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Report

Seeing Left- or Right-Asymmetric Tail Wagging Produces Different Emotional Responses in Dogs

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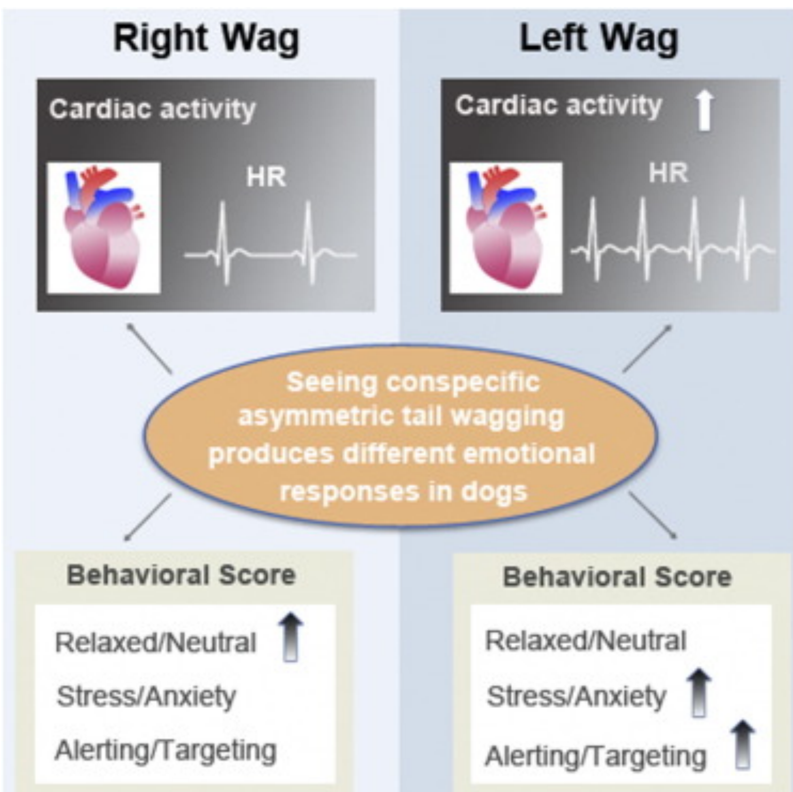
Highlights

- Seeing asymmetric tail wagging produces different emotional responses in dogs

Summary

Left-right asymmetries in behavior associated with asymmetries in the brain are widespread in the animal kingdom [1], and the hypothesis has been put forward that they may be linked to animals' social behavior [2, 3]. Dogs show asymmetric tail-wagging responses to different emotive stimuli [4]—the outcome of different activation of left and right brain structures controlling tail movements to the right and left side of the body. A crucial question, however, is whether or not dogs detect this asymmetry. Here we report that dogs looking at moving video images of conspecifics exhibiting prevalent left- or right-asymmetric tail wagging showed higher cardiac activity and higher scores of anxious behavior when observing left- rather than right-biased tail wagging. The finding that dogs are sensitive to the asymmetric tail expressions of other dogs supports the hypothesis of a link between brain asymmetry and social behavior and may prove useful to canine animal welfare theory and practice.

Graphical Abstract



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Results and Discussion

Side biases associated with left-right asymmetries in the nervous system are widespread in the animal kingdom [1, 5, 6]. In dogs, they have been shown to occur in a variety of behaviors [7, 8, 9, 10], including tail wagging [4]. Stimuli that could be expected to elicit approach tendencies, such as seeing a dog's owner, seem to be associated with higher amplitude of tail-wagging movements to the right side, whereas stimuli that could be expected to elicit withdrawal tendencies, such as seeing a dominant unfamiliar dog, seem to be associated with higher amplitude of tail-wagging movements to the left side [4]. Given that the rubrospinal tract, from the brain to the spinal cord, decussates caudally on the red nucleus and descends in the contralateral lateral funiculus [11], higher amplitude of tail wagging to the left or to the right sides reflects prevalent activation of contralateral right or left brain structures. The dogs asymmetry in tail wagging thus fits with the hypothesis [12] of a left hemisphere specialization for approach behavior and a right hemisphere specialization for withdrawal behavior (it is unclear to what extent an approach/withdrawal dichotomy would parallel a positive emotion/negative emotion dichotomy; [13]).

Asymmetry of tail wagging raises, however, a crucial issue—namely, whether dogs can detect (not just exhibit) this asymmetry. A prominent hypothesis states that directional brain asymmetries evolved and are maintained as evolutionarily stable strategies when individuals exhibiting side biases should interact to each other in social contexts [1, 2, 3]. Here we investigated whether dogs are sensitive to an asymmetric tail expression of other dogs by presenting dogs with moving video images of conspecifics showing prevalent left- or right-tail-wagging behavior. To evaluate emotional responses to asymmetrical tail wagging, we measured dogs' behavior and cardiac activity. We tested dogs with naturalistic stimuli ($n = 8$, Movie S1) and with the same stimuli digitalized and transformed to a silhouette ($n = 35$, Movie S2) to remove cues other than tail wagging.

The analyses of variances showed no heterogeneity or interactions associated with the type of stimulus used (naturalistic versus silhouette), thus we discussed here cumulative data (but see the Supplemental Experimental Procedures for the separate data sets and statistical analyses). The visual stimuli showing a dog with a left-wagging bias induced a higher maximum heart rate than the other two stimuli [F(2,84) = 22.953, p = 0.000; p < 0.001 post hoc analysis Fisher's protected least significant difference (LSD) for both comparisons]. No statistically significant differences were observed between the static stimulus and the dog stimulus with a right-biased wag (p = 0.224; Figure 1).

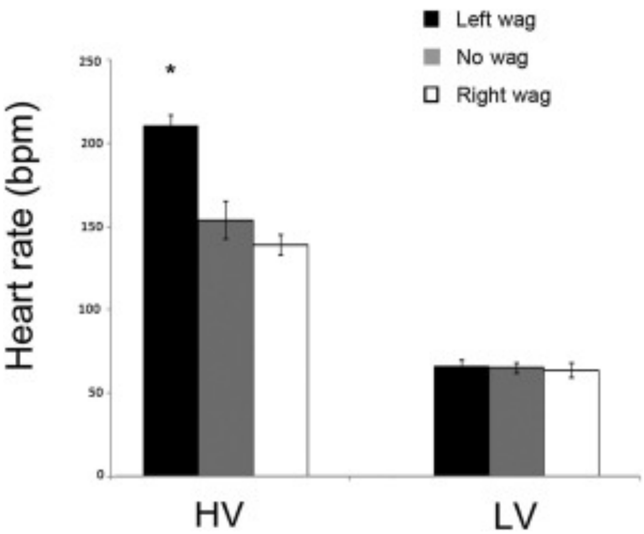

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Figure 1. Heart Rate

Highest value (HV) and lowest value (LV) of the dogs' heart rate (HR) in response to visual stimuli. *p < 0.001. Means with SEM are shown. See also Figure S3.

A significant main effect of stimulus was observed in the overall period of time in which the heart rate values were higher with respect to the basal average [i.e., the "AUC" area above baseline and under curve; F(2,84) = 27.175, p = 0.000): post hoc analysis (Fisher's protected LSD) revealed that the AUC was higher for the dog stimulus with a left-biased wag than for the other visual stimuli (p < 0.001 for all comparisons; see Figure 2A). Although there was a trend for AUC values in response to the presentations of the static dog to be higher than those in response to the dog stimulus with a right-wagging bias, this was not significant (p = 0.215).

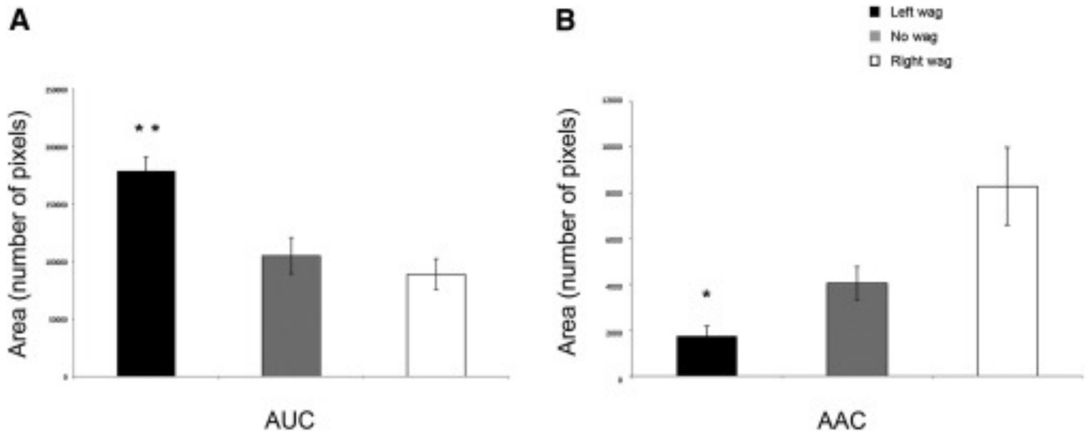

Figure 2. Cardiac Activity Areas

The areas under curve (AUC; A) and above curve (AAC; B) in response to visual stimuli (explanations can be found in the main text).**$p < 0.001$; *$p < 0.01$. Means with SEM are shown. See also Figures S2 and S3.

The overall period of time in which the heart rate values were lower respect to the basal average (i.e., the "AAC" area under baseline and above curve) was also affected by different visual stimuli [$F(2,84) = 10.564$, $p = 0.000$]: post hoc analysis revealed that this was due to the AAC values given in response to the "left-wag" stimulus being lower than those given in response to the other two stimuli ($p < 0.01$ for all comparisons, Figure 2B). No differences were observed in AAC values between the dog stimulus not wagging its tail and that exhibiting a "right-wagging" bias ($p = 0.052$).

As to behavioral score, a reactivity index was determined by calculation of the total number of manifested behaviors (each behavioral response that occurred was allocated a score of 1) for each dog, for each behavioral category (neutral/relaxed, stress/anxiety, and alerting/targeting), and for each stimulus (see the Supplemental Experimental Procedures for details). An analysis for neutral/relaxed behavioral category revealed that there was a significant difference between visual stimuli [$F(2,84) = 50,884$ $p = 0.000$]. Post hoc analyses revealed that dogs were more relaxed when they looked at projection of a dog stimulus with a right-biased wag ("right wag" versus "left wag" $p < 0.01$; "right wag" versus "no wag" $p < 0.05$); no significant differences were observed between the static dog stimulus and the stimulus exhibiting a "left-wagging" bias in terms of eliciting a neutral/relaxed response by dogs (p = 0.062; Figure 3).

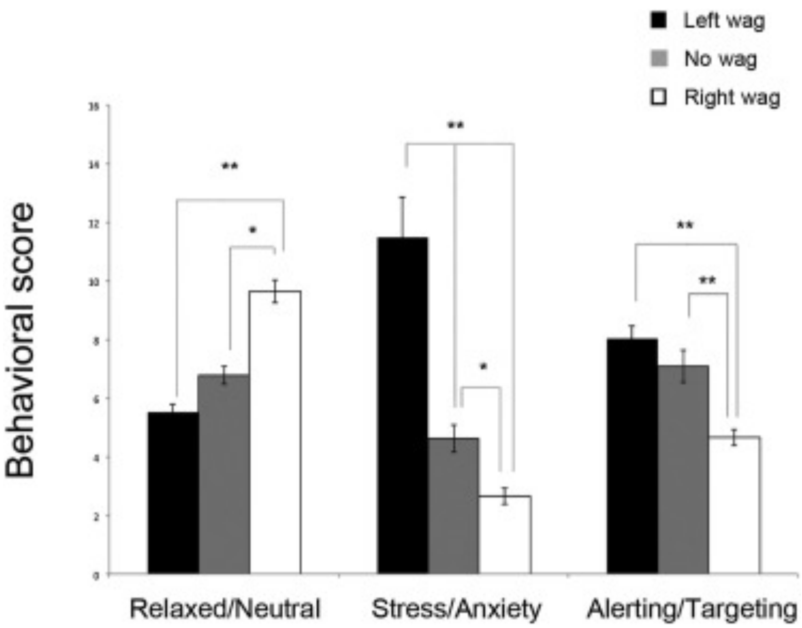

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Figure 3. Data for the Score of the Reactivity Index of the Three Behavioral Categories

*p < 0.05; **p < 0.01. Means with SEM are shown. See also Figure S4 and Table S1.

A significant main effect of visual stimuli was also observed in stress/anxiety category [F(2,84) = 29.094, p = 0.000]. The results showed that dogs were more stressed when they looked at the visual stimulus exhibiting a left-wagging bias than the other two stimuli (p < 0.01 for both comparisons). Dogs were also more stressed when looking at the static dog stimulus than to the visual stimuli displaying a right-biased wag (p < 0.05; Figure 3).

Finally, analyses revealed a significant main effect of visual stimuli on alerting/targeting behavioral index [F(2,84) = 19,379, p = 0.000]. The effect was due to the behavioral response to the dog stimulus exhibiting prevalent right-asymmetric tail wagging being lower with respect to the other two stimuli (p < 0.01 for all comparisons; see Figure 3). No differences between “left wag” and “no wag” visual stimuli were observed (p = 0.052).

No effects of sex, of age or of the breed were apparent in any of the measures (see the

Supplemental Experimental Procedures).

The results show that domestic dogs could extract communicative cues from tail-wagging direction. Dogs facing stimuli (either naturalistic or silhouette) of a dog wagging its tail with a bias to the left side revealed a greater emotional reaction than those facing similar stimuli wagging its tail to the right side. This was apparent in both cardiac activity and behavior.

During presentations of the stimuli with a left-wag bias, dogs showed higher heart-rate values for a longer period compared to presentations of both the right-wag-biased and the static stimulus. These higher levels of cardiac activity could be due to the fact that dogs perceived the tail wagged to the left side of the stimulus as associated with withdrawal responses. Previous work has shown that dogs exhibit left-biased wagging when looking at stimuli eliciting withdrawal responses (e.g., an unfamiliar dog with an agonistic approaching behavior; [4]), as a consequence of predominant right-hemisphere activation. This agrees with independent evidence that in dogs neural structures located on the right side attend prevalently to stimuli of higher emotional valence [7, 8, 9, 10].

It seems that one interpretation of these findings is that dogs might use tail-wagging direction as an indicator of the state of the other animal (in this case a "withdrawal" state) and somehow match that state (emotional transfer) or use it as a signal of impending danger in the environment. Another possible use of this information would be to capitalize on it at the expense of the tail-wagger (in this case, to approach/attempt to control an unknown individual who is signaling a withdrawal state). In both cases, heart rate may increase. However, behavioral measures showed that dogs were more anxious and stressed when they looked at the stimuli wagging the tail to the left side (right-hemisphere activation), thus somehow supporting the former interpretation.

Behavioral measures are also clearly against the hypothesis that higher heart rate (to the left-wagging stimuli) would simply reflect a generic state of increased excitement. In contrast, dogs appeared to be more relaxed when they looked at a stimulus wagging its tail to the right side (direct approaching behavior to the screen was also apparent during this condition), which suggests that dogs perceived right wagging as an expression of companionship/confidence emotional state. Supporting these findings, higher amplitude of tail-wagging movements to the right side (left-brain activation) were associated with stimuli that could be expected to elicit approach tendencies, such as seeing a dog's owner [4]. Note, also, that the results of the present experiments rule against the simple hypothesis that motion signals projected in the left visual field of an observer dogs (generated by a right-wagging stimulus image) would be associated with higher emotional responding (due to the their feeding mainly the contralateral right hemisphere).

Artelle et al. [14] investigated dogs' responses to tail wagging of a life-size robotic dog replica. They noticed a tendency for more dogs to approach the model without stopping when the tail wagged to the left, compared with to the right, which was more likely to elicit interruption of approach. The authors argued that the results could be due to the fact that dogs were presented with a signal that would otherwise be positive (right wagging) but which was not accompanied by any additional (and reciprocal) visual or acoustical responses. However, it might well be that dogs simply did not perceive robotic tail movements as biologically convincing movements.

Interestingly, in our experiments, dogs appeared to be more stressed and displayed more targeting behaviors when looking at the static stimuli than when looking at the stimuli with a right-wagging bias. This could be due to the fact that a stimulus not wagging its tail was not processed as a neutral stimulus but as a "negative" one, since freezing is associated with fear. In addition, dogs tended to look more at the stationary stimulus than at the other two stimuli (see the Supplemental Experimental Procedures). Probably, it is difficult for dogs to detect the motivational state of the "frozen" dog stimulus since, besides tail wagging, other crucial behavioral cues (e.g., eye movements and tongue flick) were absent. Similarly, studies on the judgment of human faces revealed that prototypical neutral faces (being relaxed, presenting no facial muscle contraction) were not evaluated by human subjects as neutral but in a negative way (i.e., appearing cold or threatening) [15].

The finding that dogs are sensitive to the asymmetric tail expressions of other dogs supports the hypothesis of a major role of social behavior in the evolution of brain asymmetries [2, 3, 16]; it also opens a window to the objective investigation of the emotional life of animals and has direct implications for dogs' welfare, emphasizing the crucial role of the tail movements in conspecific communication.

Experimental Procedures

Subjects

Subjects were 43 healthy domestic dogs of various breeds. See the Supplemental Experimental Procedures for details.

Stimuli

Stimuli consisted of black silhouettes obtained from a frontal presentation of a dog wagging its tail to the left or to the right of its body or without any tail wagging (see Figure 4 and Movie S2). A separate group of animals was tested with the naturalistic version of the same stimuli, without any silhouetting (see Figure 4 and Movie S1). See the Supplemental Experimental Procedures for details.

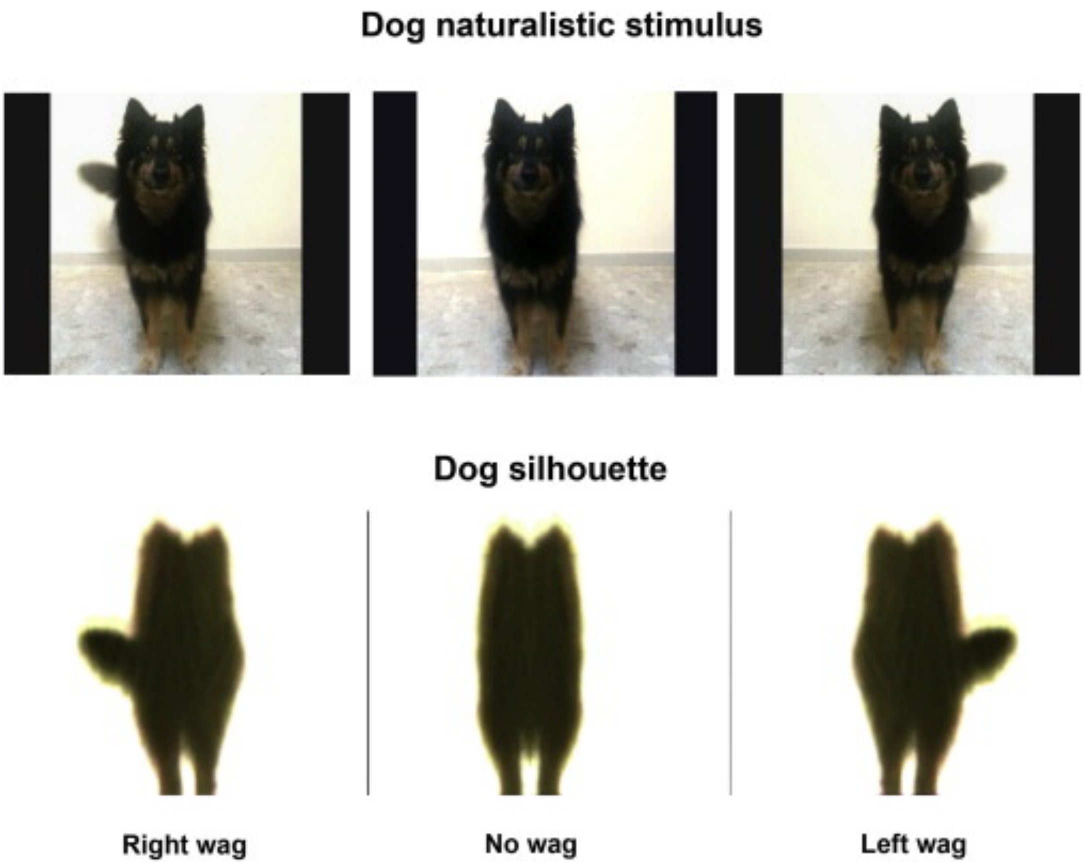

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Figure 4. Visual Stimuli

Dogs visual stimuli (naturalistic and silhouette) exhibiting prevalent left- or right-asymmetric tail wagging. Stationary stimuli not wagging their tail are also showed (pictures are single frames from moving videos).

Experimental Setup

The experiment was carried out in a large isolated room (4.80 m long, 3.50 m wide) with a white screen (2.5 × 2.5 m), on which the sequence of visual stimuli was presented. A chair for the dog's owner was placed at one side of the room facing the screen at a distance of 4 m, and the owner was asked to sit on the chair during stimulus presentation (Figure S1).

Heart Rate

The heart rate activity was recorded using the wireless system PC-Vetgard+ Multiparameter, for telemetric measurements. Dogs were accustomed to the vest during weekly visits to the laboratory before the experimental tests. See the Supplemental Experimental Procedures for details.

Behavioral Score

The behavior of the dogs was video recorded continuously during stimulus presentations and up to 5 min after a session in which the dog did not return to the starting position after the presentation of a stimulus. The video footage was subsequently analyzed by two trained observers who were blind to the testing paradigm, and interobserver reliability was assessed by means of independent parallel coding of a random sample of videotaped sessions (i.e., 40%) and calculated as percentage agreement (which was always higher than 94%).

A total of 34 behaviors were recorded which were then included into three categories (neutral/relaxed, stress/anxiety, and alerting/targeting; see Table S1). Looking times to different visual stimuli were also measured.

The experiments were conducted according to the protocols approved by the Italian Minister for Scientific Research in accordance with EC regulations; before the experiment began, the procedure was explained to owners, and written informed consent was obtained.

Acknowledgments

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Supplemental Information

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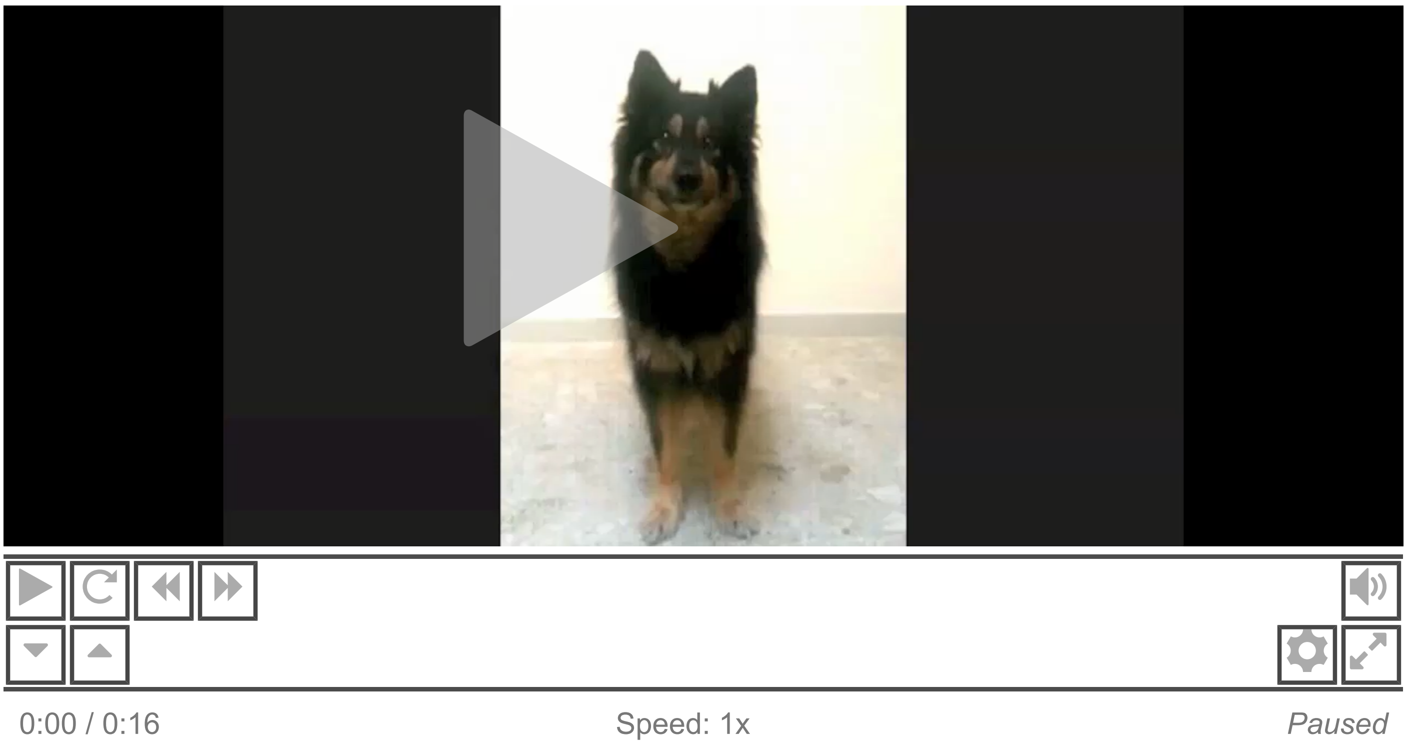
Document S1. Supplemental Experimental Procedures, Figures S1–S4, and Table S1.



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Movie S1. Dog Naturalistic Stimulus, Related to the Experimental Procedures.

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Movie S2. Dog Silhouette, Related to the Experimental Procedures.

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