



Opinion piece



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Why do dogs wag their tails?

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Tail wagging is a conspicuous behaviour in domestic dogs (*Canis familiaris*). Despite how much meaning humans attribute to this display, its quantitative description and evolutionary history are rarely studied. We summarize what is known about the mechanism, ontogeny, function and evolution of this behaviour. We suggest two hypotheses to explain its increased occurrence and frequency in dogs compared to other canids. During the domestication process, enhanced rhythmic tail wagging behaviour could have (i) arisen as a by-product of selection for other traits, such as docility and tameness, or (ii) been directly selected by humans, due to our proclivity for rhythmic stimuli. We invite testing of these hypotheses through neurobiological and ethological experiments, which will shed light on one of the most readily observed yet understudied animal behaviours. Targeted tail wagging research can be a window into both canine ethology and the evolutionary history of characteristic human traits, such as our ability to perceive and produce rhythmic behaviours.

1. Introduction

Domestic dogs (*Canis familiaris*; hereafter dogs) are the most widespread carnivore in the world: with an estimated population of one billion individuals, they are present in nearly all areas where humans occur [1,2]. Through the simple act of sharing physical space, humans directly interact with dogs in many contexts and must use different cues and modalities to effectively communicate [3,4]. Visual signals are used as communicative cues in both human–dog and dog–dog interactions [5,6]. In particular, tail attributes such as carriage (i.e. position) and wagging provide readily observable informational cues, which humans use to infer the inner states of dogs [7–9]. Tail wagging, defined as the repetitive movement of the tail across the midsagittal/median plane, may well be one of the most conspicuous of all animal behaviours for humans to observe [9–12]. The human sensitivity to and intuition for dog tail movements (with tail wagging generally associated with positive valence) is so strong that engineers have leveraged it when designing user interfaces for utility and social robots [13–15]. Despite the ubiquity of dogs in our lives and all the meaning we ascribe to tail wagging, quantitative studies to date have led to patchy results and a structured theoretical framework is missing.

We summarize existing literature on dog tail wagging by considering the mechanistic, ontogenetic, functional and evolutionary aspects of this behaviour. We tackle the question of why dogs wag their tails more frequently and in more contexts than other closely related canids, such as wolves. This overview serves as a starting point to propose empirical low-hanging fruits, recommendations and suitable methodologies for future studies.

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2. Tail wagging and Tinbergen's four questions

Why do dogs wag their tails? We can answer this question by considering tail wagging behaviour in terms of Tinbergen's four questions [16]: how does it work, mechanistically? How does it develop? What is it for? How did it evolve?

(a) Mechanism

Dog tails are an extension of the spine, but little is known about how tail movements are neuro-physiologically controlled. The cerebellum is likely involved, given that electrical stimulation in the fastigial nucleus is accompanied by an increase in wagging [17]. Wagging is an asymmetric behaviour, with dogs showing side biases depending on the stimuli they encounter. This suggests brain lateralization in dogs. Dogs exhibit a right-side wagging bias, determined by left hemisphere activation, for stimuli that have a positive emotional valence (e.g. when shown their owner or a familiar person). On the contrary, they show left-biased wagging, hence right hemisphere activation, for stimuli that elicit withdrawal (e.g. when shown an unfamiliar, dominant dog or when in aggressive situations) [8,18–20]. Dogs also perceive wagging asymmetries in robot dogs [21] and conspecifics [22]. For example, dogs show more behavioural and physiological signs of stress when watching video silhouettes of left-biased wagging dogs compared to right-biased wagging dogs [22].

Several studies have documented positive correlations between time spent tail wagging and heart rate [17,23], although links between wagging and heart rate variability are less clear [12,23]. Tail wagging is frequently associated with both positive and negative arousal, suggesting a correlation with arousal-related hormones and neurotransmitters [24–32]. For example, there is indirect evidence linking oxytocin and tail wagging, especially when dogs are reunited with a familiar human [33,34]. However, associations between tail wagging behaviour and cortisol levels are inconsistent across studies [24,35–40]. This is likely because baseline cortisol levels can co-vary with many other parameters (e.g. sex, breed, age and life history of a dog) [38,41–44]. Alternatively, or in addition, past inconsistencies may have arisen because tail wagging is typically analysed as one broad behavioural category, without taking into account its multidimensional nature and parameters (which might be modulated by different arousal, and hence cortisol, levels). This could explain why one study found that aggressive dogs wagged their tails more (and had lower serotonin levels) than non-aggressive dogs—a result that is counterintuitive to the widely held human belief linking tail wagging to positive valence in dogs [19].

(b) Ontogeny

To our knowledge, no study has tracked the development of tail wagging behaviour in the same individual(s) throughout life. One study, however, quantified several behavioural features of dog and wolf pups, including tail wagging, during object-preference tasks [45]. Pups of both species were hand-raised and then tested on their preference for their human carer versus other stimuli at three, four and five weeks of age. Four- to five-week-old dog pups frequently started to wag their tails and began displaying preferences for their carer. By contrast, wolf pups almost never wagged their tails. These results align with a short-term study (less than one week) that investigated how adult beagles interact

with a human: wagging shifted from left- to right-side biased as dogs became more familiar with an experimenter [18].

(c) Function

Both tail movement and tail carriage convey information in dog–dog [46,47], dog–human [18,38,40,48] and dog–object [49] interactions. Across canids, tail wagging with low carriage is often used as a visual sign of appeasement, submission or non-aggressive intent [50,51]. The combination of tail wagging and tail carriage seems a reliable status indicator of formal submission and subordination in dog–dog interactions [46]. Tail wagging is also used as an appeasement or affiliative signal in dog–human interactions [52,53]. One study found that during food denial situations, dogs wagged their tails more when a human was present versus not, suggesting that tail wagging may also function as a requesting signal [40]. Dogs frequently wag their tails when interacting with familiar and unfamiliar humans, but wag the most when their owners are present [34,54–57]. Dogs also wag their tails in response to non-social stimuli, such as food [23,27], fans [49] and plastic bags [35,49], with tail wagging in these situations thought to indicate positive emotions [23,27] and/or high arousal [23], but not fear [49] or stress [35].

(d) Evolution

Tails are common across vertebrates and originally evolved for locomotion, with many animals also using tails for balance and swatting pests [51,58]. In canids, tails are no longer primarily used for locomotion [58], but rather for ritualized communication [51]. While dog tail wagging can vary by individual [59,60], sex [3,32,37,55] and breed [40,60,61], dogs wag their tails more frequently and in more contexts than any other canid [51]. Differences in dog and wolf tail wagging behaviour appear as early as three weeks of age, even when pups of both species have been raised in the same way [45]. In the next section, we investigate how and why this propensity for tail wagging evolved in dogs, focusing on a strong candidate trigger: the domestication process.

3. Effects of domestication on tail wagging behaviour

Domestication is defined as an evolutionary process arising from an ecological interaction: one species actively manages the survival and reproduction of another, which ensures resources and services to the former [62,63]. Domestication is a long process that ultimately leads to a range of physiological, morphological and behavioural changes in the domesticated species [64].

Dog domestication probably began during the Upper Palaeolithic period (approx. 35 000 BP) [65,66]. In domesticated dogs, and some other mammals, changes associated with domestication include: fur depigmentation [64,67], reduced facial skeleton and teeth size [67,68], changes in overall body size and proportions [69,70], the emergence of physical attributes like floppy ears and curled tails [67], reduced brain size [66,71], reduced aggression, increased docility and variation in hormone levels resulting in behavioural changes, such as a reduced response to stress [67,69,71,72]. In addition, comparative studies between wolves and dogs have shown that the domestication process shaped dogs' cognition and sociability

in both dog–dog [73] and dog–human interactions [73–75]. Interestingly, dogs show a sophisticated ability to communicate and cooperate with humans: for example, in experimental tasks, they efficiently perceive and respond to human communicative cues, such as pointing and gaze [75–77].

Several hypotheses have tried to explain how these changes arose, outlining selective pressures that might have acted during domestication [78]. Desirable features in domesticated species are primarily the result of genetic selection by humans or an adaptation to a human-dominated environment. However, whether these traits emerged as a by-product of selection for other traits or were directly selected for is still unclear [66,67,79].

According to the ‘domestication syndrome’ hypothesis, domestication can lead to the emergence of genetically linked but unexpected traits, which are by-products of a more targeted trait selection [64,67] (but see [80] for a recent challenge). Changes in tail wagging behaviour could thus have arisen as a by-product of selection for another trait, such as tameness or friendliness toward humans. This aligns with results from a long-term experiment that tried to replicate the mammalian domestication process and track changes in behaviour, genetics and development in real-time. Silver foxes (*Vulpes vulpes*) were bred over 40 generations and directly selected for tameability and docility [81]. The resulting population of foxes exhibited behavioural, physiological and morphological traits similar to those observed in dogs (described above) [82,83]. Although tail wagging behaviour was not directly selected for, tamed foxes showed dog-like tail wagging behaviour and had more curled tails [64,81]. Based on this, we hypothesize that the domestication process may have led to changes at the behavioural and anatomical level that altered tail wagging behaviour in dogs, such that dogs wag more often and in more contexts than non-domesticated canids. This could have been due to a genetic link between the selection for tameness and tail anatomy. For instance, initial selections for docility may have triggered alterations of the neural crest cells during development, with repercussions on various phenotypic traits, including tail anatomy [72,84,85]. In line with other domestication hypotheses, such as the ‘deferential behaviour’ hypothesis [78] and the ‘emotional reactivity’ hypothesis [86], we suggest that, independently from the possible specific behavioural trait targeted during the domestication process, the altered tail wagging behaviour seen in dogs could have arisen as a direct expression of docility/friendliness.

Alternatively, tail wagging behaviour may have been one target of the domestication process, with humans (un)consciously selecting for dogs who wagged their tails more often, and potentially more rhythmically. We call this the ‘domesticated rhythmic wagging’ hypothesis. Tail wagging is a stereotyped, cyclical and rhythmic behaviour [87,88]. Extensive multidisciplinary evidence shows that humans have remarkable abilities to perceive and produce rhythmic sequences, particularly isochronous patterns where events are evenly spaced in time [89–96]. How this behavioural trait appeared in humans is still not clear, but cognitive neuroscience shows that human brains prefer rhythmic stimuli, which trigger pleasurable responses and engage brain networks that are part of the reward system [97,98]. This propensity for isochronous rhythms could have driven human selection for the conspicuous rhythmic wagging of the tail in

dogs, and could explain why dogs exhibit it so often in human–dog interactions.

Under both hypotheses, selection on tail wagging behaviour may not have been uniform across breeds; for example, hunting-type dogs wag their tails more than shepherd-type dogs, and have also experienced different selective pressures throughout domestication [40,65]. Was tail wagging behaviour a by-product of selection for other traits (i.e. the ‘domestication syndrome’ hypothesis) or was it directly selected by humans because of its rhythmic properties (i.e. the ‘domesticated rhythmic wagging’ hypothesis)? Answering this question requires dedicated experiments that not only better quantify tail wagging in general but also explicitly consider how the behaviour is controlled.

4. Recommendations and future directions

Dog tail wagging may in fact be one of the most visible, prevalent animal behaviours in the world, but it has never been analysed in a systematic way. Most studies have measured when, for how long or at what rate tail wagging (broadly defined) occurs. These types of analyses are useful but limited in scope, and make teasing apart different evolutionary hypotheses challenging. Indeed, our brief review emphasizes that tail wagging is a multidimensional trait that can differ according to various parameters, including tail carriage, wag direction, wag speed, wag (a)symmetry and wag amplitude [59]. It can also vary depending on the portion of the tail being considered (i.e. base, central portion or tip). In theory, each tail movement parameter could be under different levels of neural control, have different functions and/or convey different information.

To better characterize the behaviour as a whole and distinguish between types of tail wagging, our first suggestion is to perform precise behavioural analyses of high-quality tail wagging videos [20], in concert with newly developed automated tracking tools specific to this oscillatory behaviour [99]. By simultaneously quantifying the parameters mentioned above, we can start to determine whether and how they relate to each other. Such analyses should be performed with dogs exposed to different stimuli (e.g. social versus non-social; of positive, neutral or negative valence) and accompanied by physiological measurements (e.g. heart rate, heart rate variability, cortisol, oxytocin, serotonin, testosterone); this will clarify how context and physiology impact different tail wagging parameters.

Second, we suggest that combining techniques of behaviour, computer vision and physiology analysis with neuroscience can help disentangle between tail movements under control (thus, under possible selection) from those resulting from mere mechanical effects (e.g. the tip of the tail might move as a consequence of more cranial portions of the tail being actively moved). Dogs are one of few animals, apart from humans, for which both non-invasive electrophysiology (e.g. EEG) and neuroimaging (e.g. fMRI) have been developed [100–103]. Neuroimaging techniques will help pinpoint which brain areas and networks are involved in tail wagging perception and production. Electrophysiology will support mapping the temporal dynamics of the putative involvement of different areas in the dog’s cerebral cortex. Better understanding of tail wagging parameters and control will allow us to answer many outstanding questions, including investigating different evolutionary hypotheses for dog tail

Table 1. Outstanding questions on dog tail wagging behaviour and related suggestions for future studies.

Tinbergen domain	outstanding questions	methods
mechanism	<p>physiology: are different tail wagging parameters associated with different arousal levels and/or physiological mechanisms?</p> <p>biomechanics: is the entire tail under neurological control, or just a portion of it (e.g. base, tip)? Which brain circuits control tail wagging? Is any parameter of tail wagging under voluntary control or potentially learned?</p> <p>genetics: how much inter-individual phenotypic variation is there in tail wagging? How much of that variation can be explained by genetics?</p>	<p>—systematically quantify dog tail wagging parameters (see ‘Recommendations and future directions’ section for details) while collecting real-time physiological (e.g. heart rate, cortisol, oxytocin) and behavioural (e.g. pacing, yawning) measures of arousal [22] in different contexts (e.g. affiliative, aggressive)</p> <p>—monitor dog tail activity while simultaneously conducting non-invasive electrophysiology (e.g. EEG) and neuroimaging (e.g. fMRI) [100–103].</p>
ontogeny	<p>development: does tail wagging behaviour in the same individual change from puppyhood to adulthood? Is any age-related variability in tail wagging linked to cognitive development and/or the production of other communicative signals?</p>	<p>—use whole-genome sequencing data and comparative genomics to investigate whether tail wagging is a genetically linked trait; a logical starting point would be to build on genomic research that has already been conducted on dog tail length [104] and shape [105].</p> <p>—systematically quantify dog tail wagging parameters in the same individuals throughout development while also tracking changes in cognition and non-tail-based communication [106,107].</p>
function	<p>context: how do dog tail movements differ in social versus non-social contexts?</p>	<p>—systematically quantify dog tail wagging parameters when dogs are exposed to social and non-social stimuli and situations (e.g. [57]).</p>
audience	<p>audience: are there systematic differences in tail wagging behaviour when dogs are interacting with humans versus with conspecifics? How do receivers perceive different tail wagging parameters?</p>	<p>—systematically quantify dog tail wagging parameters in both intra- and inter-specific contexts (for an example of how differences in dog–dog and dog–human interactions can be investigated, see [108]) and investigate the effect on the receiver (human or conspecific, e.g. [22]).</p>
phylogeny	<p>phylogeny: which features of dog tail wagging are shared with other members of the class (mammals), suborder (caniforms) and family (canids)? Which features are more recent phylogenetic innovations?</p> <p>selection: is increased tail wagging in dogs a by-product of selection for other traits or was it directly selected? Is tail wagging correlated with other domestication traits (e.g. docility)?</p>	<p>—systematically quantify tail wagging parameters in a diversity of species and compare the resulting phylogeny of behavioural similarity (in terms of tail wagging) with a phylogeny of genetic relatedness (e.g. [109]).</p> <p>—compare dog tail wagging with tail wagging in other domesticated mammals (e.g. pigs or cats) to shed light on whether tail wagging results from domestication in general (i.e. a general selection for tameness) or is specific to dog domestication.</p>
perception	<p>perception: do humans and dogs have a preference for more rhythmically regular tail movements?</p>	<p>—quantify correlations between temperament traits such as docility, friendliness or deferentiality (as measured through temperament test batteries, e.g. [110]) and tail wagging parameters.</p> <p>—test the perception of tail wagging parameters in humans and dogs (and ideally in non-human primates and other canids as well) through neuroimaging and physiological studies (e.g. expose both humans and dogs to tail wagging dogs and measure attention parameters such as eye fixations) [111–114].</p> <p>—human studies should be conducted on diverse participants, given that age, cultural upbringing, and personal experience with dogs could all be confounding factors.</p> <p>—testing human populations living in close proximity to free-ranging dogs would be particularly interesting from an evolutionary perspective, since an unconscious positive selection for dogs wagging their tails, mediated by a potential preference for their rhythmicity, could still be taking place.</p>

wagging. Table 1 lists outstanding questions and suggested methods to answer them.

5. Conclusion

Dog tail wagging is a conspicuous yet scientifically elusive behaviour. Its uniqueness, complexity and ubiquity have the potential to be associated with multiple functions, but its mechanisms and ontogeny are still poorly understood. These knowledge gaps prevent us from fully understanding the evolutionary history of modern tail wagging behaviour and what role humans played in the process. A more systematic and thorough investigation of tail wagging will not only better map this iconic dog behavioural display, but also provide indirect evidence into the evolution of human traits, such as the perception and production of rhythmic stimuli.

References

- Gompper ME. 2014 The dog–human–wildlife interface: assessing the scope of the problem. In *Free-ranging dogs and wildlife conservation* (ed. ME Gompper), pp. 9–54. Oxford, UK: Oxford University Press.
- Zapata-Ríos G. 2018 Dogs are more than wet kisses and tail wags: domestic dogs as invasive species. *Anim. Conserv.* **21**, 287–288. (doi:10.1111/acv.12440)
- Fonseca MLA, Vasconcellos AS. 2021 Can dogs' origins and interactions with humans affect their accomplishments? A study on the responses of shelter and companion dogs during vocal cue training. *Animals* **11**, 1360. (doi:10.3390/ani11051360)
- Kerepesi A, Jonsson GK, Miklósi Á, Topál J, Csányi V, Magnusson MS. 2005 Detection of temporal patterns in dog–human interaction. *Behav. Processes* **70**, 69–79. (doi:10.1016/j.beproc.2005.04.006)
- Müller CA, Schmitt K, Barber ALA, Huber L. 2015 Dogs can discriminate emotional expressions of human faces. *Curr. Biol.* **25**, 601–605. (doi:10.1016/j.cub.2014.12.055)
- Siniscalchi M, d'Ingeo S, Minunno M, Quaranta A. 2018 Communication in dogs. *Animals* **8**, 131. (doi:10.3390/ani8080131)
- Beaver BV. 1999 *Canine behavior: a guide for veterinarians*. Philadelphia, PA: W.B. Saunders.
- Quaranta A, Siniscalchi M, Vallortigara G. 2007 Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Curr. Biol.* **17**, R199–R201. (doi:10.1016/j.cub.2007.02.008)
- Tami G, Gallagher A. 2009 Description of the behaviour of domestic dog (*Canis familiaris*) by experienced and inexperienced people. *Appl. Anim. Behav. Sci.* **120**, 159–169. (doi:10.1016/j.applanim.2009.06.009)
- Horowitz A. 2009 Disambiguating the 'guilty look': salient prompts to a familiar dog behaviour. *Behav. Processes* **81**, 447–452. (doi:10.1016/j.beproc.2009.03.014)
- Buckland EL, Volk HA, Burn CC, Abeyesinghe SM. 2014 Owner perceptions of companion dog expressions of positive emotional states and the contexts in which they occur. *Anim. Welf.* **23**, 287–296. (doi:10.7120/09627286.23.3.287)
- Somppi S, Törnqvist H, Koskela A, Vehkaoja A, Tiira K, Väättäjä H, Surakka V, Vainio O, Kujala MV. 2022 Dog–owner relationship, owner interpretations and dog personality are connected with the emotional reactivity of dogs. *Animals* **12**, 1338. (doi:10.3390/ani12111338)
- Singh A, Young JE. 2013 A dog tail for communicating robotic states. In *ACM/IEEE Int. Conf. on Human–Robot Interaction (HRI). Tokyo, Japan. 3–6 March 2013*. p. 417. Piscataway, NJ: Institute of Electrical and Electronics Engineers. (doi:10.1109/HRI.2013.6483625)
- Singh A, Young JE. 2013 A dog tail for utility robots: exploring affective properties of tail movement. In *Human–Computer Interaction–INTERACT 2013: Proc. of the 14th IFIP TC 13 Int. Conf., Cape Town, South Africa, 2–6 September 2013, Part II 14*, pp. 403–419. Berlin, Germany: Springer.
- Faragó T, Takács N, Miklósi Á, Pongrácz P. 2017 Dog growls express various contextual and affective content for human listeners. *R. Soc. Open Sci.* **4**, 170134. (doi:10.1098/rsos.170134)
- Tinbergen N. 1963 On aims and methods of ethology. *Z. Tierpsychol.* **20**, 410–433. (doi:10.1111/j.1439-0310.1963.tb01161.x)
- Braggio JT, Dormer KJ. 1985 Effects of fastigial nucleus stimulation on behavior and cardiovascular parameters in the freely moving dog. *Physiol. Psychol.* **13**, 80–85. (doi:10.3758/BF03326501)
- Ren W, Wei P, Yu S, Zhang YQ. 2022 Left–right asymmetry and attractor-like dynamics of dog's tail wagging during dog–human interactions. *Iscience* **25**, 104747.
- Gobbo E, Zupan Šemrov M. 2021 Neuroendocrine and cardiovascular activation during aggressive reactivity in dogs. *Front. Vet. Sci.* **8**, 683858. (doi:10.3389/fvets.2021.683858)
- Völter CJ, Lonardo L, Steinmann MGGM, Ramos CF, Gerwisch K, Schranz M-T, Doberner I, Huber L. 2023 Unwilling or unable? Using three-dimensional tracking to evaluate dogs' reactions to differing human intentions. *Proc. R. Soc. B* **290**, 20221621. (doi:10.1098/rspb.2022.1621)
- Artelle KA, Dumoulin LK, Reimchen TE. 2011 Behavioural responses of dogs to asymmetrical tail wagging of a robotic dog replica. *Laterality* **16**, 129–135. (doi:10.1080/13576500903386700)
- Siniscalchi M, Lusito R, Vallortigara G, Quaranta A. 2013 Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. *Curr. Biol.* **23**, 2279–2282. (doi:10.1016/j.cub.2013.09.027)
- Travain T, Colombo ES, Grandi LC, Heinzl E, Pelosi A, Previde EP, Valsecchi P. 2016 How good is this food? A study on dogs' emotional responses to a potentially pleasant event using infrared thermography. *Physiol. Behav.* **159**, 80–87. (doi:10.1016/j.physbeh.2016.03.019)
- Pastore C, Pirrone F, Balzarotti F, Faustini M, Pierantoni L, Albertini M. 2011 Evaluation of physiological and behavioral stress-dependent parameters in agility dogs. *J. Vet. Behav.* **6**, 188–194. (doi:10.1016/j.jveb.2011.01.001)
- Rehn T, Keeling LJ. 2011 The effect of time left alone at home on dog welfare. *Appl. Anim. Behav. Sci.* **129**, 129–135. (doi:10.1016/j.applanim.2010.11.015)
- Normando S, Corain L, Salvadoretti M, Meers L, Valsecchi P. 2009 Effects of an enhanced human interaction program on shelter dogs' behaviour analysed using a novel nonparametric test. *Appl. Anim. Behav. Sci.* **116**, 211–219. (doi:10.1016/j.applanim.2008.10.005)

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27. McGowan RTS, Rehn T, Norling Y, Keeling LJ. 2014 Positive affect and learning: exploring the 'Eureka Effect' in dogs. *Anim. Cogn.* **17**, 577–587. (doi:10.1007/s10071-013-0688-x)
28. Bosch G, Beerda B, van de Hoek E, Hesta M, van der Poel AFB, Janssens GPJ, Hendriks WH. 2009 Effect of dietary fibre type on physical activity and behaviour in kennelled dogs. *Appl. Anim. Behav. Sci.* **121**, 32–41. (doi:10.1016/j.applanim.2009.08.001)
29. Katz M, Rosales-Ruiz J. 2022 Constructional fear treatment: teaching fearful shelter dogs to approach and interact with a novel person. *J. Exp. Anal. Behav.* **118**, 278–291. (doi:10.1002/jeab.784)
30. Bremhorst A, Mills DS, Würbel H, Riemer S. 2022 Evaluating the accuracy of facial expressions as emotion indicators across contexts in dogs. *Anim. Cogn.* **25**, 121–136. (doi:10.1007/s10071-021-01532-1)
31. Bray EE, MacLean EL, Hare BA. 2015 Increasing arousal enhances inhibitory control in calm but not excitable dogs. *Anim. Cogn.* **18**, 1317–1329. (doi:10.1007/s10071-015-0901-1)
32. Beerda B, Schilder MBH, Bernadina W, Van Hooff JANA, De Vries HW, Mol JA. 1999 Chronic stress in dogs subjected to social and spatial restriction. II. Hormonal and immunological responses. *Physiol. Behav.* **66**, 243–254. (doi:10.1016/S0031-9384(98)00290-X)
33. Murata K, Nagasawa M, Onaka T, Kanemaki N, Nakamura S, Tsubota K, Mogi K, Kikusui T. 2022 Increase of tear volume in dogs after reunion with owners is mediated by oxytocin. *Curr. Biol.* **32**, 855–873. (doi:10.1016/j.cub.2022.07.031)
34. Rehn T, Lindholm U, Keeling L, Forkman B. 2014 I like my dog, does my dog like me? *Appl. Anim. Behav. Sci.* **150**, 65–73. (doi:10.1016/j.applanim.2013.10.008)
35. Beerda B, Schilder MBH, Van Hooff JA, De Vries HW, Mol JA. 1998 Behavioural, saliva cortisol and heart rate responses to different types of stimuli in dogs. *Appl. Anim. Behav. Sci.* **58**, 365–381. (doi:10.1016/S0168-1591(97)00145-7)
36. Glenk LM, Kothgassner OD, Stetina BU, Palme R, Kepplinger B, Baran H. 2014 Salivary cortisol and behavior in therapy dogs during animal-assisted interventions: a pilot study. *J. Vet. Behav.* **9**, 98–106. (doi:10.1016/j.jveb.2014.02.005)
37. Beerda B, Schilder MBH, Van Hooff J, de Vries HW, Mol JA. 2000 Behavioural and hormonal indicators of enduring environmental stress in dogs. *Anim. Welf.* **9**, 49–62. (doi:10.1017/S0962728600022247)
38. Willen RM, Mutwill A, MacDonald LJ, Schiml PA, Hennessy MB. 2017 Factors determining the effects of human interaction on the cortisol levels of shelter dogs. *Appl. Anim. Behav. Sci.* **186**, 41–48. (doi:10.1016/j.applanim.2016.11.002)
39. McCullough A *et al.* 2018 Physiological and behavioral effects of animal-assisted interventions on therapy dogs in pediatric oncology settings. *Appl. Anim. Behav. Sci.* **200**, 86–95. (doi:10.1016/j.applanim.2017.11.014)
40. Pedretti G, Canori C, Marshall-Pescini S, Palme R, Pelosi A, Valsecchi P. 2022 Audience effect on domestic dogs' behavioural displays and facial expressions. *Sci. Rep.* **12**, 9747. (doi:10.1038/s41598-022-13566-7)
41. Hennessy MB, Voith VL, Mazzei SJ, Buttram J, Miller DD, Linden F. 2001 Behavior and cortisol levels of dogs in a public animal shelter, and an exploration of the ability of these measures to predict problem behavior after adoption. *Appl. Anim. Behav. Sci.* **73**, 217–233. (doi:10.1016/S0168-1591(01)00139-3)
42. Hennessy MB, Davis HN, Williams MT, Mellott C, Douglas CW. 1997 Plasma cortisol levels of dogs at a county animal shelter. *Physiol. Behav.* **62**, 485–490. (doi:10.1016/S0031-9384(97)80328-9)
43. Beerda B, Schilder MBH, Janssen NS, Mol JA. 1996 The use of saliva cortisol, urinary cortisol, and catecholamine measurements for a noninvasive assessment of stress responses in dogs. *Horm. Behav.* **30**, 272–279. (doi:10.1006/hbeh.1996.0033)
44. Horváth Z, Igyártó B-Z, Magyar A, Miklósi Á. 2007 Three different coping styles in police dogs exposed to a short-term challenge. *Horm. Behav.* **52**, 621–630. (doi:10.1016/j.yhbeh.2007.08.001)
45. Gácsi M, Györi B, Miklósi Á, Virányi Z, Kubinyi E, Topál J, Csányi V. 2005 Species-specific differences and similarities in the behavior of hand-raised dog and wolf pups in social situations with humans. *Dev. Psychobiol. J. Int. Soc. Dev. Psychobiol.* **47**, 111–122. (doi:10.1002/dev.20082)
46. van der Borg JAM, Schilder MBH, Vinke CM, De Vries H. 2015 Dominance in domestic dogs: a quantitative analysis of its behavioural measures. *PLoS ONE* **10**, e0133978.
47. Horowitz A. 2009 Attention to attention in domestic dog (*Canis familiaris*) dyadic play. *Anim. Cogn.* **12**, 107–118. (doi:10.1007/s10071-008-0175-y)
48. Kujtkowska A, Strychalski J, Gugolek A. 2020 A pilot study on the qualitative assessment of the impact of human–canine relationships on dogs' susceptibility to stress. *Dog Behav.* **6**, 13–20.
49. Flint HE, Coe JB, Serpell JA, Pearl DL, Niel L. 2018 Identification of fear behaviors shown by puppies in response to nonsocial stimuli. *J. Vet. Behav.* **28**, 17–24. (doi:10.1016/j.jveb.2018.07.012)
50. Kleiman DG. 1967 Some aspects of social behavior in the Canidae. *Am. Zool.* **7**, 365–372. (doi:10.1093/icb/7.2.365)
51. Kiley-Worthington M. 1976 The tail movements of ungulates, canids and felids with particular reference to their causation and function as displays. *Behaviour* **56**, 69–114. (doi:10.1163/156853976X00307)
52. Firnkes A, Bartels A, Bidoli E, Erhard M. 2017 Appeasement signals used by dogs during dog–human communication. *J. Vet. Behav.* **19**, 35–44. (doi:10.1016/j.jveb.2016.12.012)
53. Cavalli CM, Dzik MV, Carballo Pozzo Ardizzi F, Bentosela M. 2016 Post-conflict affiliative behaviors towards humans in domestic dogs (*Canis familiaris*). *Int. J. Comp. Psychol.* **29**. (doi:10.46867/ijcp.2016.29.00.03)
54. Rezac P, Koru E, Havlicek Z, Zospisilova D. 2017 Factors affecting dog jumping on people. *Appl. Anim. Behav. Sci.* **197**, 40–44. (doi:10.1016/j.applanim.2017.09.008)
55. Ruiz-Izaguirre E, Bokkers EAM, Ortolani A, Ortega-Pacheco A, de Boer IJM. 2014 Human–dog interactions and behavioural responses of village dogs in coastal villages in Michoacán, Mexico. *Appl. Anim. Behav. Sci.* **154**, 57–65. (doi:10.1016/j.applanim.2014.02.002)
56. Prato-Previde E, Custance DM, Spiezio C, Sabatini F. 2003 Is the dog–human relationship an attachment bond? An observational study using Ainsworth's strange situation. *Behaviour* **140**, 225–254. (doi:10.1163/15685390321671514)
57. Stellato AC, Flint HE, Widowski TM, Serpell JA, Niel L. 2017 Assessment of fear-related behaviours displayed by companion dogs (*Canis familiaris*) in response to social and non-social stimuli. *Appl. Anim. Behav. Sci.* **188**, 84–90. (doi:10.1016/j.applanim.2016.12.007)
58. Rottier T, Schulz AK, Söhnel K, McCarthy K, Fischer MS, Jusufi A, Heisenbergstraße AJ. 2022 Tail wags the dog is unsupported by biomechanical modeling of Canidae tails use during terrestrial motion. *bioRxiv* 2022.12.30.522334. (doi:10.1101/2022.12.30.522334)
59. Ruge L, Cox E, Mancini C, Luck R. 2018 *User centered design approaches to measuring canine behavior: tail wagging as a measure of user experience*. In *ACI '18: Proc. of the Fifth Int. Conf. on Animal–Computer Interaction*. Atlanta, GA, 4–6 December, pp. 1–12. New York, NY: ACM.
60. Svartberg K, Forkman B. 2002 Personality traits in the domestic dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* **79**, 133–155. (doi:10.1016/S0168-1591(02)00121-1)
61. Handelman B. 2012 *Canine behavior: a photo illustrated handbook*. Wenatchee, WA: Dogwise Publishing.
62. Zeder MA. 2015 Core questions in domestication research. *Proc. Natl Acad. Sci. USA* **112**, 3191–3198. (doi:10.1073/pnas.1501711112)
63. Purugganan MD. 2022 What is domestication? *Trends Ecol. Evol.* **37**, 663–671. (doi:10.1016/j.tree.2022.04.006)
64. Trut L, Oskina I, Kharlamova A. 2009 Animal evolution during domestication: the domesticated fox as a model. *Bioessays* **31**, 349–360. (doi:10.1002/bies.200800070)
65. Galibert F, Quignon P, Hitte C, André C. 2011 Toward understanding dog evolutionary and domestication history. *C. R. Biol.* **334**, 190–196. (doi:10.1016/j.crv.2010.12.011)
66. Zeder MA. 2012 Pathways to animal domestication. *Biodivers. Agric. Domest. Evol. Sustain.* **10**, 227–259.
67. Darwin C. 1868 *The variation of animals and plants under domestication*. London, UK: John Murray.
68. Belyaev DK, Khvostova VV. 1974 Domestication, plant and animal. *Encycl. Br.* **15**, 936–942.
69. Belyaev DK. 1969 Domestication of animals. *Science* **5**, 47–52.
70. Herre WK. 1959 Today's status of domestication research. *Naturwissenschaftlich Rundschau* **12**, 87–94.
71. Kruska D. 1987 How fast can total brain size change in mammals? *J. Hirnforsch.* **28**, 59–70.
72. Wilkins AS, Wrangham RW, Fitch WT. 2014 The 'domestication syndrome' in mammals: a unified

- explanation based on neural crest cell behavior and genetics. *Genetics* **197**, 795–808. (doi:10.1534/genetics.114.165423)
73. Marshall-Pescini S, Rao A, Virányi Z, Range F. 2017 The role of domestication and experience in 'looking back' towards humans in an unsolvable task. *Sci. Rep.* **7**, 46636. (doi:10.1038/srep46636)
74. Lazzaroni M, Range F, Backes J, Portele K, Scheck K, Marshall-Pescini S. 2020 The effect of domestication and experience on the social interaction of dogs and wolves with a human companion. *Front. Psychol.* **11**, 785. (doi:10.3389/fpsyg.2020.00785)
75. Hare B, Rosati AG, Kaminski J, Bräuer J, Call J, Tomasello M. 2010 The domestication hypothesis for dogs' skills with human communication: a response to Udell *et al.*(2008) and Wynne *et al.*(2008). *Anim. Behav.* **79**, e1–e6. (doi:10.1016/j.anbehav.2009.06.031)
76. Range F, Virányi Z. 2015 Tracking the evolutionary origins of dog–human cooperation: the 'Canine Cooperation Hypothesis'. *Front. Psychol.* **5**, 1582. (doi:10.3389/fpsyg.2014.01582)
77. Cooper JJ, Ashton C, Bishop S, West R, Mills DS, Young RJ. 2003 Clever hounds: social cognition in the domestic dog (*Canis familiaris*). *Appl. Anim. Behav. Sci.* **81**, 229–244. (doi:10.1016/S0168-1591(02)00284-8)
78. Range F, Marshall-Pescini S. 2022 Comparing wolves and dogs: current status and implications for human 'self-domestication'. *Trends Cogn. Sci.* **26**, 337–349. (doi:10.1016/j.tics.2022.01.003)
79. Gregory TR. 2008 Artificial selection and domestication: modern lessons from Darwin's enduring analogy. *Evol. Educ. Outreach* **2**, 5–27. (doi:10.1007/s12052-008-0114-z)
80. Lord KA, Larson G, Coppinger RP, Karlsson EK. 2020 The history of farm foxes undermines the animal domestication syndrome. *Trends Ecol. Evol.* **35**, 125–136. (doi:10.1016/J.TREE.2019.10.011)
81. Trut LN. 1999 Early canid domestication: the farm-fox experiment: foxes bred for tamability in a 40-year experiment exhibit remarkable transformations that suggest an interplay between behavioral genetics and development. *Am. Sci.* **87**, 160–169. (doi:10.1511/1999.20.160)
82. Belyaev DK. 1979 Destabilizing selection as a factor in domestication. *J. Hered.* **70**, 301–308. (doi:10.1093/oxfordjournals.jhered.a109263)
83. Trut LN, Plyusnina IZ, Oskina IN. 2004 An experiment on fox domestication and debatable issues of evolution of the dog. *Russ. J. Genet.* **40**, 644–655. (doi:10.1023/B:RUGE.0000033312.92773.c1)
84. Sánchez-Villagra MR, Schneider RA, Geiger M. 2016. The taming of the neural crest: a developmental perspective on the origins of morphological covariation in domesticated mammals. *R. Soc. Open Sci.* **3**, 160107. (doi:10.1098/rsos.160107)
85. Pendleton AL, Shen F, Taravella AM, Emery S, Veeramah KR, Boyko AR, Kidd JM. 2018 Comparison of village dog and wolf genomes highlights the role of the neural crest in dog domestication. *BMC Biol.* **16**, 1–21. (doi:10.1186/s12915-018-0535-2)
86. Hare B, Tomasello M. 2005 Human-like social skills in dogs? *Trends Cogn. Sci.* **9**, 439–444. (doi:10.1016/j.tics.2005.07.003)
87. Kotz SA, Ravignani A, Fitch WT. 2018 The evolution of rhythm processing. *Trends Cogn. Sci.* **22**, 896–910. (doi:10.1016/j.tics.2018.08.002)
88. Merker BH, Madison GS, Eckerdal P. 2009 On the role and origin of isochrony in human rhythmic entrainment. *Cortex* **45**, 4–17. (doi:10.1016/j.cortex.2008.06.011)
89. Fitch WT. 2012 The biology and evolution of rhythm: unravelling a paradox. In *Language and music as cognitive systems* (eds P Rebuschat, M Rohmeier, JA Hawkins, I Cross), pp. 73–95. Oxford, UK: Oxford University Press.
90. Ravignani A, Madison G. 2017 The paradox of isochrony in the evolution of human rhythm. *Front. Psychol.* **8**, 1820. (doi:10.3389/fpsyg.2017.01820)
91. Madison G, Merker B. 2004 Human sensorimotor tracking of continuous subliminal deviations from isochrony. *Neurosci. Lett.* **370**, 69–73. (doi:10.1016/j.neulet.2004.07.094)
92. Madison G. 2009 An auditory illusion of infinite tempo change based on multiple temporal levels. *PLoS ONE* **4**, 8151. (doi:10.1371/journal.pone.0008151)
93. Fabb N, Halle M. 2012 Grouping in the stressing of words, in metrical verse, and in music. In *Language and music as cognitive systems* (eds P Rebuschat, M Rohmeier, JA Hawkins, I Cross), pp. 4–21. Oxford, UK: Oxford University Press.
94. Grabe E, Low EL. 2002 Durational variability in speech and the rhythm class hypothesis. *Pap. Lab. Phonol.* **7**, 1–16.
95. Fitch WT. 2016 Dance, music, meter and groove: a forgotten partnership. *Front. Hum. Neurosci.* **10**, 64. (doi:10.3389/fnhum.2016.00064)
96. Honing H, Ladinig O, Háden GP, Winkler I. 2009 Is beat induction innate or learned? Probing emergent meter perception in adults and newborns using event-related brain potentials. *Ann. N. Y. Acad. Sci.* **1169**, 93–96. (doi:10.1111/j.1749-6632.2009.04761.x)
97. Brodal HP, Osnes B, Specht K. 2017 Listening to rhythmic music reduces connectivity within the basal ganglia and the reward system. *Front. Neurosci.* **11**, 153. (doi:10.3389/fnins.2017.00153)
98. Zatorre RJ, Salimpoor VN. 2013 From perception to pleasure: music and its neural substrates. *Proc. Natl Acad. Sci. USA* **110**, 10 430–10 437. (doi:10.1073/pnas.1301228110)
99. Roberts DL, Park J, Pappas A, Gruen M, Carson M. 2019 Automated tail position tracking with millimeter accuracy using depth sensing and mask R-CNN. In *Proc. of the Sixth Int. Conf. on Animal-Computer Interaction*, pp. 1–12. New York, NY: ACM.
100. Andics A, Rta M, Csi G, Faragó TS, Kis A, Dá M, Miklósi Á. 2014 Report voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. *Curr. Biol.* **24**, 574–578. (doi:10.1016/j.cub.2014.01.058)
101. Berns GS, Brooks AM, Spivak M. 2015 Scent of the familiar: an fMRI study of canine brain responses to familiar and unfamiliar human and dog odors. *Behav. Processes* **110**, 37–46. (doi:10.1016/j.beproc.2014.02.011)
102. Kis A, Szakadát S, Gácsi M, Kovács E, Simor P, Török C, Gombos F, Bódizs R, Topál J. 2017 The interrelated effect of sleep and learning in dogs (*Canis familiaris*); an EEG and behavioural study. *Sci. Rep.* **7**, 41873. (doi:10.1038/srep41873)
103. Törnqvist H, Kujala MV, Somppi S, Hänninen L, Pastell M, Krause CM, Kujala J, Vainio O. 2013 Visual event-related potentials of dogs: a non-invasive electroencephalography study. *Anim. Cogn.* **16**, 973–982. (doi:10.1007/s10071-013-0630-2)
104. Lee D, Lim D, Kwon D, Kim J, Lee J, Sim M, Choi BH, Choi SG, Kim J. 2017 Functional and evolutionary analysis of Korean bob-tailed native dog using whole-genome sequencing data. *Sci. Rep.* **7**, 1–8. (doi:10.1038/s41598-017-17817-w)
105. Mansour TA *et al.* 2018 Whole genome variant association across 100 dogs identifies a frame shift mutation in DISHEVELLED 2 which contributes to Robinow-like syndrome in bulldogs and related screw tail dog breeds. *PLoS Genet.* **14**, e1007850. (doi:10.1371/journal.pgen.1007850)
106. Bray EE, Gruen ME, Gnanadesikan GE, Horschler DJ, Levy KM, Kennedy BS, Hare BA, MacLean EL. 2021 Dog cognitive development: a longitudinal study across the first 2 years of life. *Anim. Cogn.* **24**, 311–328. (doi:10.1007/s10071-020-01443-7)
107. Lampe M, Bräuer J, Kaminski J, Virányi Z. 2017 The effects of domestication and ontogeny on cognition in dogs and wolves. *Sci. Rep.* **7**, 11690. (doi:10.1038/s41598-017-12055-6)
108. Rooney NJ, Bradshaw JWS, Robinson IH. 2000 A comparison of dog–dog and dog–human play behaviour. *Appl. Anim. Behav. Sci.* **66**, 235–248. (doi:10.1016/S0168-1591(99)00078-7)
109. Hecht EE, Smaers JB, Dunn WD, Kent M, Preuss TM, Gutman DA. 2019 Significant neuroanatomical variation among domestic dog breeds. *J. Neurosci.* **39**, 7748–7758. (doi:10.1523/JNEUROSCI.0303-19.2019)
110. Turcsán B, Wallis L, Virányi Z, Range F, Müller CA, Huber L, Riemer S. 2018 Personality traits in companion dogs—results from the VIDOPET. *PLoS One* **13**, 1–27. (doi:10.1371/journal.pone.0195448)
111. Karl S, Boch M, Virányi Z, Lamm C, Huber L. 2020 Training pet dogs for eye-tracking and awake fMRI. *Behav. Res. Methods* **52**, 838–856. (doi:10.3758/s13428-019-01281-7)
112. Williams FJ, Mills DS, Guo K. 2011 Development of a head-mounted, eye-tracking system for dogs. *J. Neurosci. Methods* **194**, 259–265. (doi:10.1016/j.jneumeth.2010.10.022)
113. Pelgrim MH, Espinosa J, Buchsbaum D. 2023 Head-mounted mobile eye-tracking in the domestic dog: a new method. *Behav. Res. Methods* **55**, 1924–1941. (doi:10.3758/s13428-022-01907-3)
114. Correia-Caeiro C, Lawrence A, Abdelrahman A, Guo K, Mills D. 2023 How do children view and categorise human and dog facial expressions? *Dev. Sci.* **26**, e13332. (doi:10.1111/desc.13332)