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What smells? Gauging attention to olfaction in canine cognition research

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Abstract

One of the challenges of animal cognition research is overcoming anthropocentric sensory biases—in particular, favoring visual information and cues despite the dominance of other sensory cues in many nonhuman research subjects. As such, it is particularly important for animal cognition researchers to explicitly mention steps taken to control for and attend to the sensory world of their study species. Dogs are well known for their reliance on olfaction, but the extent to which dog cognition and behavior research accounts for olfactory cues or incorporates olfactory controls is unknown. With this bibliographic study, we reviewed canine research published in the past 10 years (2008–2018) in 13 scientific journals and coded the 481 resulting papers for mentions of olfactory or odor cues or controls. Our findings indicate that despite widespread acceptance of the significance of olfaction to dogs, scientific methodology rarely takes olfactory information processing into account. Finally, we propose a simple rubric of recommended reporting of olfactory information in research contexts, with the aims to help attune researchers to the *umwelt* of their study subjects, and to enhance the methodological reproducibility of canine cognition research.

Keywords Domestic dog · Cognition · Olfaction · Methodology · Reproducibility

Introduction

While technological advances have recently enabled researchers to examine animal behavior more closely within the animal—via methods from functional MRI in awake dogs (e.g., Andics et al. 2014; Berns et al. 2015) to two-photon miniature microscopes (Aharoni et al. 2019)—research design at times overlooks the significance of the sensory environments of subjects. Stimuli not perceptible or meaningful to the human researchers—such as smell, ultrasound or infrasound, or ultraviolet or infrared waves—may be at particular risk of being neglected. For instance, in the field of canine cognition (aka dog cognition), in many respects a subfield of comparative psychology (although not exclusively: some studies emerge from ethology or cognitive science, for instance), many of the methods that are employed were originally designed for understating non-canids—especially primates.

The field of canine cognition itself is relatively new: the number of published research papers on the topic of the cognitive abilities of dogs has grown dramatically in the last two decades (Bensky et al. 2013). Some methodological revisions appropriate to the different physiology and evolutionary history of domestic dogs have been made since the field's inception; these revisions use knowledge generated from previous studies—such as an awareness of the importance of the developmental histories, breeds, and training backgrounds of the dogs; and the influence of owner cues on dog behavior (e.g., Miklósi et al. 1998). There is growing awareness that even within the visual modality, the difference between dogs' perception and humans' is important to consider experimentally (Byosiere et al. 2018; Pongrácz et al. 2017). At the same time, given the sensitivity of dogs to odors (e.g., Walker et al. 2006) and significance of olfaction in dogs' perceptual experience (Gadbois and Reeve 2014; Horowitz and Hecht 2014), it is noteworthy that three-quarters of studies in canine cognition involve visual tasks (Bensky et al. 2013).

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As animal researchers acknowledge the importance of context in interpretation of behavior, this includes describing the context in a way sensitive to subjects' *umwelt* (Bekoff et al. 2002; Breed and Moore 2012; Horowitz and Hecht 2014; Partan and Marler 2002). In other words, regardless of the target of the investigation (visual discrimination, social cognition, personality, welfare, etc.), research can benefit from attending to and reporting on aspects of the primary sensory modalities of the species in question; for dogs, this means including an assessment of the olfactory environment. As highly salient perceptual information for dogs, odors have the potential to have an outsized influence on dog cognition—both in terms of what types of information dogs may be particularly skilled at processing and in terms of what types of information may be particularly distracting or confounding for dogs. Some work has reasoned that perceptual abilities of a tested species should be the focus of cognitive studies—especially when non-visual perception is integral to a species' behavior (Horowitz 2017). As yet, however, less attention has been drawn to the need for these perceptual abilities to be reflected in the methodological design and reporting, even when examining subjects' performance on non-olfactory tasks.

In this review, we aim to assess the current state of reporting olfactory cues in research in the field, and to suggest a new approach. Thus far, there has been little examination of how odor cues apart from food cues might affect dog behavior in testing environments. The result is a limited description of the experimental setting, at best, and the overlooking of a possible confound, at worst. While the smell of food is undoubtedly notable to dogs, what a human researcher perceives as the salient element of an odorant may not be what the dog perceives. Apart from the numerous examples of working dogs' abilities to detect odors that are seemingly imperceptible to the typical human nose, a straightforward description of odors as simply present or absent is defied by research. For instance, research has found that detection dogs do not alert to stimuli on which they have been trained, when they are combined with other stimuli (Lazarowski and Dorman 2014); further, performance can be lower when dogs have been trained on an odor chemically similar but non-identical to a target odor (Rice and Koziel 2015). In canine cognition research, possible non-food olfactory cues come from people present and recently absent, dogs who have previously been in the space, additions such as cleaning agents, and various exogenous sources. Odorants can serve as distraction, can be aversive, or can provide additional information to the dog unwanted and uncontrolled by the experimenter. Moreover, researchers describe that many dogs are unable to keep motivation through the trials; accounting for olfactory information in the experimental room may begin to give insight into reasons for attrition.

Researcher attention to the olfactory environment would reflect both a sensitivity to the relevance of stimuli to the subjects in the experiment, and would also serve a broader scientific goal: providing full details of the environment, presented stimuli, and subjects' history. Such reporting is critical to research reproducibility (Goodman et al. 2016) and results interpretation. Especially given the quasi-naturalistic nature of canine cognition studies—often involving owners or occurring in nontraditional lab spaces (such as outside)—reliable reporting of contextual information is needed if studies are to be repeated or extended.

Thus, the present research examines the degree to which studies of canine cognition report information about, or attempt to control, the olfactory environment presented to or encountered by subjects, regardless of whether olfaction is the target of the research question. We systematically review the literature in the field of canine cognition and behavior over the last decade, from 2008 until 2018, and note the reporting of any olfactory information in the studies: not only the acknowledgment of odor cues which may help to explain subject behavior, but also the means by which olfactory information was controlled, if it was.

Finally, we propose a straightforward rubric of recommended reporting of olfactory information, with the aim both to enhance the reproducibility of canine cognition research, and to help attune researchers to the *umwelt* of their study subjects.

Methods

Our search procedure was designed to track the identification of odorous cues or the use of odor controls in published studies of dog behavior and cognition over the last decade. We searched in 13 journals which could account for the majority of the published results in the field: *Animal Behaviour*, *Animal Cognition*, *Applied Animal Behavior Science*, *Behaviour*, *Behavioural Processes*, *Current Biology*, *International Journal of Comparative Psychology*, *Journal of Comparative Psychology*, *Journal of Veterinary Behavior*, *Learning & Behavior*, *Physiology and Behavior*, *PLoS One*, and *Science*. Other notable journals were surveyed but excluded if they did not contain original empirical material (*Nature*; *Neuroscience and Biobehavioral Reviews*); or if their full text was not reliably accessible in the Columbia University database (*Animal Welfare*; *Anthrozöos*). Within the 13 journals, single articles were eliminated if they were not in the scope of this review, including articles that discussed dogs but were nonetheless about other canids; articles that were biomedical, not social-science, in nature; and review papers.

Search years were 2008 through the end of 2017; we completed the searches by September, 2018. The journals were

surveyed via global searches, to identify publications on the topic of dog cognition or behavior, then refined by more selective searches. An initial search for all papers with "dog" or "dogs" in the title yielded many papers not about dog behavior; additional hand-checking eliminated those which did not include either "domestic dog", "*Canis familiaris*" (or "*Canis lupus familiaris*"), or "pet dog" in the body of the paper. The resultant papers were then searched for use of "olfactory" or "odor" as well as "cue" or "control"; the latter restrictions wound up being redundant, and we just searched for "olfactory" or "odor". After spot-checking the success of the search terms, the variants "odour" and "smell" were added. In addition, we characterized whether the study asked a question of subjects' olfactory perception or not, as represented in their title and abstract.

Results

Across the journals, we found 481 articles that met our criteria (Fig. 1). Publications in these journals on the topic of dog cognition or behavior have increased over the past 10 years (linear least-squares estimates (LLS): $\beta = 4.54$, $t(8) = 5.11$, $p < 0.001$; Fig. 2a). However, there has not been a corresponding increase in the number of dog papers mentioning odor or olfactory cues or controls [LLS: $\beta = 0.25$, $t(8) = 1.14$, $p > 0.2$]. This pattern means that relative to the total number of papers, the proportion of dog research considering olfactory information has remained consistently low over the decade of this survey [LLS: $\beta = -0.99$, $t(8) = 1.64$, $p > 0.1$; Fig. 2b].

Relatedly, there has not been a substantial increase in the number of publications studying olfaction [LLS: $\beta = 0.24$, $t(8) = 1.62$, $p > 0.1$], such that relative to the total number of papers, the proportion of dog research studying olfaction has remained consistently low [LLS: $\beta = 0.21$, $t(8) = 0.60$, $p > 0.5$; Fig. 2c].

Publications reporting research focused on olfactory stimuli, either partially or primarily, more often mentioned odor cues and controls (in terms of raw percentages). Still, rates were quite low across both study types; the difference between olfactory and non-olfactory research in reporting trends did not reach statistical significance (non-olfactory studies: 15%; olfactory studies: 28%; generalized linear model with a logit link and binomial error distribution (logistic regression) for presence (1) vs. absence (0) of a study reporting olfactory control: $z = 1.45$, $p > 0.1$; Fig. 3a).

Moreover, of the papers that made any mention of controlling for odor, in 25% of the cases (19 of 75 cases), it was only mentioned in the Introduction or Discussion sections of the paper, not in the Methods (Fig. 3b). Extra-method mentions were more likely to be allusions to the role of odor in dogs' lives, or statements about the perceived effect of odor in the study.

Discussion

The present review of the literature over the last decade finds that in studies of canine cognition, very little information about odorous cues or the olfactory environment is reported. Despite a widespread acknowledgement of the importance of olfaction to dogs, research has largely neglected addressing this dimension of their experience in the experimental setting. As the number of dog-cognition papers published each year has increased, the relative number of papers mentioning any aspect of the olfactory environment of the studies has slightly decreased. The percentage of published papers investigating subject response to odorous stimuli has

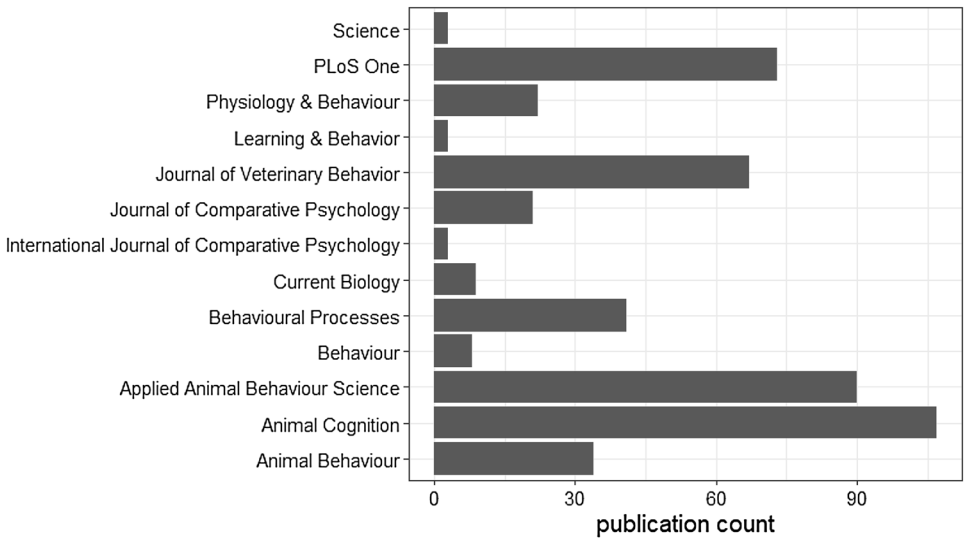

Fig. 1 Dog publications (2008–2017) by journal. Searching 13 top journals for publications on dogs yielded 481 articles for analysis. Most of these articles were published in *Animal Cognition* ($n = 107$), *Applied Animal Behaviour Science* ($n = 90$), or *PLoS One* ($n = 73$)

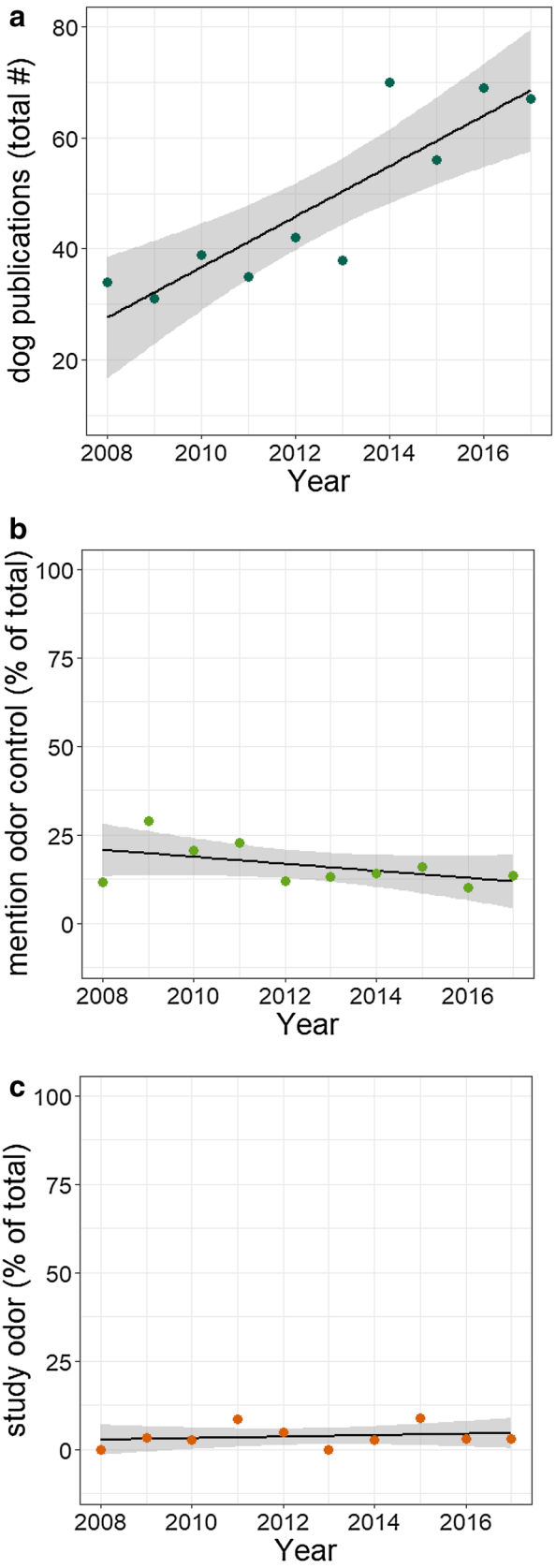

Fig. 2 Dog publications trends over time. During our search period (2008–2017), **a** the number of dog publications increased significantly ($p < 0.001$), but **b** the proportion of articles mentioning odor/olfactory controls/cues remained consistently low, as did **c** the proportion of articles investigating olfaction

remained steadily low, less than four percent of the published research.

Even when olfactory information was mentioned, a quarter of the time it was not in the Methods sections, but in the Introduction or Discussion sections of the paper—usually as recognition that olfaction could have played a role in the results, or as an assertion that it could not have. Such low reporting of olfactory cues or description of odor controls is perhaps not surprising, given the origins and motivations of the field in comparative studies, interested in how dogs fit in human society. As visually oriented animals, it may be challenging for humans to consider olfactory information in study design. Human beings are more inclined to think of the visual elements of a scene, not the odorous elements (Batty 2010). Researchers' accounting for the olfactory reality of an experimental setting is, thus, impoverished.

The limits of human reckoning with the olfactory nature of a context are apparent on closer examination of the 56 mentions of olfactory cues or controls that did arise in Methods sections. Frequently, mentions of olfactory cues were of food cues: typically, the food used in the experimental design. As also observed by Bensky et al. (2013), researchers reported various strategies to attempt to control for food cues, such as putting all apparatus in contact with food (Riedel et al. 2008), smearing containers with "abundant liver" (Barrera et al. 2015; Elgier et al. 2009) or other food (Carballo et al. 2015; Hegedüs et al. 2013), hiding food under a false-bottom (Carballo et al. 2017; Hauser et al. 2011), and not washing bowls to keep odor cues (Walker et al. 2014). Relatedly, the notion that the only olfactory cues might come from food is on display in studies that claim that by using still images (Yong and Ruffman 2015), or photographs (Nagasawa et al. 2011), any and all olfactory cues were controlled for.

A number of surveyed papers cite previous research in which dog subjects did not use olfactory cues (such as Bräuer et al. 2006; Szetei et al. 2003) to dismiss the possibility that olfaction could be a part of the subjects' experience of the task. In these studies, dogs were less likely to use olfactory cues in solving certain tasks when familiar visual communicative cues from humans were available. It is important to note that in these cases, the only olfactory cue controlled for was food odor, a narrow band of animals' sensory experience (Nielsen 2018), and the task was very narrow (object-choice). And as Szetei et al. (2003) demonstrated, dogs did use olfactory cues to solve the problem when needed. However, it is premature to thus claim that

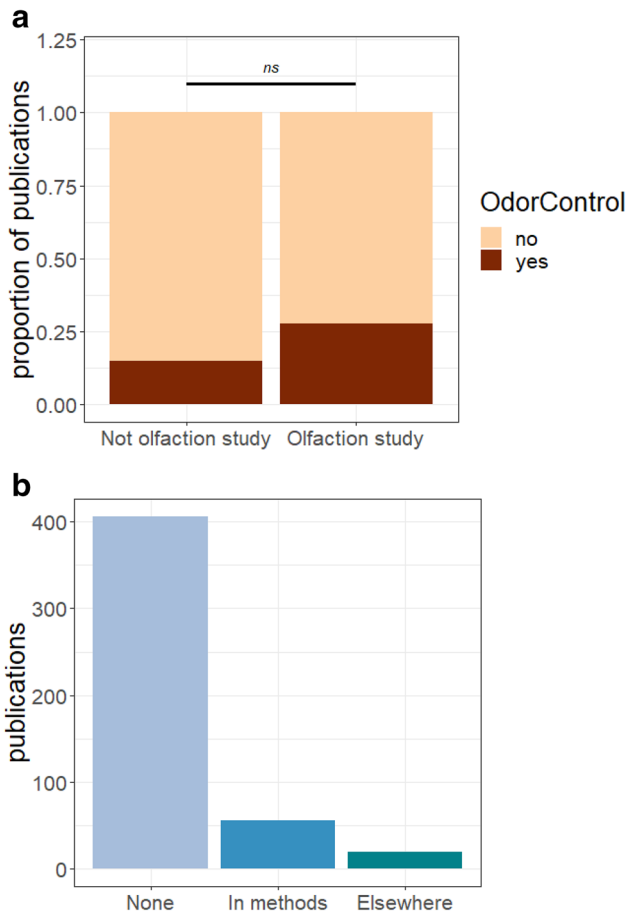

Fig. 3 Odor control by study type and location within the article. **a** Dog publications investigating olfaction mentioned odor controls at an equivalently low rate as dog publications on other subjects (28% and 15% for odor vs. non-odor studies, respectively; $p > 0.1$). **b** The majority of publications did not mention controlling for odor anywhere in the article ($n = 406$). Moreover, among the publications that did mention odor control somewhere in the article ($n = 75$), not all of them included odor control information in the Methods section, with several papers referring to odor control/cues elsewhere in the paper (e.g., the Abstract or Discussion), but not in the Methods ($n = 19$)

olfactory cues have thus been "ruled out" (e.g., Bray et al. 2014), as this implies both that dogs' behavior on that task can be generalized to all tasks, and also the only olfactory cue possible is the one that the human experimenter intentionally provides. If that were the case, of course, detection dogs would be out of a job.

Notably, even the approaches to controlling food cues are not standardized, and appear to represent researchers' intuition about the equivalence of odors. If a truly identical quantity of a food reward is used in different contexts, that intuition may be justified; however, when a different quantity of food—such as a "smear"—is used, it is suspect: research has found that dogs discriminate food quantities (Ward and Smuts 2007), and attend longer to a covered plate with five times the food of a second plate (Horowitz et al. 2013), even if they do not approach it significantly more often.

A few surveyed studies did go beyond food smells in considering the olfactory information in their experiments. For instance, in some cases the protocol required that experimenters or owners touch all parts of the equipment (Fugazza and Miklósi 2014; Fugazza et al. 2017; Pongrácz et al. 2012). Another applied the saliva of dog demonstrators and observers to the experimental apparatus, in order to control canine scent cues (Miller et al. 2009). In another study, Polgár et al. (2015) found that pet dogs did not always use olfaction as a strategy in search tasks, sometimes using other cognitive strategies—highlighting the need to understand all elements of dogs' *umwelt* in problem-solving. Given the relevance of dog and human odor for dogs (e.g., Berns et al. 2015; Hepper 1988; Nielsen et al. 2015), these approaches are appropriate and recommended.

There are some limitations to our findings of the field's reporting of olfactory information. Search methods could generate false-positives when the search terms were used to describe general species behavior, rather than olfaction's relevance in an experimental setting. In other cases, the search terms may not have captured mentions when less common synonyms for olfaction were used in the publication.

Relatedly, it should be noted that in some cases a mention of a control condition related to odor cues was mentioned in the Discussion section, but not described in the Methods. Such a finding supports, rather than undermining, our suggestion that more reliable reporting of the specifics of the olfactory context is due.

An olfactory proposal

Both for reasons of fully describing subject experience, and for reasons of reproducibility, we recommend increased attention to the presence of odors—even while we are agnostic about exactly how odor might alter or affect dogs' behavior in experimental studies (if at all). Regardless of the type of study (e.g., visually or olfactory-based), there are many kinds of contextual information that may be relevant. For example, researchers could include details about attempts to control variation in ambient odors. Similarly, information about the (unintended) odor properties of presented stimuli could be provided: is there any mention of attempts to ensure that odor is identical for each stimulus. When the stimuli are themselves odorous, but the task is a visual task, is any mention made of an attempt to ensure that stimuli- or non-stimuli odors are not the means by which the subject made a choice or the motivation for subject behavioral performance. In studies manipulating olfactory stimuli, information about the relative strengths of odors and the traces left by the stimuli is apt.

In view of the dearth of attention to olfaction in methodologies involving a species which uses olfaction, field practices and guidelines may be of value. With this in mind, we propose that research in canine cognition consider a characterization of some of the odorous elements present in experimental contexts along the following dimensions:

- *Stimuli odors* What odors are presented to the subjects? Report on odors of stimuli containers or objects, and any attempt to match odor; if food is used, include a precise measurement of how much food is used and the temperatures thereof, as temperature affects volatility of food and olfactory detection (e.g., Amerine et al. 1965). Given dogs' sensitivity to quantity (Ward and Smuts 2007), simply smearing the scent on a control stimulus, or placing and removing the food odor, is not adequate odor control. Stimuli containers and objects encountered en route to stimuli should be of the same material; if odor differences are suspected, a separate control test could be run with subjects with just the containers.
- *Mortals and mongrels* Social odors are known to be highly salient for dogs (Nielsen et al. 2015); chemosignals have been found to provide information between people and dogs (D'Aniello et al. 2018). Identify the odors of people and any other dogs in the environment, including the traces of biological matter left by past people and dogs.
- *Environmental conditions* Environmental conditions affect the movement and creation of odors, and thus directly affect olfaction (Jenkins et al. 2018). Keep a record of the temperature and humidity levels of the experimental room; if possible, include a measure of the "headspace" or rate of air flow in the experimental context. While room ambient temperature does not strongly affect human odor perception, dogs' ability of perceive odors is strongly affected by humidity and temperature: acuity rises in higher humidity, but with heat, which induces panting, olfaction is compromised (Jenkins et al. 2018). Ideally, temperature and humidity levels will be the same across subjects and trials.
- *Lab description and use* Include a description of lab floor surface; the presence or absence of windows/doors/vents which could permit airflow; and other uses to which the room is put. Dogs can detect odors on surfaces and on plumes of air; in animals whose olfactory navigational or mate-finding behavior is well studied, such as pigeons and moths, the movement of air strongly affects their behavior (Bau and Cardé 2015; Gagliardo 2013). While not studied with dogs in experimental tasks, this information could help inform the effects of air flow on dog behavior. Similar suggestions have been made of handlers working with detection dogs (Reed et al. 2011).
- *Lingering odors* Is there a cleaning process between subjects or trials? Describe what is used and how is it applied. One common cleaner, ammonia, has been shown to be aversive and to affect olfaction in many housed animal species (Nielsen 2018). Dogs more often choose to forsake a larger quantity of highly desired food for a smaller quantity when the larger quantity is presented on a plate which has been scented with common odorants, including lavender, mint, and vinegar (Horowitz et al. 2013). Consistency in cleaning practices will help standardization of methods across studies.

These elements (acronym SMELL) cover the best-known sources of odors relevant to the subjects; characterization thereof would be relatively straightforward. Reliable reporting of SMELL sources would represent the kind of methodological hygiene necessary for the kind of repetition and replication of research that is the backbone of science (Goodman et al. 2016). Complete application of the rubric may not apply to every study—for instance, research in owners' homes or outdoors, where identification of odor sources is impracticable. In all cases, best practices would include identification of the various outlined parameters, appropriate matching of conditions across subjects and trials, and avoidance of any odors known to strongly affect (adversely or otherwise) behavior, insofar as it is possible.

In canine cognition, improvements in researcher attention to and communication about various aspects of their methods are not commensurate with the growth of knowledge about the significance of various stimuli to dogs. Of course, dogs are not exclusively olfactory; and some research results point to the real possibility that in domestication itself changed the species to be more visually centered, to better fit in the anthropogenic environment. Certainly, as has been demonstrated, dogs can use both visual and olfactory means of problem-solving (Polgár et al. 2015). Still, given the dearth of attention to odor environments, more is due. To suggest that olfactory cues should be noted is only to acknowledge dogs' sensory abilities; exactly what effect they may have is an empirical question, which will be determined if the olfactory environment begins to be regularly described in research. With SMELL, it is our aim to not only enhance the methodological reproducibility of canine cognition research, but also to help researchers attend to the perceptual abilities of their study subject and thereby stimulate new discoveries that would not be possible by applying visually focused methodology to an olfactorily skilled species. Indeed, with reliable reporting of these elements researchers may gain useful information about one of the more mysterious of their subjects' perceptual experience: the role of olfaction in cognition.

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest.

Dataset The datasets generated during and analyzed in the current study are available from the corresponding author upon reasonable request.

References

Aharoni D, Khakh BS, Silva AJ, Golshani P (2019) All the light that we can see: a new era in miniaturized microscopy. Nat Methods 16:11–13

Amerine MA, Pangborn RV, Roesssler EB (1965) Principles of sensory evaluation of food. Academic Press, New York

Andics A, Gácsi M, Farago T, Kis A, Miklosi Á (2014) Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. Curr Biol 24:574–578

Barrera G, Fagnani J, Carballo F, Giamal Y, Bentosela M (2015) Effects of learning on social and nonsocial behaviors during a problem-solving task in shelter and pet dogs. J Vet Behav 10:307–314

Batty C (2010) A representational account of olfactory experience. Can J Philos 40:511–538

Bau J, Cardé RT (2015) Modeling optimal strategies for finding a resource-linked, windborne odor plume: theories, robotics, and biomimetic lessons from flying insects. Integr Comp Biol 55:461–477

Bekoff M, Allen C, Burghardt GM (2002) The cognitive animal. MIT Press, Cambridge

Bensky M, Gosling SD, Sinn DL (2013) The world from a dog's point of view: a review and synthesis of dog cognition research. Adv Study Behav 45:209–406

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 Proc 110:37–46

Bräuer J, Kaminski J, Riedel J, Call J, Tomasello M (2006) Making inferences about the location of hidden food: social dog causal ape. J Comp Psychol 120:38–47

Bray EE, MacLean EL, Hare BA (2014) Context specificity of inhibitory control in dogs. Anim Cogn 17:15–31

Breed MD, Moore J (2012) Animal behavior. Academic Press, Boston

Byosiere S-E, Chouinard PA, Howell TJ, Bennett PC (2018) What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. Psychonom Bull Rev 25:1798–1813

Carballo F, Freidin E, Putrino N, Shimabukuro C, Casanave E, Bentosela M (2015) Dog's discrimination of human selfish and generous attitudes: the role of individual recognition experience and experimenters' gender. PLoS One 10:e0116314

Carballo F, Freidin E, Casanave EB, Bentosela M (2017) Dogs' recognition of human selfish and generous attitudes requires little but critical experience with people. PLoS One 12:e0185696

D'Aniello B, Semin GR, Alterisio A, Aria M, Scandurra A (2018) Interspecies transmission of emotional information via chemosignals: from humans to dogs (*Canis lupus familiaris*). Anim Cogn 21:67–78

Elgier AM, Jakovcevic A, Mustaca AE, Bentosela M (2009) Learning and owner-stranger effects on interspecific communication in domestic dogs (*Canis familiaris*). Behav Proc 81:44–49

Fugazza C, Miklósi Á (2014) Deferred imitation and declarative memory in domestic dogs. Anim Cogn 17:237–247

Fugazza C, Mongillo P, Marinelli L (2017) Sex differences in dogs' social learning of spatial information. Anim Cogn 20:789–794

Gadbois S, Reeve C (2014) Canine olfaction: scent sign and situation. In: Horowitz A (ed) Domestic dog cognition and behavior: the scientific study of *Canis familiaris*. Springer, Berlin, pp 3–29

Gagliardo A (2013) Forty years of olfactory navigation in birds. J Exp Biol 216:2165–2171

Goodman SN, Fanelli D, Ioannidis JPA (2016) What does research reproducibility mean? Sci Transl Med 8:1–6. https://doi.org/10.1126/scitranslmedaaf5027

Hauser MD, Comins JA, Pytka LM, Cahill DP, Velez-Calderon S (2011) What experimental experience affects dogs' comprehension of human communicative actions? Behav Proc 86:7–20

Hegedüs D, Bálint A, Miklósi Á, Pongrácz P (2013) Owners fail to influence the choices of dogs in a two-choice visual pointing task. Behav 150:427–443

Hepper PG (1988) The discrimination of human odor by the dog. Perception 17:549–554

Horowitz A (2017) Smelling themselves: dogs investigate their own odours longer when modified in an "olfactory mirror" test. Behav Proc 143C:17–24

Horowitz A, Hecht J (2014) Looking at dogs: Moving from anthropocentrism to canid umwelt. In: Horowitz A (ed) Domestic dog cognition and behavior: the scientific study of *Canis familiaris*. Springer, Berlin, pp 201–219

Horowitz A, Hecht J, Dedrick A (2013) Smelling more or less: investigating the olfactory experience of the domestic dog. Learn Motiv 44:207–217

Jenkins EK, DeChant MT, Perry EB (2018) When the nose doesn't know: canine olfactory function associated with health management and potential links to microbiota. Front Vet Sci 5:56

Lazarowski L, Dorman DC (2014) Explosives detection by military working dogs: olfactory generalization from components to mixtures. Appl Anim Behav Sci 151:84–93

Miklósi Á, Polgárdi R, Topál J, Csányi V (1998) Use of experimenter-given cues in dogs. Anim Cogn 1:113–121

Miller HC, Rayburn-Reeves R, Zentall TR (2009) Imitation and emulation by dogs using a bidirectional control procedure. Behav Proc 80:109–114

Nagasawa M, Murai K, Mogi K, Kikusui T (2011) Dogs can discriminate human smiling faces from blank expressions. Anim Cognit 14:525-533

Nielsen B (2018) Making sense of it all: the importance of taking into account the sensory abilities of animals in their housing and management. Appl Anim Behav Sci 205:175–180

Nielsen BL, Jezierski T, Bolhuis JE, Amo L, Rosell F, Oostindjer M, Christensen JW, McKeegan D, Wells DL, Hepper P (2015) Olfaction: an overlooked sensory modality in applied ethology and animal welfare. Front Vet Sci 2:69. https://doi.org/10.3389/fvets201500069

Partan S, Marler P (2002) The Umwelt and its relevance to animal communication: introduction to special issue. J Comp Psychol 116(2):116–119

Polgár Z, Miklósi Á, Gácsi M (2015) Strategies used by pet dogs for solving olfaction-based problems at various distances. PLoS One 10(7):e0131610

Pongrácz P, Bánhegyi P, Miklósi Á (2012) When rank counts—dominant dogs learn better from a human demonstrator in a two-action test. Behaviour 149:111–132

Pongrácz P, Ujvári V, Faragó T, Miklósi Á, Péter A (2017) Do you see what I see? The difference between dog and human visual

perception may affect the outcome of experiments. Behav Proc 140:53–60

Reed SE, Bidlack AL, Hurt A, Getz WM (2011) Detection distance and environmental factors in conservation detection dog surveys. J Wildl Manag 75:243–251

Rice S, Koziel JA (2015) The relationship between chemical concentration and odor activity value explains the inconsistency in making a comprehensive surrogate scent training tool representative of illicit drugs. Forensic Sci Int 257:257–270

Riedel J, Schumann K, Kaminski J, Call J, Tomasello M (2008) The early ontogeny of human–dog communication. Anim Behav 75:1003–1014

Szetei V, Miklósi Á, Topál J, Csányi V (2003) When dogs seem to lose their nose: an investigation on the use of visual and olfactory cues in communicative context between dog and owner. Appl Anim Behav Sci 83:141–152

Walker DB, Walker JC, Cavnar PJ, Taylor JL, Pickel DH, Hall SB, Suarez JC (2006) Naturalistic quantification of canine olfactory sensitivity. Appl Anim Behav Sci 97:241–254

Walker JK, Waran NK, Phillips CJC (2014) The effect of conspecific removal on the behaviour and physiology of pair-housed shelter dogs. Appl Anim Behav Sci 148:46–56

Ward C, Smuts B (2007) Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). Anim Cogn 10:71–80

Yong MH, Ruffman T (2015) Domestic dogs match human male voices to faces, but not for females. Behav 152:1585–1600