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Ontogeny vs. Phylogeny in Primate/Canid Comparisons:

A Meta-analysis of the Object Choice Task

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Highlights

- The Object Choice Task (OCT) is a widely used experimental protocol that assesses the understanding of directional cues, such as pointing.
- We analysed the procedures administered to domestic dogs and nonhuman primates (sample = 2,534 subjects) and found that systematically different procedures have been administered to the two groups.
- Both domestic dogs and nonhuman primates are sensitive to many of the factors we identify as systematic confounds in between-species comparisons.
- Widely reported species differences on the OCT between domestic dogs and nonhuman primates cannot, therefore, be attributed to their different selective histories, because procedural confounds with taxonomic classification cannot isolate selective history as the relevant factor.

Abstract

The Object Choice Task (OCT) is a widely used paradigm with which researchers measure the ability of a subject to comprehend deictic (directional) cues, such as pointing gestures and eye gaze. There is a widespread belief that nonhuman primates evince only a weak capacity to use deictic cues; in contrast, domestic dogs (*Canis familiaris*) tend to demonstrate high success rates. This pattern of canid superiority has been taken to support the Domestication Hypothesis, which posits enhancing effects of artificial selection on the sociocognitive abilities of dogs and humans. Here we review nearly two decades of published findings, using variants of the OCT. We find systematic confounds with species classification in task-relevant preparation of the subjects, in the imposition of a barrier between reward and subject, and in the specific deictic cues used to indicate the location of hidden objects. Thus, the widespread belief that dogs outperform primates on OCTs is undermined by the systematic procedural differences in the assessments of these skills, differences that are confounded with taxonomic classification.

Keywords: Object choice task, canids, primates, comparative cognition.

According to some theorists, the origins of human language may be found in gestural communication (Arbib, 2005; Corballis, 2002) and there is profound interest in the effects of selection on the capacity to comprehend referential (deictic) gestures (Hare, Brown, Williamson, & Tomasello, 2002). The theoretical basis for this contemporary interest lies in two key suppositions: (a) that the ability to grasp communicative intent is an essential cognitive prerequisite for linguistic communication, in both developmental and evolutionary terms (e.g., Grice, 1975; Sperber & Wilson, 1995) and (b) that this cognitive ability can be objectively

measured (e.g., Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997; Tomasello, Call & Gluckman, 1997). It has been well-demonstrated that human children's ability to follow pointing gestures to particular loci is correlated with their later language acquisition (e.g., Colonesi, Stams, Koster, & Noom, 2010). In typical development, this likely works by facilitating audio-visual associations between the referents (the things pointed to or gazed at) with the verbal labels for those referents. Thus, a child can point to an entity and elicit its name, or a child can follow another's gaze or pointing gesture to a referent, bringing the referent into their visual field at the same time that the referent's label is spoken (e.g., Baldwin & Moses, 1996). Comprehension of deictic cues developmentally precedes speech production and seems to be functionally linked with language acquisition; this ability has therefore been characterized as one component in a human species-specific biological adaptation for language (e.g. Butterworth, 2003).

There is a variety of different techniques for measuring the comprehension of deictic cues that have been administered to children for decades. For example, a common technique is to determine whether children will visually orient in the direction of another's gaze or pointing gesture (reviewed by Butterworth, 2003). Gestures form an important part of human communication and the capacity to produce and comprehend them emerges in pre-verbal infants. In Western societies, the index-finger point is the predominant form of deictic gesture, used to direct another's attention to an object or event of interest (Butterworth, 2003; Masataka, 2003; but see, e.g., Cooperrider, Slotta, & Núñez, 2018, for descriptions of non-manual points). Human infants develop the ability to follow points at around 6 months of age (Butterworth, 2001) and begin to produce points at around 12- 15 months (Franco & Butterworth, 1996). The onset of pointing constitutes a significant developmental milestone (e.g., Flack & Leavens, 2018; Leavens & Clark, 2017), and its onset has been shown to predict the onset of speech (Colonesi, Rieffe, Koops, & Perucchini, 2008; Iverson & Goldin-Meadow, 2005), and a delay in, or lack of the development of pointing has been linked to autism (Osterling & Dawson, 1994) and

pervasive developmental disorders (Bernabei, Camaigni, & Levi, 1998).

In the last 30 years, the question of whether animals can also use these cues has generated a substantially increasing number of studies with nonhumans, testing their abilities to comprehend gaze and pointing cues (e.g., Krause, Udell, Leavens & Skopos, 2018). As noted by Hare and Tomasello (2005), one of the most scientifically interesting justifications for using dogs in this research is the possibility that dogs might display cognitive adaptations that converge on those of humans, providing the tantalizing possibility that dogs might provide a window into the selective pressures that faced our human ancestors. Nonhuman primates are an important and complementary comparison group, insofar as they may provide insight into the time frames—and associated paleoecological contexts—in which certain cognitive abilities emerged. For example, among nonhuman primates, only the great apes display mirror self-recognition (MSR) in the same experimental contexts in which human children also display MSR (Bard, Todd, Bernier, Love, & Leavens, 2006), which implicates paleoecological environments pre-dating the Miocene origins of contemporary great apes and humans. Differences between humans and their nearest living relatives in assays of sociocognitive abilities would suggest that the ability emerged in our lineage after the split between ourselves and the last common ancestor with the nonhuman primate comparison group in question.

The Object Choice Task (OCT) is a widely used experimental paradigm that measures the ability of a subject to comprehend deictic (directional) cues, usually to find food (Anderson, Sallaberry, & Barbieri, 1995). There is a widespread belief that nonhuman primates have a deficient capacity to interpret deictic gestures, evidenced by their poor performances on this task (e.g., Maclean, 2016). In contrast, domestic dogs (*Canis lupus familiaris*) tend to demonstrate high success rates on the task, and the relative performances of both taxa have been taken as evidence for selective histories that facilitate social cognition in domesticated dogs and humans (i.e. the Domestication Hypothesis), while nonhuman primates are held to lack these selective

histories (e.g., Hare et al., 2002). This point of view sits uncomfortably against a large body of evidence for the successful use of social cues by animals and their sensitivity to social information in their environments (e.g., Call & Tomasello, 1994; Flombaum & Santos, 2005; Haroush & Williams, 2015—see reviews by Lyn, 2010; Monfardini, Reynaud, Prado & Meunier, 2017). A competing theoretical perspective accounts for the performance differences on the OCT with reference to specific individual learning histories, irrespective of selective history (i.e. the Lived Experiences Model)—according to this line of reasoning, most captive great apes have impoverished social learning opportunities, relative to pet dogs, human children, enculturated primates, and their wild conspecifics (e.g., Bard & Leavens, 2014; Leavens & Bard, 2011; Racine, Leavens, Susswein & Wereha, 2008). Here we comprehensively review the OCT literature and show that experience with humans and procedural variables better explain group performance differences between dogs and nonhuman primates than do species classifications. When these mammals are matched on task-relevant pre-experimental history and on key procedural variables, species differences disappear. We find no evidence for a deficiency in social cognition, as measured by the OCT, in nonhuman primates, relative to dogs.

The OCT involves an experimenter baiting, typically, one of two or three opaque containers and then using a referential gesture, often a point or gaze cue, to indicate to the subject the container in which the bait has been placed. Human infants perform well on this task from around 12 months of age (Behne, Lizkowski, Carpenter & Tomasello, 2012) and a number of non-primate species such as horses and elephants have also been shown to be successful (Proops, Rayner, Taylor & McComb, 2013; Smet & Byrne, 2013).

Nonhuman primates, however, tend to have poor success rates on the OCT (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Kirchofer, Zimmermann, Kaminski, & Tomasello, 2012). The results from studies with our nearest relatives, the great apes, have been used to propagate theories such as the Cultural Intelligence Hypothesis (Herrmann et al., 2007),

the Shared Intentionality model (Tomasello & Carpenter, 2007), and the Vygotskian Intelligence model (Moll & Tomasello, 2011), all of which share the premise that nonhuman primates are unable to comprehend the communicative significance of informative gestural cues and that, therefore, this is a human-unique ability that contributed to the emergence of verbal communication in humans. This pattern of poor comprehension of deictic cues by nonhuman primates sits uncomfortably against a large and growing literature demonstrating that great apes frequently use pointing, themselves, in captivity, typically with no explicit training to do so, along with many other animal taxa (see Krause et al., 2018, for review).

However, there exist some disparities in the literature as to the relative abilities of different species, and, recently, some authors have begun to address these anomalous findings with reference to methodological and procedural factors in OCT experiments that are systematically confounded with species classification. In a review of ape OCT studies, Lyn (2010) found performance differences on the OCT as a function of rearing history in apes, such that enculturated apes, raised in an environment rich in human interaction, outperformed institutionalised apes and thus argued for greater consideration of rearing history when comparing across species. Mulcahy and Hedge (2012) reviewed 63 OCT papers and concluded that configurational differences in the testing of apes and dogs disadvantage the former due to decreased salience of, and attention, to the cue being given. Finally, in a review of gaze-following OCT studies with nonhuman primates Byrnie (2015) argues that there exists such disparity between different species in their performance on the OCT that taking one species' results as representative of their whole phylogenetic group leads to erroneous conclusions. Here, we develop and extend these findings in the most comprehensive OCT literature review to date, focusing primarily on domestic dogs and nonhuman primates, as it is evidence from these species that has been used to support prevailing theories of human uniqueness in social cognition and of the effects of domestication on dogs' social-cognitive abilities.

The first factor that we address is that of the systematic confound between life history and species classification of subjects. Among humans, index-finger pointing is not a universally employed communicative gesture, and, in fact, in some non-Western societies, lip-pointing or nose-pointing is more predominantly used (Cooperrider et al., 2018; Enfield, 2001; Wilkins, 2003). The comprehension of pointing is a developmental process in human infants (Butterworth & Groer, 1988); it is through repeated exposure that pointing acquires its cultural and communicative significance. In fact, one of the first OCT studies conducted with nonhuman primates (Call & Tomasello, 1994) concluded that the marked difference in both pointing comprehension and production between an enculturated and an institutionalised orangutan was due to the subjects' differential experiences of human interaction. Call and Tomasello (1994) suggested that humanlike interaction in early ontogeny, therefore, was necessary for the development of an understanding of others as intentional agents and they remarked that this was possibly also the case for human infants. In spite of these speculations, the OCT literature in the ensuing 20 years comprises a multitude of studies of nonhuman primate in which the poor performance of samples of great apes raised in institutional settings with minimal exposure to humanlike interaction is attributed to a core, phylogenetic species difference in cognitive ability (e.g., Moore, Call, & Tomasello, 2015; Povinelli et al., 1997; Tomasello et al., 1997; for critical analysis, see Leavens, Bard, & Hopkins, 2017; Lyn, 2010).

Bard and Leavens (2014) discussed the importance of social engagement in the development of socio-cognitive skills in human infants, and there is an effect of the amount and quality of human interaction on nonhuman primates' abilities to use human nonverbal cues in much the same way (Bard, Bakeman, Boysen & Leavens, 2014). Studies which have compared nonhuman primates from different rearing environments on the OCT have found marked differences in their abilities as a function of their pre-experimental exposure to human interaction (Lyn, Russell & Hopkins, 2010). Hence, we argue that it is invalid to conclude that differences

in experimental performance are due to species differences, without considering the experiential histories of all of the individuals tested.

This is further emphasised by the wealth of studies concluding that domestic dogs' superior performance on the OCT reflects specialised socio-cognitive skills evolved through their long history of domestication (Hare & Tomasello, 1999; Hare & Tomasello, 2005). Whilst pet dogs, who are extensively exposed to human interaction, are indeed adept at passing the OCT, the poor performance of dogs with alternative life histories, such as shelter dogs or kennel-bred research dogs (D'Aniello et al., 2017; Lazarowski & Dorman, 2015; Udell, Dorey & Wynne, 2010) demonstrates that this is not, in fact, an innate, evolutionarily derived adaptation. Lea and Osthaus (2018) suggested that in order to assess the extent to which dogs' cognitive skills are exceptional, it is necessary to consider their phylogenetic, ecological and anthropogenic backgrounds, comparing their abilities to representatives of taxonomic groups that share common features of these: other carnivores, other social hunters and other domestic animals, respectively. They argued that when dogs' social cognition is considered in this way, there is no evidence to show that they have unique abilities- other carnivores (e.g. sea lions, seals and dolphins) demonstrate high success rates and other domestic animals (e.g. pigs and goats) show similar abilities to follow points. With regard to social hunters, there is evidence that chimpanzees, too, can comprehend pointing cues (Leavens & Clark, 2017). Thus, as argued by Lea and Osthaus (2018), when dogs' abilities are considered from these three perspectives, there is no evidence to suggest that their sociocognitive skills are exceptional.

The second factor, we propose, is the use of incommensurate testing protocols for representatives of different taxa. For example, in order to ensure the safety of the experimenter, the testing of nonhuman primates typically involves subjects participating from within a cage, thus introducing a barrier between the subject and the experimenter and testing apparatus. Testing domestic dogs does not entail these same safety precautions, and so this barrier in the

testing paradigm is generally absent. There are, however, two notable exceptions. The first (Udell, Dorey & Wynne, 2008) involved an OCT with domestic dogs in which a tapping cue was presented to subjects tested either with or without a fence separating subject and experimenter. The authors reported a significant difference between the performance levels of the two groups, with those in the barrier condition experiencing a 31% decrement in success levels. In addition, the only study to date which has involved the presentation of a pointing cue in a testing paradigm where a barrier was present for domestic dogs found significantly lower success rates in those dogs for which a barrier was present, compared to dogs for which this barrier was absent (Kirchhofer et al., 2012). We therefore argue that this difference in the testing paradigm represents a confound with taxonomic classification, which should not be ignored when comparing species' relative abilities.

A further systematic confound we consider here concerns the broad range of types of pointing cues presented in OCT experiments. Typically, researchers use an ipsilateral point where the ipsilateral arm is extended and the index finger outstretched (i.e., a point with the hand on the same side as the baited container is used). Miklósi and Soproni (2006) differentiated between types of cues, specifically distal and proximal points, where the distances between the fingertip and the target are greater than 50cm (i.e. distal) and between 10 and 40cm (i.e. proximal), distinguished as so because the former is considered to be within reach and the latter not; and between momentary and dynamic pointing where the cue is presented for 1-2 seconds (i.e. momentary) or the cue is maintained until a choice has been made (i.e. dynamic). They reported that representatives of a number of species perform at different levels according to the type of cue presented and attribute this to the cues' differential effects on salience and memory. Udell, Hall, Morrison, Dorey and Wynne (2013) assessed dogs' performance on nine point types and found differences in levels of success as a function of the temporal and distal properties of the pointing cues.

Finally, Mulcahy and colleagues (Mulcahy & Call, 2009; Mulcahy & Hedge, 2012) argued that there is a tendency for nonhuman primates to be tested with a central version of the OCT, whereas domestic dogs are tested with a peripheral version. The distinction between the two concerns the inter-object distance between the containers, with the central version being categorised as one in which the containers are placed closer together (around 40cm. apart), whereas in the peripheral version the containers are further apart (around 2m. between containers). The authors argue that this could affect performance in several important ways. First, containers placed close together tend to be in the subject's direct line of vision, and, as such, the salience of the containers may distract subjects' attention from the cue being given. Second, retrieval of a reward from containers that are placed further apart may require increased effort, therefore increasing both attention to, and the salience of, the deictic cue. In support of this, Mulcahy and Call (2009) found that representatives of three species of great ape performed significantly better when tested with a peripheral version compared with when tested with a distal version. In addition, the one study to date with has compared dogs' performance on the two versions of the task (Kraus, van Waveren & Huebner, 2014) found that performance was lower in the peripheral version.

Thus, it is becoming apparent that there may be systematic differences across different taxa in (a) their level of familiarity with humans and human signaling conventions, (b) the physical circumstances in which representatives from different taxa are tested—especially, whether or not they are tested through cage mesh or other barriers, (c) the types of deictic cues used to test comprehension, and (d) the configurations of the key elements in the OCT: the subject, the experimenter, and the referents. If these factors are systematically confounded with taxonomic classification, then current reports of dog-primate differences in sociocognitive abilities, based in their different selective histories, would be open to alternative interpretations, based in life history and procedural factors. In order to investigate the prevalence of these

confounds, individual life history data, as classified by the original studies, and performance data were collated from OCT studies published up until 2019. Given the enormous morphological variation that exists between different dog breeds (e.g., Shearin & Ostrander, 2010), we sampled the literatures for domestic dogs (an unusually and artificially diverse species) with representatives across the order Primates.

Method

Literature Selection

This study was conducted in two phases. In Phase 1 (2013-2016) we assembled every published article on animals' comprehension of deictic cues in OCT studies that we could find, across all vertebrate species, systematically noting the rearing environments where available. This phase of data collection supported the Human Experience Scale that is depicted in Figure 1 and listed in Table S2. The literature search consisted of the following components: Electronic databases (Scopus, ScienceDirect, PsychInfo and all Citation Databases included in ISI web of knowledge) from 1990 – 2018 with keywords in abstracts: “object choice task”, “object-choice”, object choice task (and “animal”), citation search on author names, scanning reference lists, and Google scholar. We also used reference lists in the published articles to find additional reports not captured by our keyword searches. In addition, where we knew of relevant studies not captured by the above methods, we added those to the database. During a preliminary assessment of the database in 2016, it became apparent that systematic comparisons between taxa would only be possible between canids and primates, because the database was dominated by these two taxonomic groups (a finding reported by Krause et al., 2018, Tables 1 & 2). Therefore, in Phase 2 (2016-2018), we focused on dogs and nonhuman primates, extending our cut-off date from the originally planned 2015 to 2017.

Studies were included if they involved an object choice task with at least one pointing

cue condition, and, in order to collate the most individual data possible, no minimum sample size was used to determine inclusion. As noted above, initially, data were collected from 99 studies comprising 43 vertebrate species. Individual rearing history, individual performance data, or both, were available for 3277 subjects. This review focuses on nonhuman primate vs. dog comparisons, for which data was available for 2534 individuals, including representatives of 16 nonhuman primate species, from 71 studies (see Table S1). Of the nonhuman primates, 82% were great apes, with 64% of the nonhuman primate subjects comprised of chimpanzees.

Subjects

Subjects' rearing histories, as classified by the original studies, were collated. Due to the variety of rearing histories of subjects, a human experience scale was created (see Table S2, Extended Data) which defines rearing histories in terms of the quantity and quality of experiential history with humans, such that “close” is characterised by having daily, intensive contact with humans, “occasional” as having some form of exposure, typically in the form of general husbandry, and “seldom” as having experience little or no exposure to humans. Each individual was given an ordinal grade on this scale according to the rearing history given in the original study. Figure 1 shows the human experience scale and the allocation of the original reported rearing histories to this scale.

Data were also collected regarding a number of features of the testing environment, such as the presence or absence of a barrier (most often in the form of a cage), the inter-object distances of containers and the numbers of containers used *inter alia*. Subjects who took part in multiple studies (usually nonhuman primates) were highlighted as having done so, as were those subjects who took part in multiple cue conditions.

Cue Types

For the purposes of this review, performance data were analysed only where one or more pointing cues were presented, and these cues were categorised according to Miklósi and

Soproni's (2006) definitions. The following distinctions were made:

Ipsilateral point vs. contralateral point. An ipsilateral point is where the pointing cue is presented using the hand that is on the ipsilateral side of the body in relation to the baited container. A contralateral point is one where the hand is on the opposite side of the body to the baited container is used.

Static point vs. dynamic point vs. momentary point. A point is categorised as static when the pointing hand is in place before the participant views the cue and remains so until the participant chooses one of the containers. A dynamic point is when the point is enacted once the participant is in position and is held until the participant makes a choice. A momentary point is where the point is enacted in front of the participant and is presented for 1-2 seconds before the hand returns to the resting position.

Proximal point vs. distal point. A point is said to be proximal when the distance between the fingertip and the baited container is less than 40cm. A distal point is categorised as such when the distance between the fingertip and the baited container is equal to or greater than 40cm.

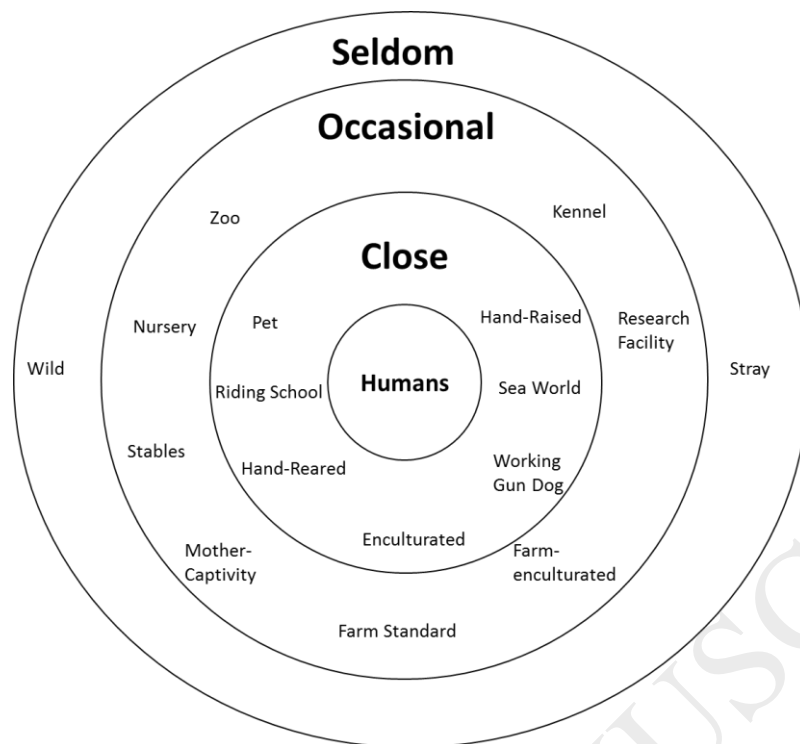


Figure 1. Rearing histories as reported in the original studies categorised according to the human experience scale. “Mother-captivity” means mother-reared in captivity.

Individual Performance Data

Although many studies present only group mean scores, individual performance data were obtained for 1137 individuals. Where possible, we recorded the number of trials in each pointing condition, the number of correct trials and the percentage of correct trials. Due to variation in the number of containers used in the studies, and thus, the differing chance levels of success, these scores were converted to Z-scores. A ‘pass’ or ‘fail’ was then obtained for each participant in each condition, with a ‘pass’ being a Z-score greater than or equal to 1.65 (one-tailed; see Rumbaugh, Washburn, & Pate, 1984, for justification).

Because lateral, temporal, and distance features of cues presented were not all systematically reported for many subjects, we analysed each of these three features separately, to maximise statistical power. Systematic confirmatory analyses were then conducted where two

of these features were known, and finally, where all three properties were known, on ever-decreasing sample sizes.

For subjects participating in multiple conditions (i.e., different cue types), where these properties were shared across the cue types presented, an aggregate score was collated. For example, if a subject participated in an ipsilateral momentary distal point condition and an ipsilateral dynamic distal point condition, these scores were aggregated, such that a total number of trials and correct trials was obtained, when analyses were conducted regarding ipsilateral or distal pointing cues, but not when examining momentary or dynamic points. Performance data for subjects who participated in multiple conditions (i.e., multiple cue types) were excluded from the performance analyses, as to include their data would be to violate the assumption of independence. These data were then analysed separately, using statistical tests that allowed for within-subjects analyses. This was the case for all analyses excepting cue type distribution analyses, as the aim of this analysis was to examine the frequency of the exposure to the different types of cue across taxonomic groups.

Where participants had participated in multiple studies, their results were taken as independent data points, because studies which had taken place in different years of their lives can be viewed as independent events.

Results

Human experience

Rearing history data were available for 2534 subjects, comprised of 2064 dogs and 470 nonhuman primates. There was a significant difference in the level of human experience between dogs and nonhuman primates (Kruskal-Wallis, $\chi^2(3, N = 2534) = 1550, p < .001$) with 91% of dogs being categorised as “close”, compared with 6% of nonhuman primates; within nonhuman primates, 87% were categorised as “occasional” and 2% as “seldom” (Figure 2). This highlights

the lack of comparability between dogs and nonhuman primates with regard to human experience, with the majority of dogs having a much more enriched experiential history with humans than their nonhuman primate counterparts.

Human experience and performance

Importantly, a relationship was also found between human experience and performance on the OCT on a number of pointing cues. For *ipsilateral* pointing cues, within nonhuman primates and dogs, there was a significant difference in performance between subjects in the different levels of the human experience scale, Kruskal-Wallis $\chi^2(2, N = 212) = 16.43, p = .001, r = .28$. Pairwise comparisons showed that subjects categorised as “close” ($N = 174, Mdn z = 1.26$) scored higher than those categorised as “occasional” ($N = 22, Mdn z = 0.00$), Mann-Whitney $U = 1209.5, p = .005$, and those categorised as “seldom” ($N = 16, Mdn z = -0.32$), Mann-Whitney $U = 731.00, p = .002$. There was no significant difference between those categorised as “occasional” ($N = 22, Mdn z = 0.00$) and “seldom” ($N = 16, Mdn z = -0.32$), Mann-Whitney $U = 135.35, p = .227$, mean $z = 0.36, SD = 0.98$). Within-nonhuman primates, sample sizes were too small (22 “occasional” subjects, 2 “seldom” subjects) for sufficient statistical power for comparisons. Within dogs, those categorised as “close” ($N = 174, Mdn z = 1.26$) scored higher than those categorised as “seldom” ($N = 14, Mdn z = -0.63$) (Mann-Whitney $U = 13.97, p < .001$). For *contralateral* pointing cues, in contrast, within nonhuman primates and dogs, those categorised as “occasional” ($N = 95, Mdn z = 1.89$) outperformed those categorised as “close” ($N = 6, Mdn z = 0.00$), (Mann-Whitney $U = 136.5, p = .029$). Those categorised as “occasional” comprised solely nonhuman chimpanzee subjects and so further analyses were not possible. This suggests that for *contralateral* cues, there may be inherent species differences in responsiveness to cue features that explain the performance differences, or, alternatively, a more complex relationship with human experience may exist

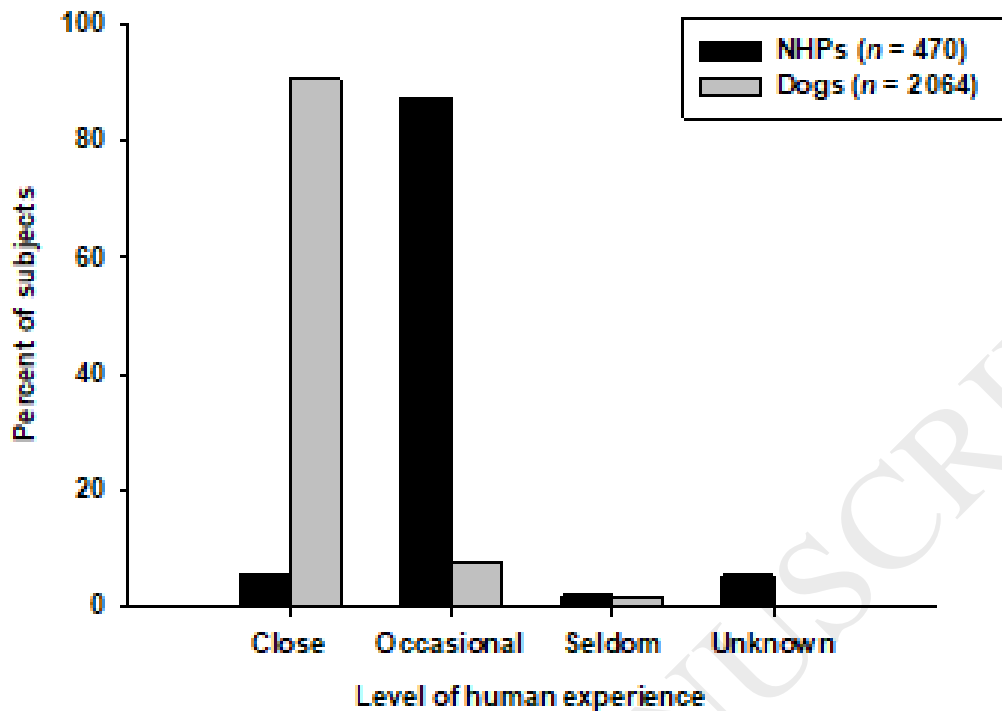


Figure 2. The distribution of levels of human experience between nonhuman primates (NHPs) and dogs.

that leads to the suppression of comprehension of contralateral cues as a result of increased exposure to humans. However, given the systematic confounds between taxonomic classification and cue type, manifest in Figure 3, these possibilities remain speculative. Where *momentary* pointing cues were presented, within nonhuman primates and dogs, subjects categorised as “close” ($N = 356$, $Mdn z = 0.89$) scored higher than those categorised as “seldom” ($N = 22$, $Mdn z = -0.63$), Mann-Whitney $U = 1235.5$, $p < .001$. This was a within-dogs difference, because no performance data were available for nonhuman primates on this cue, and thus replicates previous findings (D’Aniello et al., 2017; Lazarowski & Dorman, 2015; Udell, Dorey & Wynne, 2010) that dogs that have experienced greater exposure to humans are more capable in understanding this more difficult pointing gesture.

Where *dynamic* cues were presented, there were no differences in performance between

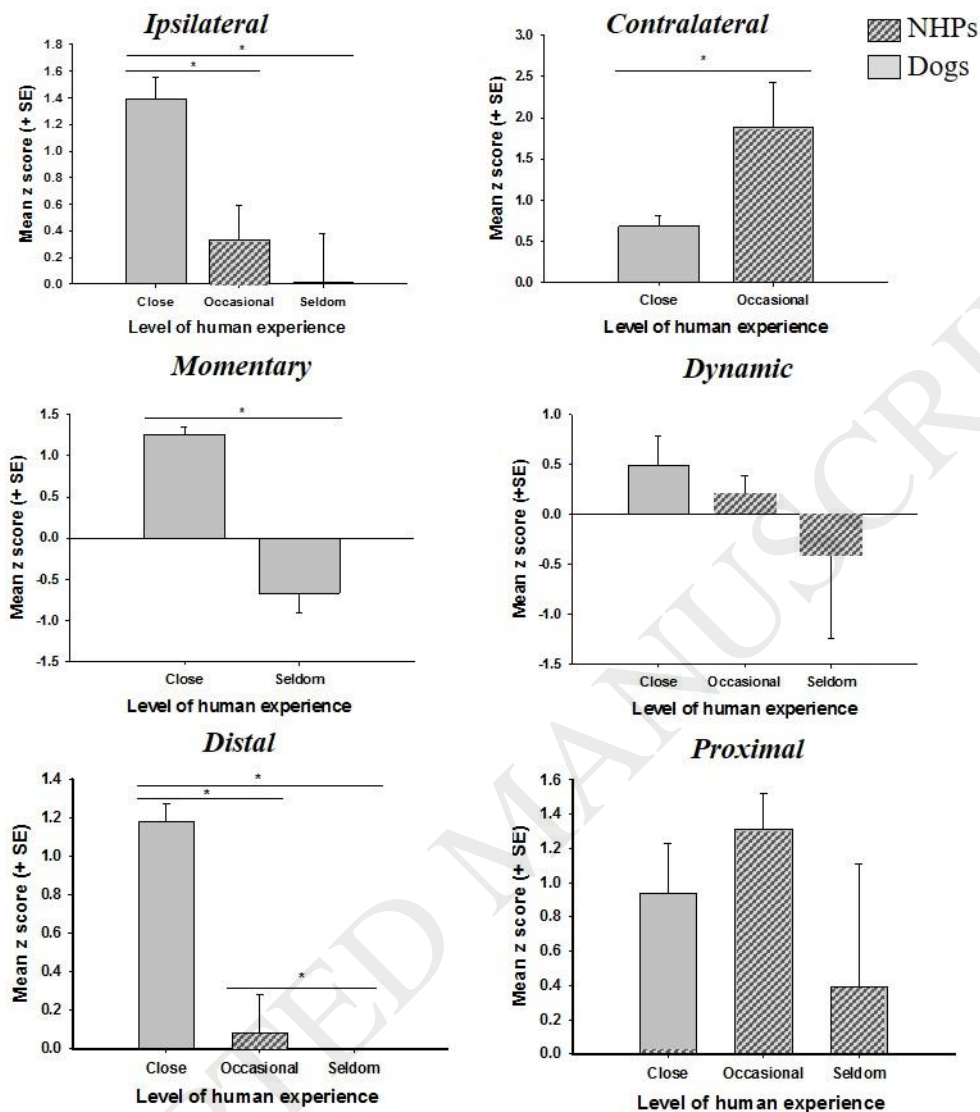


Figure 3. The mean standardised z scores (and standard errors) of nonhuman primates and dogs and the proportion of each species/ taxonomic group contributing to those means, categorised according to level of human experience on six different pointing cues. * denotes $p < .05$.

the categorisations of level of human experience within nonhuman primates and dogs, Kruskal-Wallis $\chi^2(2, N = 82) = 1.84, p = .398$, nor within nonhuman primates alone, Kruskal-Wallis $\chi^2(2, N = 36) = 2.81, p = .246$. Dogs for which there were performance data available were all

categorised as “close” so within-species analyses were not possible. This shows that level of human experience may be of less importance in the comprehension of this easier pointing cue than for those more-difficult-to-follow cues.

Where *distal* cues were presented, within nonhuman primates and dogs, there was a significant effect of level of human experience on performance, (Kruskal-Wallis χ^2 (2, $N = 395$) = 35.27, $p < .001$). Pairwise comparisons showed that those categorised as “close” ($N = 353$, $Mdn z = 0.89$) scored higher than those categorised as “occasional” ($N = 20$, $Mdn z = 0.00$), Mann-Whitney $U = 2066.00$, $p = .002$, and those categorised as “seldom” ($N = 22$, $Mdn z = -0.63$), Mann-Whitney $U = 1334.50$, $p < .001$ (this was a within-dog comparison). “Occasional” ($N = 20$, $Mdn z = 0.00$) subjects also scored higher than “seldom” subjects ($N = 22$, $Mdn z = -0.63$), Mann-Whitney $U = 126.00$, $p = .017$. Within-nonhuman primate comparisons were not possible because all subjects for which there were data were categorised as “occasional”. This shows that level of human experience may better explain performance differences than taxonomic group affiliation.

Where *proximal* cues were presented, there was no significant effect of level of human experience on performance, (Kruskal-Wallis χ^2 (2, $N = 94$) = 2.12, $p < .346$). Within nonhuman primates only, there was no significant effect of human experience on performance, (Kruskal-Wallis χ^2 (2, $N = 51$) = 2.31, $p = .315$). All 43 of the dog subjects were categorised as “close” so within-dog analyses were not possible. This shows that, for *proximal* cues, intense exposure to humans may not have as important a role in facilitating comprehension as for more difficult *distal* cues. Figure 3 shows the comparisons in performance between subjects with different levels of human experience across the different point types.

Presence of a barrier

Comparisons of the presence of a barrier in the testing environment between nonhuman primates and dogs showed that less than 1% of dogs were tested with a barrier, compared with 99% of nonhuman primates, $\chi^2(1, N=2534) = 2411.77, p < .001$, as shown in Figure 4. This highlights the systematic inconsistencies present in testing environments across the two taxonomic groups, and, therefore, the reduced validity of interpreting group differences as phylogenetic traces of differences in selective histories. Comparisons of performance between dogs tested with a barrier and those tested without were not possible because among the only

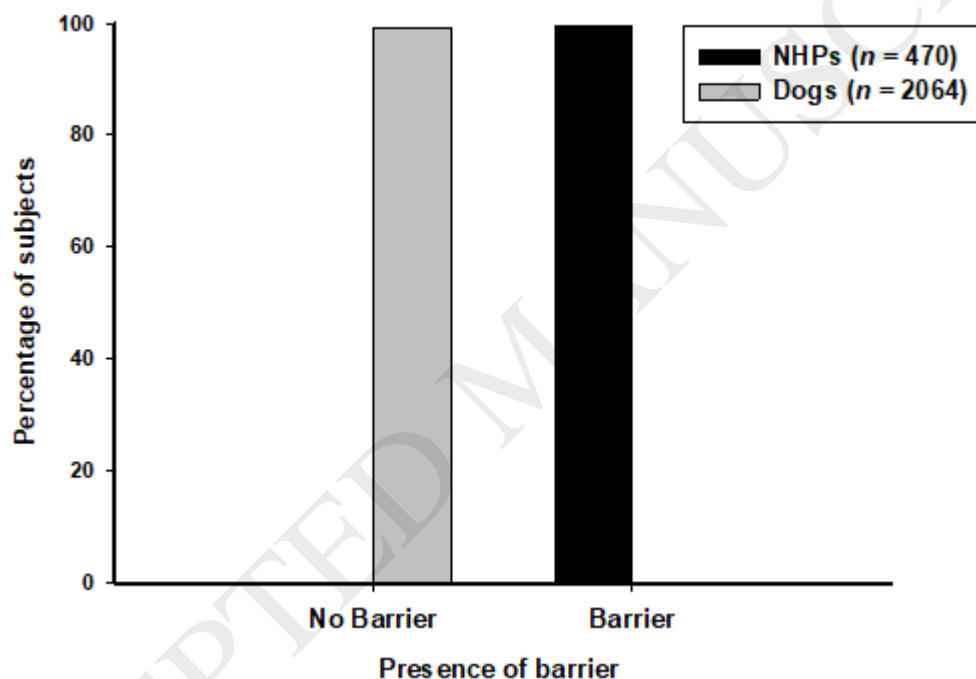


Figure 4. The percentage of nonhuman primates and dogs tested with and without a barrier.

two studies to introduce barriers to the testing protocol, Kirchofer et al. (2012) did not specify which individuals participated in the barrier condition and Udell et al.'s (2008) dogs tested with a barrier did not take part in a pointing cue condition. Comparisons between nonhuman primates tested with and without a barrier were not possible because only 3 infant chimpanzees were tested without a barrier present (Okamoto-Barth, Tomonaga, Tanaka & Matsuzawa, 2008), thus sufficient statistical power was lacking.

Cue types

Among those subjects with only one type of pointing cue, differences were also found regarding the types of cues presented to the two taxonomic groups. There was a significant difference between lateral properties (i.e. whether ipsilateral or contralateral hand was used to point) of cues presented to nonhuman primates and dogs, with 26% of points to nonhuman primates being *ipsilateral* and 74% *contralateral*, compared with 82% *ipsilateral* and 18% *contralateral* for dogs, $\chi^2(1, N = 1777) = 328.59, p < .001$, as shown in Figure 5a. For nonhuman primates, there was no significant difference in performance between *ipsilateral* ($N = 24, Mdn z = 0.25$) and *contralateral* ($N = 6, Mdn z = 1.89$), Mann-Whitney $U = 34.5, p = .05$, shown in Figure 6a. Dogs scored significantly higher on *ipsilateral* ($N = 188, Mdn z = 1.00$) than on *contralateral* ($N = 95, Mdn z = 0.00$) pointing cues, shown in Figure 6b. This shows that lateral cue features can differentially affect different species' performance.

Figure 5b shows the percentage of the different temporal cue types presented to nonhuman primates and dogs. There was a significant difference across taxa in temporal cue properties, with 4% of cues presented to nonhuman primates being static, 7% momentary and 90% dynamic, compared with 1% static for dogs, 45% momentary and 42% dynamic, Kruskal-type according to a) lateral features b) temporal features and c) distance features of the cue. Wallis $\chi^2(2, N = 2105) = 195.48, p < .001, r = .30$. This demonstrates that there are also systematic differences in the temporal properties of cue types presented to nonhuman primates and dogs, with a bias towards dynamic pointing for nonhuman primates. There were insufficient data to analyse performance differences between the three point types for nonhuman primates (see Figure 6a), and there was no significant difference in performance on *dynamic* ($N = 46, Mdn z = 0.57$) and *momentary* ($N = 378, Mdn z = 0.89$) pointing cues within

dogs, Mann-Whitney $U = 7376.0$, $p = .092$ (Figure 6b).

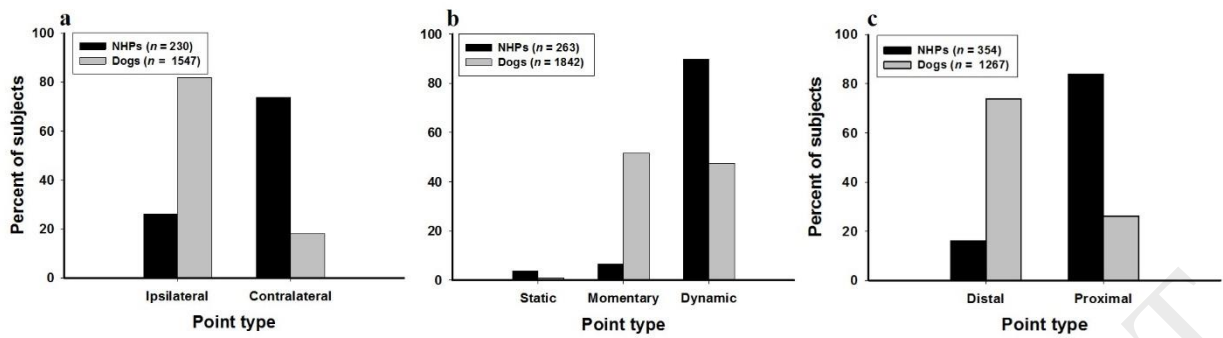


Figure 5. The percentage of nonhuman primate and dog subjects presented with each point

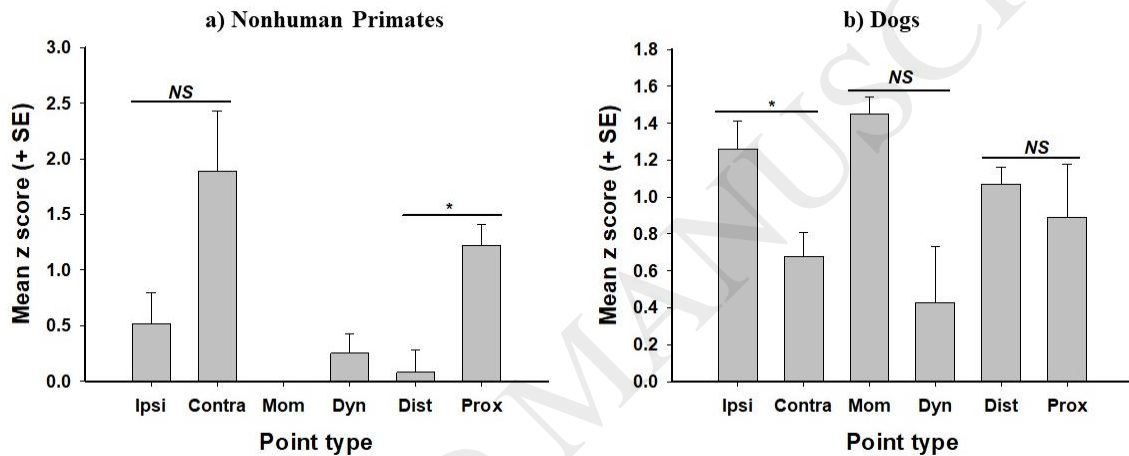


Figure 6. The mean z scores and standard errors for a) nonhuman primates and b) dogs on the different pointing cue types. Ipsi = *ipsilateral*; Contra = *contralateral*; Dyn = *dynamic*; Mom = *momentary*; Dist = *distal*; Prox = *proximal*. * denotes significant at $p < .05$. NS = not significant.

Please note difference in scale ranges for the Z-score.

There was a significant difference in the distance properties, with 16% of cues presented to nonhuman primates being distal cues, and 84% proximal, compared with 74% distal for dogs and 26% proximal, $\chi^2(1, N = 1621) = 387.86$, $p < .001$ (Figure 5c). This shows that there are marked differences in the distance properties of cue types presented between nonhuman primates and dogs, with a bias towards distal pointing cues for dogs and towards proximal pointing cues for nonhuman primates. Within nonhuman primates, subjects scored higher on

proximal ($N = 54$, $Mdn z = 0.90$) than on *distal* ($N = 20$, $Mdn z = 0.00$) pointing cues, Mann-Whitney $U = 309.50$, $p = .005$ (Figure 6a). Within dogs, there was no significant difference in performance between *distal* ($N = 375$, $Mdn z = 1.07$) and *proximal* ($N = 43$, $Mdn z = 0.63$) pointing cues, Mann-Whitney $U = 7441.00$, $p = .406$ (Figure 6b). This demonstrates that, for nonhuman primates, there are performance differences associated with the distance properties of the cue being presented.

Multiple conditions

Four hundred and two subjects took part in studies in which they were presented with multiple cue types. Individual performance data were available for 210 of these subjects. There were insufficient data to conduct statistically robust comparisons of performance according to level of human experience. Analyses were possible, however, for comparisons of performance according to cue type. Nonhuman primates scored higher when tested with *distal* cues (mean $z = 2.47$, $SD = 1.62$) than with *proximal* cues (mean $z = 0.75$, $SD = 1.62$), ($Z = -3.01$, $p = .003$). Dogs, in contrast, performed better when tested with *proximal* (mean $z = 3.90$, $SD = 0.62$) rather than *distal* cues (mean $z = 0.51$, $SD = 2.59$), ($Z = -2.37$, $p = .018$). With regard to temporal properties of cues, nonhuman primates scored higher when tested with *dynamic* (mean $z = 1.07$, $SD = 0.93$) rather than *momentary* (mean $z = 0.05$, $SD = 1.09$) cues, ($Z = -2.58$, $p = .010$). This was also the case for dogs (*dynamic* mean $z = 2.33$, $SD = 1.50$; *momentary* mean $z = 0.80$, $SD = 1.75$), ($Z = -2.94$, $p = .003$). This shows that both temporal and distance properties of pointing cues may affect individual performances, and that there may be different processes at play in terms of their effects depending on taxonomic group. There were insufficient data to analyse performance for *static*, *ipsilateral* and *contralateral* pointing cues.

Inter-object distance

Further procedural differences were found with respect to the inter-object distance between containers. Dogs ($Mdn = 155.0$ cm) were tested with significantly greater inter-object distances than nonhuman primates ($Mdn = 58.0$ cm), (Mann-Whitney $U = 4917.5$, $z = -27.99$, $p < .001$), demonstrating a bias towards greater distances between the containers for dogs than for nonhuman primates, congruent with Mulcahy and Hedge's (2012) findings. Analyses of the relationship between inter-object distance and performance by species found significant correlations between these inter-object distance and cue types, although with different patterns between the two species. For dogs, *ipsilateral*: significant positive correlation ($r_s(155) = .17$, $p = .032$), *contralateral*: significant positive correlation ($r_s(19) = .75$, $p < .001$), *static*: insufficient data, *momentary*: significant positive correlation: ($r_s(269) = .23$, $p < .001$), *dynamic*: no significant correlation ($r_s(46) = -.17$, $p = .261$), *distal*: significant positive correlation ($r_s(299) = .319$, $p < .001$), and for *proximal*: insufficient data. For nonhuman primates, *ipsilateral*: significant negative correlation ($r_s(24) = -.64$, $p = .001$), *contralateral*: insufficient data, *static*: insufficient data, *momentary*: insufficient data, *dynamic*: no significant correlation ($r_s(27) = -.04$, $p = .836$), *distal*: insufficient data, and for *proximal*: no significant correlation ($r_s(41) = -.214$, $p = .180$). Thus, for dogs, increasing inter-object distance correlates positively with performance in the face of cues that are characteristic of past research with this species (ipsilateral, momentary, distal points—see Figure 5). In contrast, for nonhuman primates, sample sizes are generally too small to invoke confidence—the only significant correlation was a negative correlation between inter-object distance and performance with ipsilateral cues, which are not the most characteristic cues used in studies with nonhuman primates (Figure 5a).

Discussion

Our results highlight the procedural and methodological factors that can influence a subject's performance on the OCT and demonstrate that the trend in the existing literature to

compare across these two taxonomic groups without considering these factors greatly reduces the legitimacy of findings. First, it is clear from the results that experiential history with humans can influence an individual's ability in the comprehension of pointing cues. This supports the results of Udell and colleagues (Udell, Dorey & Wynne, 2008; Udell et al., 2012), Lyn and her colleagues (Lyn, 2010; Lyn, Russell & Hopkins, 2010), and numerous others (e.g., Bard, Bakeman, Boysen, & Leavens, 2014; Call & Tomasello, 1994; Hopkins, Russell, McIntyre, & Leavens, 2013; Pedersen, Segerdahl, & Fields, 2009; Scheel, Shaw, & Gardner, 2016) who suggested that exposure to humans and immersion in their environment is a key factor in the development of the comprehension of human communicative cues. As shown in Figure 2, the nonhuman primate subjects in the existing literature come from a wide variety of rearing backgrounds, with only 6% of subjects being enculturated and the majority being nursery-raised or mother-reared in captivity. When this is compared with the dogs' rearing history data, it is clear that the vast majority of dogs are sampled from a pet background. Those who had more impoverished backgrounds in terms of human experience--for example, stray, shelter and free ranging dogs--demonstrated lower success rates on the OCT (e.g., Udell, Dorey & Wynne, 2008; Udell, Dorey & Wynne, 2010). Thus, to make generalisations about the relative abilities of species without considering their experiential backgrounds (e.g. Herrmann et al., 2007; Kirchofer et al., 2012) and, furthermore, to base theories of species' evolutionary histories on results from such studies (e.g. Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare & Tomasello, 2005) is not warranted, due to the pervading imbalance in task-relevant pre-experimental experience between dogs and nonhuman primates. Moreover, enculturated apes significantly outperform institutionalized apes when they are directly compared (Lyn et al., 2010; Russell, Lyn, Schaeffer, & Hopkins, 2011). Contemporary claims to the effect that dogs have greater social awareness than nonhuman primates are, thus, not supported by compelling experimental evidence.

In addition, there are large differences between the two taxonomic groups in the procedural aspect of whether or not there is an intervening barrier between subject and cue provider in the testing paradigm. For example, excepting three infant subjects, all nonhuman primate subjects experienced testing with a barrier between subject and apparatus compared with less than 1% of dogs. In fact, this 1% consists, entirely, of a sample of 16 dogs in Kirchofer et al.'s (2012) study, in which they compared performance of dogs tested with and without a barrier and found that those tested with a barrier performed significantly worse than the dogs tested without a barrier. Whilst it is accepted that a barrier is a necessary precaution when working with dangerous animals, the results of this study highlight the impact that this can have on success rate (Kirchofer et al., 2012). This absence of consistency in testing conditions represents a systemic confound with taxonomic classification in the contemporary scientific literature; dogs and nonhuman primates have not been compared on the same OCT task.

Moreover, there are substantial and systematic differences in the cue types presented to different taxonomic groups, which, again, demonstrates that the comparisons that are currently being drawn in the literature regarding the relative abilities of different species are not based on like-for-like testing paradigms. Miklósi and Soproni (2006) and Udell et al. (2013) highlighted the differential abilities involved in the comprehension of the various cue types, with regard to the salience and memory functions necessary. This shows the importance of testing representatives of any given species not just on one pointing cue type, but on several, before drawing conclusions about a species' ability to comprehend human gestural cues, and of making comparisons about ability only when the cue type is matched between samples. This is further demonstrated here, in the findings that there are advantages across different taxonomic groups of particular cue types, specifically those that involve *dynamic* pointing features.

Finally, the differences found in the distances between the containers in the testing paradigm support Mulcahy and colleagues' (Mulcahy & Call, 2009; Mulcahy & Hedge, 2012)

assertions that nonhuman primates tend to be tested with a central version of the task, whereas dogs are tested with a more peripheral version. The authors suggest that placing containers close together and within the direct line of vision of the subject can lead to the salience of the containers distracting the subjects' attention from the cue being presented. Alternatively, it may be that placing the containers further apart signifies an additional cost to make a choice, and, as such, there is an increase in the attention afforded the cues by the subject. The positive correlations found in the current review, between inter-object distance and performance on several cue types provide support for these hypotheses and further evidence that inter-species comparisons without regard for procedural factors such as these is neither appropriate nor scientifically sound.

These findings demonstrate that dogs and nonhuman primates are treated systematically differently across the OCT literature. They differ in the quality of their early interactions with humans, they are tested in different physical circumstances, they are tested with different cues to locations presented in different spatial configurations, etc., and these systematic differences have been noted by every extant review of OCT studies (Byrnit, 2015; Lyn, 2010; Mulcahy & Hedge, 2012). Moreover, dogs and nonhuman primates differ in many additional respects, in body plan, in longevity, in the relative durations of successive life history stages, and so on. How, then, should researchers compare across species? Are direct species comparisons ever legitimate? There are at least two promising approaches to species comparisons that could, in principle, ameliorate these systematic deficiencies in the OCT literature.

First, as advocated by Bard and Leavens (2014), researchers could establish performance parameters across the full range of rearing histories within a species. With respect to human experience, there is a large range of variation in the familiarity that individual animal subjects will have with human communicative conventions, and this is true both of dogs and nonhuman primates. Previous direct comparisons within species, across different levels of exposure to human communicative conventions, have revealed that subjects that have had more intensive

exposure to humans perform systematically better than conspecifics raised in greater isolation from humans on a variety of tasks, including the OCT (Bard et al., 2014; Call & Tomasello, 1994; Lyn et al., 2010; Russell et al., 2011). These studies reveal that because these organisms are developmentally responsive to quality and quantity of human contact, therefore no systematic performance difference between species—on the OCT or any other such assay—can be rationally attributed to evolutionary, as opposed to developmental factors. Consideration of rearing history differences will, therefore, significantly improve the sophistication of interpretations of these differences, as exemplified by Call and Tomasello (1994) and the researchers who have followed them in considering the effects of human exposure on cognitive development within species. In the fullness of time, as population parameters emerge from more individual studies, then the degrees of responsiveness of different taxa to human exposure will permit comparisons of these presumably different performance curves across species. The essential point is that comparative psychologists cannot legitimately continue to assume that pre-experimental developmental experience is irrelevant to performance.

A second promising approach to comparing across species is to directly manipulate the task-relevant experiences of representatives of different taxa through explicit training regimens (Leavens & Racine, 2009; Leavens et al., 2017). The ability to use others' deictic cues is a developmental milestone in our species (Butterworth, 2001), and it is clear that human children display this ability to use communicative cues only after many months of intensive exposure to cultural environments characterized by frequent referential signalling, both verbally and non-verbally. There is no reason, in principle, that human children could not learn to use these communicative cues in these reference-intensive environments, notwithstanding that many contemporary researchers have elected to interpret this developmental milestone as evidence for human-unique cognitive abilities (for discussion, see, e.g., Leavens, 2018; Moore & Corkum, 1994; Triesch, Teuscher, Deák, & Carlson, 2006). Thus, a promising corrective approach is to

intensively train animals to use referential cues; if representatives of a species are incapable of learning to use these cues even after months of intensive training to use the cue, then one might reasonably conclude that the species has an inherent difficulty understanding these cues. If, on the other hand, such representatives can acquire the ability to use directional cues, then this serves as a clear demonstration that a learning pathway exists for this species to the use of human-given cues to object location. This approach can ameliorate the deficiencies in pre-experimental learning opportunities that exist in the environments of some captive animals (e.g., Bard & Leavens, 2014; Udell et al., 2012).

In conclusion, the current review builds on existing criticisms of the current state of the OCT literature to further demonstrate that methodological and procedural confounds limit the validity of the results of many studies. Moreover, we found examples, within each group, where it was clear that certain methodological factors (e.g., cue type) were correlated with performance; this pattern of findings strongly argues against theoretical interpretations of previously published group differences between dogs and nonhuman primates as evidence for inherent differences in cognitive capabilities (*contra*, e.g., Hare & Tomasello, 2004, 2005; Kirchoffer et al., 2012); we think this pattern also provides a significant challenge to the Domestication Hypothesis, the idea that dogs' performances on the OCT are better explained with reference to their selective histories, as opposed to their ontogenetic experiences (Hare & Tomasello, 2005). To the contrary, our analysis supports numerous previous reports that the use of experimenter-given cues to find hidden objects is well within the competencies of nonhumans, when they are treated pre-experimentally and experimentally like human children or like domesticated animals (e.g., Lyn et al., 2010; Russell et al., 2011; Thomas, Murphy, Pitt, Rivers, & Leavens, 2008; Udell et al., 2012); these findings are consistent with the Lived Experiences model, the idea that organisms adapt, ontogenetically, to the specific ecological features of their rearing environments, promulgated by, Bard and colleagues (e.g. Bard & Leavens, 2014). To put this another way,

based on this pattern of evidence, it is not necessary to invoke human cognitive specializations to account for the ability to follow referential cues. In order to gain a more comprehensive understanding of the abilities of different taxonomic groups to understand human communicative cues, it is necessary for further research that controls for the abovementioned factors to be conducted. We recommend that a series of systematic experiments in which these variables are manipulated is required. This should begin by manipulating such variables with human infant participants, such that the effect of, for example, barriers or pointing cues can be established in this ‘enculturated’ sample, and then to broaden the samples of species, maintaining consistency throughout and ensuring that comparisons are only made across truly comparable groups. In addition, our analysis demonstrates that much greater consideration needs to be given to ontogenetic influences on behaviour, rather than the pervasive reliance on phylogenetic explanations that prevails in the literature (Bard & Leavens, 2014; Leavens et al., 2017). Consistent with Udell and colleagues (Udell, Dorey & Wynne, 2008a, 2008b, 2010) we argue that, prior to asserting reductionist interpretations that assume that individuals’ behaviour is solely a function of their evolutionary history, their individual learning experiences must be taken into account.

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Supplementary Materials

Table S1. Authors and dates of publication; subject species, with sample size shown in parentheses; and cuing conditions of studies for which data were obtained at the individual level.

Study	Species and Number of Subjects	Pointing Cues
Anderson, Montant & Schmitt (1996) ^b	Rhesus Macaques, <i>Macaca mulatta</i> (3)	<i>Proximal</i>
Anderson, Sallaberry & Barbier (1995) ^b	Capuchins, <i>Cebus apella</i> (3)	<i>Proximal</i>
Barth, Reaux & Povinelli (2005) ^a	Chimpanzees, <i>Pan troglodytes</i> (5)	<i>Dynamic Proximal</i>
Bhattacharjee et al. (2017) ^a	Domestic Dogs, <i>Canis familiaris</i> (209)	<i>Ipsilateral Dynamic Proximal</i>
Bräuer, Kaminski, Riedel, Call & Tomasello (2006) ^b	Domestic Dogs, <i>C. familiaris</i> (21)	<i>Ipsilateral Dynamic</i>
	Bonobos, <i>Pan paniscus</i> (4)	<i>Ipsilateral Momentary</i>
	Chimpanzees, <i>P. troglodytes</i> (12)	
Burkart & Heschl (2006) ^b	Common Marmosets, <i>Callithrix jacchus</i> (10)	<i>Ipsilateral Static Proximal</i>
		<i>Ipsilateral Static Distal</i>
Byrnit (2004) ^a	Orangutans (4), <i>Pongo pygmaeus</i>	<i>Proximal</i>
Byrnit (2009) ^a	Gorillas, <i>Gorilla gorilla</i> (3)	<i>Dynamic Proximal</i>
Call & Tomasello (1994) ^b	Orangutans, <i>P. pygmaeus</i> (2)	No properties known.
Call, Hare & Tomasello (1998) ^b	Chimpanzees, <i>P. troglodytes</i> (6)	No properties known.

Call, Agnetta & Tomasello (2000) ^b	Chimpanzees, <i>P. troglodytes</i> (15)	No pointing cues given.
Carballo, Freidin, Casanave & Bentosela (2016) ^a	Domestic Dogs, <i>C. familiaris</i> (12)	<i>Proximal Dynamic,</i> <i>Distal Dynamic</i>
Dalla Costa, Cannas, Minero & Palestini (2010) ^a	Domestic Dogs, <i>C. familiaris</i> (37)	No properties known
D'Aniello et al. (2017) ^b	Domestic Dogs, <i>C. familiaris</i> (29)	<i>Distal Dynamic,</i> <i>Proximal Dynamic</i>
Dorey, Udell & Wynne (2010) ^b	Domestic Dogs, <i>C. familiaris</i> (33)	<i>Ipsilateral Momentary Proximal</i>
Essler, Schwartz, Rossettie & Judge (2017) ^a	Capuchins, <i>C. apella</i> (10)	<i>Ipsilateral Dynamic Proximal</i>
Gácsi et al. (2009) ^a	Domestic Dogs, <i>C. familiaris</i> (23)	<i>Momentary Distal</i> <i>Momentary Proximal</i>
Gácsi et al. (2009) ^a	Domestic Dogs, <i>C. familiaris</i> (180)	<i>Momentary Distal</i>
Gácsi, McGreevy, Kara & Miklósi (2009) ^b	Domestic Dogs, <i>C. familiaris</i> (140)	<i>Momentary Distal</i>
Hare & Tomasello (1999) ^b	Domestic Dogs, <i>C. familiaris</i> (10)	<i>Contralateral</i>
Hare, Brown, Williamson & Tomasello (2002) ^a	Domestic Dogs, <i>C. familiaris</i> (12)	<i>Contralateral Proximal</i>
Hare & Tomasello (2004) ^b	Chimpanzees, <i>P. troglodytes</i> (12)	<i>Contralateral Proximal</i>
Hare et al. (2005) ^a	Domestic Dogs, <i>C. familiaris</i> (11)	<i>Dynamic</i>

Hattori, Kurashima & Fujita (2007) ^a	Capuchins, <i>C. abella</i> (5)	No pointing cues given.
Hegedüs Bálint, Miklósi & Pongrácz (2013) ^a	Domestic Dogs, <i>C. familiaris</i> (61)	<i>Momentary Distal</i>
Hernádi, Kis, Turcsán & Topál (2012) ^a	Domestic Dogs, <i>C. familiaris</i> (18)	<i>Momentary Proximal</i>
Herrmann, Melis & Tomasello (2005) ^b	Chimpanzees, <i>P. troglodytes</i> (12)	No pointing cues given.
	Orangutans, <i>P. pygmaeus</i> (6)	
	Gorillas, <i>G. gorilla</i> (6)	
	Bonobos, <i>Pan paniscus</i> (4)	
Herrmann et al. (2007) ^a	Chimpanzees, <i>P. troglodytes</i> (106)	<i>Contralateral Dynamic Proximal</i>
	Orangutans, <i>P. pygmaeus</i> (32)	
Hopkins, Russell, McIntyre & Leavens (2013) ^b	Chimpanzees, <i>P. troglodytes</i> (35)	<i>Proximal</i>
Inoue, Inoue & Itakura (2004) ^b	White-Handed Gibbon, <i>Hylobates lar</i> (1)	<i>Proximal</i>
Itakura & Tanaka (1998) ^b	Chimpanzees, <i>P. troglodytes</i> (2)	<i>Proximal</i>
	Orangutan, <i>P. pygmaeus</i> (1)	
Itakura, Agnetta, Hare & Tomasello (1999) ^b	Chimpanzees, <i>P. troglodytes</i> (13)	No properties known.
Kaminski, Schulz & Tomasello (2011) ^a	Domestic Dogs, <i>C. familiaris</i> (50)	<i>Contralateral Momentary Distal</i>

Kirchhofer, Zimmermann, Kaminski & Tomasello (2012) ^b	Domestic Dogs, <i>C. familiaris</i> (32) Chimpanzees, <i>P. troglodytes</i> (20)	<i>Ipsilateral Dynamic Distal</i>
Kraus, van Waveren & Huebner (2014) ^a	Domestic Dogs, <i>C. familiaris</i> (40)	<i>Ipsilateral Momentary Proximal</i>
Lakatos, Dóka, Miklósi (2007) ^a	Domestic Dogs, <i>C. familiaris</i> (14)	<i>Ipsilateral Momentary Distal</i> <i>Contralateral Momentary Distal</i>
Lakatos, Soproni, Dóka & Miklósi (2009) ^a	Domestic Dogs, <i>C. familiaris</i> (15)	<i>Ipsilateral Momentary Distal</i> <i>Contralateral Momentary Distal</i>
Lyn, Russell & Hopkins (2010) ^b	Chimpanzees, <i>P. troglodytes</i> (10) Bonobos, <i>P. Paniscus</i> (7)	<i>Proximal</i>
Maclean, Krupenye & Hare (2014) ^a	Domestic Dogs, <i>C. familiaris</i> (40)	<i>Ipsilateral Dynamic</i>
Maclean, Herrmann, Suchindran & Hare (2017) ^a	Domestic Dogs, <i>C. familiaris</i> (552)	<i>Ipsilateral Dynamic</i>
Marsh (2012) ^b	Orangutans, <i>P. pygmaeus</i> (5)	No pointing cues given.
McKinley & Sambrook (2012) ^b	Domestic Dogs, <i>C. familiaris</i> (16)	<i>Dynamic</i>
Miklósi et al. (2005) ^a	Domestic Dogs, <i>C. familiaris</i> (21)	<i>Dynamic Proximal</i> <i>Dynamic Distal</i> <i>Momentary Proximal</i> <i>Momentary Distal</i>
Mulcahy & Call (2009) ^b	Chimpanzees, <i>P. troglodytes</i> (12)	<i>Contralateral Dynamic Distal</i>

	Bonobos, <i>P. paniscus</i> (4)	<i>Contralateral Dynamic Proximal</i>
	Orangutans, <i>P. pygmaeus</i> (3)	
Mulcahy & Suddendorf (2011) ^a	Orangutan, <i>P. pygmaeus</i> (1)	<i>Dynamic Proximal</i>
		<i>Dynamic Distal</i>
Nakajima, Fukuoka, Takamatsu & Chin (2009) ^b	Domestic Dogs, <i>C. familiaris</i> (9)	<i>Contralateral Dynamic Distal</i>
Neiworth, Burman, Basile & Lickteig (2002) ^a	Cotton-Top Tamarins, <i>Saguinis oedipus</i> (6)	<i>Proximal</i>
Okamoto-Barth, Tomonaga, Tanaka & Matsuzawa (2008) ^a	Chimpanzees, <i>P. troglodytes</i> (3)	<i>Proximal</i>
Okamoto et al. (2002) ^a	Chimpanzee, <i>P. troglodytes</i> (1)	<i>Proximal</i>
Peignot & Anderson (1999) ^a	Gorillas, <i>G. gorilla</i> (5)	<i>Proximal</i>
Pettersson, Kaminski, Herrmann & Tomasello (2011) ^b	Domestic Dogs, <i>C. familiaris</i> (76)	<i>Contralateral Momentary Distal</i>
Plaude & Fiset (2013) ^b	Domestic Dogs, <i>C. familiaris</i> (10)	<i>Ipsilateral Momentary Proximal</i>
Pongrácz, Gácsi, Hegedüs, Péter & Miklósi (2013) ^b	Domestic Dogs, <i>C. familiaris</i> (115)	<i>Ipsilateral Momentary Distal</i>
		<i>Contralateral Momentary Distal</i>
Povinelli, Nelson & Boysen (1990) ^a	Chimpanzees, <i>P. troglodytes</i> (4)	No properties known.
Povinelli, Parks & Novak (1991) ^a	Rhesus Macaques, <i>M. mulatta</i> (4)	No properties known.

Povinelli, Reaux, Bierschwale, Allain & Simon (1997) ^b	Chimpanzees, <i>P. troglodytes</i> (7)	<i>Distal</i>
Povinelli, Bierschwale & Čech (1999) ^a	Chimpanzees, <i>P. troglodytes</i> (7)	No properties known.
Riedel, Schumann, Kaminski, Call & Tomasello (2007) ^b	Domestic Dogs, <i>C. familiaris</i> (64)	<i>Contralateral Dynamic Proximal</i>
Schmidjell, Range, Huber & Virányi (2004) ^a	Domestic Dogs, <i>C. familiaris</i> (102)	<i>Ipsilateral Momentary Distal</i>
Schmitt, Schloegl & Fischer (2014) ^b	Long-Tailed Macaques, <i>Macaca fascicularis</i> (10)	<i>Contralateral Dynamic Proximal</i>
Takaoka, Maeda, Hori & Fujita (2015) ^a	Domestic Dogs, <i>C. familiaris</i> (65)	<i>Momentary Proximal</i>
Tan, Tao & Su (2014) ^b	Golden Snub-Nosed Monkeys, <i>Rhinopithecus roxellana</i> (4)	<i>Ipsilateral Dynamic</i>
Tomasello, Call & Gluckman (1997) ^b	Chimpanzees, <i>P. troglodytes</i> (6) Orangutans, <i>P. pygmaeus</i> (3)	<i>Dynamic Proximal</i>
Udell, Dorey & Wynne (2008) ^b	Domestic Dogs, <i>C. familiaris</i> (46)	<i>Momentary Distal</i>
Udell, Dorey & Wynne (2010) ^b	Domestic Dogs, <i>C. familiaris</i> (23)	<i>Ipsilateral Momentary Distal</i> <i>Ipsilateral Dynamic Proximal</i>

Udell, Ewald, Dorey & Wynne (2014) ^a	Domestic Dogs, <i>C. familiaris</i> (36)	<i>Ipsilateral Momentary Distal</i>
Udell et al. (2013) ^a	Domestic Dogs, <i>C. familiaris</i> (58)	<i>Static Proximal</i> <i>Dynamic Proximal</i> <i>Momentary Proximal</i> <i>Static Distal</i> <i>Dynamic Distal</i> <i>Momentary Distal</i>
Udell, Giglio & Wynne (2008) ^b	Domestic Dogs, <i>C. familiaris</i> (6)	<i>Momentary Distal</i>
Udell, Spencer, Dorey & Wynne (2012) ^b	Domestic Dogs, <i>C. familiaris</i> (7)	<i>Dynamic Proximal</i> <i>Contralateral Dynamic Distal</i>
Vick & Anderson (2000) ^a	Capuchins, <i>C. apella</i> (3)	<i>Proximal</i>
Vick & Anderson (2003) ^a	Olive Baboons, <i>Papio anubis</i> (4)	No pointing cue given.
Wobber et al. (2009) ^a	Domestic Dogs, <i>C. familiaris</i> (59)	<i>Contralateral Dynamic Distal</i>
Zaine, Domeniconi & Wynne (2015) ^a	Domestic Dogs, <i>C. familiaris</i> (60)	<i>Ipsilateral Momentary Distal</i> <i>Ipsilateral Momentary Proximal</i> <i>Ipsilateral Dynamic Proximal</i>
Zlatev, Madsen, Lenninger, Persson, Sayehli et al.	Chimpanzees, <i>P. troglodytes</i> (4)	<i>Dynamic Proximal</i>

Notes: ^a Denotes studies for which only life history data was available. ^b Denotes studies for which life history and individual performance data

(2013)^b

were available (except Bräuer et al., 2006, where performance data were only available for dogs and Itakura and Tanaka, 1998, where performance data were only available for orangutans).

Table S2: Rearing histories as reported in the original studies categories according to the human experience scale.

Human Experience Scale	Rearing History
Close	Pet
	Enculturated (incl. language-trained)
	Human-Reared
	Hand-Raised
	Riding School
	Sea World
	Working Gun Dog
Occasional	Nursery
	Mother-Captivity
	Farm- Enriched
	Farm- Standard
	Research Facility
	Stables

Zoo

Kennel

Free-ranging (dogs)

Seldom

Wild

Stray
