Lateralized behaviour in dogs during positive anticipation

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Recent research has used behavioural asymmetries in dogs as an indirect measure of their emotional states from inferred asymmetries in brain activity. Different hypotheses predict differences in behaviour based on emotional salience (right-hemisphere hypothesis), valence (valence hypothesis) or motivation (approach—withdrawal hypothesis). As testing different hypotheses requires having a measure of the consistency of a lateralized response across stimuli of similar emotional significance, we investigated dogs' responses to two emotionally positive and approach-motivating stimuli (food and toy) presented within an apparatus in which dogs could see the positive stimulus (anticipatory phase) before being given access to it. Moreover, to assess the degree to which expressions of lateralized behaviour are similar across different functional responses to an emotionally competent stimulus (and, thus, to explore the generalizability of different hypotheses), biases were analysed both at the level of sensory processing (i.e. lateralized eye use) as well as 'postprocessing' motor action (i.e. lateralized tail-wagging behaviour) during stimulus inspection. Overall, dogs showed a right-eye/left-hemisphere dominance when inspecting the food, but no population level bias for the toy; although they displayed consistent individual level biases. This difference cannot be explained by simply referring to the stimuli with regards to their general emotional salience (right-hemisphere hypothesis), valence (valence hypothesis), or general motivational tendencies (approach—withdrawal hypothesis). In relation to tail wagging, laterality patterns for both stimuli involved considerable inter-/intraindividual variability, with no common directional bias at a population level. Expressions of lateralized activity can therefore vary between sensory perceptual and expressive motor processes. These results suggest that emotion-related behavioural/brain lateralization reflects a complex phenomenon that probably involves processes modulated by multiple factors. The contribution of laterality patterns to informing assessments of animals' emotions might be more limited than generally assumed.

There is growing scientific interest in the emotional states of nonhuman animals (hereafter referred to as 'animals'). Emotions are relatively short-lasting states that can occur in response to particular external stimuli (i.e. changes in the environment) and/or internal (mental) representations that typically involve (1) appraisal processes assessing the stimuli/internal representations as salient to current goals (Adolphs, 2010; Ben-Ze'ev, 2010; Scherer, 2005); (2) changes in different response systems (e.g. peripheral physiological, behavioural, experiential, Mendl et al., 2010; Moors, 2009; Scherer, 2005); and (3) the activation of relatively distinct neuronal networks (Palomero-Gallagher & Amunts, 2021; Panksepp, 1998). Unlike humans, animals cannot give verbal, self-reflective descriptions of their emotional states. Therefore,

research relies exclusively on nonlinguistic measures to study animal emotions. As such, various (neuro)physiological, cognitive and behavioural markers are used to investigate animals' emotional lives.

Inter alia, emotions in (both humans and) animals can be studied by investigating correlates of brain lateralization. Brain lateralization refers to functional asymmetries between the right and the left hemisphere of the brain. Although emotional states are widely accepted as being associated with asymmetric activity between the two sides of the brain, the precise contribution of each remains unclear (Demaree et al., 2005; Gainotti, 2019; Leliveld et al., 2013; Ocklenburg & Güntürkün, 2018; Palomero-Gallagher & Amunts, 2021; Simon, Guo et al., 2022). Competing hypotheses are proposed including, for example, the right-hemisphere hypothesis, which maintains that all emotional states predominantly involve the activation of right hemisphere networks (Gainotti, 1972,

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2019). By contrast, the valence and the approach–withdrawal hypotheses claim that both hemispheres can play a dominant role: the valence hypothesis suggests that emotional states with a negative emotional valence predominantly involve the activation of the right hemisphere, whereas the left hemisphere is relatively more involved in emotional states with a positive valence (Silberman & Weingartner, 1986); the approach–withdrawal hypothesis predicts that emotional states that involve approach and withdrawal motivations are associated with a dominant activity of the left and right hemisphere, respectively (Davidson, 1995). All three hypotheses were originally introduced in the context of human research and later applied in research on (vertebrate) animals.

In animals, most findings on emotion-related brain asymmetries are not inferred from direct measurements of the animals' brain activity, but indirectly through observation of behavioural biases reflecting brain lateralization (Leliveld et al., 2013; Rogers et al., 2013; Siniscalchi et al., 2021); that is, behavioural asymmetries can be considered signatures of hemispherically lateralized activity. In the vertebrate nervous system, both afferent and efferent neurons to and from one side of the body cross the midline of the body and are mainly connected to the contralateral brain hemisphere. As a result, sensory input from and movements of the left or right half of the body are mainly processed or controlled by the opposite side of the brain (the olfactory system, however, represents a notable exception: input processed by the right or left nostril is transmitted to networks of the same side of the brain, Rogers et al., 2013; Royet & Plailly, 2004). Given this organization of the nervous system, brain lateralization in emotionally salient contexts can be studied indirectly by investigating behavioural biases. For instance, if an emotionally significant stimulus is inspected predominantly with the right or left eye/ear/nostril and/or induces emotionally motivated (expressive and/or other) asymmetric motor behaviour, conclusions about the relative activation of the two sides of the brain can be inferred.

Given the unique position of dogs, *Canis familiaris*, in human society, especially in their role as social companions, there is particular interest in their emotional lives. Given that behavioural observations are noninvasive, relatively easy and cost effective, lateralization research is considered a valuable methodological approach to assess dogs' (and other animals') emotions (Leliveld et al., 2013; Siniscalchi et al., 2017, 2021). Two particular types of emotionally salient stimuli are commonly used in this work: (1) stimuli that are appraised as alarming and that were probably associated with negatively valenced emotions, and (2) stimuli that are assessed as prosocial and thus related to positively valenced emotions (see Simon, Guo et al., 2022 for a detailed review of the previous literature). Dogs preferentially used their left eye to inspect alarming visual stimuli (e.g. image of a snake or a cat displaying a threatening posture, Siniscalchi et al., 2010; pictures showing an angry/fearful human, Siniscalchi, d'Ingeo, & Quaranta, 2018 and threatening conspecific facial expressions, Racca et al., 2012) and their left ear when attending to alarming sounds (e.g. sounds of thunderstorm, Siniscalchi et al., 2008; threatening cat vocalizations, Reinholz-Trojan et al., 2012; nonverbal human emotional vocalizations, such as screaming, sobbing, growling, Siniscalchi, d'Ingeo & Fornelli, 2018). Moreover, they displayed a right nostril bias to sniff at alarming odours (e.g. smell of adrenaline and veterinary sweat, Siniscalchi et al., 2011; and secretions of a conspecific collected soon after a distressing situation, Siniscalchi et al., 2016). Given the organization of the vertebrate nervous system, the reported behavioural biases during alarming sensory stimulus inspection indicate a stronger engagement of networks in the right hemisphere. By contrast, when dogs were presented with (presumably) emotionally salient prosocial stimuli (e.g. pictures with friendly conspecific facial expressions, Racca et al., 2012;

nonverbal prosocial emotional vocalizations of humans, such as laughing, Siniscalchi, d'Ingeo & Fornelli, 2018), they displayed patterns of lateralized behaviour during sensory stimulus inspection that overall suggest a dominant role of the left hemisphere.

While most work has focused on behavioural asymmetries in dogs' sensory functioning when attending to emotionally relevant stimuli, few studies have analysed other behavioural asymmetries, such as emotionally expressive motor behaviours. For instance, dogs showed left-lateralized tail-wagging movements (i.e. the angles of tail-wagging movements to the left side were larger compared to the right side of the dog's body) when facing an alarming stimulus (e.g. appearance of an agonistic conspecific, Quaranta et al., 2007), but right-biased movements in prosocial contexts (e.g. appearance of the owner, Quaranta et al., 2007; prosocial interactions with a human being, Ren et al., 2022). Like behavioural asymmetries in the context of sensory functioning, the observed lateralized tail-wagging movements indicate a predominant activation of motor networks in the right hemisphere in response to an alarming stimulus, but the converse when responding to prosocial stimuli.

Taken together, in the context of presumably emotionally relevant alarming and prosocial stimuli, the observed patterns of behavioural lateralization of both sensory and motor functions provide stronger evidence for the valence hypothesis compared to the right-hemisphere hypothesis. Supposing that the alarming stimuli presented to the dogs were more likely to induce withdrawal tendencies, while the prosocial stimuli were associated with approach motivation, the reported findings can also be explained by the approach–withdrawal hypothesis (see Simon, Guo et al., 2022, for a critical reflection on the evidential weight of previous research findings on the different hypotheses about emotion-related brain lateralization).

A systematic investigation of asymmetric behavioural markers for emotional states in dogs requires exploration of a wider range of different emotionally salient settings (Simon, Guo et al., 2022). Therefore, we explored behavioural biases during emotional states of positive anticipation (i.e. an expectation of a future, positively valenced event). While previous work (Bremhorst et al., 2019; Pedretti et al., 2022) reported behavioural indicators of positive anticipation in dogs, behavioural asymmetries have not yet been investigated. We trained dogs to anticipate access to a visually presented stimulus that was likely to be associated with both a positive emotional valence and stimulus-directed approach motivation. To test different hypotheses on emotion-related brain lateralization (e.g. right-hemisphere hypothesis, valence hypothesis, approach–withdrawal hypothesis), it is essential to have a measure of the consistency of a lateralized response across different stimuli of the same emotional quality. In this way stimulus-specific functional/motivational effects can potentially be teased out from more general emotional effects (consistent effects across the stimuli). For this reason, we exposed dogs to two different stimulus types with the same emotional valence (i.e. positive) and motivational tendency (i.e. stimulus-directed approach motivation): food and toy stimuli.

Recent research with humans suggests that different emotionally salient contexts and different components of emotions (according to the Component Process Theory, emotions are multicomponent states that can be analysed with regards to their functional structure in terms of appraisal, arousal, behavioural tendencies, emotion expression and communicative content; e.g. Scherer, 2005) may involve different interconnected brain networks that are associated with distinct patterns of lateralization (Fusar-Poli et al., 2009; Killgore & Yurgelun-Todd, 2007; Neumann et al., 2008; Palomero-Gallagher & Amunts, 2021; Simon, Guo et al., 2022). Multiple interrelated but differently lateralized networks

might be best explained by an integrative model according to which the right-hemisphere, valence and approach—withdrawal hypotheses are not mutually exclusive, but relate to different aspects of emotional states. To further investigate the relationship between brain lateralization and specific emotional states such an integrative hypothesis should also be explored in other nonhuman species. To investigate the integrative hypothesis, it is not only important to investigate behavioural/brain lateralization in various emotionally relevant settings, but also to compare lateralization patterns relating to different components of emotion. However, most previous work with dogs (and other animals) has focused on behavioural asymmetries in sensory functioning (e.g. lateralized visual/ auditory/olfactory processing), which relates to the appraisal component of emotional processing (Simon, Guo et al., 2022; Siniscalchi et al., 2021). By contrast, other components of emotion (e.g. arousal, behavioural tendencies and communicative signals) have been less studied. To address this gap, we analysed behavioural lateralization both at the level of sensory (i.e. visual) stimulus inspection and 'postprocessing' motor action (i.e. emotionally expressive tail-wagging behaviour) while dogs awaited the reward.

While both the food and the toy stimulus presumably involved the same (i.e. positive) emotional valence and induced stimulus-directed approach motivation in the dogs participating in this study, the two stimulus types may have varied with regard to the specific intensity of valence and/or the elicited motivational tendencies (e.g. some dogs may appraise food as a more positive stimulus, whereas other dogs may perceive the toy as more positive). Yet, regardless of potential differences in the intensity of the emotional valence and/or motivation, different hypotheses allow for different predictions about lateralized responses to both the food and the toy stimulus: based on the right-hemisphere hypothesis, we would expect left-lateralized behavioural expressions (i.e. preferential use of the left eye and left-biased tail-wagging behaviour) reflecting dominant activation of the right brain in response to both stimulus types. By contrast, assuming either the valence or approach—withdrawal hypothesis, we would expect left-lateralized brain activity and right-lateralized behavioural correlates for both stimulus types. Assuming a more integrative model, according to which the right-hemisphere, valence and approach—withdrawal hypotheses are not mutually exclusive, but relate to different aspects of emotional states, dogs' visual stimulus processing and tail-wagging behaviour may exhibit distinct lateralization patterns corresponding to different hypotheses. For instance, left-biased behaviour/right-lateralized brain activation (corresponding to the right-hemisphere hypothesis) may be observed for one behavioural variable, whereas the other behavioural variable may be associated with right-biased behaviour/left-lateralized brain activation (corresponding to the valence or approach—withdrawal hypothesis).

Our study contributes to comparative research on emotion-related behavioural and brain lateralization; hypothesized relationships between brain lateralization and specific emotional states that have been originally proposed in the context of human research are further explored in a different vertebrate species using dogs as a model.

METHODS

Subjects

Pet dogs of various breeds were recruited by directly approaching dog owners (e.g. in dogs parks or pet food stores) in the Bielefeld area, Germany. As this study involved the investigation of dogs' visual inspection of rewarding stimuli (i.e. either a piece of food or a toy) at close distance, only dogs that had, according to their owners' judgement, both unimpaired vision and a high motivation (1) for some kind of (dog-appropriate) food, and/ or (2) to play with a toy ball were used in this study. Extreme versions of both brachycephalic (i.e. short-nosed) dogs, such as pugs or French bulldogs, and dolichocephalic (i.e. long-nosed) dogs, such as whippets or greyhounds, were not considered for participation to reduce effects from morphology-related interindividual variation in the dogs' field of vision (McGreevy et al., 2004). In total, 40 pet dogs were recruited (20 purebred dogs, 20 mixed breed; 22 females of which 13 were neutered, 18 males of which eight were neutered; age (mean ± SD): 5.21 ± 2.98 years; see Supplementary Material for details).

Stimuli

Dogs were trained to expect to gain access to a rewarding (1) food or (2) toy item, 2 s after the item had been initially presented in an experimental apparatus. The presentation of the reward was intended to induce a state of positive anticipation (positive emotion) that is associated with a stimulus-directed approach motivation. A similar paradigm has also been used in previous investigations of positive anticipation (Bremhorst et al., 2019; Pedretti et al., 2022). The type of food was selected for each dog individually, according to what the owner said their dog particularly liked. For each dog, the individually selected food was cut into cylindrical pieces (ca. 15 mm diameter and 5 mm high; Fig. 1a). An apple corer was used to ensure a uniform shape of the food pieces. A rubber ball (60 mm diameter) was used as an appropriate toy item for all dogs (Fig. 1b); the same ball was used throughout the study.

Experimental Set-up

Dogs were tested in an experimental room (5 m × 4 m) in Bielefeld, Germany. The set-up consisted of two interconnected and equally sized barriers, A and B (150 × 120 cm and 2 cm thick; Fig. 2). In the centre of barrier A was an opening (50 × 50 cm). The distance of the opening from the floor could be varied so that the lower edge of the opening was level with the dog's chest. Behind barrier A, there was a board upon which the rewarding stimulus (i.e. food or toy) was presented. The presentation board was also adjustable in its distance from the floor and was set to the height of the lower edge of the opening, depending on the size of the dog.

Below the presentation board was another board on which several more versions of the stimulus presented were arranged (they were identical in type, size and shape to the stimulus displayed on the presentation board). The items on the lower board were not visible to the dog at any time but were present to encourage a homogeneous diffusion of the odour; they were evenly distributed over the entire lower board. This was intended to encourage the dog to visually (rather than olfactorily) inspect the food or toy stimulus on the presentation board during stimulus presentation.

In front of barrier A, there was an enclosure into which the dogs had to enter to allow the orientation measurements during the test. The enclosure consisted of two equally sized parallel wooden boards (50 × 38 cm and 1.5 cm thick), which were connected at their front base (i.e. directly adjacent to barrier A) at 30 cm via another wooden board (30 × 13 cm and 1.5 cm thick).

Two vertically movable sliding panels (i.e. one transparent and one opaque; Fig. 2) were used to block the visibility of (opaque) and/or access to (transparent) the stimulus on the presentation board when the dogs stood inside the enclosure (in front of barrier A). Only when both panels were moved upwards could the dogs see and access the reward stimulus on the presentation board. When
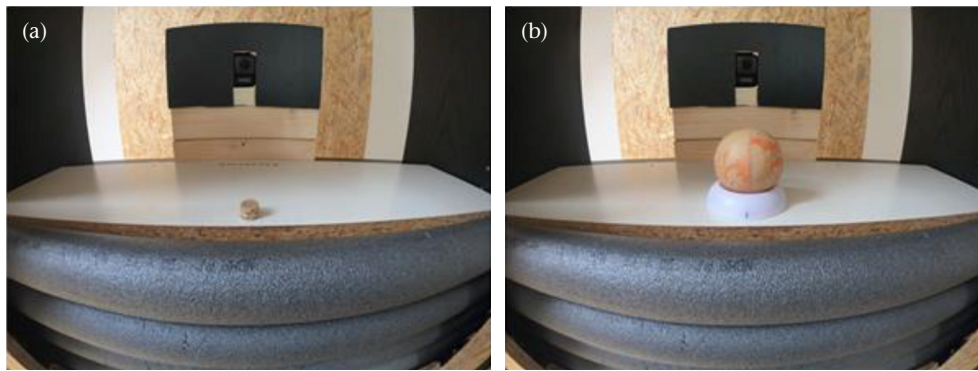
Figure 1. Presentation of (a) a food item and (b) a toy ball in the experimental apparatus.
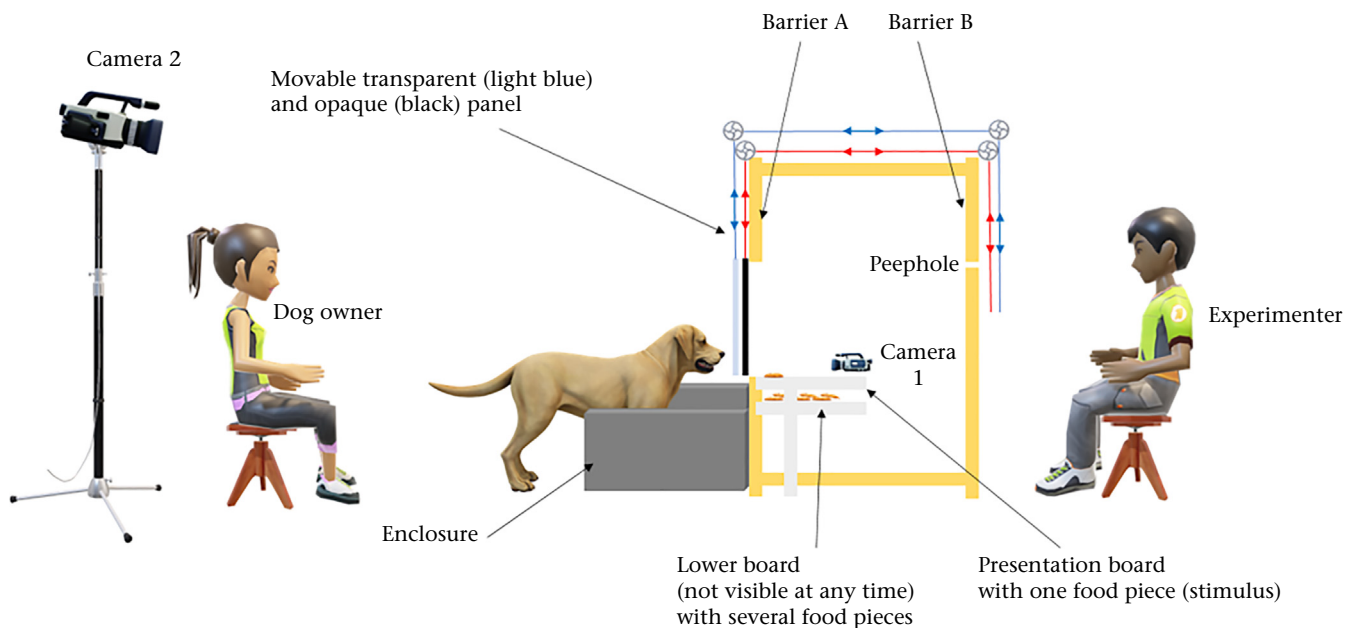

Figure 2. Experimental apparatus.

only the opaque panel was moved upwards and the transparent panel still blocked the opening, the dogs could see the presentation board with the stimulus but had no access to it.

The dog owner sat on a chair centrally behind the dog (ca. 2.5 m in front of barrier A). The experimenter was positioned behind barrier B. The position of the vertically movable panels could be modified by the experimenter via a cable pull system. When the opaque panel was lifted, the experimenter could observe the dog through a peephole in barrier B (Fig. A1).

All test sessions were video recorded with two cameras (GoPro Hero 7 Black, resolution 1440p, 30 fps, GoPro Inc., U.S.A.). To record the relative involvement of the eyes during visual inspection of the stimulus, a camera was attached to the presentation board (camera 1 in Fig. 2). To record tail-wagging behaviour, a second camera was attached above the box in front of barrier A (camera 2 in Fig. 2).

Design and Procedure

Depending on their specific stimulus preferences, dogs were either presented with one (i.e. food or toy) or two (i.e. food and toy) types of rewarding stimuli. If dogs were exposed to only one stimulus type, participation in the study required four visits for each dog and its owner (Fig. 3). During the first visit, the dog was habituated to the experimental setting: the dog could familiarize with both the experimenter and the experimental apparatus (e.g. the dog was introduced to the sliding panels of the apparatus and it could take some pieces of food or a toy ball from the presentation board of the apparatus when both sliding panels were lifted). On the second visit, the dog received an initial training session. On both the third and fourth visit, it received a training session followed by a test session. Each of the visits lasted approximately 15–20 min. The minimum interval between two successive of the four visits was 2 days. If dogs were exposed to both food and the toy stimulus, three additional visits were required; these consisted of one training session (fifth visit) followed by two training and test sessions (sixth and seventh visits; Fig. 3). The minimum interval between the last test session of the first stimulus (fourth visit) and the initial training session for the second stimulus (fifth visit) was one week. For dogs that were exposed to both the food and the toy stimulus, the order in which the two stimulus types were presented was randomized for each dog, using Urbaniak and Plous's (2013) Research Randomizer, and counterbalanced between individuals. Before a visit involving food, dogs were food deprived for at least 5 h, and before a visit involving a toy stimulus, they did not play
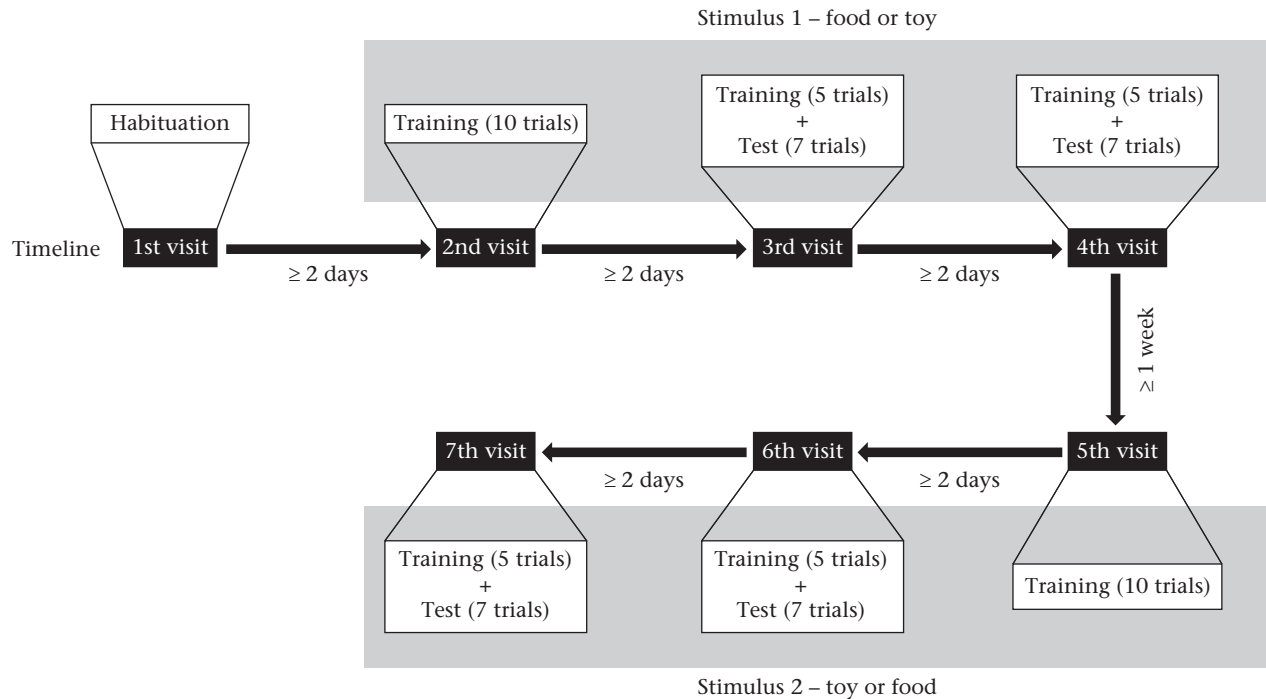
Stimulus 1 – food or toy

Figure 3. Experimental procedure. If a dog was exposed to only one stimulus type (i.e. food or toy), participation in the study required four visits: first visit (habituation session), second visit (a longer training session), third and fourth visits, respectively (both a short training and a test session for each visit). If a dog was also presented with the other stimulus type (i.e. toy or food), three additional visits were required for the second stimulus: fifth visit (a longer training session), sixth and seventh visits, respectively (both a short training and a test session for each visit).

with a toy or engage in intense physical activity (e.g. intense running, swimming) on the same day prior to the session; this was supposed to help maximize their motivation for either food or toy. After a dog's visit, the experimental apparatus and (if a toy was involved during that visit) the ball were cleaned.

Training sessions

Each training session consisted of a series of trials in which the dog was trained to anticipate access to the stimulus (i.e. food or toy) after it was visually presented in the apparatus. Prior to the start of each training trial, the experimenter prepared the stimulus at the centre of the presentation board. Meanwhile, both the transparent and opaque panel blocked the opening so that the dog could not see stimulus preparation. The training trial started as soon as the dog entered the enclosure in front of barrier A, so that at least its head, shoulders and both front legs were in the enclosure (verbally indicated by the dog owner). 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 (ca. 2 s), the experimenter also lifted the transparent panel. If the dog was presented with a food stimulus, the training trial ended after the dog had eaten the food. When a toy was presented to the dog, the training trial ended after a short (ca. 10–15 s) play session after the dog had taken the toy from the presentation board: depending on its preferred style of play, the dog could chew on the toy, carry it around, chase it or engage in interactive play with its owner. After a trial, the dog was called back by its owner and remained close to them. When the experimenter had prepared the next trial, the dog could approach the apparatus again to start the trial.

The initial training session for the specific stimulus type (on the second visit and, for dogs that were exposed to both stimulus types, also on the fifth visit) was considered complete when the dog finished 10 consecutive training trials in which it directed its (visual) attention to the stimulus (according to the judgement of the

experimenter observing the dog through the peephole in the apparatus; Fig. A1) when it was visible but not yet accessible. Each of the subsequent two training sessions (on the third and fourth visits and, for dogs that were exposed to both stimulus types, also on the sixth and seventh visits) was completed when the dog showed such stimulus-directed attention in five consecutive training trials. As both the third and fourth/sixth and seventh visits involved test trials (see Test sessions) in addition to the training trials, the number of training trials was reduced compared to the second/fifth visit in order to not overburden the dogs or lose their motivation and attention due to too many training and test trials. Where possible, the dog would start the 10 (second/fifth visit) and five (third and fourth/sixth and seventh visits) consecutive training trials, respectively, by entering the enclosure independently (without its owner's help). Where this was not possible, the dog owner could support their dog by guiding it into the enclosure and then stepping behind it to start the training trial. Some dogs repeatedly pushed against the panels with their muzzles and/or paws when they went into the enclosure on their own. In this case, the owner would gently hold the dog by its hindquarters while the dog stood in the enclosure with its body straight in front of the apparatus. Only after both panels were lifted would the owner release the dog so that it could access the food stimulus.

Test sessions

Once the dog successfully completed the training, it moved onto the test sessions. Each session comprised seven test trials, the procedure for which was similar to that of the training trials, differing only in that they involved a manipulation of the dog's body position relative to the stimulus presented. As it was expected that the dog's relative lateral body position could affect their behavioural response to the stimulus (especially the relative involvement of the eyes during visual stimulus inspection), the dogs' body position was manipulated to control for this possible

effect. For this purpose, the food stimulus was shown at one of seven possible positions on the presentation board, so that in each experimental session the stimulus was shown once at each position. The order of the positions in which the food stimulus was presented was randomized, using Urbaniak and Plous's (2013) Research Randomizer, for each experimental session and each dog. All positions were in a straight line parallel to the edge of the presentation board with adjacent positions being 10 mm apart. Thus, the possible positions were either in the centre of the presentation board or 10, 20 or 30 mm to either side of the centre (Fig. A2). Through this manipulation, stimulus-induced behavioural responses could be analysed for different relative body positions. This allowed an estimation of the influence of relative lateral position on displayed behavioural responses and thereby any responses could be corrected for lateral position effects (described below in Data Analyses: Relative eye use).

Measurements

For each stimulus type (i.e. food and toy), dogs' relative eye use and tail-wagging behaviour during stimulus inspection were both measured from video recordings. Video analysis was performed using Kinovea software (version 0.8.15; www.kinovea.org).

Relative eye use

Both the right-eye angle and the relative body position were determined during the 2 s time window from the time at which the opaque panel was initially lifted, while the transparent panel still blocked the opening of the apparatus, so that the dog could see but not yet access the stimulus on the presentation board. All measurements were done as soon as the dog held its body and head still for at least 0.1 s (three frames) and appeared focused on the stimulus in the respective time window.

To investigate dogs' relative eye use in experimental trials, the angle between the inner canthus of the right eye, the midpoint

between the right and the left eye's canthus and the stimulus was assessed (Fig. 4a).

In addition, for each angle measurement, the corresponding lateral body position of the dog relative to the presented stimulus was estimated. For this purpose, the lateral displacement of the dog's body centre relative to the stimulus was measured. The body centre was determined as follows. When the dog stood centrally in front of the opening of the apparatus, both the distance between the two forelimbs and the width of the chest was measured at two different positions. The midpoints of all measured distances were calculated. The average of all midpoints was used to determine the body centre of the dog (Fig. 4b). This additional measurement provided an estimate of the influence of relative lateral position on the dogs' visual stimulus inspection and thus allowed an analysis of their relative eye use corrected for lateral position effects (described below in Data Analyses: Relative eye use).

To standardize measurements across dogs and experimental trials, the dog's right-eye angle and the corresponding relative lateral body position were measured only for those trials in which the dog's body was positioned straight in front of the apparatus. This was considered to be the case only if, from the perspective of the camera recording the dog within the apparatus, at least one of the dog's front legs partially covered the ipsilateral hindleg (Fig. A3).

Tail-wagging behaviour

To investigate tail-wagging behaviour in experimental trials, the sweep of tail-wagging movements to the right and left side of the dog's body was measured. Specifically, for each sweep, the maximum displacement was recorded by measuring the maximum angle of the tail after the lower third with reference to the anteroposterior body axis (Fig. 5). The anteroposterior body axis was represented by a software-generated (Kinovea software) straight line between the midpoint of both points of the hip and the midpoint of the tail base (both reference points were marked with a sticker at the beginning of each experimental session; Fig. 5). For
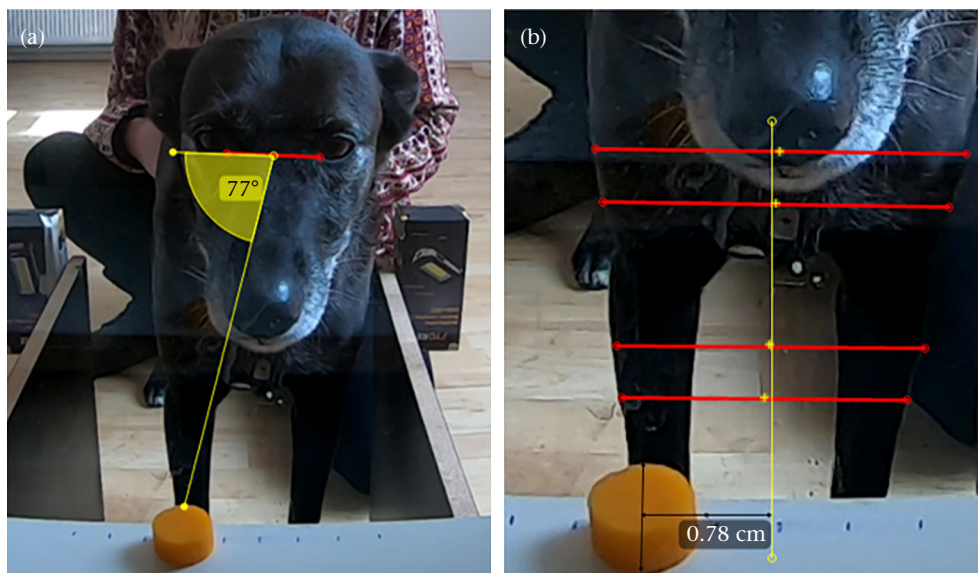

Figure 4. Relative eye use and relative lateral body position. (a) Angles between the inner canthus of the right eye, the midpoint between the two eyes' canthi and the stimulus were used to assess the dog's relative eye use. (b) The estimation of the body centre was based on both the distance between the two front legs (indicated by the two lower red lines) and the width of the rib cage (indicated by the two upper red lines). The average of the midpoints of all four red lines (indicated by the yellow crosses) was used to estimate the centre of the dog's body (indicated by the yellow line). The lateral body position in relation to the stimulus was defined as the distance between the body centre and the stimulus.

each experimental trial, tail-wagging behaviour was measured during the same time window as dog's relative eye use.

Data Analyses

Statistical analyses were performed in RStudio 1.3.1056.1 (R Core Team, 2021).

Relative eye use

For each stimulus type (i.e. food and toy), each dog and each experimental trial, the right-eye angle and the lateral body position (relative to the presented stimulus) were measured as outlined above (see Measurements: Relative eye use). To subsequently estimate the effect of the dog's relative lateral body position on the right-eye angle measurements, a linear regression was used with the dog's relative lateral body position as the independent variable and the right-eye angle as the dependent variable. Based on the slope of the regression line 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 observed in the respective experimental trial.

For each stimulus type and dog, the median of all (corrected) right-eye angles was used to assess the relative eye use across trials. A median <90° indicates that the stimulus is predominantly processed within the visual field of the right eye (i.e. right-eye bias), a median >90° indicates that the stimulus is predominantly perceived in the left visual field (i.e. left-eye bias) and a median = 90° means that there is no bias. In addition, for each stimulus type and dog, the degree of lateralized eye use was assessed by the absolute deviation of the median right-eye angle from 90°: |right eye angle − 90°|. The more the degree of lateralized eye use is greater than 0°, the stronger is a dog's preferential eye use (i.e. regardless of which eye is preferentially used) and the closer the degree of lateralization is to 0°, the weaker is the preferential eye use.

For each stimulus type, a one-sample *t* test was run to test whether the dogs' median right-eye angles were significantly different from 90°. For the dogs that completed both the food and toy condition, a paired *t* test was used to see whether the medians

of the dogs' right-eye angles differed significantly between the two stimulus types; a Pearson correlation test was performed to further analyse the relationship between the medians of both stimulus types.

A one-sample Wilcoxon signed-rank test was performed for each stimulus type to test whether the dogs' degree of lateralized eye use was significantly larger than 0°. For the dogs that completed both the food and toy condition, a Wilcoxon signed-rank test was to estimate whether the degree of asymmetric eye use differed significantly between the two stimuli; a Spearman correlation test was performed to further analyse the relationship between the medians of both stimulus types.

To assess the consistency of dogs' relative eye use for each stimulus type across time, the dogs' medians of their right-eye angles of both experimental sessions were compared using a paired *t* test. To further explore the relationship between the medians of both experimental sessions, a Pearson correlation test was performed. A similar procedure was used with regard to the degree of lateralized eye use; in this case, however, nonparametric tests (i.e. Wilcoxon signed-rank test and Spearman correlation test) were used.

For each *t* test and Wilcoxon test, effect sizes were estimated by Cohen's *d*.

Tail-wagging behaviour

For each stimulus type, dog and experimental trial, tail-wagging movements were assessed by calculating the median angle of all sweeps to each direction (i.e. left and right). For each stimulus type and dog, overall medians (i.e. across trials) for left and right movements, respectively, were determined based on the trials' medians.

For each stimulus type and dog, a directional index of lateralized tail-wagging behaviour was determined. For dogs with greater (overall) median left than right angles, the directional index was calculated by:

$$\frac{\text{angle right sweep}}{\text{angle left sweep}} - 1$$

For dogs with greater (overall) median right than left angles, the index was computed by:

$$1 - \frac{\text{angle left sweep}}{\text{angle right sweep}}$$

This directional index thus quantifies lateralized tail wagging on a scale from −1 to +1: just as the more the directional index is smaller than 0, the greater the left-lateralization of the tail-wagging behaviour, so the more the index is greater than 0, the stronger the right-lateralization of the tail-wagging behaviour, thus the closer the index is to 0, the less lateralized is the behaviour. In addition, for each stimulus type and dog, the degree of lateralized tail-wagging movements was assessed by the absolute value of the directional index:

$$\left|\frac{\text{angle right sweep}}{\text{angle left sweep}} - 1\right| \text{ and } \left|1 - \frac{\text{angle left sweep}}{\text{angle right sweep}}\right|$$

respectively. The more the degree of lateralized tail wagging is greater than 0, the stronger is a dog's tail wagging asymmetry (regardless of the direction) and the closer the degree of lateralization is to 0, the weaker is the lateral bias.

For each stimulus type, a one-sample *t* test was performed to test whether the dogs' directional index of lateralized tail-wagging behaviour was significantly different from 0. A paired *t* test was employed to test whether the dogs' directional indices were
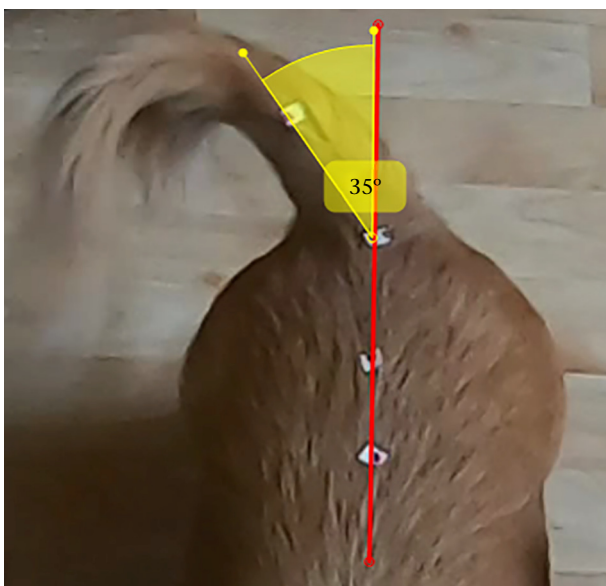

Figure 5. Tail-wagging behaviour. For each tail wag, the maximum displacement was recorded by measuring the maximum angle of the tail after the lower third with reference to the anteroposterior body axis (indicated by the red line).

significantly different between the two stimulus types. In addition, a Pearson correlation test was used to investigate the relationship between the directional indices of both stimulus types. The procedure was then repeated for the data on the dogs' degrees of lateralized tail wagging.

To assess the consistency of dogs' lateralized tail-wagging behaviour for each stimulus type across time, the directional indices of lateralized tail movements were compared between experimental sessions using a Wilcoxon signed rank test. To further explore the relationship between the directional indices of both experimental sessions, a Pearson correlation test was used. This procedure was repeated for the degree of lateralized tail-wagging movements.

For each t test and each Wilcoxon test, the effect size was estimated using Cohen's d.

Correlation between relative eye use and tail-wagging behaviour

For each stimulus type, the relationship between the lateralization patterns of dogs' relative eye use and tail-wagging behaviour was explored by performing a Spearman correlation test based on the dogs' medians for their right-eye angle and the directional index of lateralized tail-wagging movements. This procedure was then repeated for the degrees of lateralized behaviours.

Intercoder reliability

For each stimulus and behavioural variable (i.e. relative eye use and tail-wagging behaviour), data of 20% of the dogs (randomly selected using the sample() function in R) were analysed by a second coder. For relative eye use, the intercoder reliability was assessed by performing a Spearman correlation test for each selected dog based on their (corrected) right-eye angles for all experimental trials. For tail-wagging behaviour, the intercoder reliability was assessed by running a Spearman correlation test for each selected dog based on their experimental trials' median angles of all tail-wagging movements to each direction (i.e. left and right).

Ethical Note

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

RESULTS

Of the 40 dogs that were recruited for this study, data from a total of 35 dogs were analysed (17 purebred dogs, 18 mixed breeds; 20 females of which 12 were neutered, 15 males of which seven were neutered; age (mean ± SD): 5.39 ± 2.87 years; see Supplementary Material for details). Five dogs were excluded from the analysis because they did not meet the criteria for the behavioural measurements (i.e. the dogs neither focused visually on the presented stimuli nor showed tail-wagging behaviour).

Relative Eye Use

For the food stimulus, the relative eye use was analysed for 19 dogs. Of these 19 dogs, 17 individuals completed two experimental sessions, whereas two individuals completed one session (for one dog, the camera did not record the second session, while the other dog met the criteria for the behavioural measurements only in one session); on average, 9.37 ± 2.63 trials were analysed per dog. For 18 dogs, eye data were assessed for the toy stimulus. Of these 18 dogs, 17 completed two experimental sessions and one dog did one session (this dog met the criteria for the behavioural measurements

only in one session); on average, 8.72 ± 2.59 trials were analysed per dog. For eight dogs, eye data were measured for both the food and the toy stimulus.

In response to food stimuli, dogs' right-eye angles were significantly less than 90° (mean = $87.5° \pm 4.2°$, $t_{18} = 2.6$, $N = 19$, $P = 0.017$, effect size $d = 0.6$; Fig. 6a), suggesting a common right-eye bias during stimulus inspection at a population level. By contrast, when dogs were presented with the toy stimulus, their right-eye angles were not significantly different from 90° (mean = $89.5° \pm 4.6°$, $t_{17} = 0.5$, $N = 18$, $P = 0.621$, effect size $d = 0.1$; Fig. 6b), indicating no common directional (i.e. left or right) eye bias at a population level. While the range of right-eye angles was similar for both stimulus types, relatively more dogs showed angles < 90° (right-eye bias) than > 90° (left-eye bias) in the food compared to the toy stimulus (Fig. 6c,d). For the subsample of dogs that provided eye data for both the food and the toy stimulus, right-eye angles did not vary significantly between stimulus types ($t_7 = 0.458$, $N = 8$, $P = 0.661$, effect size $d = 0.162$) and were significantly positively correlated ($r = 0.836$, $N = 8$, $P = 0.01$).

The degree of lateralized eye use (i.e. regardless of which eye is preferentially used) was significantly larger than 0° for both the food and the toy stimulus (food: median = $3.212°$, interquartile range, IQR = $4.53°$, $V = 190$, $N = 19$, $P < 0.001$, effect size $d = 1.259$; Fig. 6e; toy: median = $3.212°$, IQR = $4.53°$, $V = 190$, $N = 18$, $P < 0.001$, effect size $d = 1.731$; Fig. 6f). That is, regardless of whether the dogs' right-eye angles indicated a common directional bias in response to the food or toy stimulus at the population level, they showed left- or right-biased eye use for both stimulus types at the individual level (i.e. in single individuals, regardless of a common directional bias in the population). The distributions of the degrees of lateralized eye use were similar for both stimulus types (Fig. 6g,h). In the subsample of dogs that completed both the food and the toy condition, the degree of lateralized eye use did not significantly differ between the two stimuli ($V = 7$, $N = 8$, $P = 0.148$, effect size $d = 0.480$) and tended to be positively correlated across stimulus types (rho = 0.714, $N = 8$, $P = 0.062$).

For both stimulus types, the right-eye angles were consistent between the two experimental sessions: neither for the food nor for the toy stimulus did the dogs' right-eye angles differ between the two experimental sessions (food: $t_{16} = -0.546$, $N = 17$, $P = 0.593$, effect size $d = 0.132$; toy: $t_{16} = 0.417$, $N = 17$, $P = 0.682$, effect size $d = 0.101$) and, for both stimulus types, right-eye data were significantly and positively correlated between experimental sessions (food: $r = 0.664$, $N = 17$, $P = 0.004$; toy: $r = 0.512$, $N = 17$, $P = 0.036$). By contrast, the degree of lateralization was less consistent across experimental sessions: although neither the food nor the toy data were significantly different between the two sessions (food: $V = 66$, $N = 17$, $P = 0.644$, effect size $d = 0.085$; toy: $V = 86$, $N = 17$, $P = 0.678$, effect size $d = 0.116$), the degree of lateralization tended to be correlated between experimental sessions only for the toy (rho = 0.426, $N = 17$, $P = 0.091$) but not the food stimulus (rho = 0.306, $N = 17$, $P = 0.233$).

Tail-Wagging Behaviour

For the food stimulus, tail wagging data were assessed for 15 dogs. Two dogs were excluded from the statistical analyses as their eye data were identified as statistical outliers (based on Tukey's fence test with $k = 1.5$). This resulted in a final sample size of 13 dogs. For 12 of these 13 dogs, data were analysed for two experimental sessions, whereas for one individual, data were assessed for only one session (average number of analysed trials per dog: 11.38 ± 2.93). For the toy stimulus, tail-wagging data were obtained from 15 dogs. For 11 of these 15 dogs, data were analysed for two experimental sessions, whereas for four individuals, data were
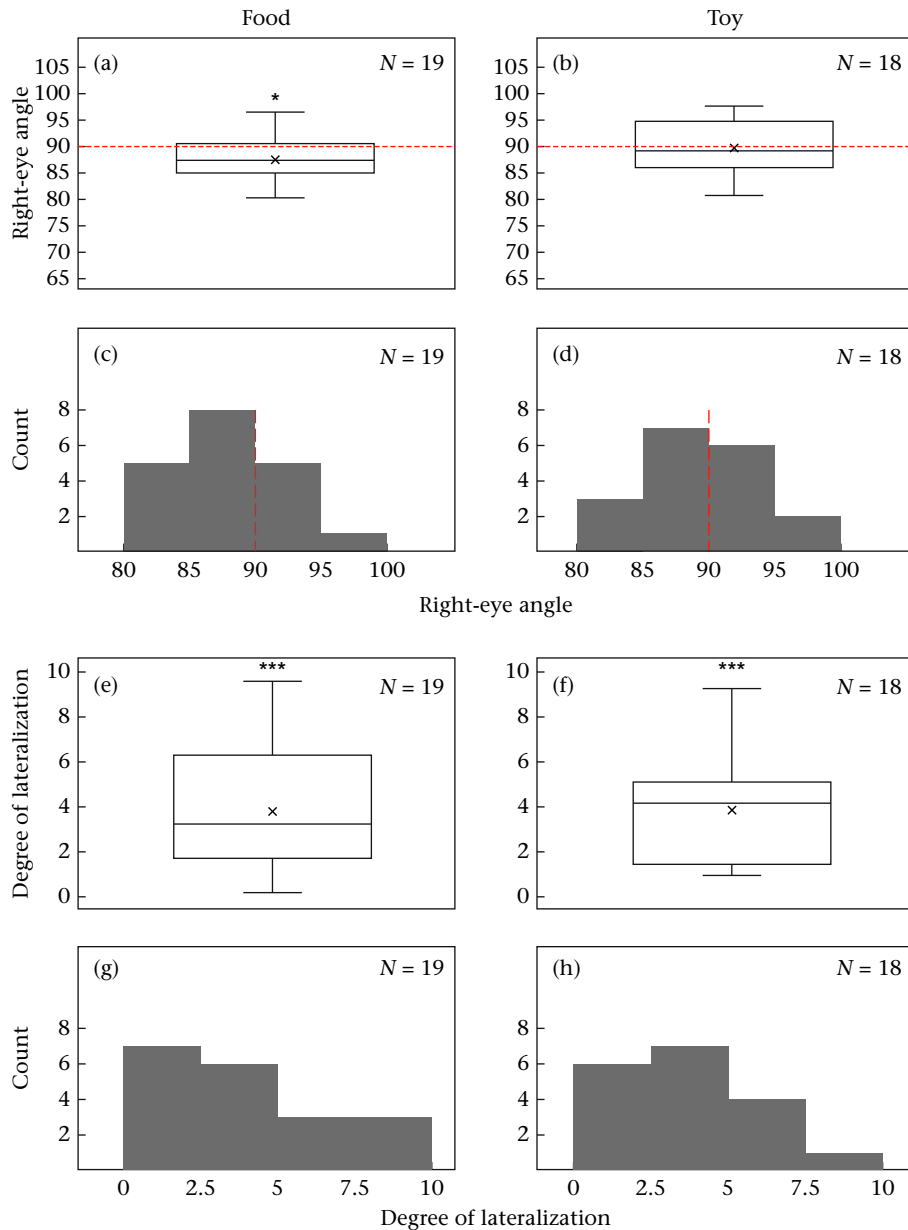
Figure 6. Lateralized eye use. Dogs' right-eye angles when attending to (a) the food and (b) the toy stimulus; distribution of dogs' right-eye angles for (c) the food and (d) the toy stimulus; dogs' degrees of lateralized eye use for (e) the food and (f) the toy stimulus; distribution of dogs' degrees of lateralized eye use for (g) the food and (h) the toy stimulus. The box plots show the median (horizontal line) and 25th and 75th percentiles, the whiskers indicate the values within 1.5 times the IQR. Asterisks indicate significant deviations from 90° and 0°, respectively (* $P < 0.05$; *** $P < 0.001$).

assessed for only one session (average number of analysed trials per dog: 10.53 ± 3.85). For five individuals, tail-wagging behaviour was analysed for both the food and the toy stimulus.

For both the food and the toy stimulus, the directional index of lateralized tail movements was not significantly different from 0 (food: mean $= 0.070 \pm 0.219$, $t_{12} = 1.160$, $N = 13$, $P = 0.269$, effect size $d = 0.321$; Fig. 7a; toy: mean $= 0.050 \pm 0.387$, $t_{14} = 0.500$, $N = 15$, $P = 0.625$, effect size $d = 0.129$; Fig. 7b); i.e. for neither stimulus type did the tail-wagging data indicate any common directional bias at a population level. Looking at the distribution of the dogs' directional indices for tail wagging, most dogs had scores between -0.25 and $+0.25$ in the food condition (Fig. 7c), whereas for the toy stimulus, scores were more evenly dispersed between scores of -0.75 and $+0.75$ (Fig. 7d). For the subsample of dogs for which tail-wagging behaviour was measured for both stimulus

types, a small but nonsignificant difference in the directional index of asymmetric tail movements was measured between the two stimuli ($t_4 = 1.031$, $N = 5$, $P = 0.368$, effect size $d = 0.453$). There was no significant correlation between the directional indices of the two stimulus types ($r = 0.084$, $N = 5$, $P = 0.893$).

The degree of lateralized tail wagging (i.e. regardless of the direction) was significantly greater than 0 for both the food and the toy stimulus (food: mean $= 0.189 \pm 0.121$, $t_{12} = 5.631$, $N = 13$, $P < 0.001$, effect size $d = 1.562$; Fig. 7e; toy: mean $= 0.333 \pm 0.182$, $t_{14} = 7.077$, $N = 15$, $P < 0.001$, effect size $d = 1.83$; Fig. 7f). Thus, although the dogs' tail-wagging behaviour did not suggest a directional population level asymmetry for either stimulus type, dogs showed left- or right-biased tail wagging for both stimulus types at the individual level. Relatively more dogs had degrees of lateralization >0.25 in the toy compared to the food condition,
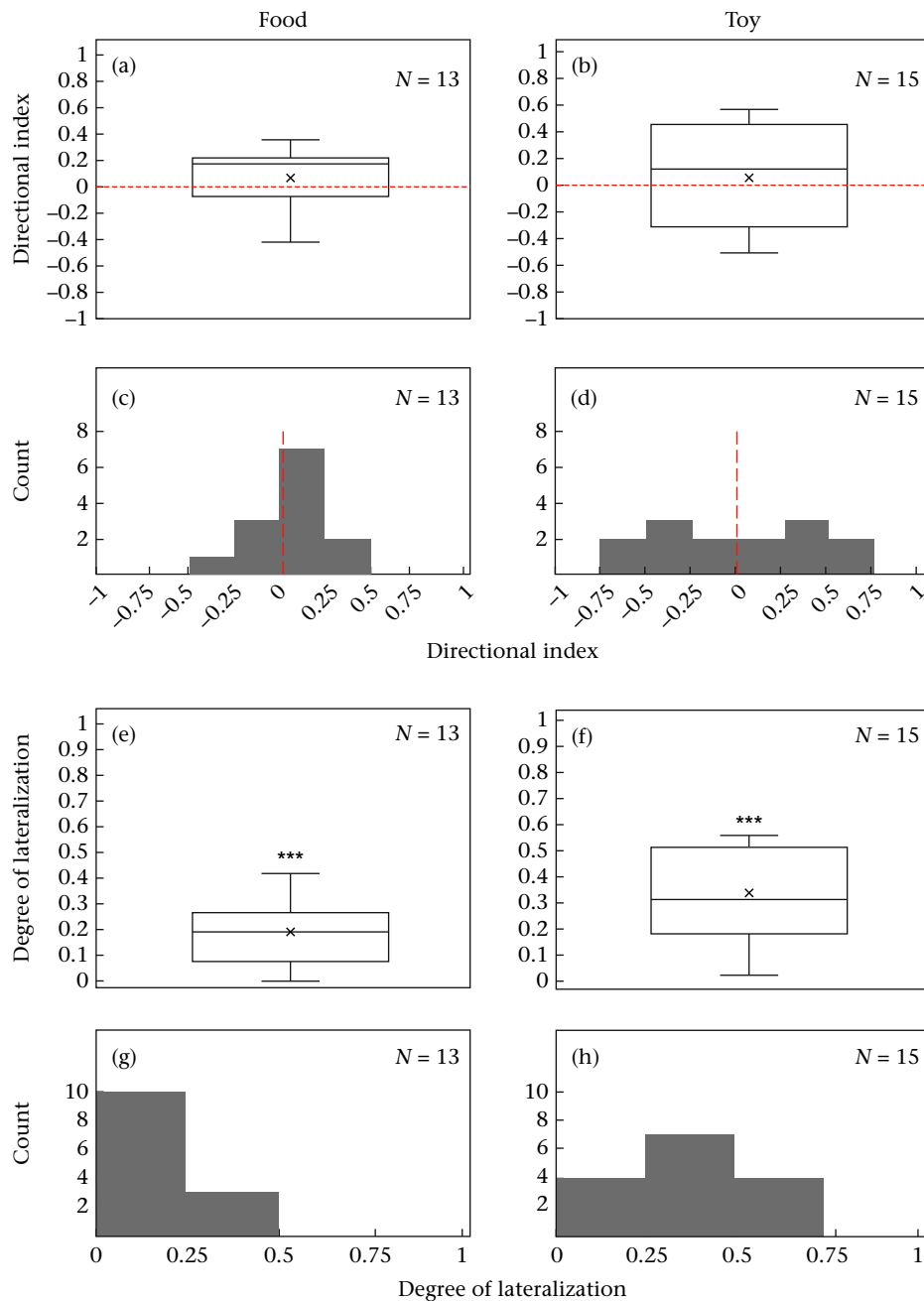
Figure 7. Tail-wagging behaviour. Dogs' directional index for lateralized tail-wagging behaviour when attending to (a) the food and (b) the toy stimulus; distributions of dogs' degrees of lateralized tail-wagging movements for (c) the food and (d) the toy stimulus; dogs' degrees of lateralized tail-wagging movements for (e) the food and (f) the toy stimulus; distributions of dogs' degrees of lateralized tail-wagging movements for (g) the food and (h) the toy stimulus. The box plots show the median (horizontal line) and 25th and 75th percentiles, the whiskers indicate the values within 1.5 times the IQR. Asterisks indicate significant deviations from 0 (*** $P < 0.001$).

suggesting relatively stronger asymmetries in tail wagging for the toy stimulus. In the subsample of dogs that completed both the food and the toy condition, the degree of lateralized tail wagging was significantly larger for the toy compared to the food stimulus ($t_4 = 2.911$, $N = 5$, $P = 0.044$, effect size $d = 1.302$). The degree of lateralization was not significantly correlated between stimulus types ($r = -0.151$, $N = 5$, $P = 0.809$).

Compared to dogs' relative eye use, their tail-wagging data were less consistent between experimental sessions. For neither stimulus type did the directional indices of lateralized tail movements differ significantly between experimental sessions (food: $V = 38$,

$N = 12$, $P = 0.970$, effect size $d = 0.072$; toy: $V = 33$, $N = 11$, $P = 1.000$, effect size $d = 0.034$). Yet, the directional indices of the two experimental sessions were significantly and positively correlated only for the food stimulus ($r = 0.674$, $N = 12$, $P = 0.016$), but not for the toy stimulus ($r = 0.210$, $N = 11$, $P = 0.536$). For the food stimulus, the degree of lateralization tended to be larger in the first compared to the second experimental session ($V = 64$, $N = 12$, $P = 0.052$, effect size $d = 0.706$). A small but nonsignificant difference between sessions was observed for the toy stimulus ($V = 21$, $N = 11$, $P = 0.320$, effect size $d = 0.427$). While the degree of lateralized tail wagging tended to be positively correlated between

experimental sessions for the food stimulus ($r = 0.542$, $N = 12$, $P = 0.069$), there was no significant correlation for the toy stimulus ($r = -0.207$, $N = 11$, $P = 0.541$).

Correlation Between Relative Eye Use and Tail-Wagging Behaviour

For 10 dogs, both the relative eye use and tail-wagging movements were analysed for the food stimulus. In the context of the toy stimulus, 13 dogs provided data for both behavioural variables. There was no significant correlation between dogs' right-eye angles and their directional indices for tail-wagging behaviour (food: rho = 0.042, $N = 10$, $P = 0.448$; toy: rho = 0.05, $N = 13$, $P = 0.579$). In relation to the degrees of lateralized eye use and tail-wagging behaviour, there was a large and significant negative correlation for the food stimulus (rho = -0.637, $N = 10$, $P = 0.042$), but no correlation for the toy stimulus (rho = 0.11, $N = 13$, $P = 0.911$).

Intercoder Reliability

For both the food and the toy stimulus, the second coder analysed data of relative eye use for four dogs (i.e. 21–22% of all data). For the food stimulus, the median correlation coefficient (rho) was 0.814 (IQR = 0.164, all $P \leq 0.05$); for the toy stimulus, the median correlation coefficient (rho) was 0.94 (IQR = 0.041, all $P < 0.001$). For tail-wagging behaviour, the second coder analysed data of three dogs for each stimulus type (i.e. 20% of all data). For food, the median for angles of tail movements to the left and right was 0.968 (IQR = 0.297, all $P \leq 0.007$); for the toy stimulus, the median for angles of tail movements to the left and right was 0.943 (IQR = 0.032, all $P < 0.001$).

DISCUSSION

Relative Eye Use

The results for the food stimulus indicate a right-eye bias at a population level, while the results for the toy stimulus do not suggest any specific directional bias at a population level. However, there was no significant difference in the dogs' right-eye angles between the food and the toy. These findings seem to be robust: given the measured effect sizes (see Results: Relative Eye Use), the absence of any significant directional population level bias for the toy stimulus and the lack of difference between the food and the toy stimulus do not seem to be the result of sample size but rather indicate a genuine lack of effect. For both stimuli, eye use was generally lateralized (i.e. not only during the inspection of the food but also for the toy, dogs preferentially used one eye over the other). Compared to the food stimulus, however, the toy was associated with a left or right-eye bias only at the individual level (dogs' values for the degree of lateralized eye use, regardless of the direction, were significantly greater than 0°), without a common directional bias in the population.

Food stimulus: population level right-eye bias

In response to the food stimulus, dogs displayed a population level right-eye dominance. This result is consistent with increased use of the left hemispheric networks subserving visual reward processing associated with the food stimulus. Due to their rather frontally placed eyes, dogs will probably not have perceived the food exclusively with their right eye/left hemisphere, but, to a certain extent, also with their left eye/right hemisphere. However, the observed right-eye angles nevertheless indicate that the food stimulus was predominantly processed within the right visual field

and the left brain. If the food item was appraised as an emotionally salient, positively valenced stimulus that motivated stimulus-directed approach behaviour, the right eye/left hemisphere dominance provides greater evidential support for the valence and approach–withdrawal hypotheses, compared to the right-hemisphere hypothesis. Yet, the results do not discriminate between the valence and the approach–withdrawal hypotheses. It is particularly challenging to do this as the two models often overlap in their predictions (see Simon, Guo et al., 2022, for a review of these three hypotheses and their scientific exploration). Emotions that are typically classified as positive (e.g. joy, positive anticipation) are likely to motivate approach behaviour, whereas emotions that are typically assessed as negative (e.g. disgust, fear) are often associated with withdrawal behaviour.

Behavioural biases during sensory inspection of putatively emotionally salient food stimuli have been reported previously. For example, on presentation with cotton swabs impregnated with the odour of dog food, dogs showed asymmetric nostril use when sniffing the samples (Siniscalchi et al., 2011): while the first sniff during a 3 min presentation of the odour sample revealed no common directional (i.e. left or right) nostril bias in the population, most dogs preferentially used their left nostril for the last sniff. Due to the ipsilateral organization of the olfactory system (unlike other sensory systems), the preferential use of the left nostril suggests a relatively higher activity of left-brain networks subserving olfactory functioning. From a comparative perceptual processing basis, it might seem that the first rather than the last sniff would equate to the measurement of the first visual fixation of the food stimulus in the current study. However, differences in the processes associated with detection through these stimulus modalities may be critical here. Whereas the visual system captures input from a spatially wide field from the outset, that can then be rapidly focused on, the olfactory system may require more general engagement (a general sniff) to evaluate the salience of the target odour, before any lateralized bias based on this becomes apparent. In the current study, dogs were also trained to anticipate the visual presentation of food and so may have become emotionally 'primed'; by contrast, there was no training involved in the food odour test of Siniscalchi et al. (2011). Both factors may explain why there might be expected to be a shift from nonlateralized nostril use for the initial sniff to a left-biased nostril use during the final sniff. Thus, across different sensory domains, both the current and previous work by Siniscalchi et al. (2011) indicate a general population level dominance of left-brain networks in the context of processing attractive food-related stimuli.

However, even if the food-related stimuli are emotionally relevant, it cannot be conclusively determined that the dogs' lateralized sensory (olfactory and visual) stimulus processing was the result of emotion-related brain lateralization. Food-induced lateralized behaviour/brain activation could also arise from other processes that are not linked to emotional states. Indeed, feeding behaviour is associated with left-brain specialization, which indirectly manifests itself in different behavioural biases in various vertebrate species (e.g. Güntürkün et al., 2020; Leliveld, 2019; MacNeilage et al., 2009; Rogers, 2002; Rogers et al., 2013). In this instance, it might be that both the emotional and food-related processes are congruent with regards to their hemispherical biases and thus synergistic in the lateralized effect; this could explain the clear directional population level bias reported here and elsewhere. However, this might not be the case with other attractive stimuli. It is also possible that the dogs' patterns of behavioural/brain asymmetries did not reflect any emotion-related functioning and were only driven by food-related/emotion-unspecific processes.

Preferential eye use when inspecting a food stimulus has also been reported in other animals. For instance, Sichuan snub-nosed monkeys preferentially used their left or right eye when observing a food item in a box through a small observation hole (Zhao et al., 2020). Although most monkeys showed a right-eye preference (right-eye bias: $N = 9$; left-eye bias: $N = 4$), there was no significant directional population level bias. Yet, the lack of a population level bias might be the result of sample size ($N = 13$) rather than indicating a genuine lack of effect. When piglets were trained to associate the presentation of an object with a food reward, covering their right eye (i.e. reducing stimulus processing by the left hemisphere) with a patch was related to a longer latency to touch the object, a longer interruption of vocalization, a shorter duration of exploring the arena and an increased vagal activity compared to piglets without any patches on their eyes (Goursot et al., 2019). These findings might suggest an important role of the left hemisphere in the recognition of a positively valenced stimulus (in line with the valence hypothesis) and/or in controlling stimulus-directed approach tendencies (in line with the approach–withdrawal hypothesis).

Toy stimulus: no directional population level eye bias

Although the toy stimulus showed evidence of lateralization within individuals, there was not a common directional (left- or right-) eye bias at the population level. Given the emotional salience of the toy stimulus and likely behavioural approach response triggered by it, this finding seems equally unlikely if either the right-hemisphere, valence or approach–withdrawal hypothesis is correct. None the less, this result has important implications for the scope of the different hypotheses about brain lateralization in emotional states. If two different emotionally relevant stimuli (i.e. food and toy) are both associated with a positive valence and elicit stimulus-directed approach behaviour, but result in different patterns of behavioural eye lateralization, then this difference cannot be explained by simply referring to the quality of the stimuli with regards to their general emotional salience (right-hemisphere hypothesis), their emotional valence (valence hypothesis) or general stimulus-induced motivational tendencies (approach–withdrawal hypothesis).

It might be hypothesized that the expression of some behavioural biases represents the manifestation of complex brain states integrating the activation of multiple individually lateralized brain networks based on the nature of the specific emotionally relevant stimuli. While some of these networks might show activation patterns that specifically reflect the emotional significance of a certain stimulus (in terms of their general emotional salience, their emotional valence, or emotionally motivated behavioural tendencies), other coactivated neuronal networks might be more related to less emotion-specific brain processes. When dogs are visually presented with an anticipated food or toy stimulus, the dogs' overall brain state might include the activation of both neural networks that are specifically sensitive to the emotional significance of the situation and those that are involved in processing other information and performing operations that are not directly linked to the emotional specificity of the situation. For example, in relation to an anticipated food reward, our finding of a population level right-eye bias might be the behavioural manifestation of a cumulative or synergistic effect of both emotion-specific (e.g. valence-sensitive) and other stimulus-specific (e.g. food specific; see Food stimulus: population level right-eye bias) activation in the left hemisphere including the visual cortex. By contrast, the individual level left- and right-biased eye use (without any common directional population level bias) in response to the toy stimulus

might reflect correlation of brain states with asymmetry between lateralized emotion-specific (e.g. valence-related) networks relating to specific behavioural systems in the context of play behaviour. For some dogs, playing with a toy can include the expression of elements of predatory activity: e.g. running after a ball may relate to the 'chase' element of the predatory sequence, whereas grabbing and shaking a toy may relate to the elements 'grab-bite' and 'head-shake' (performed to immobilize and kill (small) prey, respectively; Coppinger et al., 2015). Elements of the predatory sequence 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 that they involve a strong element of the positive emotion referred to as 'seeking'. Different elements of the predatory sequence might be associated with specific lateralization patterns within the brain. Indeed, in attack-trained dogs, burst and rapid movements towards a target have shorter latencies to reach the target when the target is predominantly analysed with the right eye/left brain (Siniscalchi, Pergola et al., 2013). Perhaps the right eye/left hemisphere system plays a specialized role in selective attention and focused pursuit, abilities that are important when performing behaviours related to the 'chase' element of the predatory sequence. A specialized role of the right eye/left brain system for selective attention, prey capture and discriminating food against a distracting background has been suggested in other vertebrate species: for instance, zebrafish preferentially use their right eye/left brain to fixate on a prey target (Miklósi & Andrew, 1999), toads display a right-eye preference for directing tongue strikes at prey (Robins & Rogers, 2004) and chicks show a right eye/left brain bias for pecking at food items that have to be discriminated against a distracting background (Andrew et al., 2000).

Different behavioural/brain asymmetries might, however, be indicated in the context of the 'grab-bite' element; for example, sheepdogs exposed to a flock of sheep showed higher frequencies of livestock-directed behaviours that can be interpreted as a reduced expression of the 'grab-bite' when the sheep were mainly processed in the dogs' left visual hemifield (Siniscalchi et al., 2019). This finding is consistent with a specialized role for the right hemisphere in mediating behaviour related to the predatory 'grab-bite'. If an anticipated toy reward motivates play behaviour relating to specific elements of predatory-related action patterns, with different dogs predisposed towards different elements of the predatory sequence (e.g. 'chase'-related action patterns versus 'grab-bite'/'head-shaking'-related patterns), different individuals may display differing brain asymmetry patterns when attending to the same toy stimulus. The integration of both the emotion-related hemispheric asymmetries (e.g. similar valence-sensitive patterns as for the food stimulus) and specific play-/predation-related brain asymmetry patterns in relation to the toy stimulus may thus result in overall brain states that vary between subjects. This could explain why dogs' lateralized eye use in response to the toy was associated with increased variability between subjects and, compared to the food stimulus, revealed no common directional bias at the population level. Apart from predatory behaviour, a dog's interaction with a toy might be also motivated by object manipulation such as chewing on the toy. Chewing on objects may relieve stress (Koizumi et al., 2011; Ono et al., 2012; Tasaka et al., 2014) and is recommended by practitioners for dogs as well (Rooney et al., 2009). For dogs that learned to chew on toys to relieve stress and frustration, the used toy may represent an emotionally more ambiguous stimulus; this might additionally contribute to the increased variability in lateralized eye use.

As discussed above, food-related specialized functioning may occur in the left hemisphere independently of any potential emotional processing. This might complement emotion-specific functioning in this hemisphere to create a population-level bias in the case of the food but not the toy, if there is no such synergy in the case of the toy. However, the focus should perhaps not be on what context-/stimulus-specific aspects might lead to a directional population level behavioural/brain asymmetry for the food but not the toy stimulus, but rather on which factors determine that some (e.g. alarming and prosocial stimuli; Simon, Guo et al., 2022) but not all (e.g. food and toy stimuli) emotionally relevant stimuli, and/or some (e.g. fear, prosocial emotions; Simon, Guo et al., 2022) but not all (e.g. positive anticipation) types of emotional states result in common directional behavioural/brain lateralization in the population. To investigate these issues further, future studies should examine both (1) states of positive anticipation elicited by types of stimuli other than food and toys (e.g. positive anticipation to gain access to a preferred social partner), and (2) contexts in which food and toys do not elicit states of positive anticipation but instead other types of emotional states (e.g. states of frustration due to denied access to positively anticipated food or toy stimuli).

In summary, our results reveal how emotion-related behavioural/brain lateralization in dogs may not be exclusively determined by the emotional salience of stimuli (right-hemisphere hypothesis), their valence (valence hypothesis) or stimulus-directed motivational approach/withdrawal tendencies (approach–withdrawal hypothesis). Greater consideration needs to be given to the potential for emotion-related laterality patterns to be modulated by more specific context-/stimulus-related aspects and/or the specific quality of the emotional state.

Population level versus individual level lateralization

Although the toy stimulus did not produce any directional population level behavioural/brain asymmetries, dogs did show lateralized eye use at an individual level (since the values for laterality regardless of direction were significantly greater than 0°). The toy stimulus was thus associated with greater interindividual variability as to which eye/hemisphere was predominantly used during stimulus inspection, compared to the food stimulus. This suggests that, in some cases, emotion-related patterns of behavioural/brain lateralization might involve increased variation regarding the direction of laterality between subjects. The factors that might underlie such variation in emotion-related lateralization are not well understood in dogs. A recent meta-analysis investigating lateralized paw use in dogs in different, partially emotionally relevant tasks (e.g. holding a toy with one paw while retrieving food placed inside the toy, reaching for a reward under a piece of furniture, removing an adhesive tape from the dogs' head) also suggests directional lateralization only at an individual but not at the population level (Ocklenburg et al., 2019). In fact, some studies investigating preferential paw use in dogs have reported asymmetries in paw use influenced by a variety of factors, including age and an interaction between age and neuter-status (Duncan et al., 2022), sex (Laverack et al., 2021; McGreevy et al., 2010; Quaranta et al., 2004, 2006; Wells, 2003), breed (Tomkins et al., 2010), chronic and acute stress (Salgirli Demirbas et al., 2019, 2023) and dogs' temperament and personality (Barnard et al., 2017; Batt et al., 2009; Schneider et al., 2013; Wells et al., 2018). Most of these findings are not replicated in other studies (see Simon, Frasnelli et al., 2022, for a review) and so the influence of these factors remains uncertain. It should also be noted that paw preferences reflect a motor behavioural output and this might be subject to different lateralization effects (associated with the location of

structures involved in the organization of these outputs) compared to motor activity relating to sensory processing (e.g. eye movement). Thus, even though the tasks used to test paw preference might have been emotionally salient, it is not clear whether asymmetries in paw use reflect emotion-specific brain lateralization or are the result of one or more nonemotional factors (e.g. inadvertent training effects; Simon, Frasnelli et al., 2022). Undoubtedly, further investigations are needed to identify and explore potential factors that may underlie interindividual differences in emotion-related behavioural/brain lateralization. That some emotion-related behavioural/brain asymmetries may involve considerable variation between subjects further challenges the assumption that lateralization in emotional states can be explained by referring exclusively to the right-hemisphere, valence or approach–withdrawal hypothesis. In this regard the results of the tail-wagging behaviour are particularly insightful.

Tail-Wagging Behaviour

The data for dogs' tail-wagging movements did not reveal any common directional (left or right) bias in the population for either stimulus type. These findings seem to be robust: given the measured effect sizes (see Results: Tail-Wagging Behaviour), the lack of directional population level biases does not seem to be the result of sample size but rather indicates a genuine lack of effect. For both the food and the toy stimulus, the degree of lateralized tail wagging was significantly larger than 0, indicating that dogs displayed left- or right-biased tail-wagging movements at an individual level. For dogs that were presented with both stimuli, no significant difference in the directional tail-wagging index was found between the two stimulus types. Yet, given the measured effect size, an increase in the sample size (minimum required sample size: $N = 41$) might have seen a significant effect. Regarding the degree of lateralization, the dogs' values were significantly larger for the toy compared to the food stimulus. For both stimulus types, dogs' tail-wagging asymmetries increased in intraindividual variability over time (i.e. between subsequent test sessions), compared to their relative eye use during stimulus inspection: while dogs' directional indices of lateralized tail movements did not vary significantly between test sessions for either stimulus type, their indices were significantly correlated between test sessions only for the food but not the toy stimulus. While the degree of lateralized tail wagging (regardless of the direction) tended to be larger in the first compared to the second session for the food stimulus, there was no significant difference between sessions for the toy stimulus. For the food stimulus, the degrees of lateralization tended to be correlated between the two sessions, whereas no significant correlation was found for the degree of lateralization between sessions for the toy stimulus. Given the effect sizes observed, the findings for the toy seem to represent a genuine lack of effect, whereas a larger sample for the food stimulus (minimum required sample size: $N = 24$) might have seen both a significant difference and a significant correlation between the two sessions.

No directional population level tail-wagging bias

While the current study identified patterns of lateralized tail-wagging behaviour only at the individual level, previous work on emotionally relevant social contexts reported tail-wagging asymmetries also at a population level: when dogs were presented with different emotionally relevant stimuli, for instance the appearance of an agonistic conspecific (Quaranta et al., 2007), or a prosocially acting person (Ren et al., 2022), they displayed directional population level tail-wagging behaviour/hemispheric asymmetries

(agonistic conspecific: left-biased tail movements; prosocially acting person: right-biased movements). A possible explanation for the difference between previous and the current research could be that in the former studies, tail wagging may have played a communicative role, whereas in the current study it might be the product of more general arousal. Whereas previous research investigated tail wagging when dogs were facing emotionally salient social stimuli, our study analysed behavioural lateralization as a response to nonsocial objects (i.e. food and toy items). In support of the suggestion that patterns of asymmetric tail wagging might have an important signalling function in (intraspecific) communication, Siniscalchi, Lusito et al. (2013) demonstrated that dogs are sensitive to asymmetric tail wagging displayed by a conspecific. Dogs showed relatively increased cardiac activity and more fear-related behaviours when observing left- compared to right-lateralized tail movements. Whether certain emotionally relevant social compared to certain non-social contexts are more likely to be associated with directional population level biases in tail wagging remains an open question for future research.

If reported lateralization patterns of tail wagging reflect emotion-related brain asymmetries, the difference between previous research and the current study adds further weight to the argument that patterns of behavioural/brain lateralization in emotional states may not be determined exclusively by the emotional salience of stimuli (right-hemisphere hypothesis), their emotional valence (valence hypothesis), or stimulus-induced motivational tendencies (approach–withdrawal hypothesis), and that other contextual circumstances and/or more specific stimulus-related aspects may be important.

Intraindividual variability

Asymmetries in tail-wagging behaviour not only varied between but also within subjects. Compared to measures of asymmetric eye use, patterns of lateralized tail wagging were less stable in time. If dogs' tail-wagging asymmetries, when attending to the positively anticipated food and toy stimuli, respectively, reflected an emotion-related response, our findings suggest that patterns of behavioural/brain lateralization in emotional states can be modulated by both inter- and intraindividually varying parameters. Like between-subject variation (see Population level versus individual level lateralization), within-subject variability is largely unexplored in dogs and requires further investigation. Yet, a recent investigation with dogs on lateralized motor behaviour (i.e. preferential paw use) in potentially emotionally salient tasks (e.g. holding a toy with one paw while retrieving food placed inside the toy) has reported asymmetries affected by (intraindividually variable levels of) acute stress (Salgirli Demirbas et al., 2023).

However, it cannot be conclusively determined whether the observed inter- and intraindividually varying asymmetries represent emotion-related brain lateralization or are potentially the result of other mechanisms. For instance, approximately 20% of all dogs (in North America) over 1 year of age have been reported to be affected by osteoarthritis (Johnston, 1997). Since arthritis may result in lateralized differences in muscle use and tension around the hips, such as in the gluteals, it is possible that this could interfere with the symmetry of tail-wagging behaviour. Moreover, lateralized issues with anal sacs (i.e. fluid-filled pouches that are located on the right and left side of a dog's anus) may also interfere with tail posture. These have a relatively high prevalence in dogs, with 12% of animals experiencing some problems during their lifetime (Potanas et al., 2015). Other medical problems like pinched nerves in the lower back might also cause asymmetries in tail wagging and explain the high levels of inter- and intraindividual variability of lateralization patterns. This hypothesis deserves further investigation and these conditions should certainly be controlled for in studies of tail lateralization.

Different Components of Emotions: Different Lateralization Patterns?

In response to the food stimulus, dogs showed a population level right-eye bias, whereas tail-wagging movements were associated with directional biases only at an individual level, without revealing any patterns of directional population level lateralization. If dogs' behavioural asymmetries reflect emotion-related brain lateralization rather than other mechanisms not related to emotions, these findings show that different components of emotional states might involve varying patterns of behavioural/brain lateralization. Component Process Theory provides a framework for understanding the functional structure of the various physiological, cognitive and behavioural elements of emotion (Scherer, 2005). Within this theoretical framework, dogs' visual inspection of the presented stimuli might be primarily associated with the component of stimulus appraisal (i.e. how a stimulus is assessed emotionally), whereas tail wagging would be related to the communicative output or arousal component.

That different components of emotional responses might involve distinct patterns of behavioural/brain lateralization is not only indicated by dogs' population level laterality patterns but is also suggested by their individual asymmetry patterns. Neither for the food nor for the toy stimulus did we find any significant correlations between the dogs' eye and tail-wagging data, neither with regard to laterality measures conveying information about the directionality of lateralization (i.e. dogs' right-eye angles and their directional indices of tail-wagging movements), nor with regard to laterality measures assessing the strength of lateralization, regardless of the directionality (i.e. degree of lateralized eye use and tail-wagging behaviour, respectively). The absence of any positive correlations demonstrates that individuals' relative eye use and tail-wagging movements can involve independent behavioural asymmetries. The absence of any significant correlation (i.e. positive or negative) indicates considerable variation between individuals with regard to their profiles for differently lateralized responses: for some dogs, lateralization measures between the two behavioural variables were positively correlated, whereas a negative or no association was found for other dogs. If dogs' behavioural asymmetries represented emotion-related responses, these findings show that distinct components of emotional states might relate to different patterns of behavioural/hemispheric asymmetries not only at a population level, but also within each individual.

The possibility that distinct components of emotional responses are associated with varying patterns of emotion-related behavioural/brain lateralization has important implications: if a specific component of an emotional state is associated with a certain pattern of behavioural/brain asymmetry, we cannot assume that other components of this emotional state necessarily show concordant patterns of lateralization. That is, emotion-related 'hemispheric dominance' may not imply a global dominance of one brain hemisphere over the contralateral counterpart in the sense that all neuronal processes subserving the various constituent components of a particular emotional state (e.g. stimulus appraisal, emotional expression, subjective feelings, action tendencies etc.) exhibit congruent patterns of hemispheric lateralization. Rather, it may be more appropriate to conceptualize emotion-related 'hemispheric dominance' within a more local phenomenological context. Accordingly, 'hemispheric dominance' may occur

in the context of specific neuronal networks that are constitutive for certain components of a given emotional state, and relates to the relative activation of these constituent neuronal networks in one (i.e. the dominant) of the two hemispheres. This understanding is in line with recent developments in lateralization research with humans, which allows for multiple interconnected emotion-related neural networks that may be associated with different lateralization patterns (Fusar-Poli et al., 2009; Killgore & Yurgelun-Todd, 2007; Morawetz et al., 2020; Neumann et al., 2008; Ocklenburg & Güntürkün, 2018; Palomero-Gallagher & Amunts, 2021). In this context, research with humans has postulated that different hypotheses such as the right-hemisphere, valence and approach–withdrawal hypotheses are not necessarily mutually exclusive but may rather relate to different components of emotional states (Fusar-Poli et al., 2009; Killgore & Yurgelun-Todd, 2007; Neumann et al., 2008). Since the current investigation indicates that some behavioural/brain asymmetries might involve considerable inter-/intraindividual variability, the picture might be even more complex (in dogs): apart from different emotion-related neural networks with varying population level patterns of specialized hemispheric functions that relate to different (complementary) hypotheses about brain asymmetries, some brain networks subserving certain components of emotional states might display hemispheric biases involving higher variability between/within subjects. Such inter-/intraindividually variable hemispheric biases do not suggest general hemispheric specialized functioning but rather a functional equivalence of both hemispheres and a flexible/adaptive distribution of relative activation between the two sides of the brain. A further possible explanation for the increased variation between/within subjects could be that, while there may be distinct emotion-related neural networks with varying population level patterns of specialized hemispheric functioning, the relative activation of the different lateralized networks may vary between/within subjects, potentially leading to increased variability in asymmetric behavioural correlates as a result.

To further explore the relationship between patterns of behavioural/brain lateralization relating to different components of emotional states, more research is needed. Future studies should analyse lateralization patterns of multiple components of different emotional states. So far, many studies with dogs investigating behavioural/hemispheric biases in emotionally salient situations focused on lateralized sensory (visual, auditory, olfactory) processing of emotionally relevant stimuli, which probably reflects the appraisal component. By contrast, other components of emotional states have been less explored and should receive more attention. To investigate laterality patterns of different emotional components, analyses of behavioural/brain lateralization related to sensory functioning and the component of stimulus appraisal should be combined with analyses of behavioural/brain asymmetries of different motor goal-related functions associated with emotion expression (e.g. facial expression, tail wagging, body posture) or other components of emotional states (e.g. self-directed behaviours and 'displacement activities' that can occur in emotional situations, such as scratching, autogrooming, body shaking). However, with respect to both dogs' visual stimulus inspection and their tail-wagging movements, we have already discussed the possibility that the observed behavioural asymmetries are not manifestations of emotion-related brain asymmetries but rather the result of other nonemotional factors.

Implications for Practical Assessments of Dogs' Emotional States

An important goal of recent studies investigating the behavioural/brain lateralization of emotional states in dogs (and other species) has been the potential development of a tool that helps inform assessments of animals' emotional states (Leliveld et al., 2013; Siniscalchi et al., 2021). However, the current study indicates that behavioural/brain lateralization in emotional states might be a highly complex phenomenon that is modulated by a myriad of factors: e.g. different types of stimuli, specific types of emotional states (see Toy stimulus: no directional population level eye bias), certain contextual circumstances (see No directional population level tail-wagging bias), distinct components of dogs' emotional states (see Different Components of Emotions: Different Lateralization Patterns). In some cases, emotion-related behavioural/brain asymmetries might also involve considerable inter-/intraindividual variability (see Population level versus individual level lateralization). To establish behavioural/brain asymmetries as a tool to inform assessments of dogs' emotional states, findings need to be clear and unambiguous. This might be an unrealistic expectation, especially without greater specification of relevant contexts.

As already discussed, dogs' relative eye use when attending to the toy stimulus and their tail-wagging movements in response to both the food and the toy stimulus did not indicate any directional population level asymmetries; left- or right-biased behaviour/hemispheric activity was only indicated at an individual level. In general, if certain behavioural biases that reflect emotion-related hemispheric lateralization occur only at an individual level, without any common directional bias in the population, the potential to use asymmetries for the assessment of dogs' emotional states is more limited compared to directional laterality patterns at the population level. Therefore, future research into behavioural/brain asymmetries as indicators for emotional states in dogs should primarily focus on the identification of population level biases.

Awareness must be raised of the possibility that certain measures of emotion-related behavioural/brain asymmetries may not only vary between individuals but also within subjects. In the current study, although the procedure of each test session was the same for each stimulus type and dogs probably experienced emotional states of the same broad type in subsequent experimental sessions (i.e. states of positive anticipation for food or a toy), intraindividual variability was observed between test sessions (i.e. within a relatively short period of time). In the context of dogs' relative eye use, only the degree of lateralization was associated with intraindividual variability. For dogs' tail-wagging behaviour, not only the degree of lateralization but also the directional index of lateralized tail-wagging movements was subject to within-subject variability. When similar stimuli that occur in similar contexts are appraised in similar ways emotionally and yet induce different behavioural/brain asymmetry patterns, the contribution of such laterality patterns to the assessment of the individual's emotional states will be marginal, without detailed additional information about the individual (e.g. specific knowledge about factors that might modulate the individual's particular laterality patterns in certain emotionally significant situations). To establish behavioural/brain asymmetries as potential markers of emotional state in dogs, research should focus on behavioural/hemispheric biases and laterality measures that are little influenced by factors that may cause intraindividual variation.

Previous work suggests a general population level dominance of right-hemisphere networks in response to alarming stimuli, which is reflected in various behavioural correlates (Quaranta et al., 2007; Reinholz–Trojan et al., 2012; Siniscalchi et al., 2008, 2010, 2011, 2016, 2018, 2018). Thus, in relation to situations involving stimuli that are likely to be appraised as alarming, behavioural/brain asymmetries might indeed be used as markers for emotional states (e.g. fear). Compared to that, dogs' asymmetry patterns in other emotionally salient situations (e.g. positive anticipation when

awaiting a reward) might be more difficult to interpret and may require considerably more additional information to make inferences about an individuals' emotional state.

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 (Berlinghieri et al., 2021; Leliveld, 2019; Leliveld et al., 2013; Rogers, 2010, 2011; Rogers & Kaplan, 2019; Siniscalchi et al., 2021). For instance, it is generally assumed that emotional states reflect improvements or decrements in individuals' wellbeing depending on their valence: while positively valenced emotions probably enhance an individual's wellbeing, negatively valenced emotions have rather compromising effects on welfare. Thus, if particular brain networks show valence-specific patterns of hemispheric asymmetry, as claimed by the valence hypothesis, the observation of lateralized behavioural correlates could provide a valuable, noninvasive and cost-effective approach to assess emotion-related effects on animal welfare. Moreover, since emotion-related approach tendencies are often associated with a positive emotional valence (states of anger and frustration might represent exceptions; see Carver & Harmon-Jones, 2009; Simon, Guo et al., 2022), 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. From an ethical and welfare-oriented perspective, it seems particularly important to be aware of potential limitations of the marker function of behavioural biases for emotion-related brain asymmetries. Practical assessments of welfare-relevant emotional states should not rely solely on expressions of behavioural lateralization, but should also always consider other physiological, cognitive and behavioural indicators to draw conclusions about emotional states and their effects on animals' welfare.

Limitations and Future Directions

In this study, data for both the food and toy stimuli were obtained from a limited number of dogs. Hence, observed differences in visual lateralization (i.e. in terms of a common directional bias at a population level) between the two stimulus types may not solely be attributed to stimulus-specific effects (food versus toy), but also to interindividually varying factors. However, the disparity in effect sizes between the food and the toy stimulus nevertheless suggests the observed difference between the two stimulus types is a robust finding, which is unlikely to be primarily driven by interindividual variation.

While a 2 s time window might be sufficient to detect the preferential eye use at the first fixation of a stimulus, a larger time window might be required to detect laterality patterns in 'post-processing' tail-wagging behaviour. Previous work reporting directional population level biases in tail-wagging behaviour used time windows ≥60 seconds (Quaranta et al., 2007; Ren et al., 2022).

While the population level right-eye/left-hemisphere bias in response to the food stimulus provides greater evidential support for the valence and approach–withdrawal hypotheses, compared to the right-hemisphere hypothesis, this finding cannot discriminate between the former two hypotheses. To further explore whether the found right-eye/left-brain asymmetry might be driven by the positive valence of the stimulus (valence hypothesis) or rather by stimulus-induced approach motivation (approach-–withdrawal hypothesis), future research could investigate dogs' patterns of lateralized eye use in both emotional states of positive anticipation when awaiting a food reward and frustration when the dogs' expectation of getting access to the reward is not satisfied (e.g. when the access to the reward is delayed). While states of positive anticipation involve a positive and states of frustration a negative emotional valence, both states probably motivate stimulus-directed approach behaviour. This, therefore, allows discrimination between the valence and the approach–withdrawal hypotheses: the former model predicts a population level right-eye/left-brain dominance for states of positive anticipation but the reverse pattern for frustration, whereas the latter model always predicts a right-eye/left-brain dominance.

Both previous and the current work were designed to analyse dogs' behavioural/brain asymmetries in response to different emotionally salient stimuli involving a specific valence (i.e. positive or negative) and (sometimes) stimulus-directed motivational tendencies (i.e. approach or withdrawal). However, potential effects of the intensity of the emotional valence and/or induced motivational tendencies on laterality patterns have not yet been investigated. For instance, while many dogs may perceive food or toy stimuli as positively valenced, there is probably variation in the intensity with which they appraise the stimulus as positive. Future research could explore whether more positive food/toy stimuli involve different patterns of lateralization compared to less positive food/toy stimuli. For example, this could involve comparing individuals' responses to higher quality (i.e. more positive) stimuli (e.g. individuals' preferred food/toy) versus lower quality (i.e. less positive) stimuli (e.g. individuals' less preferred food/toy). Potential differences between stimuli with regard to their valence intensity could be validated by additional physiological measures: relatively increased cardiac activity or pupil dilation, for instance, may be used as potential indicators for relatively higher arousal in response to greater valence intensity. However, based on the different models regarding emotion-related lateralization (i.e. right-hemisphere, valence, approach–withdrawal hypotheses), variation in intensity may affect the degree of lateralization rather than the direction.

Conclusions

This study raises questions about many assumptions underpinning the use of behavioural/brain asymmetries as potential markers for animals' emotional states. The patterns of lateralization observed appear to reflect complex phenomena involving various modulators and may not be explained by referring only to the emotional salience of stimuli (right-hemisphere hypothesis), their emotional valence (valence hypothesis), or stimulus-induced motivational tendencies (approach–withdrawal hypothesis). While laterality patterns may provide valuable information about emotional states in certain situations, their contribution to informing assessments of emotions in other situations might be more limited than is generally supposed.

Author Contributions

Tim Simon: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Anna Wilkinson:** Writing – review & editing, Supervision, Conceptualization. **Elisa Frasnelli:** Writing – review & editing, Supervision, Conceptualization. **Kun Guo:** Writing – review & editing, Supervision, Conceptualization. **Daniel S. Mills:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Data Availability

The data presented in this study are available in the Supplementary Material.

Declaration of Interest

The authors have no competing interests to declare that are relevant to the content of this article.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.08.005.

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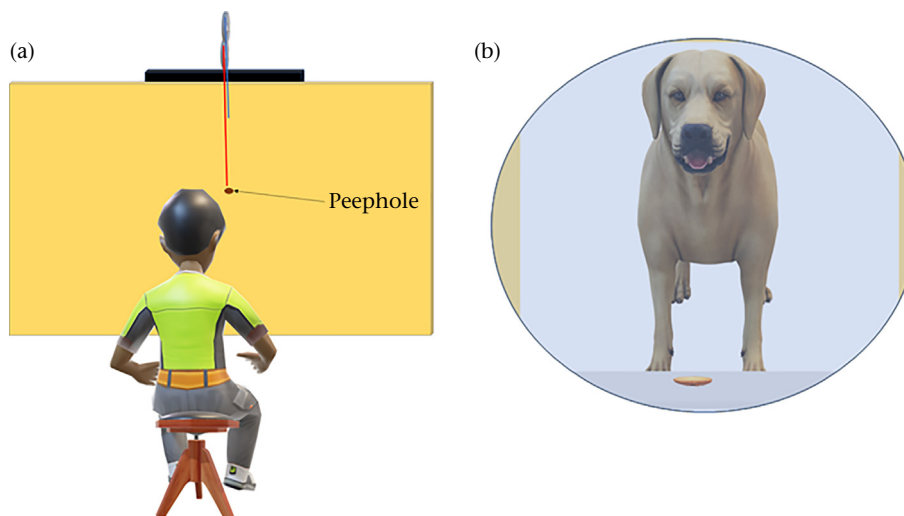
Appendix

Figure A1. Experimental apparatus (view from behind). (a) The experimenter could observe the dog through a peephole in barrier B. (b) Viewing the dog through the peephole when the opaque but not the transparent panel was lifted.

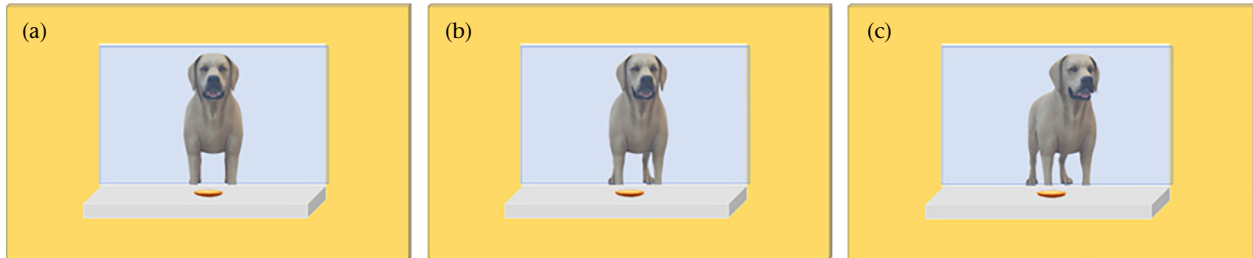**Figure A2.** Stimuli presentation. Stimuli were presented at seven possible positions.

Figure A3. Dog from the perspective of the camera within the apparatus. (a), (b) The dog was considered to be positioned straight in front of the apparatus if and only if at least one of their front legs (partially) covered the ipsilateral hindleg. (c) If neither front leg (partially) covered their ipsilateral hindleg, the condition was not met.