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Performance of domestic dogs on an olfactory discrimination of a homologous series of alcohols

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ABSTRACT

Dogs are deployed for the detection of a wide variety of chemical stimuli. Despite their wide use, little basic research has explored canine olfactory generalization and discrimination. In the present study, we assessed canine odor discrimination amongst a series of chemically-related aliphatic alcohols. Domestic dogs were trained to discriminate 1-pentanol from air in a two-choice operant discrimination procedure until reaching an 85% accuracy criterion. In a series of transfer tasks, we assessed dogs' generalization and discrimination between related odorants by replacing the S^- stimulus with an alcohol related to pentanol, differing only in the length of the carbon chain. Dogs showed an increase in discrimination performance with an increase in the difference in the number of carbon atoms between pentanol and the comparison alcohol ($p < 0.001$). These results indicate that this graded series of alcohols may be a useful stimulus set for studying olfactory generalization and discrimination processes in dogs, and that dogs show the same relationship between chemical similarity and discrimination performance as has been observed with humans, monkeys, honeybees, elephants, and rats.

1. Introduction

Dogs are thought to have keen olfactory capabilities, making them useful for the detection of chemical stimuli. They have been deployed globally to match police suspects by odor (Schoon and Haak, 2002), detect narcotics (Dean, 1972), detect explosives (Goldblatt et al., 2009), or even to detect wildlife (Duggan et al., 2011; Long et al., 2007). Despite their wide range of use and importance, there is little basic research exploring canine olfactory discrimination abilities.

Some basic research has explored dogs' threshold detection for a limited range of odorants (see Passe and Walker, 1985). In particular, however, little basic science has explored dogs' ability to discriminate between odorants. Some applied research has indicated that dogs are capable of discriminating complex odor profiles, such as discriminating between human identical twins (Hepper, 1988; Kalmus, 1955; Pinc et al., 2011). However, no basic science has explored dogs' ability to discriminate monomolecular stimuli of known chemical structure.

Several studies have attempted to characterize the relationship between chemical structure and the perceptual quality of odorants in other species. One apparent relationship is a link between odor similarity and chemical structure of homologous odorants with the same functional group, differing only in the number of carbon atoms in the carbon chain. In general, the greater the difference between two odorants in the length of their carbon chains, the more different the two odorants tend to be perceived. This general phenomenon has been demonstrated in humans (Laska and Teubner, 1998), several species of monkeys (Laska and Freyer, 1997; Laska and Seibt, 2002; Laska and Teubner, 1998), honeybees (Laska et al., 1999), Fisher 344 rats (Yoder et al., 2014), Sprague–Dawley rats (Cleland et al., 2002), and elephants (Arvidsson et al., 2012; Rizvanovic et al., 2013).

Interestingly, this finding does not generalize to all species or chemical classes. For example, CD1 mice showed this chemical structure similarity-discrimination performance correlation for *n*-acetic esters and 2-ketones, but not with 1-alcohols, *n*-aldehydes or *n*-carboxylic acids (Laska et al., 2008). Similarly, South African fur seals only showed a trend correlation between odorant structure and perception for 1-alcohols, and no significant correlation between structure and perception for any of the other four classes of odorants tested (Laska et al., 2010). Thus, there appear to be species differences across this chemical structure-perception relationship that may even depend on the class of odorants (Laska et al., 2010).

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Table 1
Subject information. Table gives the age (in years), sex, sexual status (intact or altered), and breed for each subject.

Subject	Age	Sex	Status	Breed
Bessa	5	Female	Spayed	Lab Mix*
Rowdy	~5	Male	Neutered	Chihuahua*
Joey	~3	Male	Neutered	Lab Mix*
Paco	3	Male	Intact	Yorkshire Terrier
Rex	~4	Male	Neutered	Pit-bull Mix*
Ben	~2	Male	Neutered	Rhodesian Ridgeback Mix*

~ Indicates the age was estimated from the adoption agency, and is not known exactly.
* Indicates the breed was estimated by the adoption agency.

Table 2
Odorants and dilutions. Table shows the S- odorant used, the dilution used, the differences in carbon chain length and CAS#. Pentanol (CAS# 71-41-0) was diluted to 0.1% v/v.

Odorant	Concentration (v/v in Mineral oil)	$|\Delta C|$	CAS #
Ethanol	0.1%	3	64-17-5
Propanol	0.1%	2	71-23-8
Butanol	0.1%	1	71-36-3
Hexanol	0.3%	1	111-27-3
Heptanol	2.0%	2	111-70-6
Octanol	4.0%	3	111-87-5

$|\Delta C|$ indicates the absolute value of the difference in carbons between the odorant and pentanol. Purity for all odorants was greater than 99% and odorants were obtained from Sigma Aldrich.

Despite the diversity of species that have been tested for a relationship between the difference in the length of the carbon chain and odor perception, we have found no reports on this phenomenon in dogs. The aim of the present study was to assess whether dogs show a chemical structure-perception relationship amongst homologous odorants that only differ in the length of the carbon chain.

There were two main motivations for this study. The first was to extend the species generality of this chemical structure-perception relationship to dogs. The second aim was to develop a stimulus set of known perceptual similarity that could be used for the study of generalization and discrimination processes in dogs. Dogs are an important applied detection tool. Their performance is dependent on their ability to discriminate between target and non-target odors and also to generalize among similar odors that are exemplars of the target. For example, Lazarowski and Dorman (2014) showed that dogs trained to a pure explosive component (potassium chlorate) failed to generalize to mixtures containing this component. Thus, understanding processes that relate to olfactory discrimination and generalization could have important applied implications. Unfortunately, however, it is difficult to develop basic studies of generalization and discrimination with complex odor mixtures, such as explosives, because determining the *a priori* perceptual similarity prior to an experimental manipulation of these complex mixtures is difficult. The development of a stimulus set of known perceptual quality for dogs could be useful for future studies looking at olfactory generalization and discrimination.

In the present study, we tested dogs' discrimination of a homologous series of alcohols. Domestic dogs were trained in a two-choice operant task to alert to a five-carbon alcohol (pentanol). The dogs were then transferred to a task in which they were required to discriminate pentanol from homologous alcohols differing by 1, 2, or 3 carbons from pentanol. Accuracy was used as an index of similarity between the two odorants presented.

2. Methods

2.1. Subjects

Six companion-animal domestic dogs were recruited for the present study. Dogs were household pets and were tested in the owners' homes, during times convenient for the owner. Five dogs had previously participated in studies in which they were trained on an odor discrimination task to dig in a bin of pine shavings containing a cotton pad with a target odorant. All dogs, however, were, to the best of our and their owners' knowledge, naïve to the odorants used in the present study. Information on the age, sex and breed of the dogs are presented in Table 1. All procedures were approved by the University of Florida Institutional Animal Care and Use Committee.

2.2. Odorants

Table 2 indicates the odorants used and their v/v dilutions in mineral oil; mineral oil is a common diluent in olfactory studies. Pentanol was diluted to 0.1% v/v. Prior research has used a range alcohol concentrations in mineral oil or diethyl phthalate; elephants: 10% v/v (Rizvanovic et al., 2013), fur seals: 10% v/v (Laska et al., 2010), humans: ~1% v/v (Laska and Teubner, 1999), CD-1 mice: 0.0001% v/v (Laska et al., 2008), Fisher 344 rats: 0.0001% v/v (Yoder et al., 2014). We selected 0.1% as it was well within the range of concentrations used in previous studies. Odorant dilutions for the remaining odorants were informed by odorant vapor pressures, obtained from PubChem (pubchem.ncbi.nlm.nih.gov). Because the shorter chained alcohols such as ethanol have a higher vapor pressure (59 mmHg at 25 °C), compared to the longer chain alcohols such as octanol (0.079 mmHg at 25 °C), we diluted the shorter chain alcohols more than the longer chain alcohols. The minimum concentration used for this study was 0.1% (see Table 2). For the longer chain alcohols, the concentration was increased so that the theoretical partial pressure of the odorant was near approximately 0.01 mmHg at 25° C (ranging from 0.008–0.012 mmHg). The partial pressure for butanol, propanol and ethanol were higher, ranging from approximately 0.03–0.43 mmHg. In calculations, we assumed the molecular weight for mineral oil to be 335 g/mol, that the odorants were miscible with mineral oil, and that the partial pressures of the odorant was the product of the pure odorant vapor pressure and the mole fraction of the odorant.

2.3. Odorant presentation

Dogs were trained to alert to pentanol using a custom built two-choice odor delivery device. The device contained two odor ports in which one port delivered the S- odorant while the other delivered the S+ (pentanol). Olfactory stimuli were created by delivering a stream of air from an air pump, to a manifold containing a series of calibrated needle valves to regulate each line to a flow rate of 0.5 l/min and solenoid valves to control directional flow. When a valve was activated via a relay controller board (Numato Laboratories™, Bangalore, India), the headspace of the odorant saturation bottle (750 ml glass jar) was delivered to the odor port to which it was connected at a rate of 0.5 l/min, where it was mixed with a continuous air stream of 0.5 l/min. The final mixture (a nominal 50% air dilution of the odorant) then entered a standard PVC tube (Nominal size: 1.5") with a 5 × 5 cm opening where the dog could sniff to sample the air stream. The physical dimensions of, and airflow rates in, both odor ports were identical and were continuously exhausted via a connected T-junction that was fitted with an exhaust fan. The odor ports were suspended 5 cm above the ground by two bins with pine shavings. The bins provided support for the odor ports but also provided a substance the dogs could alert to by scratching or digging to indicate the target odor.

Tubing was composed of polyethylene (1/4" ID Tubing) for its chemical resistance and availability. Odorants were held in glass saturation jars with polyethylene lids. There was 35 cm of ¼" ID tubing running from the saturation jars to the odor port, yielding a dead volume of approximately 11 cm^3. To insure accuracy, the flow rates of each air stream were calibrated prior to each session using a variable area flowmeter (Dwyer™ OMA-1).

2.4. Training

Dogs were first trained to approach the bins and PVC tubing and to root or paw in the pine shavings or at the PVC tube. The pine shavings provided a simple substrate which the dogs could manipulate to indicate a response (see Hall et al., 2013). Once the dogs successfully responded to the bins, they were then shaped to sniff at the odor port (which was suspended 5 cm above the shavings). Once dogs reliably sniffed at an odor port and responded to a bin, they were trained to respond only to the odor port containing pentanol and not the alternative port that contained the diluent odorant (mineral oil).

Each training session consisted of 40 discrimination trials and each trial started with the handler holding the dog back from the odor ports approximately 1 m. All experimental parameters and stimulus presentations, via activation of the solenoid valves, were under computer control. Each trial was initiated by activation of the solenoids to present the S^+ odorant to one port and the S^- odorant to the other port. The computer then printed, "Start", and prompted the handler to release the dog, without telling him which odor port contained pentanol (i.e., the handler was always blind to the correct response). The trial order, and whether the S^+ or S^- was at the left port or right port, was determined pseudo-randomly so the left port and right port were each correct 50% of the time, and the same port was not correct for more than two trials in a row.

After the dog was released, the handler waited for the dog to respond. Once the dog responded, the handler entered the dog's choice in the computer, which provided feedback to the handler as to whether the choice was correct or incorrect. Correct responses were reinforced by the handler saying, "good dog," and delivering a commercial dog treat. Incorrect responses simply led to the dog being called back to wait for the next trial without a treat. It took approximately 3 s for the handler to enter the choice in the computer and deliver the appropriate consequence for a response. The inter-trial-interval was 10s to insure odorants were cleared before starting the next trial. If a dog failed to respond within 30s of the start of a trial, a 'no choice' was scored and coded as incorrect.

To facilitate training, two additional contingencies were in place to prevent side biases or dogs failing to participate. If a dog chose the same odor port for four trials in a row (e.g., chose left for 4 consecutive trials), and that trial was an error (left was incorrect), a correction trial was run to inhibit side biases (repeatedly choosing left). During this trial, the dog was guided to the alternative side (where pentanol was present), and reinforced for responding to that side. If, during training, a dog made three incorrect choices in a row or failed to respond for two trials in a row, two "motivation" trials were conducted. In these trials, the handler guided the dog to the correct, pentanol port, to prevent an incorrect response and delivered a reinforcer. The dog was then walked back to the start location and the computer then switched the pentanol to the alternative side. The dog was then walked to this side and was delivered another reinforcer. These trials insured the dog was motivated to participate.

After every six training trials a control trial was conducted to test whether the dogs were potentially following audible "clicks" from the solenoids or other unintended stimuli. Although the solenoids were arranged closely together in an overlapping fashion to reduce the use of the sound of a solenoid valve as a response cue, dogs could have theoretically used subtle cues to identify the correct response. To test this, control trials, which were identical to training trials except that the solenoids were only activated for a fraction of second before being closed again. This produced the audible click associated with turning on the solenoid valve (movement of the plunger), but by the time the dog could approach the odor ports there would be insufficient odorant to guide choice. If dogs responded to the "correct" port, they were reinforced identically as during non-control trials. If dogs could utilize auditory cues from the activation of solenoids connected to the S^+ odorant, we expected they would be able to maintain above chance performance on control trials as these same solenoids are activated on these control trials. If, however, the subjects could not perform above chance on control trials, this would indicate that they were responding to the olfactory stimuli.

2.5. Testing

Dogs were trained on the pentanol vs. diluent (mineral oil) discrimination until reaching an 85% correct accuracy criterion in two consecutive sessions of 40 trials before moving on to testing. During testing, all procedures were identical to training, except that for each session, the S^- odorant was replaced with one of the six odorants in Table 2. In principle, the more perceptually similar the S^- was to pentanol, the more likely the subjects would be to make discrimination errors, than would be the case for a perceptually dissimilar S^-. After the dogs completed one session with each S^- odorant, they were given a brief re-training phase of pentanol vs. diluent alone until again reaching the 85% criterion, followed by a second block of testing in which one session was again conducted with each S^- odorant. The order of S^- presentation was counterbalanced across dogs.

2.6. Intensity control

Although the odorant dilutions were adjusted based on vapor pressures, this does not necessarily indicate each odorant was perceived with equal intensity. Vapor pressure describes the relationship between the odorants condensed phase and vapor phase. Intensity perception can vary across subjects and odorants. Thus, presenting two odorants at identical vapor concentrations does not imply they will be perceived at identical intensity. To test whether dogs were potentially using odorant intensity as a cue in the present study, rather than odorant quality, we conducted an additional test with four dogs at the conclusion of the study. They were presented with a more difficult discrimination (butanol vs. pentanol) using either the dilution level in the main study (0.1%) or a dilution 10 times greater (1%) for either the S^+ or S^-. Thus, these dogs received an additional three sessions in which butanol and pentanol were both diluted to 0.1%, butanol was diluted to 1% and pentanol to 0.1%, or pentanol was 1% and butanol was 0.1%. If concentration was a critical determinant of the dog's performance, manipulating the concentration of the S^+ and S^- odorants should have a disrupting effect on performance. If however, dogs were not utilizing intensity to guide performance, they should be able to maintain stable responding when the odorants are diluted to different concentrations.

2.7. Statistical analyses

Mixed-effects logistic regression was used to assess the effect of the difference in the number of carbons (ΔC) on discrimination accuracy. A model was fit in which whether a response was correct or incorrect (binomial outcome) across both testing sessions was predicted by ΔC, whether the ΔC was a positive (i.e. the distractor was a longer chain than pentanol) or negative value (i.e. shorter

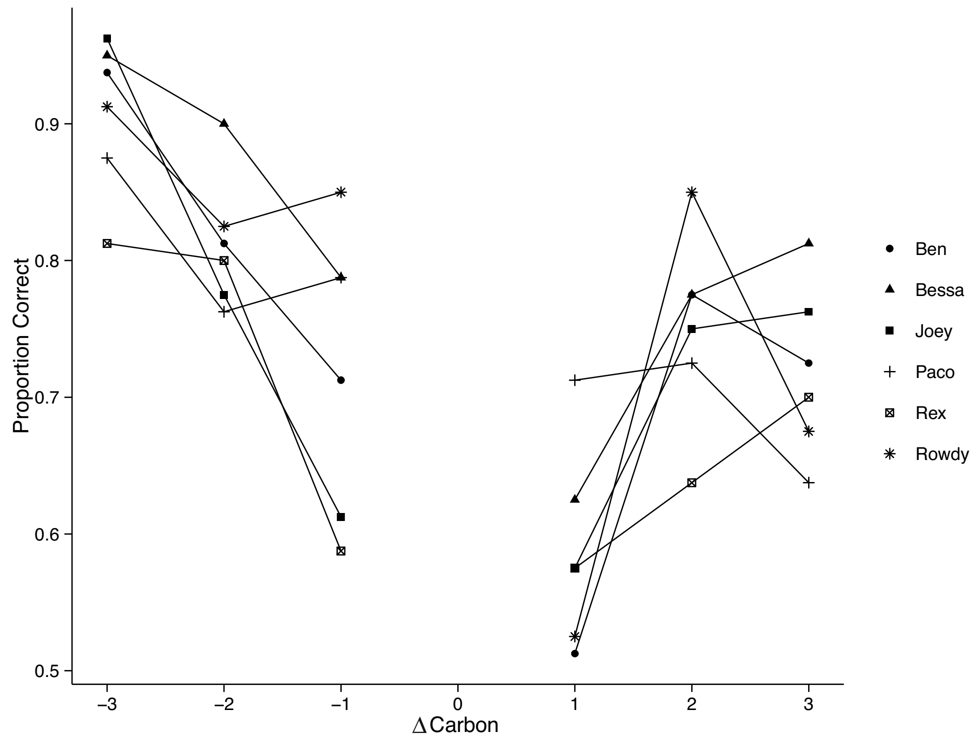

Fig. 1. Proportion correct (Response accuracy) as a function of difference in number of carbons. Performance increased as the difference in the number of carbons from pentanol increased in either the positive (more carbons then pentanol) or negative direction (fewer carbons then pentanol). Each point indicates a dog's mean performance across both sessions.

chain), and an interaction term between these two variables. A random intercept term was included to model within-subject correlation. Analyses were conducted using R (www.r-project.org; R Core Team, 2013) and the *lme4* and lmerTest packages. P-values and Z-tests of the logistic regression model were obtained from the summary function of the lmerTest package.

To test whether the intensity manipulation significantly influenced performance, a mixed effect logistic regression was conducted in which accuracy (modeled as a binomial, correct/incorrect, response) was predicted by the change in the odorant concentration. Significance of the effect of the concentration manipulation was determined by comparing a model including this variable to a model excluding this variable with a likelihood ratio test.

3. Results

The results indicate that there is a clear increasing trend in performance as the difference in the number of carbons between the S^+ and S^- increases (Fig. 1). They also indicate that the effect of ΔC on response accuracy is not symmetric for odorants with fewer carbons compared to odorants with more carbons than pentanol. Dogs tended to perform better in discriminating pentanol from alcohols with fewer carbons than alcohols with more carbons. The statistical model indicated that there was a significant increase in performance with an increase in ΔC ($z = 7.34$, $p < 0.001$). There was also a significant interaction between the effect of the carbon difference and whether the S^- was a longer or shorter chain then pentanol ($z = -2.955$, $p = 0.003$). When the S^+ and S^- differed by one carbon, the estimated difference in accuracy between the discrimination with the lower carbon S^- (Butanol) compared to the longer chain carbon S^- (hexanol) was only 0.09 in proportion correct. When the S^+ and S^- differed by three carbons, however, the difference in response accuracy between the shorter and longer chain S^- discrimination (ethanol vs. pentanol and octanol vs. pentanol) increased to 0.15.

To test whether the concentration of the odorants served as a critical discrimination cue, dogs were given the pentanol vs. butanol discrimination in which one of the odorants was increased 10-fold. The results of this manipulation are shown in Fig. 2. For three of the four dogs, accuracy was consistent regardless of the dilution for the S^+ and S^-. One dog (Rowdy), however, showed a large detrimental effect of increasing the concentration of the S^-. Overall, there was a significant effect of the concentration manipulation ($\chi^2 = 6.19$, df = 2, p = 0.05). Excluding Rowdy, however, there was no indication that the remaining three dogs' performance was influenced by manipulating odorant concentration ($\chi^2 = 0.03$, df = 2, p = 0.98).

Throughout testing, there was also no indication that dogs were utilizing unintentional cues to identify the correct response. Mean proportion correct on control trials across all dogs was 0.45 (SD = 0.04), which never exceeded chance. This slightly lower than chance (50%) performance was caused by dogs occasionally not responding when no odorant was present. When considering only trials for which dogs made a response, performance was indistinguishable from chance (mean = 0.51, SD = 0.05, one sample *t*-test, $t_5 = 0.84$, $p = 0.44$)

4. Discussion

Using a series of homologous alcohol pairs, dogs showed a significant increase in discrimination performance as the difference in number of carbon atoms (ΔC) between the odorant pairs increased. Dogs showed the same structure-perception relationship that has been observed for rats (Yoder et al., 2014), honeybees (Laska et al., 1999), humans (Laska and Teubner, 1999), elephants (Rizvanovic et al., 2013), and monkeys (Laska and Freyer, 1997; Laska and Seibt, 2002; Laska and Teubner, 1998). This contrasts the lack of correla-

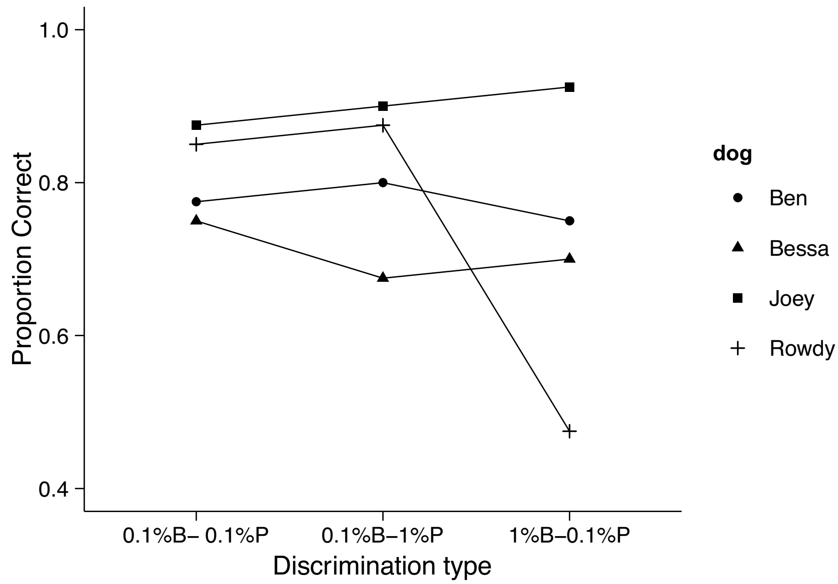

Fig. 2. The performance of the four dogs tested on the intensity discrimination. 0.1% B-0.1% P indicates a 0.1% butanol vs. a 0.1% pentanol discrimination, which was used during the initial study. In the other conditions, a 10-fold increase in concentration was used for pentanol (0.1%B-1% P) and butanol (1%B-0.1%P) to assess the effects of changing concentration on discrimination performance.

tion observed for CD-1 mice (Laska et al., 2008) and South African fur seals (Laska et al., 2010). As suggested by Laska et al. (2010), these differences may represent different selection pressures on olfaction for the different species.

In the present study, we also observed a pattern that has not been explicitly described in prior studies. Specifically, we observed that discriminating between pentanol and an odorant with more carbon atoms was consistently more difficult than discriminating between pentanol and an odorant with fewer carbon atoms.

One variable potentially confounding the present results is differences in vapor pressures across the different alcohols and the final concentrations. We attempted to account for some variability in vapor pressure by increasing the concentration of the lower vapor pressure odorants. This unfortunately does not necessarily indicate that the stimulus was perceived with equal intensity. Prior research in humans using supra-threshold concentrations of the same odorant series suggests that intensity decreases with increases in carbon chain length (Engen, 1965). To test for odorant intensity effects we conducted a separate test in which we varied the concentration of the S^+ and S^- systematically 10-fold. For three of the four dogs tested, we saw no effect of the intensity manipulation on performance, but we did see an effect for one dog, indicating that odorant concentration might have been influencing its performance. Thus, it appears that odorant concentrations might have been an influential factor for one dog, but does not readily explain the pattern observed for the remaining three dogs tested.

Another important consideration is the possibility that the olfactory discrimination performance was mediated by the nasal trigeminal system. The dilutions of the alcohols in the present study (e.g., pentanol 0.1% v/v) were selected in part from prior studies which have used a range of odorant concentrations from 10% v/v to 0.0001% v/v (Laska et al., 2010, 2008; Laska and Teubner, 1999; Rizvanovic et al., 2013; Yoder et al., 2014). Thus, although it is unclear how the present results may have been influenced by trigeminal stimulation, our dilutions were similar to those used in prior studies investigating the same structure-discrimination relationship.

The present research has potential applications for future applied work with dogs. Given that dogs are charged with detection tasks that rely on their ability to discriminate between target and non-target odors and generalize to a variety of exemplars of targets (see Lazarowski and Dorman, 2014), having a thorough understanding of olfactory generalization and discrimination processes in dogs is important. Unfortunately, little work has investigated this topic. The present study provides data regarding odor perceptual similarity in a homologous series of alcohols, and defines a stimulus set of known odor similarity for dogs. This will allow future research to capitalize on the known relationship between these alcohols to study how experimental manipulations may lead to enhanced generalization and discrimination amongst similar odors.

In conclusion, dogs show a correlation between the number of carbon atoms by which two odorants differ in a homologous series of alcohols and the perceptual similarity of those odorants. Alcohols that differ by more carbons are perceived more differently. In addition, the present data indicate that there was a performance difference with the shorter carbon chains compared to the longer carbon chains. Future research is needed, however, to explore the effects of this difference and its relationship with the carbon difference. Last, the results indicate that a homologous series of alcohols may be a useful stimulus set of odorants for further study of olfactory generalization and discrimination in dogs.

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