant context determines which hemisphere is predominantly active, AWH asserts that hemispheric dominance is a function of the behavioural motivational dimension (i.e., approach vs. withdrawal) of the emotion. The two hypotheses often overlap in their predictions about the direction of brain lateralization. Emotions that are typically classified as positive (e.g., happiness) are likely to motivate approach behaviour, while emotions that are typically classified as negative (e.g., disgust or fear) are often associated with behavioural withdrawal. However, frustration and anger (emotions associated with a reduction in autonomy) are negatively valenced but may be associated with approach behaviour tendencies (Carver and Harmon-Jones, 2009): For example, to protect a resource from another, an individual may move forward to place itself between the resources and the one who is perceived as potentially trying to take it from them. While VH predicts a dominant role of the right hemispheric networks in such circumstances, AWH predicts a relatively higher activity of the left hemisphere. While some research findings provide support for one or more hypotheses, other findings show stronger evidence for one or more of the other hypotheses. To date, there is no consensus as to whether any particular hypothesis is epistemically superior to the others (Demaree et al., 2005; Gainotti, 2019; Leliveld et al., 2013; Ocklenburg and Güntürkün, 2018; Palomero-Gallagher and Amunts, 2021).

2.1. Brain lateralization and emotional states in pet dogs

Given the unique position of domestic dogs (*Canis familiaris*) in society and their increasingly important role as social companions, there is particular interest in dogs' emotional lives. Their close association with humans in diverse, complex social relationships, also makes them interesting potential models for comparative work concerning the phylogenetic development of emotional processes. In the last 15 years, research has shown a growing interest in studying lateralized behaviour in dogs as an indirect marker for asymmetric brain activity in dogs' emotional states. Most work has focussed on behavioural asymmetries in dogs' sensory functioning (e.g., lateralized eye/ear/nosril use) when attending to emotionally salient stimuli, whereas only few studies explored other behavioural asymmetries, such as emotionally expressive motor behaviours (e.g., lateralized tail wagging or facial expressions). To investigate behavioural signatures of brain lateralization during emotional states, researchers often analysed dogs' responses to two particular types of emotionally relevant stimuli: (i) Stimuli that were assessed as presumably alarming (e.g., threatening facial expression of a conspecific) and that were likely associated with negative emotions, and (ii) stimuli that were evaluated as pro-social (e.g., friendly facial expression of a conspecific) and thus related to positive emotions. Research suggests that dogs' responses to potentially alarming stimuli invoke relatively increased engagement of the right hemisphere, whereas most responses to prosocial stimuli indicate a left hemispherical dominance. Lateralized responses in dogs have also been observed in

relation to stimuli that may have been appraised as emotionally relevant, but for which it was less clear either how they were perceived emotionally (iii), or whether the stimulus-induced lateralization pattern reflected brain processes subserving non-emotional functions rather than emotion-specific asymmetric brain activity (iv). In the following sections, previous research on dogs is reviewed and critically evaluated with regard to what they tell us about the competing hypotheses on emotion-related brain lateralization (i.e., RHH, VH, and AWH).

2.2. Alarming stimuli

2.2.1. Right hemisphere superiority in response to alarming stimuli

Several studies investigating behavioural asymmetries at the level of sensory functions suggest a predominant involvement of the right hemisphere in response to different, presumably alarming stimuli (see Table 1). In the visual domain, for example, researchers observed a superior role of the left eye in dogs when attending to images featuring potentially alarming motifs. Given the contralateral organisation of the vertebrate visual system, this left eye dominance suggests increased use of right hemispheric networks subserving visual processing. For instance, a relatively increased activity of the left eye/right hemisphere system was indicated by dogs' head orienting response, when they were shown images of a snake or a cat displaying a threatening posture (Siniscalchi et al., 2010). In particular, when two drawings (showing a snake or cat) were presented simultaneously in dogs' right and left visual hemifield, they turned their head predominantly with the left eye leading. Compared to that, no eye bias was observed in response to drawings of a conspecific in a relaxed posture. In a similar head orienting paradigm, dog head movements also indicated dominant involvement of the left eye/right hemisphere system in response to pictures showing angry or fearful human facial expressions (Siniscalchi et al., 2018a). However, the researchers also documented the same pattern of lateralization for happy human faces. Based on further physiological and behavioural indicators, Siniscalchi et al. (2018a) argued that the dogs may have misjudged the happy faces and evaluated them as alarming too. Specifically, happy faces were associated with cardiac activity and behavioural "stress/anxiety" scores which were similar to those in response to angry and fearful faces, but higher compared to other emotionally expressive (e.g., sad, surprised, and disgusted) faces. The reported left eye/right hemisphere advantage when viewing presumably alarming human facial expressions corroborates findings of previous studies (Racca et al., 2012; Barber et al., 2016). Compared to Siniscalchi et al. (2018a), previous studies also discovered a left eye advantage in attending to neutral, i.e. supposedly less emotionally expressive, human faces (Racca et al., 2012; Barber et al., 2016). Yet, since research on humans shows that neutral faces are sometimes processed in a similar way to fearful faces (Lee et al., 2008), dogs' display of a left eye/right hemisphere lateralization may be interpreted as a response to stimuli that were appraised as aversive rather than neutral. This is also consistent with the work of Guo et al. (2009) on dogs' gaze bias towards human faces (although see the later work, Siniscalchi et al., 2018a for a different result). Alternatively, dogs' response to neutral faces may suggest a general specialisation of the left eye/right hemisphere system in processing facial expressions rather than demonstrating a right hemisphere dominance for processing alarming stimuli in particular, which was the original interpretation of the work by Guo et al. (2009). For instance, experiments in sheep (Kendrick, 2006; Peirce et al., 2000, 2001) and non-human primates (Hamilton and Vermeire, 1998; Pinsk et al., 2005) support the idea of a general specialisation of the right hemisphere for facial recognition – a function that has presumably descended from abilities by early vertebrates to visually recognise other individuals (MacNeilage et al., 2009) and which can be explained by a general superiority of the right hemisphere for processing spatial and configurational relations between visual objects and their properties (Rogers et al., 2013). However, given that dogs can display a right eye/left hemisphere system advantage in

Table 1

List of studies reporting behavioral biases in response to emotionally relevant alarming stimuli.

Alarming stimuli					
	Publication	Stimulus	Finding	Dominant hemisphere	Relative evidence for
Sensory processing (visual)	Siniscalchi et al., 2010	Simultaneous presentation of two identical pictures with alarming motives (e.g., picture of a cat showing a threatening posture) in the dogs' left and right visual field	Head turns to the left picture (left eye dominance)	Right	RHH & VH vs. AWH
	Racca et al. (2012)	Pictures with threatening (i) conspecific, and (ii) human facial expressions	Left eye dominance	Right	RHH & VH vs. AWH
	Siniscalchi et al. (2018a)	Simultaneous presentation of two identical pictures with alarming (e.g., angry, fearful) human facial expressions in the dogs' left and right visual field	Head turns to the left picture (left eye dominance)	Right	RHH & VH vs. AWH
	Barber et al. (2016)	Pictures with alarming human (e.g., angry) facial expressions	Left eye dominance	Right	RHH & VH vs. AWH
Sensory processing (auditory)	Siniscalchi et al., 2008	(i) Sounds of thunderstorm, and (ii) alarming conspecific vocalisations (e.g., during contexts of "isolation"), broadcasted simultaneously from two speakers installed symmetrically to the left and right side of the dogs' head	(i) Head turns to the left speaker (left ear dominance)	(i) Right	(i) RHH & VH vs. AWH
			(ii) Head turns to the left speaker (right ear dominance)	(ii) Left	(ii) AWHvs. RHH & VH
	Reinholz-Trojan et al., 2012	(i) Alarming conspecific vocalisations (i.e., dog barking at an unfamiliar conspecific), and (ii) threatening cat vocalisations, broadcasted from a single speaker positioned centrally behind to the dogs	Head turns to the left (left ear dominance)	Right	Alternative explanation: Left hemisphere dominance reflects a general hemispheric specialisation for processing conspecific vocalisations RHH & VH vs. AWH
	Siniscalchi et al. (2018b)	Alarming non-verbal human emotional (e.g., screaming) vocalisations, broadcasted simultaneously from two speakers installed symmetrically relative to the dogs' head	Head turns to the left speaker (left ear dominance)	Right	RHH & VH vs. AWH
Sensory processing (olfactory)	Siniscalchi et al., 2011	Odours of adrenaline and veterinary sweat	Right nostril dominance	Right	RHH & VH vs. AWH
	Siniscalchi et al., 2016	Odour of (i) a conspecific's secretions collected soon after a distressing situation, and (ii) human sweat of fear	(i) Right nostril dominance	(i) Right	(i) RHH & VH vs. AWH
			(ii) Left nostril dominance	(ii) Left	(ii) AWHvs. RHH & VH
Motor behaviour (expressive)	Quaranta et al. (2007)	Appearance of an agonistic conspecific	Left-biased tail wagging movements	Right	RHH & VH vs. AWH

response to other emotionally relevant, presumably non-alarming, (conspecific and human) faces (e.g., see [Racca et al., 2012](#) and Sections 3.2 and 3.3), the idea of a general right hemisphere specialisation that dominates for all facial processing in dogs is challenged.

In the auditory domain, a prevailing role of the left ear was observed in dogs when attending to presumably alarming acoustic stimuli. Like the visual system, the vertebrate auditory system is largely contralaterally organised. Hence, the reported left ear predominance suggests an advantage of right hemispheric networks controlling auditory functions. For example, in several studies using a head orienting paradigm, a right hemisphere advantage was indicated when dogs preferentially turned their heads with the left ear leading in response to presumably alarming sounds, broadcasted either simultaneously from two speakers installed symmetrically relative to the dogs' head, or from a single speaker positioned centrally behind the dog: Sounds of thunderstorm ([Siniscalchi et al., 2008](#)), threatening cat meows ([Reinholz-Trojan et al., 2012](#)), and non-verbal human emotional vocalisations (i.e., screaming, sobbing, and growling) that may have been appraised as alarming ([Siniscalchi et al., 2018b](#)). In response to vocalisations of conspecifics, dogs' head turning behaviour suggests lateralized hemispheric activity as well. Listening to vocalisations associated with a

"disturbance situation" (a stranger knocked on the door of the dog owner's house), an "isolation situation" (the dog was in a room of the house isolated from their owner), and a "play situation" (either two dogs or a human and a dog played together), dogs showed an overall bias to orient their heads with the right ear leading ([Siniscalchi et al., 2008](#)). However, a bias towards turning the head with the left ear leading was observed when any of the presented sounds induced behaviours which were associated with an increase in the additionally computed "stress/anxiety" scores. While the right ear advantage in dogs (without elevated "stress/anxiety" levels) may be explained by the general specialisation of the right ear/left hemisphere system of the vertebrate brain in processing conspecific vocalisations ([Ocklenburg et al., 2013](#)), the left ear bias in dogs (with elevated "stress/anxiety" levels) may substantiate a dominant role of the right hemisphere in attendance to alarming stimuli. Playbacks of a dog barking at an unfamiliar conspecific which might also have been perceived as alarming, were found to be associated with a left ear/right hemisphere superiority as well ([Reinholz-Trojan et al., 2012](#)).

In the olfactory domain, dogs have shown an asymmetric use of their nostrils when sniffing at different odours. In exposure to odours of veterinary sweat and adrenaline, dogs preferentially used their right nostril

during stimulus inspection (Siniscalchi et al., 2011). Due to the ipsilateral organisation of the olfactory system, the predominant role of the right nostril indicates a relatively higher activity of the right hemisphere. Non-alarming odours (e.g., odours of dog food, lemon, vaginal secretion of a female dog) were not associated with the same right nostril bias. In a more recent study, lateralized sniffing behaviour was also observed for secretions of a conspecific collected soon after a distressing situation and human sweat of fear (Siniscalchi et al., 2016). Additionally, recorded behaviours related to the categories of “stress/anxiety” and “alerting/targeting” indicated that both odours were likely perceived as more alarming than other stimuli (e.g., conspecific/human odour samples collected during situations of relaxation, joy or sportive activities). However, while conspecific secretions involved a prevalent activity of the right nostril/right hemisphere, dogs displayed a left nostril/left hemisphere bias when sniffing at samples of human sweat of fear.

Apart from sensory functions, lateralized behaviour in response to alarming stimuli has also been observed at the level of emotionally expressive motor behaviours. When facing an agonistic conspecific, dogs exhibited emotionally expressive left-biased tail wagging movements (i.e., the amplitudes of tail-wagging to the left side were higher compared to the right side) (Quaranta et al., 2007). Since left-lateralized tail movements suggest a relatively increased engagement of motor networks in the contralateral hemisphere, this finding also points to a special role of the right hemisphere for potentially alarming contexts. Non-alarming stimuli (e.g., dog owner) were associated with a different pattern of lateralized tail wagging movements (see Section 3.2). Moreover, a follow-up study demonstrated that dogs are sensitive to asymmetric tail wagging displayed by a conspecific: They showed relatively increased cardiac activity and more fear-related behaviours when observing left- compared to right-lateralized tail movements (Siniscalchi et al., 2013), indicating that patterns of asymmetric tail wagging behaviour may have a signalling function in intra-specific communication.

2.2.2. Lateralized responses to alarming stimuli in evidence for/against competing hypotheses on lateralization and emotional states

To discuss the evidential bearing of the suggested right hemisphere advantage in response to alarming stimuli on competing hypotheses concerning brain lateralization, it is necessary to go beyond considering falsification a simple binary concept, as is commonly implied in scientific research – i.e., Huxley’s “slaying of a beautiful hypothesis by an ugly fact” (Huxley, 1870). With conflicting data (that lacks overt experimental flaws that might explain the conflict) and multiple potentially viable explanations, a notion of evidence needs to be assumed which recognises it as both a probabilistic and genuinely comparative concept. Evidence can thus be defined as information that changes the probability with which a hypothesis H_1 is (believed to be) correct, relative to another, competing hypothesis H_2 (Hájek and Joyce, 2008; Meester and Slooten, 2021; Royall, 1997). Hence, assessing the relative evidentiary importance of a finding F on H_1 vs. H_2 requires us to explore how F changes the evidence for each hypothesis, i.e. if $P(H_n|F)$ denotes the probability with which H_n is (believed to be) correct when F is known, and $P(H_n)$ denotes the probability with which H_n is (believed to be) correct prior to observing F , thus we are seeking to determine the relative value of $\frac{P(H_1|F)}{P(H_1)}$ to $\frac{P(H_2|F)}{P(H_2)}$. Hence, the strength of evidence for H_1 vs. H_2 is expressed by x in the equation: $\frac{P(H_1|F)}{P(H_1)} = \frac{P(H_2|F)}{P(H_2)} \times x$. If $x > 1$, then the evidence for H_1 is stronger than the evidence for H_2 . In accordance with Bayes’ theorem: $P(H_n|F) = \frac{P(F|H_n) \times P(H_n)}{P(F)}$, i.e. a mathematical formula in probability theory describing the calculus of conditional probabilities, the equation $\frac{P(H_1|F)}{P(H_1)} = \frac{P(H_2|F)}{P(H_2)} \times x$ can be transformed to $x = \frac{P(F|H_1)}{P(F|H_2)}$, with $P(F|H_n)$ denoting the probability of observing F assuming that H_n is correct.

$\frac{P(F|H_1)}{P(F|H_2)}$ is defined as the likelihood ratio $LR(H_1, H_2; F)$ which thus measures the evidence that F provides for/against H_1 vs. H_2 by comparing F ’s predictability on the basis of H_1 with F ’s predictability on the basis of H_2 (Hájek and Joyce, 2008; Meester and Slooten, 2021; Royall, 1997). The likelihood ratio does not measure the evidence of a finding for/against a single hypothesis, but instead it quantifies the evidential weight of a finding on a certain hypothesis, *relative to another*. Just as the more $LR(H_1, H_2; F)$ is greater than 1, the stronger the evidence of F for H_1 vs. H_2 and the closer $LR(H_1, H_2; F)$ is to 0, the stronger the evidence of F against H_1 vs. H_2 , so the closer $LR(H_1, H_2; F)$ is to 1, the less relevant F is to distinguishing between H_1 and H_2 .

In the previous section, if we consider that F denotes one of the findings indicating a dominant right hemispheric involvement in response to presumably emotionally relevant, alarming stimuli, the probability of obtaining F was high assuming that RHH was correct: $P(F|RHH) \approx 1$. Given that alarming stimuli are typically associated with negative emotions, the probability of obtaining F was also high on the assumption that VH was correct: $P(F|VH) \approx 1$. Since the ratio of these two hypothesis-specific probabilities $LR(RHH, VH; F) \approx 1$, F does not provide evidence for/against RHH vs. VH. Thus, each of the above-mentioned study findings is evidentially irrelevant when comparing these two hypotheses. If AWH were correct, the probability of observing F depends on the dogs’ motivational state when attending to the alarming stimulus. Alarming stimuli may induce a stimulus-withdrawal motivation (e.g., “flight” response), but could also produce a stimulus-directed approach motivation (e.g., “fight” response), or the absence of any approach/withdrawal motivation (e.g., “freeze” response). Only in the case of a withdrawal motivation, would the probability of obtaining F have been high, i.e. $P(F|AWH \& Withdrawal Motivation) \approx 1$. Yet, information about the dogs’ motivational tendencies is largely lacking for the studies reviewed above. Only in a few cases, were further behavioural responses additionally recorded that may give information about the motivational dimension. In some of the work by Siniscalchi and colleagues (2016, 2018a, 2018b) there are behavioural “stress/anxiety” scores computed on the basis of a display of multiple possible behaviours some of which were associated with withdrawal (i.e., 4 of ≥ 26 behaviours) or freezing behaviour (i.e., 1 of ≥ 26 behaviours). However, we do not have the specific details relating to these. Nonetheless, given that dogs’ “stress/anxiety” scores were highest when attending to alarming compared to non-alarming stimuli, and that this was associated with increased right hemispheric activity, it seems reasonable to suggest that withdrawal or freezing tendencies were more likely to occur than approach behaviour in these conditions. Thus, the experiment does provide some potential evidence in support of AWH. However, in another part of the study, the researchers also calculated “alerting/targeting” scores, based on behaviours some of which were related to approach (i.e., 1 of 14 behaviours) or freezing behaviour (i.e., 1 of 14 behaviours) (Siniscalchi et al., 2016). When dogs’ behavioural responses indicated predominant right hemispherical involvement in relation to putatively alarming stimuli, not only were there higher scores for the “stress/anxiety” dimension (relative to other less alarming stimuli), but also there were higher scores on this “alerting/targeting” dimension. Overall, the few available (indirect) indicators of the dogs’ motivation provide little information: Based on the two behavioural scores, all three motivational states (i.e., approach motivation, withdrawal motivation, freezing or absence of approach/withdrawal motivation) could be expressed in relation to the “alerting/targeting” score, and there is no basis on which to assume that any of these states were more likely to occur than the others. Therefore, it could be justified to remain agnostic about dogs’ motivational state and to assume that each possible state could have been observed with similar probability. In that case, the probability of observing F was ≈ 0.33 , if AWH were correct. Comparing this hypothesis with RHH and VH, the likelihood ratios $LR(RHH, AWH; F) \approx LR(VH, AWH; F) \approx 3$ indicate that each of the reported study findings evidentially supports both RHH and VH more than

AWH.

If the finding F is repeated on multiple occasions, i.e. in separate studies or with separate stimuli, then we will have a series of findings F_1, \dots, F_n for which dogs' motivational states remains unknown, then the combined likelihood ratios will increase beyond 3:

$$LR(RHH, AWH; F_1, \dots, F_n) : \frac{P(F_1|RHH) \times \dots \times P(F_n|RHH)}{P(F_1|AWH) \times \dots \times P(F_n|AWH)}$$

\approx

$$LR(VH, AWH; F_1, \dots, F_n) : \frac{P(F_1|VH) \times \dots \times P(F_n|VH)}{P(F_1|AWH) \times \dots \times P(F_n|AWH)}$$

$\approx 3^n$

A combined likelihood ratio of 3^n says that the probability of obtaining all the above presented findings suggesting a right hemisphere advantage is 3^n times higher if either RHH or VH are correct, compared to when AWH is correct, where n is the number of observations (experiments) where this result is found.

In summary, we argue that given the studies presented, pairwise comparisons of the competing hypotheses using likelihood ratios yield greater evidential support for both RHH and VH, relative to AWH (see Table 1). The findings can however not discriminate between RHH and VH. The relative advantage of RHH and VH over AWH is apparent both in the context of lateralized sensory functioning and in relation to emotionally expressive motor asymmetries.

2.3. Pro-social stimuli

2.3.1. Most findings suggest a left hemisphere dominance in response to pro-social stimuli

Compared to the right hemispherical dominance reported for alarming stimuli, most studies investigating lateralized behaviour in dogs attending to presumably emotionally relevant pro-social stimuli suggest a left hemispherical dominance (see Table 2). For example, dogs frequently analyse putatively pro-social facial expressions of conspecifics with their right eye/left hemisphere system (Racca et al., 2012). A relatively increased activity of left hemispheric structures is also indicated when dogs preferentially orient their heads with the right ear leading in response to non-verbal pro-social emotional vocalisations of humans (laughing), broadcasted simultaneously from two speakers installed symmetrically relative to the dogs' head (Siniscalchi et al., 2018b).

However, in contrast to these findings, there have also been reports of different lateralization patterns for dogs' behavioural responses when presented with human faces that were supposed to be emotionally

relevant and pro-social stimuli, including no preferential eye use (Racca et al., 2012), or a left eye bias (Barber et al., 2016) during stimulus inspection. Neither Racca et al. (2012) nor Barber et al. (2016) collected additional behavioural and/or physiological measures to provide further information about how the dogs perceived the human faces. Therefore, it cannot be excluded, at least in the former case, that the supposedly friendly faces were deemed not to be emotionally salient. Indeed, it has been suggested that dogs may sometimes misunderstand images with happy human faces and perceive them as potentially alarming (Siniscalchi et al., 2018a), and this might explain the left eye dominance reported by Barber and colleagues (2016).

Apart from asymmetric sensory functions, dogs have also been reported to show lateralized emotionally expressive motor behaviour in response to presumably pro-social stimuli. For instance, after being left alone for a short period, dogs showed right-lateralized tail wagging behaviour when their owner appeared, indicating dominant left hemisphere activity (Quaranta et al., 2007). A more recent study recorded lateralized tail wagging behaviour of laboratory Beagles during social interactions with a previously unfamiliar human (i.e., the experimenter) for one 5-minute session per day on 3 consecutive days (Ren et al., 2022). Whereas the dogs showed either left-lateralized or no asymmetric tail wagging during the first day's session, they subsequently developed a bias to the right side during the sessions on the following days. While, in general, the dogs' tail wagging likely represented emotional expressive behaviour, the different lateralization patterns could be associated with a change in how the dogs' appraised the context emotionally over time. Considering that laboratory dogs usually interact less frequently with (unknown) humans compared to pet dogs, their left- or non-lateralized tail wagging during their first encounter with the unknown experimenter could be related to tentativeness and being insecure about the situation. Compared to this, the shift toward right-biased tail wagging movements could be associated with the development of increasing confidence and the appraisal of the context as more comfortable and pro-social once the dogs had become more familiar with the experimenter in subsequent encounters.

2.3.2. Lateralized responses to pro-social stimuli – consideration of evidential weight in relation to competing hypotheses on lateralization and emotional states

If F denotes one of the reported findings suggesting a left hemispherical advantage in dogs when presented with a presumably emotionally relevant pro-social stimulus, the probability of observing F would be low, if the RHH is correct: $P(F|RHH) \approx 0$. Compared to this, the probability of F is high, if the VH is correct: $P(F|VH) \approx 1$. Regarding AWH, the probability of observing F depends on dogs' motivational

Table 2

List of studies reporting behavioral biases in response to emotionally relevant pro-social stimuli.

	Pro-social stimuli		Finding	Dominant hemisphere	Relative evidence for
	Publication	Stimulus			
Sensory processing (visual)	Racca et al. (2012)	Pictures with pro-social (friendly) (i) conspecific and (ii) human facial expressions	(i) Right eye dominance	(i) Left	(i) VH & AWH vs. RHH
	Barber et al. (2016)	Pictures with pro-social (happy) human facial expressions	(ii) No eye dominance Left eye dominance	(ii) No dominance Right	(ii) Neither hypothesis RHH vs. VH & AWH
Sensory processing (auditory)	Siniscalchi et al. (2018b)	Pro-social non-verbal human emotional (laughing) vocalisations, broadcasted simultaneously from two speakers installed symmetrically to the left and right side of the dogs' head	Head turns to the right speaker (right ear dominance)	Left	VH & AWH vs. RHH
Motor behaviour (expressive)	Quaranta et al. (2007)	Appearance of the dog owner	Right-biased tail wagging movements	Left	VH & AWH vs. RHH
	Ren et al. (2022)	Pro-social interaction with a human	Right-biased tail wagging movements	Left	VH & AWH vs. RHH

state. Only in the case of stimulus-directed approach motivation, would the probability be high: $P(F|AWH \& \text{Approach Motivation}) \approx 1$. However, when studies do not give information about dogs' motivational state, it is not clear whether this condition is met. On the one hand, it seems reasonable to argue that especially the appearance of an owner will induce an approach motivation in dogs (e.g., Topál et al., 1998); but on the other hand, it is less certain whether abstract 2-dimensional pictures of conspecific faces and broadcasted laughing-vocalisations induce stimulus-directed approach behaviour or if any approach-avoidance tendencies remain absent. For dogs' lateralized responses in which the motivational state is not entirely certain, it may be assumed that $P(F|AWH)$ is less than 1. Based on the reported left hemisphere advantage for pro-social stimuli, pairwise comparisons of the three competing hypotheses using likelihood ratios yield clear evidence for both VH and AWH, compared to RHH. However, since the likelihood ratio $LR(VH, AWH; F)$ may be only slightly larger than 1, the evidence-based discrimination between VH and AWH is less clear. The non-lateralized visual processing of friendly faces reported by Racca et al. (2012) does not provide relative support for any of the competing hypotheses but contradicts what any of the hypotheses would have predicted. If the happy human faces shown by Barber et al. (2016) were perceived as pro-social (and not as alarming as presumably happened in the study by

Siniscalchi et al., 2018a), the probability of finding the left eye/right hemisphere bias reported was high if RHH were correct, and low if VH or AWH were correct.

Taken together, these findings on both dogs' asymmetric sensory functioning and emotionally expressive motor behaviours in response to supposedly pro-social stimuli seem to provide greater support for both VH and AWH, than RHH (see Table 2). The findings do not sufficiently discriminate between VH and AWH, though.

2.4. Other emotionally relevant stimuli

In some studies, dogs have been presented with stimuli that may also have been emotionally salient, but for which it is less clear how they were appraised and, thus, what qualified them as emotionally competent stimuli or of a particular valence (see Table 3). For instance, in exposure to surprised human facial expressions, dogs displayed a right eye/left hemisphere bias (Siniscalchi et al., 2018a). Assuming that dogs perceived this stimulus as emotionally relevant, the probability of this finding is low if RHH is correct: $P(F|RHH) \approx 0$. If either VH or AWH were correct, the probability of the left hemispherical dominance depends, respectively, on the valence appraised in the faces by the dogs and on the motivational state which the stimulus induced in the dogs. The reported

Table 3

List of studies reporting behavioral biases in response to stimuli that may have been appraised as emotionally relevant, but for which it was less clear either how they were perceived emotionally, or whether the stimulus-induced lateralization pattern reflected brain processes subserving non-emotional functions rather than emotion-specific asymmetric brain activity.

Other stimuli					
	Publication	Stimulus	Finding	Dominant hemisphere	Relative evidence for
Sensory processing (visual)	Siniscalchi et al. (2018a)	Simultaneous presentation of two identical pictures with surprised human facial expressions in the dogs' left and right visual field	Head turns to the right picture (right eye dominance)	Left	Unclear
	Siniscalchi et al., 2019	Flock of sheep	Higher frequencies of aggressive behaviours when sheep were seen in the left visual field	Right	RHH vs. VH & AWH Alternative explanation: Right hemisphere dominance reflects hemispheric specialised processes in the context of non-emotional predatory behaviour
Sensory processing (olfactory)	Siniscalchi et al., 2011	Odour of food	Left nostril bias	Left	VH & AWH vs. RHH Alternative explanation: Left hemisphere dominance reflects food-related lateralization that occurs independent of the emotional salience of the stimulus
Motor behaviour (expressive)	Nagasawa et al., 2013	Appearance of the owner or an unfamiliar person after a short period of being left alone	left-lateralized facial movements	Right	RHH vs. VH & AWH Alternative explanation: Right hemisphere dominance reflects hemispheric specialised processing in the context of individual recognition and/or novelty-sensitivity
	Quaranta et al. (2007)	Appearance of a cat	Right-biased tail wagging movements	Left	Unclear
Motor behaviour (other)	Charlton and Frasnelli (2022); Duncan et al. (2022); Laverack et al. (2021)	Food or toy	Right paw bias when reaching for the food or toy item	Left	VH & AWH vs. RHH Alternative explanation: Left hemisphere dominance reflects food-related lateralization that occurs independent of the emotional salience of the stimulus

results give insufficient information to determine either of these. Depending on the context, an unexpected, surprising event may have a negative (negative surprise) or positive (positive surprise) valence. Human facial expressions to surprising events are dynamic: Initial responses are primarily driven by the unexpectedness of the surprising event and reflect a state in which the event does not make sense yet, whereas later expressions, after sense-making, are more likely to incorporate the valence of the event itself (Noordewier and van Dijk, 2019). While initial human facial expressions to negative and positive surprising events are similar, expressions at a later stage, after sense-making, differ as a function of valence: Positive surprising events are associated with an increase in smiles (increased activity of the zygomaticus) and negative surprising events are linked to brow lowering (Noordewier and van Dijk, 2019). Whereas the initial valence-unspecific facial expression can be considered as the actual surprise face, the later more valence-specific responses are more likely associated with facial expressions of emotional states that follow after having made sense of the surprising event. Hence, without additional information, it is uncertain how dogs appraised the surprised human face presented to them. Without further information, dogs' motivational state also remains undetermined. Thus, given the missing information, the probability of the bias found was clearly larger than 0 but smaller than 1, if either VH or AWH are correct. Since the likelihood ratio $LR(VH, AWH; F)$ can be assumed to be close to 1, this finding cannot discriminate between VH and AWH. Yet, given that the likelihood ratios $LR(VH, RHH; F)$ and $LR(AWH, RHH; F)$ are certainly larger than 1, this finding supports both VH and AWH over RHH.

When attending to a cat, dogs showed right-lateralized tail wagging behaviour (Quaranta et al., 2007) suggesting a relatively stronger engagement of motor networks in the left hemisphere. While the dogs' tail wagging behaviour, regardless of any lateralization, likely demonstrates an emotionally expressive display, this motor behaviour, however, does not allow any conclusions as to how dogs perceived the cat emotionally: Depending on individual dogs' previous experiences, the cat may have been associated with a negative or positive emotional valence and may have induced withdrawal or approach behaviour. Thus, as with the dogs' preferential eye use in response to human surprise faces, the documented right-biased emotionally expressive tail wagging behaviour supports VH and AWH over RHH but cannot discriminate between VH and AWH.

2.5. Some lateralized responses might be the result of other hemispherically specialised processes not related to emotional states

In some contexts, the display of asymmetric behavioural responses might correlate to other specialized hemispherical functions not related to emotional states (see Table 3). For instance, dogs have been reported to show a left nostril/left hemisphere superiority when presented with the odour of dog food (Siniscalchi et al., 2011). This finding may be interpreted as a lateralized response to an emotionally salient stimulus that was likely associated with both a positive valence and approach behaviour. The probability of left hemispherical advantage is low if RHH is correct: $P(F|RHH) \approx 0$, but high if either VH or AWH are correct: $P(F|VH) \approx P(F|AWH) \approx 1$; thus this finding provides evidence-based support for VH and AWH over RHH without discriminating between VH and AWH. Yet, given that feeding behaviour is associated with a general specialisation of left-brain networks, which indirectly manifests itself in different lateralized behaviours in various species (Güntürkün et al., 2020; Leliveld, 2019; MacNeillage et al., 2009; Rogers, 2002; Rogers et al., 2013; Vallortigara and Rogers, 2020), dogs' left nostril/left hemisphere bias could also be the result of other food-related lateralization activity that occurs independent of the emotional salience of the food stimulus. Therefore, it cannot be said for certain whether dogs' response reflected emotion-specific hemispheric lateralization or rather non-emotional food-related specialised activation of the left side of the brain.

When sheepdogs were exposed to a flock of sheep, dogs showed higher frequencies of livestock-directed aggressive behaviours (i.e., gripping at sheep's leg) during counter-clockwise movements around the flock compared to clockwise turns (Siniscalchi et al., 2019). Given that sheep were mainly seen in the left visual hemifield during counterclockwise movements, this finding might indicate a role for the right hemisphere in mediating the aggressive behaviour. If the aggressive display was related to an emotional state, the probability of right hemispherical dominance is high if RHH is correct: $P(F|RHH) \approx 1$. Although "affective aggression" is often associated with negative emotions, predatory behaviour (predatory aggression) and its derivatives are associated with positive valence (Panksepp, 1998). The latter is the more reasonable basis to the behaviour of interest here. Thus, the probability of the observed aggression is low if VH is correct: $P(F|VH) \approx 0$. Given that these dogs' aggressive displays included approach behaviour, the probability of this finding is also low if AWH is correct: $P(F|AWH) \approx 0$. That is, the ratios of these hypothesis-specific probabilities provide evidence for RHH vs. VH and AWH. However, it might be questioned whether the aggressive behaviour was actually part of dogs' emotional functioning. Gripping at sheep's legs can be interpreted as a reduced expression of the predatory "grab-bite": being an element of the carnivorous predatory modal action pattern sequence, the "grab-bite" is performed to immobilise prey (Coppinger and Feinstein, 2015). These sequences are relatively intrinsic, stereotyped traits with a strong genetic basis (Coppinger et al., 2015). It is unclear whether they necessarily involve an emotional dimension, although affective neuroscientists like Panksepp (1998) argue they involve a strong element of the positive emotion referred to as SEEKING. In the former case, the right hemispherical dominance might reflect hemispheric specialised processes in the context of predatory behaviour rather than emotion-specific brain asymmetries.

At the level of emotionally expressive motor behaviour, left-lateralized facial movements have been observed in dogs when they were presented with either their owner or an unfamiliar person after a short period of being left alone in a room (Nagasawa et al., 2013). Considering that, after a period of social isolation, the appearance of the owner or unfamiliar person elicits a positive emotional reaction and approach tendencies in dogs, right hemispherical dominance is highly probable if RHH is correct: $P(F|RHH) \approx 1$, but unforeseen if either VH or AWH were correct: $P(F|VH) \approx P(F|AWH) \approx 0$. Hence, the resulting likelihood ratios $LR(RHH, VH; F)$ and $LR(RHH, AWH; F)$ seem to support RHH over both VH and AWH. Alternatively, left-lateralized facial movements/predominant right hemispheric involvement could be explained by a hemispheric specialised processing of unexpected and novel stimuli. The experimenter, while being invisible to the dogs, called the dogs' name to attract their attention. Shortly after, the owner/unfamiliar person appeared. This particular combination of auditory (i.e., familiar experimenter's voice) and visual information (i.e., appearance of the owner/unfamiliar person) would be unexpected. A special role of the right hemisphere in individual recognition (Hamilton and Vermeire, 1988; Kendrick et al., 2001; Leliveld, 2019; Ocklenburg and Güntürkün, 2018; Vallortigara and Andrew, 1994) and its sensitivity to unexpected and novel stimuli (Leliveld, 2019; MacNeillage et al., 2009; Rogers et al., 2013; Siniscalchi et al., 2021; Vallortigara and Rogers, 2020) has been documented in various species and might explain the dogs' left-biased facial movements in this case.

Asymmetric motor behaviour has also been observed when dogs preferentially used their right paw to reach for a rewarding food or toy stimulus that was placed under a piece of furniture (Charlton and Frasnelli, 2022; Duncan et al., 2022; Laverack et al., 2021). Compared to the previously reported tail wagging and facial movements, this reaching behaviour represents an emotionally motivated, operative goal-directed approach behaviour rather than emotionally expressive behaviour. Lateralized paw use has also been reported in other potentially emotionally relevant contexts: For instance, dogs showed paw preferences when holding a Kong™ (KONG Company, Golden, CO,

USA), a hollow, conical-shaped toy, while retrieving food placed inside it (Barnard et al., 2018; Simon et al., 2022; Tomkins et al., 2010; Wells et al., 2018), or when removing an adhesive tape from their head (Wells et al., 2018). While both stimuli motivate stimulus-directed approach behaviour, a food-stuffed Kong™ might be associated with a positive emotional valence whereas a sticky tape on the dogs' head could be appraised as negatively valenced. However, compared to the "reaching for food/toy" task, dogs' preferential paw use to hold a Kong™ or to remove a tape occurred only at an individual level, i.e. in single individuals, regardless of any common directional bias in the population (Barnard et al., 2018; Simon et al., 2022; Tomkins et al., 2010; Wells et al., 2018). While the observed paw use when holding the Kong™ or removing the tape is evidentially irrelevant for the competing hypotheses on lateralization and emotion, the right paw/left hemisphere dominance in the reaching for food/toy task seems highly probable if VH or AWH are correct: $P(F|VH) \approx P(F|AWH) \approx 1$, but unlikely if RHH is correct: $P(F|RHH) \approx 0$. Hence, the resulting likelihood ratios $LR(VH, RHH; F)$ and $LR(AWH, RHH; F)$ seem to support VH and AWH over RHH. However, as with the reported left nostril/left hemisphere dominance in response to the odour of food, the preferential use of the right paw to reach for food might reflect a food-related dominant engagement of left-hemispheric networks, that occurs independent of the emotional salience of the stimulus. Considering that research in various vertebrate species suggests a specialised role of the left hemisphere for prey-catching behaviour (Rogers et al., 2013), and given that playing with a toy can involve prey-related behaviours in dogs, the observed right paw bias to reach for a toy could possibly also reflect a dominant activation of the left brain which occurred regardless of the emotional salience of the presented stimulus. Moreover, since dogs show preferential paw use also in contexts that seem neither emotionally salient nor involve food/toy rewards, the observed lateralized pattern in dogs' reaching behaviour might also be explained by brain lateralization of functions outside emotional functioning or feeding/prey-catching behaviour. For example, a right-paw preference was also documented in a simple locomotor task investigating which paw dogs preferentially use when starting walking (Tomkins et al., 2010). However, more recent studies on preferential paw use in locomotor behaviour could not reproduce this finding and documented lateralized paw use only at an individual level (Barnard et al., 2017; Wells et al., 2018; Simon et al., 2022; Wells et al., 2018).

These examples illustrate that some of the dogs' lateralized behaviours could also reflect asymmetric brain activity relating to non-emotional functions rather than emotion-specific hemispheric asymmetries. Possibly, the final lateralized behavioural output might reflect the overall sum of several lateralized brain processes that subserve both emotion-specific and non-emotional functions. While a finding may supply evidence for one of the three hypotheses, i.e. RHH, VH or AWH, compared to the other two hypotheses, the same finding may be insufficient to support this particular hypothesis over other hypotheses which concern brain lateralization of non-emotional functions. Assessing the relative evidential weight of a finding on a particular hypothesis on brain lateralization in emotional states requires not only determining the likelihood ratios between this particular hypothesis and competing hypotheses on lateralization and emotions, but also consideration of hypotheses relating to brain asymmetries associated with non-emotional functions.

2.6. Overall relative support for VH?

In response to potentially alarming stimuli, the lateralization patterns of both the dogs' sensory functions and motor behaviour (i.e., emotional expressive or other emotionally motivated behaviour) provide support for RHH and VH over AWH. In comparison, the lateralization of the dogs' sensory functions and motor responses in relation to other emotionally salient stimuli indicate an advantage of VH and AWH over RHH. Taken together, this indicates greater relative support for the

VH. It is however crucial to note that the presented comparative assessment of the three competing hypotheses might be biased by the lack of important information in the published literature, which might allow a fuller assessment. In particular, the reviewed studies did not provide sufficient information about the dogs' motivational state in the emotional contexts being investigated. This is an oversight which should be addressed in future. For several studies, it remains unknown whether the presented stimuli induced approach or withdrawal tendencies or no such motivation at all. Not knowing the stimulus-driven motivational tendencies affects the relative probabilities of obtaining the reported findings, if AWH is correct. This leads to likelihood ratios indicating an epistemic superiority of RHH and VH vs. AWH in the context of alarming stimuli and overall advantage of VH over AWH. Thus, if more information had been available for the studies conducted so far, the comparative assessment of the three hypotheses might have come to a different conclusion. To carry out more informed comparisons between the competing hypotheses, future research needs to include assessments of dogs' motivational dimension.

2.7. Research on more varied emotional contexts is needed

A better-informed comparative assessment of the three hypotheses on lateralization and emotional states requires specification/evidence of dogs' motivational states. Taking into account the motivational aspect alone, however, will not provide sufficient information to discriminate between the different hypotheses. For instance, most of the reviewed findings on potentially positively valenced emotional stimuli suggested a predominant engagement of the left hemisphere. Yet, even if the required information about motivational states had been available, the dogs' lateralized responses would not have been sufficient to discriminate between VH and AWH: Since rewarding, positively valenced stimuli likely motivate approach behaviour, the left hemisphere advantage would have been equally probable if either VH or AWH were correct. Only scenarios that involve both a negative emotional valence and engagement in approach behaviour, or the converse, can produce the lateralization patterns that can provide relative evidence for/against these two different hypotheses. The probability of observing behavioural asymmetries suggesting either left- or right-lateralized brain activation in such a scenario would be different if either VH or AWH were correct and, thus, the resulting likelihood ratio $LR(VH, AWH; F)$ would supply support for/against VH vs. AWH. In this regard, contexts associated with anger or frustration seem particularly valuable. Anger- and frustration-eliciting stimuli are typically appraised as negatively valenced but can motivate stimulus-directed approach tendencies (Carver and Harmon-Jones, 2009).

Apart from contexts of anger and frustration, a systematic, evidence-based assessment of the three hypotheses needs to extend to various further, not yet investigated, emotionally relevant scenarios. So far, most research on dogs has examined lateralization in relation to attending to emotionally salient alarming or pro-social stimuli. Some work also suggests lateralized brain activation in response to stimuli for which it was less clear how dogs perceived them emotionally, or whether the stimulus-induced lateralized response was due to emotional functioning at all. Given that the three competing hypotheses claim validity for all kinds of emotional contexts, a more comprehensive comparative evaluation of the different hypotheses requires the investigation of lateralization in a wider range of different settings involving more diverse types of emotional stimuli.

3. Are the different hypotheses mutually exclusive?

Most of the previous dog literature and, thus far, also the current review has presented the different hypotheses about lateralization and emotional states as supporting the concept of a generalized dominance of a particular brain hemisphere over its contralateral counterpart. If, within the framework of one of the three hypotheses, predictions are

made about lateralization in the context of a particular emotional state, all brain processes subserving the constituent components of this emotional state (e.g., stimulus appraisal, emotional expression, subjective feelings, action tendencies etc.) are predicted to exhibit an identical consistent directional hemispheric asymmetry pattern. In this context, RHH, VH and AWH are seen as being mutually exclusive, competing hypotheses in that they predict incompatible brain lateralization patterns in specific emotionally relevant situations.

Lateralization research with humans is increasingly challenging the simplistic view of a generalized hemispheric unilateral dominance in emotional states. Studies on brain asymmetries and emotions in humans have reported conflicting results (Demaree et al., 2005; Ocklenburg and Güntürkün, 2018): For each of the three hypotheses, i.e. RHH, VH and AWH, experimental findings can be cited that provide evidence for one of these hypotheses, relative to the other two. While some studies provide strong relative support for RHH, other findings show more relative evidence for VH; still others supply relative evidence for AWH (studies providing relative evidence for either RHH, VH, or AWH are reviewed in: Demaree et al., 2005; Ocklenburg and Güntürkün, 2018). In human research, these inconsistencies between studies have finally resulted in a shift in the research question: The question "Is RHH, VH or AWH the best hypothesis?" has given way to the question "Are there specific emotionally salient contexts and particular brain networks subserving certain components of emotions for which right-hemispheric activity or valence-/motivation-modulated brain asymmetries are relevant?" (Ocklenburg and Güntürkün, 2018; Palomero-Gallagher and Amunts, 2021). While the former question suggests pitting competing and seemingly incompatible hypotheses against each other, the latter question allows for a more integrative approach. In this context, it has been proposed that the three hypotheses may reflect different aspects of emotions. This allows for multiple interconnected emotion-related brain networks that may be associated with different patterns of lateralization (Fusar, Poli et al., 2009; Killgore and Yurgelun, Todd, 2007; Neumann et al., 2008).

Future research in dogs (and other animals) should take these developments into account. Indeed, compared to human research, the reviewed studies on dogs documented fewer conflicting results and indicate an overall epistemic superiority of VH over RHH and AWH. However, as demonstrated in Sections 3.5 and 3.6, this superiority of VH may be biased by the lack of information on the dogs' motivational states and the limited range of emotional contexts investigated. Awareness must be raised of the possibility that different contexts and different components of dogs' emotional states may be associated with varying lateralization patterns that can be best explained by an integrative model according to which RHH, VH and AWH are not mutually exclusive hypotheses but relate to different aspects of emotional states and complement each other. To explore such an integrative hypothesis, it is not only important to investigate behavioural/brain lateralization in various settings involving many different emotionally salient stimuli, but also to study lateralization relating to different aspects of emotional states. According to the Component Process Modell, emotions are multicomponent states involving different physiological, cognitive and behavioural components (Scherer, 2005). So far, most studies focussed on lateralized sensory processing of emotionally salient stimuli. Within the Component Process Modell, asymmetric visual, auditory and olfactory processing of emotional stimuli might be primarily associated with the component of stimulus appraisal (i.e., how a stimulus is assessed emotionally). Compared to this, other components have been less studied and should receive more attention in future work. For example, lateralized emotional expression or other emotionally motivated motor behaviour of dogs are components that has been rarely addressed to date. Indeed, a few findings on lateralized emotional expressive and other emotionally motivated motor behaviours have been published and, as with the findings on lateralized sensory functioning, these findings offer relative support for VH. Yet further studies on different emotionally motivated motor behaviours in response to various

emotionally relevant stimuli are needed to validate this as a generalisation. For instance, future studies could explore asymmetries in various emotionally expressive/communicative behaviour, during emotionally relevant social interactions, and in the context of self-directed behaviours and "displacement activities" (e.g., scratching, autogrooming, body shaking) occurring in emotional situations.

4. Implications for the assessment of dogs' well-being

A central motivation for recent studies exploring behavioural manifestations of emotion-related brain asymmetries in dogs (and other species) is related to research into potential indicators of animals' states of welfare: If patterns of behavioural lateralization allow conclusions about welfare-relevant aspects of emotional states, such patterns could contribute to assessing animals' well-being (Berlinghieri et al., 2021; Leliveld, 2019; Leliveld et al., 2013; Rogers, 2010, 2011; Rogers and Kaplan, 2019; Siniscalchi et al., 2021).

It is generally assumed that emotional states reflect improvements or decrements in individuals' well-being depending on their valence: While positively valenced emotions likely enhance an individual's well-being, negatively valenced emotions have rather compromising effects on welfare. Thus, if particular brain networks show valence-specific patterns of hemispheric asymmetry, as claimed by VH, the observation of lateralized behavioural correlates could provide a valuable, non-invasive, and cost-effective approach to assess emotion-related effects on animal welfare. For example, if a dog constantly uses the right nostril/right hemisphere when sniffing at the scent mark of a conspecific that walks a few meters ahead, or shows frequent behavioural biases in a shelter environment indicating a relatively increased right hemisphere activation, this could indicate that the dog may be predisposed to negatively valenced emotional states. Specifically in the absence of other clear behavioural (e.g., avoidance behaviour, aggressive display, vocalisations) and physiological (e.g., piloerection) signs, the dog's right nostril use could help to indicate a dog's emotional appraisal of the situation and potential welfare-related consequences. This could inform the actions required to well-being.

Considering that previous research with dogs suggests an overall relative support for VH, emotion-related behavioural biases indeed appear to be a promising tool for assessing dogs' well-being. However, as discussed in Section 3.5, this epistemic superiority of VH may be biased by the lack of important information in the published literature. Specifically, the studies reviewed did not include sufficient information on the motivational state of the dogs in the emotional contexts studied and have thus not been able to discriminate well between VH and AWH. Moreover, since recent studies with humans suggest that different contexts and different components of emotional states may be associated with different patterns of hemispheric asymmetries, RHH, VH, and AWH are possibly not mutually exclusive but complementary hypotheses that relate to different aspects of emotion (Fusar, Poli et al., 2009; Killgore and Yurgelun, Todd, 2007; Neumann et al., 2008; Ocklenburg and Güntürkün, 2018; Palomero-Gallagher and Amunts, 2021). That is, there is currently no certainty as to whether – and if so, which – behavioural/brain asymmetries in dogs are indicative of emotional valence, or emotionally motivated approach and withdrawal tendencies, or emotional salience in general.

If patterns of lateralized activity in certain brain networks and their potential behavioural correlates do not reflect the valence of an emotional state, but motivational tendencies or emotional salience in general, as hypothesised by AWH and RHH, respectively, it is less clear how this might contribute to informing on an animal's welfare state. Compared to emotions' positive and negative valence, respectively, the association between emotionally motivated approach/withdrawal tendencies and enhancing/compromising effects on well-being is less straightforward. Certainly, since emotion-related approach tendencies are often associated with a positive emotional valence, whereas withdrawal motivations usually occur in the context of an emotionally

negatively valenced situation, motivational tendencies (and potential lateralized behavioural markers) might be indicative of welfare-relevant implications in many cases. However, the link between motivational approach tendencies, positive emotional valence and welfare-enhancing effects is not expected in all contexts. Specifically, approach motivation can occur in association with positively valenced emotions that might promote well-being, as well as in the context of negatively valenced emotions that probably reduce well-being. For example, if a dog expects to gain access to a desired object (e.g., food, toy, social partner), they may experience an emotional state of positive anticipation (Boissy et al., 2007; Spruijt et al., 2001; Van Den Bos et al., 2003). Yet, when the access to the desired object is delayed or denied, the state of positive anticipation can easily turn into frustration (Bremhorst et al., 2019; McPeake et al., 2019; Pedretti et al., 2022). While both emotional states are likely associated with object-directed approach motivation, they differ in their emotional valence (i.e., positive anticipation: positive; frustration: negative) and may involve opposite effects on the animal's well-being (i.e., positive anticipation: enhancing effect; frustration: compromising effect). Considering that contexts eliciting positive anticipation and frustration are likely to occur frequently in a dog's daily life, transitions between the two states might be fluid and the predominant predisposition might be difficult to determine. Episodes of frustration can be associated with aggressive behaviour (Panksepp and Zellner, 2004) and therefore have potentially wider welfare-relevant implications, nonetheless it is important to identify biomarkers that can distinguish between positive anticipation and frustration within a specific individual at a given time. Given that the described contexts of positive anticipation and frustration are both associated with approach motivation, behavioural/hemispheric asymmetries that simply reflect goal-directed motivational tendencies cannot distinguish between these two states and so allow evaluation of associated welfare-related implications. By contrast, valence-sensitive patterns of behavioural/brain asymmetries could indeed contribute to discriminate between episodes of positive anticipation (i.e., positive emotional valence) and frustration (i.e., negative emotional valence), and to estimate associated effects on well-being.

If there are patterns of lateralized activation in particular brain networks that do not reflect any specific aspects of emotional-motivational states (e.g., emotional valence, motivational tendencies), but simply indicate the general emotional salience of a certain context, as proposed by RHH, the observation of potential lateralized behavioural manifestations does not allow any inferences about emotion-related welfare consequences. However, assuming that the strength of behavioural/brain lateralization may correlate with the intensity of emotions (Larose et al., 2006; Siniscalchi et al., 2016), the degree of lateralization could be indicative of the extent to which particular emotional states (inferred through other means (e.g., Mills, 2017) enhance or reduce well-being.

In summary, particularly in the case of valence-specific patterns of hemispheric asymmetries, the observation of correlated behavioural biases could be a powerful tool for assessing welfare-relevant effects of emotions, complementing other behavioural, cognitive, and physiological indicators of dogs' well-being. In the case of behavioural/brain asymmetry patterns that are indicative of motivational approach and withdrawal tendencies or emotional salience in general, the potential contribution of behavioural biases for assessing states of welfare is more limited. To establish behavioural asymmetries as potent indicators of emotion-related well-being, research needs to determine whether and in what circumstances behavioural/brain asymmetries are indicative of emotional valence, or emotionally motivated approach and withdrawal tendencies, or general emotional salience. It is important to note that, when using behavioural asymmetries as potential indicators of emotion-related well-being, one should always bear in mind the possibility that, in some emotionally relevant contexts, behavioural biases could also reflect other specialised hemispheric functions unrelated to emotional states (see Section 3.4)."

5. Implications for research with other animal species

Emotion-related behavioural biases have been studied in various animal species (for reviews, see Berlinghieri et al., 2021; fish: Leliveld, 2019; ungulates: Leliveld et al., 2013; various vertebrate species; Siniscalchi et al., 2021; domestic animals). The current review of the literature published on dogs revealed some important conclusions which are just as relevant for research with other animal species. For instance, a comprehensive knowledge of emotion-related behavioural/brain lateralisation in dogs, but also in any other species, requires the exploration of a wide range of different situations with different types of emotionally salient stimuli. Similar to the literature reviewed on dogs, most studies with other pet and farm animals examined lateralized behaviour in response to presumably emotionally salient alarming stimuli and pro-social stimuli (Berlinghieri et al., 2021; Leliveld, 2019; Siniscalchi et al., 2021). However, some studies also investigated other emotionally relevant situations: For instance, Gygas et al. (2013) documented lateralized haemodynamic prefrontal activation in dwarf goats during situations of frustration. Moreover, two earlier studies reported lateralized behaviour in situations related to sex and mating behaviour in domestic chickens (Rogers et al., 1985; Workman and Andrew, 1986). Sex-related behaviours might be associated with different emotional states: e.g., positively valenced emotions related to the LUST system (Panksepp, 1998) and, in case of competitive courtship behaviour, potentially also negatively valenced emotions related to frustration. More studies investigating diverse different emotionally relevant contexts in various species are needed.

Since different components of emotional states might involve distinct neuronal networks that are associated with various patterns of hemispheric asymmetries, brain lateralization and correlating behavioural manifestations should be studied in relation to different components of emotions (e.g., asymmetric sensory processing of emotionally salient information, emotionally expressive behaviour, other emotionally induced motor actions). Like most studies with dogs, many with other pet and farm animal species focused on lateralized sensory functioning in response to emotionally relevant contexts (Leliveld, 2019; Siniscalchi et al., 2021). Yet, several studies on various species also examined other behavioural biases, including for instance asymmetric flight/escape turning behaviour in response to an alarming stimulus, e.g. in fish (Bisazza et al., 1997, 2000; Heuts, 1999; Lippolis et al., 2009) and horses (Austin and Rogers, 2007), lateralized ear and tail postures in sheep (Reefmann et al., 2009), and lateralized facial emotional expressions and self-directed behaviours (e.g., scratching, autogrooming) during emotional states in primates (see Gainotti, 2022 for review). More research into lateralized emotionally expressive and other asymmetric motor behaviours in different species is required.

Our review of emotion-related behavioural biases in dogs has shown the importance of assessing emotionally motivated, goal-directed (approach and withdrawal) tendencies: Both from a theoretical perspective that considers the evidential weight of lateralized behaviour in relation to different hypotheses about emotion-related brain asymmetries, and from a more applied animal welfare perspective that refers to patterns of lateralized behaviour to assess welfare-relevant aspects of emotional states. While previous studies on dogs are largely lacking sufficient information on the motivational state, several studies investigating other species include measures of goal-directed motivational tendencies (e.g., in domestic chickens: McKenzie et al., 1998; Vallortigara et al., 2001; in horses: Austin and Rogers, 2007; d'Ingeo et al., 2019; Smith et al., 2016, 2018; in cattle: Phillips et al., 2015). Whenever possible, future studies investigating lateralization in animals should integrate measures of motivational tendencies.

It is important to note that patterns of behavioural and brain lateralization may vary not only depending on the particular emotional situation and in relation to different components of emotional states, but also between different animal species. For example, while behavioural responses in most vertebrate species indicate a specialized role of the

right side of the brain in relation to alarming stimuli (Leliveld et al., 2013), several species of fish present notable exceptions and show behavioural biases indicating a left hemisphere dominance (Berlinghieri et al., 2021; Leliveld et al., 2013). Whereas dogs' behavioural biases indicate a left hemisphere superiority when attending to emotionally competent pro-social stimuli (Quaranta et al., 2007; Racca et al., 2012; Ren et al., 2022; Siniscalchi et al., 2018b), research with ungulate species point to a dominant involvement of the right hemisphere (Leliveld, 2019). To reveal the evolutionary trajectories of emotion-related brain asymmetries and their behavioural manifestations, further comparative research is needed that analyses lateralization patterns in emotional states in the various aspects previously discussed.

That patterns of lateralization might be species-specific is of crucial importance when considering the potential use of behavioural biases as indicators of animals' well-being. Presumably, there is no simple, general and species-overarching rule according to which states of emotion-related welfare can be determined. Instead, research needs to specify whether – and if so, which – species-specific behavioural/brain asymmetries can serve as markers of welfare-relevant aspects of emotional states. The identification of welfare-relevant patterns of species-specific behavioural/brain asymmetries has promising potential applications in monitoring well-being in various companion, zoo, and farm animals, and could inform assessments of welfare-relevant aspects of different housing forms, management and training practices (Berlinghieri et al., 2021; Gourso et al., 2021; Leliveld, 2019; Leliveld et al., 2013; Rogers, 2010, 2011; Siniscalchi et al., 2021).

6. Future directions

Previous research with dogs focussed on behavioural asymmetries as indirect markers for lateralized brain activation in emotional states. Given the availability of technologies such as fMRI or EEG, dogs are also a promising model in comparative affective neuroscience to explore asymmetric activation in specific brain networks that might not be reflected in behavioural asymmetries. For instance, investigating voice-sensitive regions in the dog brain using fMRI, Andics et al. (2014) found that dogs' right central ectosylvian gyrus (cESG), a structure close to the primary auditory cortex, is sensitive to emotional valence: Compared to the homotopic structure in the left hemisphere, the right cESG responded stronger to positively valenced human and conspecific vocalisations; no structures showed elevated activation in attendance to negatively valenced stimuli. However, previous observations of behavioural asymmetries indicate different patterns of brain lateralization: Asymmetric behavioural responses to positively valenced human (Siniscalchi et al., 2018b) and conspecific (Siniscalchi et al., 2008) vocalisations suggest a relatively increased engagement of left hemisphere structures, but dominant activation of the right hemisphere in attendance to negatively valenced vocalisations (Siniscalchi et al., 2008, 2018b). This apparent inconsistency between the behavioural investigations and the fMRI study supports the idea of an integrative model incorporating multiple networks with varying independent lateralization patterns. More recent fMRI studies on dogs exploring brain activation in the context of emotionally salient social stimuli reported relatively stronger activation in dogs' left hippocampus for happy and higher responsiveness in the right parahippocampal gyrus for angry human faces (Karl et al., 2020), and left-lateralized amygdala activation when viewing more compared to less emotionally salient social interactions (Karl et al., 2021). While fMRI provides a promising approach to reveal lateralization patterns in various interrelated networks subserving emotions, the contribution of fMRI technology in studying motivation-modulated asymmetric brain activity may be limited. The use of this technology requires extensive training where dogs are conditioned to lie motionless in the fMRI scanner for several seconds. This training might in itself produce an affective bias associated with the scanner, that might reduce the impact of mildly aversive sensory stimuli. Given that any impulse for approach/withdrawal behaviour must be

suppressed during the presentation of emotional stimuli, patterns of brain lateralization related to goal-directed motivation are also likely affected. In this context, a combination of behavioural measures of dogs' motivational states and the potential to develop mobile EEG or mobile fNIRS technology, which is already used in research with humans (Mehlhose and Risius, 2021; Packheiser et al., 2021), for dogs appears to be a potentially more fruitful approach. At present, EEG and fNIRS technology can however only measure brain activity from regions close to the cortical surface. Compared to that, fMRI technology can also be used, for example, to investigate the activity of (emotionally relevant) subcortical structures (e.g., amygdala).

To date, research on behavioural/brain lateralization in animals' emotional states has largely asked whether individuals share common lateralization patterns in the same direction at the population level. However, future studies should also pay more attention to the possibility of both inter- and intra-individual variation in lateralization patterns. Studies with humans, for instance, suggest that emotion-related behavioural/brain lateralization is influenced by several, individually varying factors, including the level of acute stress (Brüne et al., 2013; Stanković and Nešić, 2020), the severity and the risk of developing affective disorders (e.g., depression: Bourne and Vlădeanu, 2013; Bruder et al., 2016; social anxiety: Bourne and Watling, 2015), age (Abbassi and Joannette, 2011; Kelley and Hughes, 2019), sex (Antyukhov, 2016; Cahill et al., 2004; Schneider et al., 2011; Uematsu et al., 2012; Wager et al., 2003), and steroid hormones such as testosterone (Beking et al., 2020). In dogs, the potential effects of such factors on patterns of behavioural/brain lateralization are not yet well understood. Bolló et al. (2020) found that macrostructural characteristics of dogs' sleep affected their patterns of lateralized behaviour in response to human emotional expressions. Following three hours of sleep, dogs were simultaneously exposed to both non-verbal vocal emotional expressions and to a screen with two images of emotionally expressive human faces (i.e., with one on the left and one on the right side of the screen). In response to vocalisations of crying, dogs with a higher number of awakenings during the sleep phase looked more to the image on the left side of the screen, regardless of the type of expression that was displayed on the image (i.e., a sad or happy face). Furthermore, several studies explored potential effects of inter- and intra-individual variation on dogs' lateralized motor behaviour in the form of preferential paw use in (presumably) emotionally relevant tasks. However, different studies reported inconsistent findings. For instance, investigating dogs' preferential paw use when reaching for a rewarding food or toy stimulus, Duncan et al. (2022) found that age and an interaction between age and neuter-status influenced the degree of lateralization (i.e., regardless of the direction). Yet, this finding could not be replicated by Charlton and Frasnelli (2022). Although age could not be identified as a main factor influencing which paw dogs preferentially used to hold a Kong™ while retrieving food placed inside it (Batt et al., 2008; McGreevy et al., 2010; Tomkins et al., 2010), or to remove an adhesive (presumably disturbing) tape from their head (Batt et al., 2008), a two-way interaction between age and breed (Tomkins et al., 2010) and a three-way interaction between age, sex and coat colour (Batt et al., 2008) affected dogs' paw use in the Kong™ and tape removal task, respectively. Some studies also reported main effects of sex and breed. Sex effects were detected in dogs' lateralized paw use when retrieving food from a container (Laverack et al., 2021; Wells, 2003), when holding a Kong™ (McGreevy et al., 2010), or when removing an adhesive tape from their head (Quaranta et al., 2004, 2006). However, other studies did not find any sex effects in food retrieving or tape removal tasks (Barnard et al., 2017; Branson and Rogers, 2006; Charlton and Frasnelli, 2022; Wells et al., 2017, 2018). While Tomkins and colleagues (2010) documented breed effects in the context of the Kong™ test, other authors could not confirm this effect (Batt et al., 2008; McGreevy et al., 2010). A study on shelter dogs revealed that stronger left-pawedness in the Kong™ test was associated with an increased frequency of changes in body position, the display of vocalizations, and lower body postures, indicating a higher vulnerability

to stress (Barnard et al., 2018). Compared to that, a study by Demirbas et al. (2019) reported that weaker pawedness (i.e., regardless of the direction) in the Kong™ test was linked to higher levels of chronic stress. Whereas some studies suggest an association between dogs' preferential paw use in the Kong™ test and their scores in different psychometric temperament and personality tests (e.g., Canine Behavioural Assessment & Research Questionnaire (Hsu and Serpell, 2003); Dog Mentality Assessment (Svartberg and Forkman, 2002); Positive and Negative Activation Scale (Sheppard and Mills, 2002)) (Barnard et al., 2017; Batt et al., 2009; Schneider et al., 2013; Wells et al., 2018), a more recent study could not identify such a link (Simon et al., 2022). As the reaching tasks, the Kong™ task, and the tape removal task might be biased by other (non-emotional) specialised hemispherical functioning (see Section 3.4; Simon et al., 2022) and inadvertent learning effects (Simon et al., 2022), limitations of these tasks might account for the inconsistencies between the reported findings. Therefore, future investigations of the potential influence of different aspects of inter- and intra-individual variation should focus on other emotion-related behavioural asymmetries.

7. Summary

In recent years, research has shown a growing interest in studying lateralized behaviour in dogs as an indirect marker for asymmetric brain activity in dogs' emotional states. In this context, several studies have explored behavioural lateralization in response to different emotionally salient stimuli (e.g., potentially alarming/threatening or pro-social stimuli). Using a likelihood-ist concept of evidence, we discussed the evidential weight of previous lateralization research with dogs on different hypotheses about brain lateralization and emotional states (i. e., Right-Hemisphere-Hypothesis (RHH), Valence-Hypothesis (VH), Approach-Withdrawal-Hypothesis (AWH)): Taken together, the reviewed findings indicate an overall relative support for VH. However, the comparative evaluation of the three competing hypotheses presented may be biased by the lack of important information in the published literature that would allow for a more comprehensive evaluation. Specifically, the studies reviewed did not include sufficient information on the motivational state of the dogs in the emotional contexts studied. Since the assessment of dogs' motivational states in terms of goal-directed approach and withdrawal tendencies are crucial for the evaluation of AWH, this is an omission that should be addressed in future.

A systematic, evidence-based assessment of the three hypotheses needs to extend to various further, not yet investigated, emotionally relevant contexts. Given that the different hypotheses claim validity for all kinds of emotional contexts, a more comprehensive comparative evaluation of the competing hypotheses requires the investigation of lateralization in a wider range of different settings involving more diverse types of emotional stimuli. Specifically, to better discriminate between VH and AWH, future research should consider scenarios that involve both a negative emotional valence and engagement in approach behaviour, or the converse; only such contexts can produce the lateralization patterns that can provide relative evidence for/against these two different hypotheses. In this regard, contexts associated with anger or frustration seem particularly valuable since anger- and frustration-eliciting stimuli are typically appraised as negatively valenced but can motivate stimulus-directed approach tendencies (Carver and Harmon-Jones, 2009).

More recent research with humans suggests that multiple interconnected emotion-related brain networks that may be associated with different patterns of lateralization (Fusar-Poli et al., 2009; Killgore and Yurgelun, Todd, 2007; Neumann et al., 2008). Thus, it is possible that different contexts and different components of dogs' (and other animals') emotional states may be associated with varying lateralization patterns that can be best explained by an integrative model according to which RHH, VH and AWH are not mutually exclusive hypotheses, but relate to different aspects of emotional states. To explore such an

integrative hypothesis, it is not only important to investigate behavioural/brain lateralization in various emotionally relevant settings, but also to study lateralization relating to different components of emotion.

The observation of asymmetric behavioural correlates of emotion-specific brain lateralization provides a potential approach to assess dogs' (and other animals') well-being. Specifically in the case of valence-specific patterns of lateralization, as proposed by VH, behavioural biases could serve as valuable tools to estimate welfare-relevant aspects of emotions. Compared to that, the welfare-indicative value is more limited in the case of behavioural/brain asymmetries reflecting emotionally induced goal-directed motivational (approach and withdrawal) tendencies or emotional salience in general, as suggested by AWH and RHH, respectively. Potential differences between species and intra-/inter-individual variation in emotion-related behavioural/brain asymmetries might require identifying species-specific and individualised profiles of lateralization patterns to inform assessments of welfare-related aspects of emotional states.

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None.

Appendix A. Supporting information

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