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Seeing both sides: dogs' eyes reveal valence-sensitive shifts between emotional states

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Left-right asymmetries in behaviour, reflecting underlying asymmetries in brain activity, can serve as indirect markers of internal states. However, the underlying mechanisms driving asymmetry patterns remain unclear. This study tested two competing hypotheses concerning behavioural lateralization, using pet dogs as a model: the Valence hypothesis, which posits that lateralization is shaped by emotional valence (positive vs. negative), and the Approach–Withdrawal hypothesis, which suggests that left-right asymmetries reflect motivational tendencies (approach vs. withdrawal). We examined dogs' visual behaviour asymmetries in two distinct emotional states: positive anticipation and frustration, while awaiting a reward. Anticipation has a positive and frustration has a negative emotional valence, but both contexts motivate reward-directed approach tendencies. This allowed us to distinguish between the competing hypotheses. Dogs showed a right visual field/left-brain bias when inspecting the reward during states of positive anticipation, whereas states of frustration were associated with a left visual field/right-brain bias. Our results provide the first evidence favouring the Valence over the Approach–Withdrawal hypothesis in a non-human animal. Additionally, this study is the first to demonstrate the dynamic and fluid nature of lateralization in a non-human species, showing that dogs' visual field preference shifts within seconds as emotional states change.

1. Introduction

Brain lateralization refers to functional asymmetries between the right and left side of the brain, which includes differences relating to emotional processing. While there is broad consensus that emotional states correspond with asymmetric brain activity, the exact roles of the right and left hemispheres remain debated [1–5]. Several theoretical frameworks have been put forward. The Right-Hemisphere hypothesis argues that all emotional states largely involve activation of the right hemisphere [2]. By contrast, the Valence hypothesis contends that only negative emotions preferentially engage the right brain, while positive emotions are more strongly represented in the left [6]. A third model, the Approach–Withdrawal hypothesis, posits that lateralization depends more on the direction (approach–avoidance) of emotion-related behavioural motivations, rather than emotional valence—suggesting that approach-oriented responses are linked to the left brain, and withdrawal-related responses to the right [7].

In animals, evidence for emotion-related brain asymmetries is typically drawn from indirect behavioural indicators rather than direct assessments of neural activity [8–10]. Specifically, asymmetries in behaviour are often

considered indirect markers of lateralized brain function. This inference is grounded in the organization of the vertebrate nervous system, where the majority of afferent and efferent pathways cross over and connect primarily with the contralateral hemisphere. Consequently, sensory input and motor control are largely processed or regulated by the hemisphere opposite to the side of the body involved. A key exception is the olfactory system, in which sensory information from each nostril is primarily routed to the same-side (ipsilateral) brain structures [11]. Given this neuroanatomical arrangement, behavioural biases in response to emotionally relevant stimuli—such as a preference for using one eye, ear or nostril, or the exhibition of lateralized motor behaviours in response to emotionally relevant contexts—can be used to infer differential engagement of the two hemispheres.

In domestic dogs (*Canis familiaris*), several studies have investigated emotion-related behavioural asymmetries, focusing on their responses to two types of stimuli: (i) those appraised as alarming, presumably associated with negatively valenced and (ii) those assessed as prosocial, probably associated with positively valenced [5]. When exposed to alarming visual stimuli, dogs preferentially process these within their left visual field. For example, Siniscalchi *et al.* [12] reported that dogs showed a left visual bias in their head-orienting response when presented with images of a snake or a cat in a threatening posture. Specifically, when drawings of a snake and a cat were presented simultaneously in the right and left visual hemifield, dogs tended to turn their head with the left eye leading. Left visual field biases have also been observed in response to threatening human and conspecific facial expressions [13, 14]. Similar asymmetries have been reported for alarming auditory stimuli. When exposed to sounds such as thunderstorms [15], threatening cat vocalizations [16] and non-verbal human emotional vocalizations (e.g. screaming, sobbing, growling) [17], dogs consistently showed a left-ear bias, indicated by preferential head turns with the left ear leading. This was observed when sounds were broadcasted simultaneously from two speakers positioned symmetrically to either side of the head, or when presented from a single speaker placed centrally behind the dog. Dogs also exhibit asymmetrical nostril use when investigating emotionally salient odours. When exposed to potentially alarming olfactory stimuli, such as veterinarian sweat or adrenaline, they preferentially use the right nostril when sniffing [18]. Given the contralateral organization of the visual and auditory systems and the ipsilateral organization of the olfactory system in vertebrates, these behavioural biases indicate a stronger engagement of right-hemisphere networks during the processing of alarming stimuli. By contrast, when dogs were presented with emotionally salient prosocial stimuli—such as pictures of friendly human or conspecific facial expressions [13] or non-verbal human vocalizations like laughing [17]—they displayed right visual field and right ear biases, pointing to a dominant role of the left hemisphere.

Although previous findings clearly demonstrate that emotional states in dogs are associated with behavioural and brain asymmetries, they do not conclusively distinguish among competing theoretical models. In the context of alarming and prosocial stimuli, lateralized behavioural responses align more closely with the Valence hypothesis than with the Right-Hemisphere hypothesis. However, assuming that prosocial stimuli probably promote approach tendencies, while alarming stimuli tend to elicit withdrawal, these findings are also compatible with the Approach-Withdrawal hypothesis. Contexts that differ in emotional valence (i.e. positive vs. negative) but elicit similar behavioural motivations (i.e. approach or withdrawal), or vice versa, are essential for differentiating between these models [5,19].

To address this gap, we investigated behavioural lateralization in dogs during two emotional states: positive anticipation and frustration, both elicited while awaiting access to the same attractive food stimulus. Positive anticipation involves positive valence, whereas frustration reflects negative valence; yet both states involve stimulus-directed approach behaviour associated with trying to get access to the resource. We pre-trained the pet dogs to expect to gain access to a food item shortly after it had been visually presented within a specifically designed apparatus. The apparatus allowed the dogs to see, but not reach, the food during the *anticipatory phase*. To induce frustration, an additional and, from the dog's perspective, unpredicted *delay phase* was introduced, keeping the food inaccessible beyond the anticipatory phase. This allowed shifting of the dogs' emotional state from one of positive anticipation to frustration. Both during the anticipatory phase and the unexpected delay phase, dogs' visual orientation towards the food reward was assessed.

By analysing dogs' visual behaviour across two contexts that differ solely in emotional valence—while holding constant factors such as experimental set-up, physical stimulus characteristics (thus controlling for stimulus-specific processing effects [20]) and stimulus-directed motivation—this design provides a critical test of the Valence versus Approach-Withdrawal hypotheses by dissociating emotional valence from behavioural motivation. According to the Valence hypothesis, dogs should process the food reward primarily within their right visual field/left hemisphere during positive anticipation (anticipatory phase), but exhibit a left visual field/right-hemisphere bias during states of frustration, when access to the expected reward is blocked (delay phase). In contrast, the Approach-Withdrawal hypothesis predicts a consistent right visual field/left-hemisphere bias in both conditions. While no study to date has definitively favoured one hypothesis over the other in non-human animals, research in humans suggests that negative but approach-oriented emotions—such as anger and frustration elicited by blocked reward access—may engage left-hemisphere networks, potentially favouring the Approach-Withdrawal hypothesis [19,21]. Furthermore, our study contributes to our understanding of the dynamic nature of lateralization in a non-human species by examining changes in dogs' preferential eye use as their emotional state shifts.

2. Material and methods

(a) Subject details

Pet dogs of various breeds were recruited by directly approaching dog owners in public areas such as dog parks and pet food stores in the Bielefeld region (Germany). Since this study examined dogs' visual inspection of food stimuli at close distance,

only dogs that, according to their owners, had unimpaired vision and a strong motivation for food were included. To minimize the influence of morphology-related variations in dogs' field of vision [22], extreme brachycephalic (e.g. Pugs, French Bulldogs) and dolichocephalic breeds (e.g. Whippets, Greyhounds) were excluded. In total, 16 pet dogs participated in the study (11 pure-bred, 5 mixed breed; 9 females—6 neutered, 8 males—4 neutered; mean age \pm s.d.: 4.45 ± 2.13 years). Further details can be found in the electronic supplementary material.

(b) Method details

The materials and methods were largely reproduced from a previous study by the same authors examining dogs' lateralized behaviour during states of positive anticipation when awaiting a reward, including details of the general experimental set-up and procedures for data collection and analysis [20].

(c) Stimuli

Dogs were trained to expect to gain access to a food item approximately 2 s after the item had been visually presented to them in an experimental apparatus. The presentation of the food was intended to induce a state of positive anticipation (positive emotion). However, states of frustration (negative emotion) were also elicited: because, on some occasions (i.e. in 4 out of 14 trials), the dogs' access to the anticipated food stimulus was delayed (unmet expectation). While states of frustration differ from states of positive anticipation in their emotional valence (i.e. negative emotion), both emotional states motivate stimulus-directed approach behaviour in contexts such as the current study. The type of food was selected for each dog individually, according to what the owner said their dog particularly liked. For each dog, the selected food was then cut into cylindrical pieces (approx. 15 mm in diameter and 5 mm in height) using an apple corer to ensure a consistent shape.

(d) Experimental set-up

Dogs were tested in an experimental room measuring 5×4 m. The set-up included two interconnected barriers, A and B, of equal size (150×120 cm, 2 cm thick; [figure 1](#)). Barrier A featured a centrally located opening (50×50 cm). The height of the opening from the floor could be adjusted so that its lower edge was level with the dog's chest. Behind Barrier A, a board was positioned upon which a rewarding food stimulus was presented. The presentation board's height was also adjustable and was set to match the lower edge of the opening, depending on the dog's size.

Below the presentation board, there was another board on which several more versions of the presented stimulus were arranged (they were qualitatively identical in type, size and shape to the food stimulus displayed on the presentation board). These items on the lower board were not visible to the dog at any time but were included to ensure a homogeneous diffusion of the odour. They were evenly distributed across the lower board to promote visual rather than olfactory inspection of the food stimulus on the presentation board during stimulus presentation.

In front of Barrier A, there was an enclosure that the dogs needed to enter for orientation measurements during the test. This enclosure was made up of two parallel wooden boards of equal size (50×38 cm, 1.5 cm thick), which were connected at their front base—directly adjacent to Barrier A—by an additional wooden board (30×13 cm, 1.5 cm thick) at a distance of 30 cm.

Two vertically movable sliding panels—one transparent and one opaque ([figure 1](#))—were used to control the dogs' visibility and access to the stimulus on the presentation board while they stood inside the enclosure (in front of Barrier A). To both see and access the food stimulus, both panels needed to be moved upwards. If only the opaque panel was lifted while the transparent panel remained in place, the dogs could see the stimulus on the presentation board but were unable to reach it.

The dog owner sat on a chair centrally behind the dog, approximately 2.5 m in front of Barrier A. The experimenter was positioned behind Barrier B and controlled the position of the vertically movable panels using a cable pull system. Lifting the opaque panel allowed the experimenter to observe the dog through a peephole in Barrier B ([figure 1](#)).

All test sessions were recorded using two cameras (GoPro Hero 7 Black, 1440 p resolution, 30 fps, GoPro Inc., USA). To capture the relative involvement of the eyes during visual inspection of the stimulus, one camera was mounted on the presentation board (camera 1 in [figure 1](#)).

(e) Design and procedure

Participation in the study required four visits for each dog and its owner. During the first visit, the dog was acclimatized to the experimental setting, allowing it to familiarize itself with both the experimenter and the experimental apparatus. This included interacting with the sliding panels of the apparatus and taking some pieces of food from the presentation board when both sliding panels were lifted. The second visit involved an initial training session, while the third and fourth visits included a training session followed by a test session. Each of the four visits lasted approximately 15–20 minutes, with a minimum interval of 2 days between successive visits. To increase motivation for the food reward, dogs were food deprived for at least 5 hours before each session. After each visit, the experimental apparatus was thoroughly cleaned.

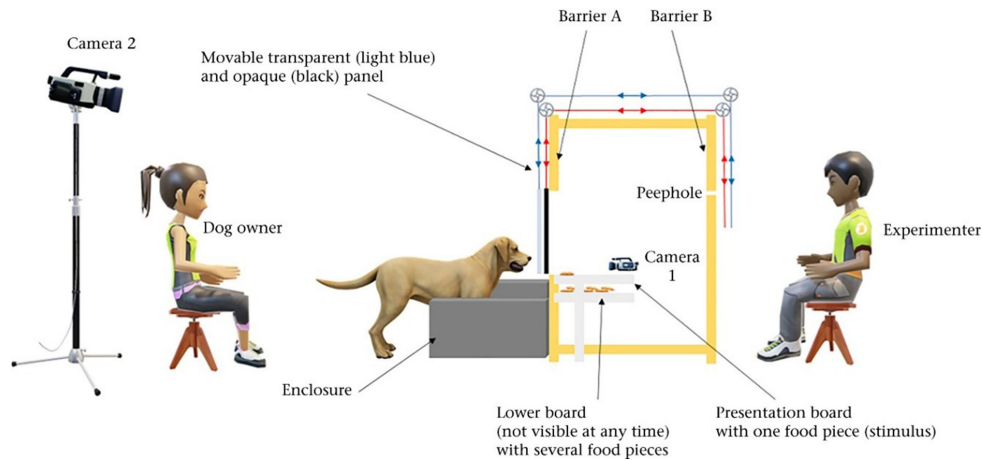


Figure 1. Experimental apparatus. Reproduced from previous work by the same authors [20].

(i) Training sessions

Each training session involved a series of trials in which the dog was trained to anticipate access to the rewarding food stimulus after it was visually presented in the apparatus. Before each training trial began, the experimenter placed the stimulus at the centre of the presentation board. Meanwhile, both the transparent and opaque panel blocked the opening, preventing the dog from seeing the stimulus preparation. The training trial began once the dog entered the enclosure in front of Barrier A, ensuring that at least its head, shoulders and both front legs were inside the enclosure (as indicated verbally by the dog's owner). The experimenter then lifted the opaque panel, allowing the dog to see the stimulus but not access it. Approximately 2 seconds later, the experimenter also raised the transparent panel. The training trial concluded once the dog had consumed the food. After each trial, the dog was called back by its owner and remained nearby. The owner ensured that the dog waited until the experimenter had prepared the next trial but did not actively engage with the dog (e.g. through play, praise or verbal interaction). Once the set-up was complete, the dog was allowed to approach the apparatus to begin the new training trial. The interval between trials ranged from approximately 30 to 45 s.

The initial training session was considered complete when the dog successfully completed 10 consecutive training trials, during which it immediately directed its visual attention to the stimulus (as assessed by the experimenter, who observed the dog through a peephole in the apparatus; [figure 1](#)) once the stimulus became visible but not yet accessible. Each of the following two training sessions (during the third and fourth visits) was completed when the dog exhibited stimulus-directed attention across five consecutive training trials. Since both the third and fourth visits included test trials (see Test sessions) in addition to the training trials, the number of training trials was reduced compared with the second visit to avoid overloading the dogs and to maintain their motivation and focus. Where possible, the dog was encouraged to begin the 10 trials (on the second visit) and five trials (on the third and fourth visits) independently by entering the enclosure without assistance from its owner. In cases where this was not possible, the dog owner could help by guiding the dog into the enclosure and then stepping behind it to start the training trial. Some dogs, when entering the enclosure on their own, would push against the panels with their muzzles or paws. In such cases, the owner would gently hold the dog's hindquarters to ensure the dog stood correctly in the enclosure with its body aligned in front of the apparatus; the owner would only release the dog to access the food stimulus once both panels had been lifted.

(ii) Test sessions

After the dog had successfully completed the training, the test sessions began. Each session consisted of seven test trials. Five of the seven test trials (henceforth '*positive anticipation trials*') were similar to the training trials: a *positive anticipation trial* began as soon as the dog entered the enclosure positioned in front of Barrier A. After that, the experimenter lifted the opaque panel so that the dog could see but not access the stimulus on the presentation board. Shortly afterwards (approx. 2 s), the experimenter also lifted the transparent panel. Each test session also involved two trials (henceforth '*delayed trials*') in which there was a delay in lifting the transparent panel. After the first 2 s from when the opaque panel was moved, lifting the transparent panel was delayed until the dog lost visual attention to the food stimulus (e.g. turning away from the stimulus or leaving the enclosure in front of the apparatus). This was judged by the experimenter observing the dog through a peephole in Barrier B. For each dog, the *delayed trials* were interspersed at positions 3 and 7 in the sequence of test trials in one test session and at positions 4 and 7 in the other test session. This order of trials across sessions was counterbalanced across dogs.

Test (i.e. *positive anticipation* and *delayed*) trials were distinct from training trials as they involved controlling the dog's body position in relation to the presented stimulus. This was done to account for the possibility that the dog's relative lateral body position could affect their behavioural response to the stimulus. During the test trials, the food stimulus was presented at one of seven possible positions on the presentation board, with each test session displaying the stimulus at each position once. The order of the positions in which the food stimulus was displayed was randomized, using Urbaniak and Plous's [23] Research Randomizer, ensuring a unique random order for each test session and dog. The positions were arranged in a straight line along the edge of the board, with adjacent positions separated by 10 mm. Thus, the possible positions were either in the centre of the



Figure 2. Stimuli presentation. Stimuli were displayed at seven possible positions. Reproduced from previous work by the same authors [20].

presentation board or 10, 20 or 30 mm to either side of the centre (figure 2). This design enabled the analysis of behavioural responses to the stimulus at various relative body positions. This allowed us to estimate the impact of relative lateral position on the observed behavioural responses, and thereby any responses could be corrected for lateral position effects (as outlined in the Statistical analysis section).

(f) Measurements

Dogs' visual behaviour during stimulus inspection was assessed by measuring the angles of their right eye relative to the food. Right-eye angles smaller than 90° indicate that the stimulus is predominantly processed within the visual field of the right eye (figure 3A), while angles larger than 90° indicate that the stimulus is primarily perceived in the left visual field (figure 3B). Visual behaviour asymmetries were assessed from video recordings using Kinovea software (version 0.8.15; <https://www.kinovea.org/>).

For *positive anticipation trials*, both the angle of the dog's right eye and the relative body position were measured during the 2-second time interval, starting when the opaque panel was lifted. During this time, the transparent panel still blocked the opening of the apparatus, allowing the dog to see the stimulus on the presentation board without being able to access it (referred to here as the 'anticipatory phase'). Yet, in the context of *delayed trials*, multiple 2 s measurements were performed: given individual differences in frustration tolerance, our primary time window of interest for assessing frustration was the 2 s before the end of visual orientation towards the stimulus (end of delay), since the latter was considered to mark a change in focused attention during the delay. Additionally, seconds 0–2 of the *delayed trials* (identical to the anticipatory phase of *positive anticipation trials*) and seconds 2–4 (onset of the delay) were analysed. Compared with the individualized final 2 s at the end of delay, which temporally varied between dogs, the other two 2 s time windows of the *delayed trials* were temporally equivalent for all dogs. Similar to the *positive anticipation trials*, dogs' right-eye angles and their relative body position were assessed for each 2 s time window of the *delayed trials*. For both *positive anticipation* and *delayed trials*, all measurements during the respective 2 s time window were from the dog's first visual fixation of the food, when the dog held its body and head still for at least 0.1 s (three frames) and appeared focused on the stimulus.

To evaluate dogs' visual behaviour asymmetries in test trials, the angle between the inner canthus of their right eye, the midpoint between the inner canthi of both eyes, and the stimulus was determined (figure 4A).

In addition, for each angle measurement, the dog's lateral body position relative to the presented stimulus was also estimated. To achieve this, the displacement of the dog's body centre in relation to the stimulus was calculated. The body centre was defined as follows. When the dog was positioned centrally in front of the apparatus, the distance between its two forelimbs and the width of its chest were measured at two distinct positions. The midpoints of these measurements were then estimated. The average of these midpoints was used to determine the dog's body centre (figure 4B). This supplementary measurement allowed for an evaluation of the influence of lateral position on the dog's inspection of the visual stimulus, thus enabling an analysis of their eye usage while controlling for lateral position effects (explained in the Statistical analysis section below).

To standardize measurements across dogs and test trials, the dog's right-eye angle and the corresponding relative lateral body position were analysed only in trials where the dog's body was positioned straight in front of the apparatus. This was defined as the case when, from the perspective of the recording camera, at least one of the dog's front legs partially covered the ipsilateral hind leg (for more details, see previous work by the same authors [20]).

(g) Statistical analysis

Statistical analyses were performed in RStudio 1.3.1056.1.

For each dog and each test (i.e. *positive anticipation* and *frustration*) trial, the angle of the right eye and the lateral body position relative to the presented stimulus were measured as described earlier (see Measurements). To assess the influence of the dog's body position on the right-eye angle, a linear regression analysis was conducted, using the dog's relative lateral body position as the independent variable and the right-eye angle as the dependent variable. However, not all measurements were considered for the linear regression, but only those taken in the anticipatory phase (i.e. measures taken for *positive anticipation trials* and seconds 0–2 of *delayed trials* and that were probably associated with states of positive anticipation). Based on the slope of the regression line which was used as an estimate of the position effect, each measured right-eye angle was then corrected for the deviation caused by the dog's lateral distance from the stimulus that was measured in the specific 2 s time window of the respective *positive anticipation* or *delayed trial*.

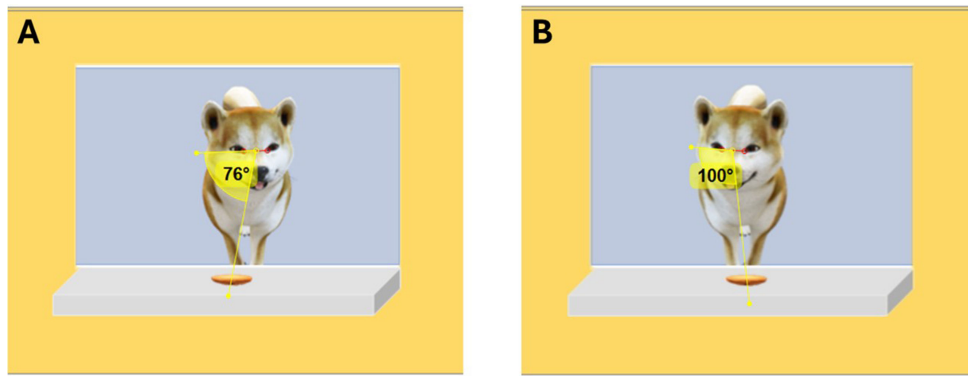


Figure 3. (A) The dog preferentially processes the stimulus within the right visual field (the angle between the right eye, the midpoint between the two eyes and the food stimulus is smaller than 90°). (B) The dog predominantly processes the stimulus within the left visual field (the angle between the right eye, the midpoint between the two eyes and the food stimulus is larger than 90°).

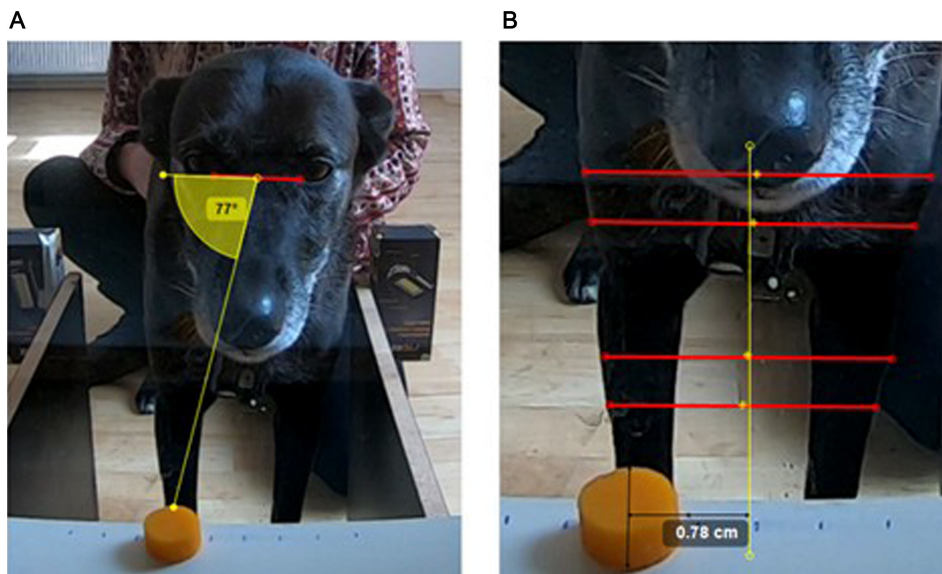


Figure 4. Measuring right-eye angles and relative lateral body positions. (A) Angles between the inner canthus of the right eye, the midpoint between the canthi of both eyes, and the stimulus were used to evaluate the dog's visual field bias. (B) The estimation of the body centre was based on both the distance between the two front legs (represented by the two lower red lines) and the width of the rib cage (represented by the two upper red lines). To estimate the body centre, the average of the midpoints of all four red lines (shown by the yellow crosses) was calculated. The lateral position of the dog's body in relation to the stimulus was defined as the distance between the body centre and the stimulus. Reproduced from previous work by the same authors [20].

To assess each dog's visual behaviour asymmetries across trials when they were probably in emotional states of positive anticipation, we estimated their median of all the (corrected) right-eye angles measured during the anticipatory phase (i.e. *positive anticipation trials* and seconds 0–2 of *delayed trials*). To quantify each dog's visual behaviour asymmetries when they might have experienced states of frustration, the median of all (corrected) right-eye angles was calculated across trials for each of the 2 s time windows of the delay phase (i.e. seconds 2–4 and the individualized final 2 s of *delayed trials*). A median less than 90° indicates that the stimulus is predominantly processed within the visual field of the right eye, a median greater than 90° means that the stimulus is predominantly perceived in the left visual field and a median = 90° suggests that there is no bias.

To evaluate whether the dogs' median right-eye angles during the anticipatory phase and/or any of the time windows in the delay phase were significantly different from 90° , one-sample t-tests were run.

To determine if dogs' median right-eye angles during the anticipatory phase differed from those measured during the delay phase, we used Wilcoxon signed-rank tests for pairwise comparisons.

To assess the consistency of dogs' responses over time, right-eye angles during the anticipatory and delay phases were compared across sessions using Wilcoxon signed-rank tests and Spearman correlations.

For all t-tests and Wilcoxon tests, effect sizes were calculated as Cohen's *d* using G*Power 3.1.9.7.

G*Power was also used to conduct *post hoc* power analyses to assess the sensitivity of the study to detect key effects.

3. Results

All 16 dogs that participated in this study provided data for both the anticipatory phase and the onset of the delay, while data from 13 dogs were available for the individualized end of the delay; three dogs were excluded from the latter analysis because they did not visually attend to the presented stimuli. For the anticipatory phase (seconds 0–2), each dog contributed on

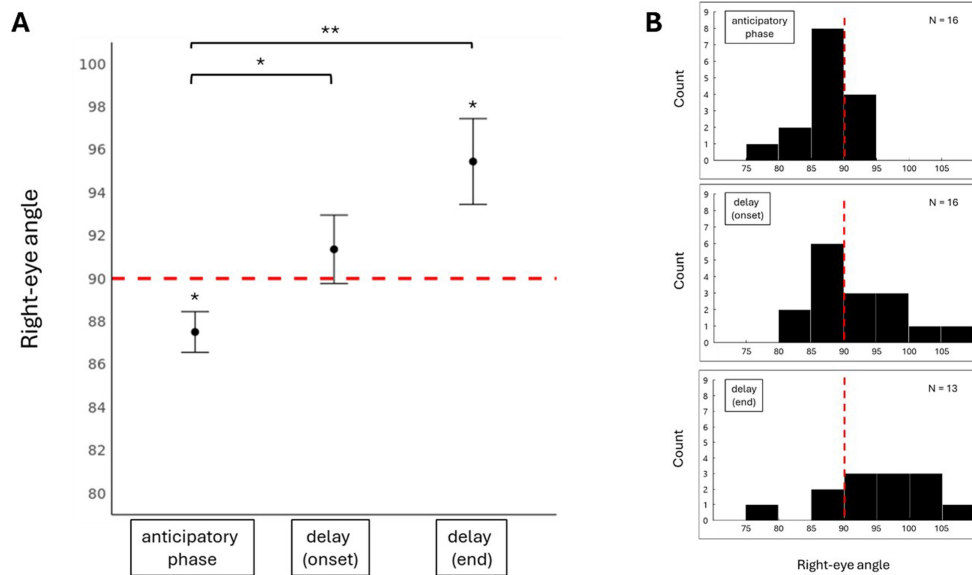


Figure 5. (A) Dogs' right-eye angles during the anticipatory and the delay phase (mean \pm s.e.). Asterisks indicate significant deviations from 90° (* $p < 0.05$; ** $p < 0.001$). (B) Histograms showing the distribution of dogs' right-eye angles during the anticipatory and the delay phase.

average 9.5 ± 3.37 of the 14 possible right-eye angle measurements used to determine visual field bias; in the remaining trials, the criteria for behavioural measurements were not met. For the onset of the delay (seconds 2–4), dogs contributed on average 2.63 ± 0.89 of the four possible successful measurements, and for the individualized end of the delay, 2.38 ± 1.04 of the four possible measurements per dog were obtained.

Most dogs exhibited right-eye angles smaller than 90° when viewing the food stimulus during the anticipatory phase (mean \pm s.e.: $87.51^\circ \pm 0.95^\circ$, $t = -2.635$, d.f. = 15, $n = 16$, $p = 0.019$, Cohen's $d = 0.659$; figure 5A,B). As expected, this indicates a right visual field bias, consistent with predominant left-brain activation related to processing an anticipated reward. During the individualized end of the delay phase, most dogs showed right-eye angles larger than 90° (mean \pm s.e.: $95.450^\circ \pm 1.995^\circ$, $t = 2.727$, d.f. = 12, $n = 13$, $p = 0.018$, Cohen's $d = 0.756$; figure 5A,B), suggesting a left visual field/right-brain preference. At the onset of the delay, dogs' right-eye angles were not different from 90° (mean \pm s.e.: $91.361^\circ \pm 1.594^\circ$, $t = 0.854$, d.f. = 15, $n = 16$, $p = 0.406$, Cohen's $d = 0.214$; figure 5A,B).

Both at the onset and the end of the delay phase, dogs showed larger right-eye angles compared with the anticipatory phase (all $p \leq 0.013$, Cohen's $d \geq 0.753$; figure 5A), suggesting a relative shift towards increased use of the left visual field/right brain.

Dogs' right-eye angles were consistent across sessions. No significant differences were found between sessions for the anticipatory phase ($n = 15$; $W = 72$, $p = 0.525$, Cohen's $d = 0.400$), the onset of the delay phase ($n = 11$; $W = 36$, $p = 0.831$, Cohen's $d = 0.450$) or the end of the delay phase ($n = 7$; $W = 18$, $p = 0.578$, Cohen's $d = 0.360$). Moreover, right-eye angles were positively correlated between sessions for the anticipatory phase ($q = 0.843$, $p < 0.001$), the onset of the delay phase ($q = 0.611$, $p = 0.046$) and the end of the delay phase ($q = 0.857$, $p = 0.030$).

Based on the observed effect sizes and assuming an α -level of 0.05, statistical power ($1-\beta$) exceeded 0.80 for key effects of interest—including dogs' right-eye angle deviations from 90° during the anticipatory phase and the individualized end of the delay phase, as well as pairwise comparisons of visual behaviour asymmetries across phases (anticipatory phase vs. onset or end of delay).

The key assumptions of the statistical tests used were met (see electronic supplementary material for details).

4. Discussion

Our data demonstrate a right visual field/left-brain preference for processing a desirable stimulus during the anticipatory phase, aligning with previous findings [20]. However, the delay phase was associated with a left visual field/right-brain shift. Assuming that the anticipatory phase involved positive emotions (i.e. positive anticipation) and the delay phase negative emotions (i.e. frustration), while both phases motivated food-directed approach tendencies, these findings challenge the Approach-Withdrawal hypothesis in favour of the Valence hypothesis, marking the first evidence for the latter in a non-human animal.

The left visual field/right-brain bias appeared only during the final 2 s of the delay phase, just before the dogs shifted attention from the stimulus. As frustration presumably increased over time during the delay, the left visual field bias at this time reflects each dog's frustration peak. By contrast, at the onset of the delay, some dogs probably had not yet reached peak frustration, accounting for the initial lack of a visual field bias.

Some previous work suggests that behavioural asymmetries in dogs are influenced by individually varying factors, including age and neuter status [24], sex [25,26], breed [27], chronic and acute stress [28], temperament and personality [29,30]. While such individual differences between dogs may contribute to variability in their responses, such heterogeneity reflects the natural diversity of the dog population and enhances the ecological validity of our findings. Specifically, random error

associated with individual variation further supports the inference of the general effect observed in our study. Importantly, the measured effects were statistically significant and sufficiently powered, indicating that the reported group-level lateralization effects are robust despite individual variation.

While our results favour the Valence over the Approach–Withdrawal hypothesis in a specific context of emotionally salient visual reward processing, they do not necessarily imply that *all* emotion-related behavioural/brain asymmetries are valence-driven. Recent research with humans suggests that different emotionally salient contexts and different components of emotions (e.g. appraisal, arousal, behavioural tendencies, emotion expression, communicative content; e.g. [31]) may involve different interconnected brain networks that are associated with their own patterns of lateralization [4,32–34]. The existence of multiple, functionally linked but differently lateralized networks may be best captured by an integrative framework according to which the Right-Hemisphere, Valence and Approach–Withdrawal hypotheses are not mutually exclusive, but relate to different aspects of emotional processing. Further research is needed to investigate the relationship between lateralization and various aspects of emotional states and to explore such an integrative hypothesis.

In light of this, the differences between our results and previous findings from research with humans are particularly salient. In humans, frustration (blocked reward access) has been linked to predominant activation of distinct left-brain networks, while showing no lateralized activation in the visual cortex [21], which presumably contributes to the right/left-eye biases in the current study. Moreover, negatively valenced and approach-motivating states of anger are associated with dominant activation of the left prefrontal cortex [19]. These findings from human research support the Approach–Withdrawal hypothesis over the Valence hypothesis. These inconsistencies may reflect species-specific patterns of emotional lateralization. Comparative research will be essential to investigate modulators of lateralization across species (which may be related to cognitive differences) and the evolutionary trajectory of behavioural/brain lateralization and its association with affective states.

Apart from emotion-related lateralized brain processes, further specialized hemispheric functions might also contribute to our findings. While networks in the left brain are specialized in mediating routine behaviour according to learnt and well-established response patterns, right hemispheric networks are particularly sensitive to novelty and are specialized in controlling responses to unexpected situations (e.g. [9,35–37]). Thus, a right visual field preference when processing the food stimulus during positive anticipation might be facilitated by specialized functioning of the left hemisphere for learnt routine behaviour, whereas a shift towards a left visual field bias when access to the food was unexpectedly delayed may reflect right-hemisphere dominance for unexpected or novel contexts. Potentially, both valence-sensitive processes and hemispheric specialization for routine versus unexpected contexts act synergistically in producing the observed lateralization patterns. To disentangle these effects, future research could compare dogs' responses with unexpected events with (i) negative valence (e.g. a rewarding event that turns out worse than expected) and (ii) positive valence (e.g. a rewarding event that turns out better than expected).

At the transition between the anticipatory phase and the onset of the delay, dogs showed a shift to increased left-eye use within a few seconds. This is the first demonstration of swift lateralization changes between distinct mental states in a non-human species, highlighting the dynamic and fluid nature of lateralization [38].

Ethics. The study was approved by the College of Science Research Ethics Committee, University of Lincoln (UK) (Ethics reference: UoL2021_7817 and 2021_3889). Written consent was obtained from the dog owners who participated in this study with their pets.

Data accessibility. The raw data and analysis code supporting the findings of this study are available in the supplementary material [39].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. T.S.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft; A.W.: conceptualization, supervision, writing—review and editing; K.G.: conceptualization, supervision, writing—review and editing; D.M.: conceptualization, supervision, writing—review and editing; E.F.: conceptualization, supervision, writing—review and editing.

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References

- Demaree HA, Everhart DE, Youngstrom EA, Harrison DW. 2005 Brain lateralization of emotional processing: historical roots and a future incorporating 'dominance'. *Behav. Cogn. Neurosci. Rev.* **4**, 3–20. (doi:10.1177/1534582305276837)
- Gainotti G. 2019 Emotions and the right hemisphere: can new data clarify old models? *Neurosci.* **25**, 258–270. (doi:10.1177/1073858418785342)
- Ocklenburg S, Güntürkün O. 2024 *The lateralized brain: the neuroscience and evolution of hemispheric asymmetries*. London, UK: Elsevier.
- Palomero-Gallagher N, Amunts K. 2021 A short review on emotion processing: a lateralized network of neuronal networks. *Brain Struct. Funct.* **227**, 673–684. (doi:10.1007/s00429-021-02331-7)
- Simon T, Guo K, Frasnelli E, Wilkinson A, Mills DS. 2022 Testing of behavioural asymmetries as markers for brain lateralization of emotional states in pet dogs: a critical review. *Neurosci. Biobehav. Rev.* **143**, 104950. (doi:10.1016/j.neubiorev.2022.104950)
- Silberman EK, Weingartner H. 1986 Hemispheric lateralization of functions related to emotion. *Brain Cogn.* **5**, 322–353. (doi:10.1016/0278-2626(86)90035-7)
- Davidson RJ. 1995 Cerebral asymmetry, emotion, and affective style. In *Brain asymmetry* (eds RJ Davidson, K Hugdahl), pp. 361–387. Cambridge, MA, USA: MIT Press.
- Leliveld LMC, Langbein J, Puppe B. 2013 The emergence of emotional lateralization: evidence in non-human vertebrates and implications for farm animals. *Appl. Anim. Behav. Sci.* **145**, 1–14. (doi:10.1016/j.applanim.2013.02.002)
- Rogers LJ, Vallortigara G, Andrew RJ. 2013 *Divided brains: the biology and behavior of brain asymmetries*. Cambridge, UK: Cambridge University Press.

10. Siniscalchi M, d'Ingeo S, Quaranta A. 2021 Lateralized emotional functioning in domestic animals. *Appl. Anim. Behav. Sci.* **237**, 105282. (doi:10.1016/j.applanim.2021.105282)
11. Royet JP, Plailly J. 2004 Lateralization of olfactory processes. *Chem. Senses* **29**, 731–745. (doi:10.1093/chemse/bjh067)
12. Siniscalchi M, Sasso R, Pepe AM, Vallortigara G, Quaranta A. 2010 Dogs turn left to emotional stimuli. *Behav. Brain Res.* **208**, 516–521. (doi:10.1016/j.bbr.2009.12.042)
13. Racca A, Guo K, Meints K, Mills DS. 2012 Reading faces: differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. *PLoS One* (ed. M Brass), **7**, e36076. (doi:10.1371/journal.pone.0036076)
14. Siniscalchi M, d'Ingeo S, Quaranta A. 2018 Orienting asymmetries and physiological reactivity in dogs' response to human emotional faces. *Learn. Behav.* **46**, 574–585. (doi:10.3758/s13420-018-0325-2)
15. Siniscalchi M, Quaranta A, Rogers LJ. 2008 Hemispheric specialization in dogs for processing different acoustic stimuli. *PLoS One* **3**, e3349. (doi:10.1371/journal.pone.0003349)
16. Reinholz-Trojan A, Włodarczyk E, Trojan M, Kulczyński A, Stefańska J. 2012 Hemispheric specialization in domestic dogs (*Canis familiaris*) for processing different types of acoustic stimuli. *Behav. Process.* **91**, 202–205. (doi:10.1016/j.beproc.2012.07.001)
17. Siniscalchi M, d'Ingeo S, Fornelli S, Quaranta A. 2018 Lateralized behavior and cardiac activity of dogs in response to human emotional vocalizations. *Sci. Rep.* **8**, 8. (doi:10.1038/s41598-017-18417-4)
18. Siniscalchi M, Sasso R, Pepe AM, Dimatteo S, Vallortigara G, Quaranta A. 2011 Sniffing with the right nostril: lateralization of response to odour stimuli by dogs. *Anim. Behav.* **82**, 399–404. (doi:10.1016/j.anbehav.2011.05.020)
19. Carver CS, Harmon-Jones E. 2009 Anger is an approach-related affect: evidence and implications. *Psychol. Bull.* **135**, 183–204. (doi:10.1037/a0013965)
20. Simon T, Wilkinson A, Frasnelli E, Guo K, Mills DS. 2024 Lateralized behaviour in dogs during positive anticipation. *Anim. Behav.* **216**, 155–173. (doi:10.1016/j.anbehav.2024.08.005)
21. Yu R, Mobbs D, Seymour B, Rowe JB, Calder AJ. 2014 The neural signature of escalating frustration in humans. *Cortex* **54**, 165–178. (doi:10.1016/j.cortex.2014.02.013)
22. McGreevy P, Grassi TD, Harman AM. 2003 A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. *Brain Behav. Evol.* **63**, 13–22. (doi:10.1159/000073756)
23. Urbaniak GC, Plous S. 2013 *Research Randomizer (version 4.0)* [computer program] <http://www.randomizer.org/>
24. Duncan A, Simon T, Frasnelli E. 2022 Investigating the influence of neuter status on paw preference in dogs and cats. *Laterality* **27**, 359–378. (doi:10.1080/1357650x.2022.2086563)
25. Laverack K, Pike TW, Cooper J, Frasnelli E. 2021 The effect of sex and age on paw use within a large sample of dogs (*Canis familiaris*). *Appl. Anim. Behav. Sci.* **238**, 105298. (doi:10.1016/j.applanim.2021.105298)
26. McGreevy PD, Brueckner A, Thomson PC, Branson NJ. 2010 Motor laterality in 4 breeds of dog. *J. Vet. Behav.* **5**, 318–323. (doi:10.1016/j.jveb.2010.05.001)
27. Tomkins LM, Thomson PC, McGreevy PD. 2010 First-stepping test as a measure of motor laterality in dogs (*Canis familiaris*). *J. Vet. Behav.* **5**, 247–255. (doi:10.1016/j.jveb.2010.03.001)
28. Salgirli Demirbas *et al.* 2023 Acute and chronic stress alter behavioral laterality in dogs. *Sci. Rep.* **13**, 4092. (doi:10.1038/s41598-023-31213-7)
29. Barnard S, Wells DL, Hepper PG, Milligan ADS. 2017 Association between lateral bias and personality traits in the domestic dog (*Canis familiaris*). *J. Comp. Psychol.* **131**, 246–256. (doi:10.1037/com0000074)
30. Wells DL, Hepper PG, Milligan ADS, Barnard S. 2018 Stability of motor bias in the domestic dog, *Canis familiaris*. *Behav. Process.* **149**, 1–7. (doi:10.1016/j.beproc.2018.01.012)
31. Scherer KR. 2005 What are emotions? And how can they be measured? *Soc. Sci. Inf.* **44**, 695–729. (doi:10.1177/0539018405058216)
32. Fusar-Poli *Pet et al.* 2009 Laterality effect on emotional faces processing: a meta-analysis of evidence. *Neurosci. Lett.* **452**, 262–267. (doi:10.1016/j.neulet.2009.01.065)
33. Killgore WDS, Yurgelun-Todd DA. 2007 The right-hemisphere and valence hypotheses: could they both be right (and sometimes left)? *Soc. Cogn. Affect. Neurosci.* **2**, 240–250. (doi:10.1093/scan/nsm020)
34. Neumann J, von Cramon DY, Lohmann G. 2008 Model-based clustering of meta-analytic functional imaging data. *Hum. Brain Mapp.* **29**, 177–192. (doi:10.1002/hbm.20380)
35. Leliveld LMC. From science to practice: a review of laterality research on ungulate livestock. *Symmetry* **11**, 1157. (doi:10.3390/sym11091157)
36. MacNeillage PF, Rogers LJ, Vallortigara G. 2009 Origins of the left & right brain. *Sci. Am.* **301**, 60–67. (doi:10.1038/scientificamerican0709-60)
37. Rogers LJ. 2010 Relevance of brain and behavioural lateralization to animal welfare. *Appl. Anim. Behav. Sci.* **127**, 1–11. (doi:10.1016/j.applanim.2010.06.008)
38. Frasnelli E. 2021 Looking at lateralization as a dynamic and plastic feature of nervous systems. *Laterality* **26**, 323–326. (doi:10.1080/1357650x.2021.1876083)
39. Simon T, Wilkinson A, Guo K, Mills D, Frasnelli E. 2025 Supplementary material from: Seeing Both Sides: Seeing both sides: dogs' eyes reveal valence-sensitive shifts between emotional states. Figshare. (doi:10.6084/m9.figshare.c.8175071)