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6 Ontogeny vs. Phylogeny in Primate/Canid Comparisons:

7 A Meta-analysis of the Object Choice Task

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Highlights

17 1. The Object Choice Task (OCT) is a widely used experimental protocol that assesses the
18 understanding of directional cues, such as pointing.

19 2. We analysed the procedures administered to domestic dogs and nonhuman primates (sample
20 = 2,534 subjects) and found that systematically different procedures have been administered to
21 the two groups.

22 3. Both domestic dogs and nonhuman primates are sensitive to many of the factors we identify
23 as systematic confounds in between-species comparisons.

24 4. Widely reported species differences on the OCT between domestic dogs and nonhuman
25 primates cannot, therefore, be attributed to their different selective histories, because
26 procedural confounds with taxonomic classification cannot isolate selective history as the
27 relevant factor.

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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.

43 According to some theorists, the origins of human language may be found in gestural
44 communication (Arbib, 2005; Corballis, 2002) and there is profound interest in the effects of
45 selection on the capacity to comprehend referential (deictic) gestures (Hare, Brown,
46 Williamson, & Tomasello, 2002). The theoretical basis for this contemporary interest lies in
47 two key suppositions: (a) that the ability to grasp communicative intent is an essential cognitive
48 prerequisite for linguistic communication, in both developmental and evolutionary terms (e.g.,
49 Grice, 1975; Sperber & Wilson, 1995) and (b) that this cognitive ability can be objectively
50 measured (e.g., Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997; Tomasello, Call &
51 Gluckman, 1997). It has been well-demonstrated that human children's ability to follow
52 pointing gestures to particular loci is correlated with their later language acquisition (e.g.,
53 Colonna, Stams, Koster, & Noom, 2010). In typical development, this likely works by
54 facilitating audio-visual associations between the referents (the things pointed to or gazed at)
55 with the verbal labels for those referents. Thus, a child can point to an entity and elicit its name,
56 or a child can follow another's gaze or pointing gesture to a referent, bringing the referent into
57 their visual field at the same time that the referent's label is spoken (e.g., Baldwin & Moses,
58 1996). Comprehension of deictic cues developmentally precedes speech production and seems
59 to be functionally linked with language acquisition; this ability has therefore been characterized
60 as one component in a human species-specific biological adaptation for language (e.g.
61 Butterworth, 2003).

62 There is a variety of different techniques for measuring the comprehension of deictic
63 cues that have been administered to children for decades. For example, a common technique is
64 to determine whether children will visually orient in the direction of another's gaze or pointing
65 gesture (reviewed by Butterworth, 2003). Gestures form an important part of human
66 communication and the capacity to produce and comprehend them emerges in pre-verbal
67 infants. In Western societies, the index-finger point is the predominant form of deictic gesture,

68 used to direct another's attention to an object or event of interest (Butterworth, 2003;
69 Masataka, 2003; but see, e.g., Cooperrider, Slotta, & Núñez, 2018, for descriptions of non-
70 manual points). Human infants develop the ability to follow points at around 6 months of age
71 (Butterworth, 2001) and begin to produce points at around 12- 15 months (Franco &
72 Butterworth, 1996). The onset of pointing constitutes a significant developmental milestone
73 (e.g., Flack & Leavens, 2018; Leavens & Clark, 2017), and its onset has been shown to predict
74 the onset of speech (Colonnesi, Rieffe, Koops, & Perucchini, 2008; Iverson & Goldin-
75 Meadow, 2005), and a delay in, or lack of the development of pointing has been linked to
76 autism (Osterling & Dawson, 1994) and pervasive developmental disorders (Bernabei,
77 Caramigni, & Levi, 1998).

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

93 and the last common ancestor with the nonhuman primate comparison group in question.

94 The Object Choice Task (OCT) is a widely used experimental paradigm that measures
95 the ability of a subject to comprehend deictic (directional) cues, usually to find food
96 (Anderson, Sallaberry, & Barbieri, 1995). There is a widespread belief that nonhuman primates
97 have a deficient capacity to interpret deictic gestures, evidenced by their poor performances on
98 this task (e.g., Maclean, 2016). In contrast, domestic dogs (*Canis lupus familiaris*) tend to
99 demonstrate high success rates on the task, and the relative performances of both taxa have
100 been taken as evidence for selective histories that facilitate social cognition in domesticated
101 dogs and humans (i.e. the Domestication Hypothesis), while nonhuman primates are held to
102 lack these selective histories (e.g., Hare et al., 2002). This point of view sits uncomfortably
103 against a large body of evidence for the successful use of social cues by animals and their
104 sensitivity to social information in their environments (e.g., Call & Tomasello, 1994;
105 Flombaum & Santos, 2005; Haroush & Williams, 2015—see reviews by Lyn, 2010;
106 Monfardini, Reynaud, Prado & Meunier, 2017). A competing theoretical perspective accounts
107 for the performance differences on the OCT with reference to specific individual learning
108 histories, irrespective of selective history (i.e. the Lived Experiences Model)—according to this
109 line of reasoning, most captive great apes have impoverished social learning opportunities,
110 relative to pet dogs, human children, enculturated primates, and their wild conspecifics (e.g.,
111 Bard & Leavens, 2014; Leavens & Bard, 2011; Racine, Leavens, Susswein & Wereha, 2008).
112 Here we comprehensively review the OCT literature and show that experience with humans
113 and procedural variables better explain group performance differences between dogs and
114 nonhuman primates than do species classifications. When these mammals are matched on task-
115 relevant pre-experimental history and on key procedural variables, species differences
116 disappear. We find no evidence for a deficiency in social cognition, as measured by the OCT,
117 in nonhuman primates, relative to dogs.

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

124 Nonhuman primates, however, tend to have poor success rates on the OCT (Herrmann,
125 Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Kirchofer, Zimmermann, Kaminski, &
126 Tomasello, 2012). The results from studies with our nearest relatives, the great apes, have been
127 used to propagate theories such as the Cultural Intelligence Hypothesis (Herrmann et al., 2007),
128 the Shared Intentionality model (Tomasello & Carpenter, 2007), and the Vygotskian
129 Intelligence model (Moll & Tomasello, 2011), all of which share the premise that nonhuman
130 primates are unable to comprehend the communicative significance of informative gestural
131 cues and that, therefore, this is a human-unique ability that contributed to the emergence of
132 verbal communication in humans. This pattern of poor comprehension of deictic cues by
133 nonhuman primates sits uncomfortably against a large and growing literature demonstrating
134 that great apes frequently use pointing, themselves, in captivity, typically with no explicit
135 training to do so, along with many other animal taxa (see Krause et al., 2018, for review).

136 However, there exist some disparities in the literature as to the relative abilities of
137 different species, and, recently, some authors have begun to address these anomalous findings
138 with reference to methodological and procedural factors in OCT experiments that are
139 systematically confounded with species classification. In a review of ape OCT studies, Lyn
140 (2010) found performance differences on the OCT as a function of rearing history in apes, such
141 that enculturated apes, raised in an environment rich in human interaction, outperformed
142 institutionalised apes and thus argued for greater consideration of rearing history when

143 comparing across species. Mulcahy and Hedge (2012) reviewed 63 OCT papers and concluded
144 that configurational differences in the testing of apes and dogs disadvantage the former due to
145 decreased salience of, and attention, to the cue being given. Finally, in a review of gaze-
146 following OCT studies with nonhuman primates Byrnie (2015) argues that there exists such
147 disparity between different species in their performance on the OCT that taking one species'
148 results as representative of their whole phylogenetic group leads to erroneous conclusions.
149 Here, we develop and extend these findings in the most comprehensive OCT literature review
150 to date, focusing primarily on domestic dogs and nonhuman primates, as it is evidence from
151 these species that has been used to support prevailing theories of human uniqueness in social
152 cognition and of the effects of domestication on dogs' social-cognitive abilities.

153 The first factor that we address is that of the systematic confound between life history
154 and species classification of subjects. Among humans, index-finger pointing is not a
155 universally employed communicative gesture, and, in fact, in some non-Western societies, lip-
156 pointing or nose-pointing is more predominantly used (Cooperrider et al., 2018; Enfield, 2001;
157 Wilkins, 2003). The comprehension of pointing is a developmental process in human infants
158 (Butterworth & Grover, 1988); it is through repeated exposure that pointing acquires its
159 cultural and communicative significance. In fact, one of the first OCT studies conducted with
160 nonhuman primates (Call & Tomasello, 1994) concluded that the marked difference in both
161 pointing comprehension and production between an enculturated and an institutionalised
162 orangutan was due to the subjects' differential experiences of human interaction. Call and
163 Tomasello (1994) suggested that humanlike interaction in early ontogeny, therefore, was
164 necessary for the development of an understanding of others as intentional agents and they
165 remarked that this was possibly also the case for human infants. In spite of these speculations,
166 the OCT literature in the ensuing 20 years comprises a multitude of studies of nonhuman
167 primate in which the poor performance of samples of great apes raised in institutional settings

168 with minimal exposure to humanlike interaction is attributed to a core, phylogenetic species
169 difference in cognitive ability (e.g., Moore, Call, & Tomasello, 2015; Povinelli et al., 1997;
170 Tomasello et al., 1997; for critical analysis, see Leavens, Bard, & Hopkins, 2017; Lyn, 2010).

171 Bard and Leavens (2014) discussed the importance of social engagement in the
172 development of socio-cognitive skills in human infants, and there is an effect of the amount
173 and quality of human interaction on nonhuman primates' abilities to use human nonverbal cues
174 in much the same way (Bard, Bakeman, Boysen & Leavens, 2014). Studies which have
175 compared nonhuman primates from different rearing environments on the OCT have found
176 marked differences in their abilities as a function of their pre-experimental exposure to human
177 interaction (Lyn, Russell & Hopkins, 2010). Hence, we argue that it is invalid to conclude that
178 differences in experimental performance are due to species differences, without considering the
179 experiential histories of all of the individuals tested.

180 This is further emphasised by the wealth of studies concluding that domestic dogs'
181 superior performance on the OCT reflects specialised socio-cognitive skills evolved through
182 their long history of domestication (Hare & Tomasello, 1999; Hare & Tomasello, 2005).
183 Whilst pet dogs, who are extensively exposed to human interaction, are indeed adept at passing
184 the OCT, the poor performance of dogs with alternative life histories, such as shelter dogs or
185 kennel-bred research dogs (D'Aniello et al., 2017; Lazarowski & Dorman, 2015; Udell, Dorey
186 & Wynne, 2010) demonstrates that this is not, in fact, an innate, evolutionarily derived
187 adaptation. Lea and Osthaus (2018) suggested that in order to assess the extent to which dogs'
188 cognitive skills are exceptional, it is necessary to consider their phylogenetic, ecological and
189 anthropogenic backgrounds, comparing their abilities to representatives of taxonomic groups
190 that share common features of these: other carnivores, other social hunters and other domestic
191 animals, respectively. They argued that when dogs' social cognition is considered in this way,
192 there is no evidence to show that they have unique abilities- other carnivores (e.g. sea lions,

193 seals and dolphins) demonstrate high success rates and other domestic animals (e.g. pigs and
194 goats) show similar abilities to follow points. With regard to social hunters, there is evidence
195 that chimpanzees, too, can comprehend pointing cues (Leavens & Clark, 2017). Thus, as
196 argued by Lea and Osthaus (2018), when dogs' abilities are considered from these three
197 perspectives, there is no evidence to suggest that their sociocognitive skills are exceptional.

198 The second factor, we propose, is the use of incommensurate testing protocols for
199 representatives of different taxa. For example, in order to ensure the safety of the experimenter,
200 the testing of nonhuman primates typically involves subjects participating from within a cage,
201 thus introducing a barrier between the subject and the experimenter and testing apparatus.
202 Testing domestic dogs does not entail these same safety precautions, and so this barrier in the
203 testing paradigm is generally absent. There are, however, two notable exceptions. The first
204 (Udell, Dorey & Wynne, 2008) involved an OCT with domestic dogs in which a tapping cue
205 was presented to subjects tested either with or without a fence separating subject and
206 experimenter. The authors reported a significant difference between the performance levels of
207 the two groups, with those in the barrier condition experiencing a 31% decrement in success
208 levels. In addition, the only study to date which has involved the presentation of a pointing cue
209 in a testing paradigm where a barrier was present for domestic dogs found significantly lower
210 success rates in those dogs for which a barrier was present, compared to dogs for which this
211 barrier was absent (Kirchhofer et al., 2012). We therefore argue that this difference in the
212 testing paradigm represents a confound with taxonomic classification, which should not be
213 ignored when comparing species' relative abilities.

214 A further systematic confound we consider here concerns the broad range of types of
215 pointing cues presented in OCT experiments. Typically, researchers use an ipsilateral point
216 where the ipsilateral arm is extended and the index finger outstretched (i.e., a point with the
217 hand on the same side as the baited container is used). Miklósi and Soproni (2006)

218 differentiated between types of cues, specifically distal and proximal points, where the
219 distances between the fingertip and the target are greater than 50cm (i.e. distal) and between 10
220 and 40cm (i.e. proximal), distinguished as so because the former is considered to be within
221 reach and the latter not; and between momentary and dynamic pointing where the cue is
222 presented for 1-2 seconds (i.e. momentary) or the cue is maintained until a choice has been
223 made (i.e. dynamic). They reported that representatives of a number of species perform at
224 different levels according to the type of cue presented and attribute this to the cues' differential
225 effects on salience and memory. Udell, Hall, Morrison, Dorey and Wynne (2013) assessed
226 dogs' performance on nine point types and found differences in levels of success as a function
227 of the temporal and distal properties of the pointing cues.

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

243 performance was lower in the peripheral version.

244 Thus, it is becoming apparent that there may be systematic differences across different
245 taxa in (a) their level of familiarity with humans and human signaling conventions, (b) the
246 physical circumstances in which representatives from different taxa are tested—especially,
247 whether or not they are tested through cage mesh or other barriers, (c) the types of deictic cues
248 used to test comprehension, and (d) the configurations of the key elements in the OCT: the
249 subject, the experimenter, and the referents. If these factors are systematically confounded with
250 taxonomic classification, then current reports of dog-primate differences in sociocognitive
251 abilities, based in their different selective histories, would be open to alternative interpretations,
252 based in life history and procedural factors. In order to investigate the prevalence of these
253 confounds, individual life history data, as classified by the original studies, and performance
254 data were collated from OCT studies published up until 2019. Given the enormous
255 morphological variation that exists between different dog breeds (e.g., Shearin & Ostrander,
256 2010), we sampled the literatures for domestic dogs (an unusually and artificially diverse
257 species) with representatives across the order Primates.

258

259 **Method**

260 **Literature Selection**

261 This study was conducted in two phases. In Phase 1 (2013-2016) we assembled every
262 published article on animals' comprehension of deictic cues in OCT studies that we could find,
263 across all vertebrate species, systematically noting the rearing environments where available.

264 This phase of data collection supported the Human Experience Scale that is depicted in Figure
265 1 and listed in Table S2. The literature search consisted of the following components:

266 Electronic databases (Scopus, ScienceDirect, PsychInfo and all Citation Databases included in
267 ISI web of knowledge) from 1990 – 2018 with keywords in abstracts: “object choice task”,

268 “object-choice”, object choice task (and) “animal”), citation search on author names, scanning
269 reference lists, and Google scholar. We also used reference lists in the published articles to find
270 additional reports not captured by our keyword searches. In addition, where we knew of
271 relevant studies not captured by the above methods, we added those to the database. During a
272 preliminary assessment of the database in 2016, it became apparent that systematic
273 comparisons between taxa would only be possible between canids and primates, because the
274 database was dominated by these two taxonomic groups (a finding reported by Krause et al.,
275 2018, Tables 1 & 2). Therefore, in Phase 2 (2016-2018), we focused on dogs and nonhuman
276 primates, extending our cut-off date from the originally planned 2015 to 2017.

277 Studies were included if they involved an object choice task with at least one pointing
278 cue condition, and, in order to collate the most individual data possible, no minimum sample
279 size was used to determine inclusion. As noted above, initially, data were collected from 99
280 studies comprising 43 vertebrate species. Individual rearing history, individual performance
281 data, or both, were available for 3277 subjects. This review focuses on nonhuman primate vs.
282 dog comparisons, for which data was available for 2534 individuals, including representatives
283 of 16 nonhuman primate species, from 71 studies (see Table S1). Of the nonhuman primates,
284 82% were great apes, with 64% of the nonhuman primate subjects comprised of chimpanzees.

285 **Subjects**

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

293 original study. Figure 1 shows the human experience scale and the allocation of the original
294 reported rearing histories to this scale.

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

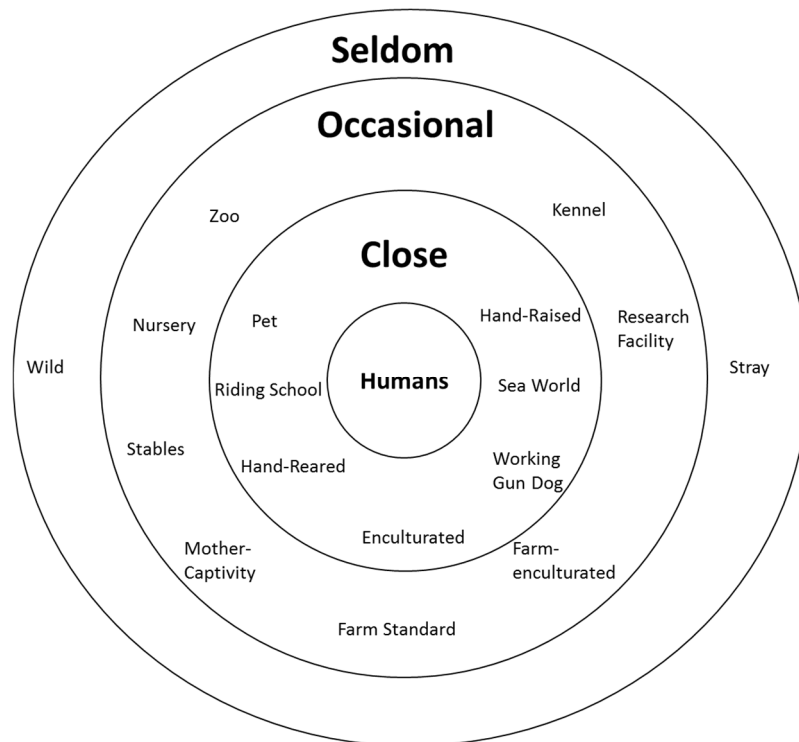
300 **Cue Types**

301 For the purposes of this review, performance data were analysed only where one or
302 more pointing cues were presented, and these cues were categorised according to Miklósi and
303 Soproni's (2006) definitions. The following distinctions were made:

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

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

314 **Proximal point vs. distal point.** A point is said to be proximal when the distance
315 between the fingertip and the baited container is less than 40cm. A distal point is categorised as
316 such when the distance between the fingertip and the baited container is equal to or greater than
317 40cm.



318

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

321

322 **Individual Performance Data**

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

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

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

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

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

350

351 **Results**

352 **Human experience**

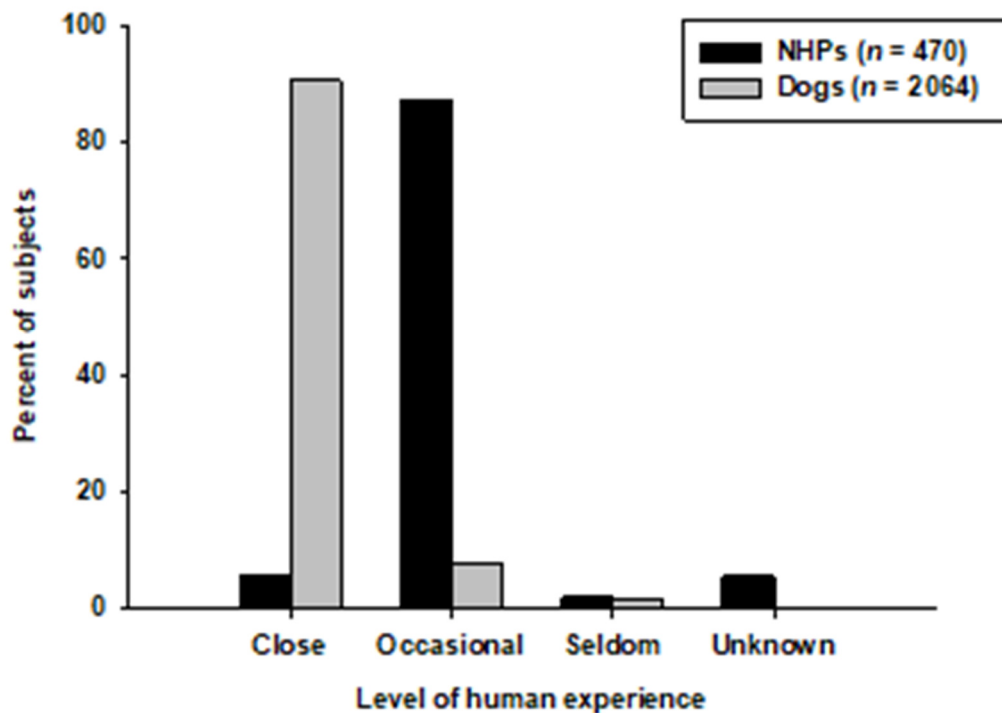
353 Rearing history data were available for 2534 subjects, comprised of 2064 dogs and 470
354 nonhuman primates. There was a significant difference in the level of human experience
355 between dogs and nonhuman primates (Kruskal-Wallis, $\chi^2(3, N = 2534) = 1550, p < .001$) with
356 91% of dogs being categorised as “close”, compared with 6% of nonhuman primates; within
357 nonhuman primates, 87% were categorised as “occasional” and 2% as “seldom” (Figure 2).

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

361

362 **Human experience and performance**

363 Importantly, a relationship was also found between human experience and performance
364 on the OCT on a number of pointing cues. For *ipsilateral* pointing cues, within nonhuman
365 primates and dogs, there was a significant difference in performance between subjects in the
366 different levels of the human experience scale, Kruskal-Wallis $\chi^2(2, N = 212) = 16.43, p =$
367 $.001, r = .28$. Pairwise comparisons showed that subjects categorised as “close” ($N = 174, Mdn$
368 $z = 1.26$) scored higher than those categorised as “occasional” ($N = 22, Mdn z = 0.00$), Mann-
369 Whitney $U = 1209.5, p = .005$, and those categorised as “seldom” ($N = 16, Mdn z = -0.32$),
370 Mann-Whitney $U = 731.00, p = .002$. There was no significant difference between those
371 categorised as “occasional” ($N = 22, Mdn z = 0.00$) and “seldom” ($N = 16, Mdn z = -0.32$),
372 Mann-Whitney $U = 135.35, p = .227$, mean $z = 0.36, SD = 0.98$). Within-nonhuman primates,
373 sample sizes were too small (22 “occasional” subjects, 2 “seldom” subjects) for sufficient
374 statistical power for comparisons. Within dogs, those categorised as “close” ($N = 174, Mdn z =$
375 1.26) scored higher than those categorised as “seldom” ($N = 14, Mdn z = -0.63$) (Mann-
376 Whitney $U = 13.97, p < .001$). For *contralateral* pointing cues, in contrast, within nonhuman
377 primates and dogs, those categorised as “occasional” ($N = 95, Mdn z = 1.89$) outperformed
378 those categorised as “close” ($N = 6, Mdn z = 0.00$), (Mann-Whitney $U = 136.5, p = .029$). Those
379 categorised as “occasional” comprised solely nonhuman chimpanzee subjects and so
380 further analyses were not possible. This suggests that for *contralateral* cues, there may be
381 inherent species differences in responsiveness to cue features that explain the performance
382 differences, or, alternatively, a more complex relationship with human experience may exist



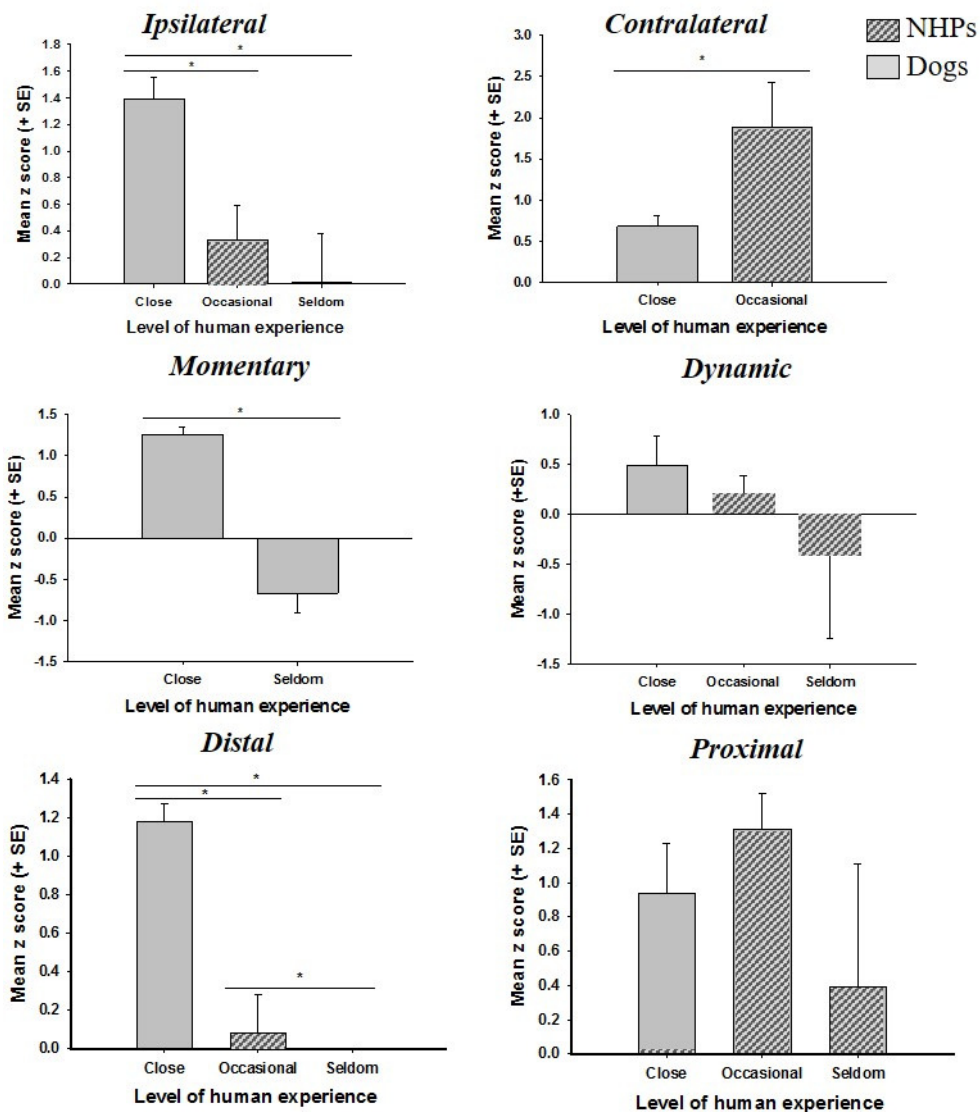
383 **Figure 2.** The distribution of levels of human experience between nonhuman primates (NHPs)
 384 and dogs.

385

386 that leads to the suppression of comprehension of contralateral cues as a result of increased
 387 exposure to humans. However, given the systematic confounds between taxonomic
 388 classification and cue type, manifest in Figure 3, these possibilities remain speculative. Where
 389 *momentary* pointing cues were presented, within nonhuman primates and dogs, subjects
 390 categorised as “close” ($N = 356$, $Mdn z = 0.89$) scored higher than those categorised as
 391 “seldom” ($N = 22$, $Mdn z = -0.63$), Mann-Whitney $U = 1235.5$, $p < .001$. This was a within-
 392 dogs difference, because no performance data were available for nonhuman primates on this
 393 cue, and thus replicates previous findings (D’Aniello et al., 2017; Lazarowski & Dorman,
 394 2015; Udell, Dorey & Wynne, 2010) that dogs that have experienced greater exposure to
 395 humans are more capable in understanding this more difficult pointing gesture.

396

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



398

399 **Figure 3.** The mean standardised *z* scores (and standard errors) of nonhuman primates and
 400 dogs and the proportion of each species/ taxonomic group contributing to those means,
 401 categorised according to level of human experience on six different pointing cues. * denotes *p*
 402 < .05.

403

404 the categorisations of level of human experience within nonhuman primates and dogs, Kruskal-
 405 Wallis $\chi^2 (2, N = 82) = 1.84, p = .398$, nor within nonhuman primates alone, Kruskal-Wallis χ^2

406 (2, $N = 36$) = 2.81, $p = .246$. Dogs for which there were performance data available were all
407 categorised as “close” so within-species analyses were not possible. This shows that level of
408 human experience may be of less importance in the comprehension of this easier pointing cue
409 than for those more-difficult-to-follow cues.

410 Where *distal* cues were presented, within nonhuman primates and dogs, there was a
411 significant effect of level of human experience on performance, (Kruskal-Wallis χ^2 (2, $N = 395$)
412 = 35.27, $p < .001$. Pairwise comparisons showed that those categorised as “close” ($N = 353$,
413 $Mdn z = 0.89$) scored higher than those categorised as “occasional” ($N = 20$, $Mdn z = 0.00$),
414 Mann-Whitney $U = 2066.00$, $p = .002$, and those categorised as “seldom” ($N = 22$, $Mdn z = -$
415 0.63), Mann-Whitney $U = 1334.50$, $p < .001$ (this was a within-dog comparison). “Occasional”
416 ($N = 20$, $Mdn z = 0.00$) subjects also scored higher than “seldom” subjects ($N = 22$, $Mdn z = -$
417 0.63), Mann-Whitney $U = 126.00$, $p = .017$. Within-nonhuman primate comparisons were not
418 possible because all subjects for which there were data were categorised as “occasional”. This
419 shows that level of human experience may better explain performance differences than
420 taxonomic group affiliation.

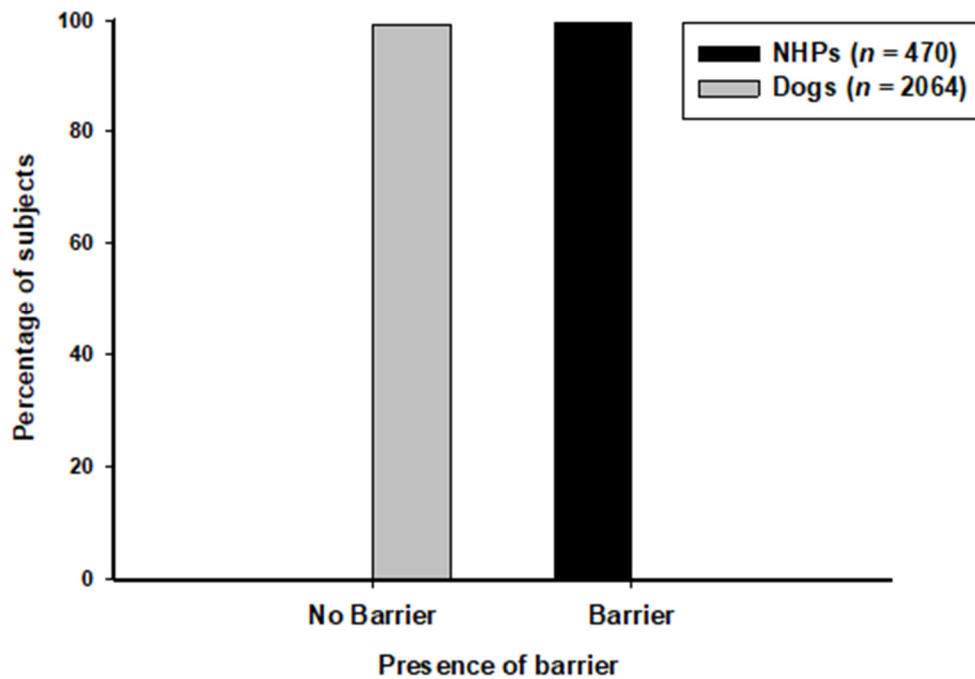
421 Where *proximal* cues were presented, there was no significant effect of level of human
422 experience on performance, (Kruskal-Wallis χ^2 (2, $N = 94$) = 2.12, $p < .346$. Within nonhuman
423 primates only, there was no significant effect of human experience on performance, (Kruskal-
424 Wallis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

429

430

431 **Presence of a barrier**

432 Comparisons of the presence of a barrier in the testing environment between nonhuman
433 primates and dogs showed that less than 1% of dogs were tested with a barrier, compared with
434 99% of nonhuman primates, $\chi^2(1, N= 2534) = 2411.77, p <.001$, as shown in Figure 4. This
435 highlights the systematic inconsistencies present in testing environments across the two
436 taxonomic groups, and, therefore, the reduced validity of interpreting group differences as
437 phylogenetic traces of differences in selective histories. Comparisons of performance between
438 dogs tested with a barrier and those tested without were not possible because among the only



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

440
441 two studies to introduce barriers to the testing protocol, Kirchofer et al. (2012) did not specify
442 which individuals participated in the barrier condition and Udell et al.'s (2008) dogs tested with
443 a barrier did not take part in a pointing cue condition. Comparisons between nonhuman
444 primates tested with and without a barrier were not possible because only 3 infant chimpanzees
445 were tested without a barrier present (Okamoto-Barth, Tomonaga, Tanaka & Matsuzawa,

446 2008), thus sufficient statistical power was lacking.

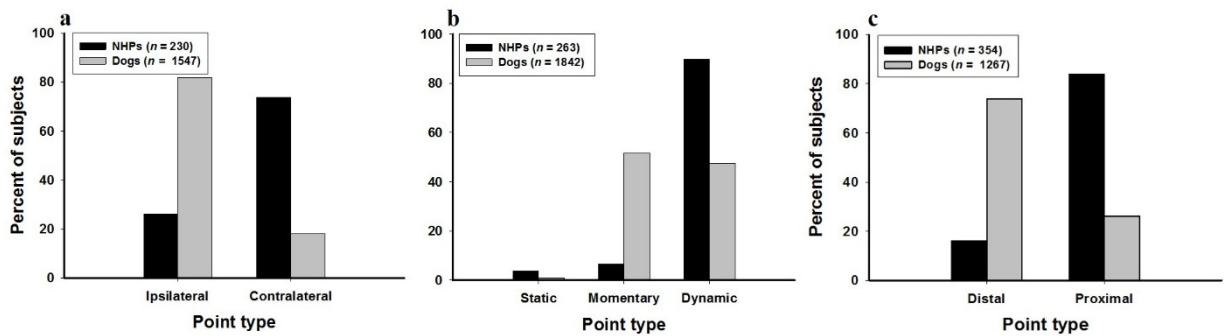
447

448 **Cue types**

449 Among those subjects with only one type of pointing cue, differences were also found
450 regarding the types of cues presented to the two taxonomic groups. There was a significant
451 difference between lateral properties (i.e. whether ipsilateral or contralateral hand was used to
452 point) of cues presented to nonhuman primates and dogs, with 26% of points to nonhuman
453 primates being *ipsilateral* and 74% *contralateral*, compared with 82% *ipsilateral* and 18%
454 *contralateral* for dogs, $\chi^2(1, N = 1777) = 328.59, p < .001$, as shown in Figure 5a. For
455 nonhuman primates, there was no significant difference in performance between *ipsilateral* (N
456 $= 24, Mdn z = 0.25$) and *contralateral* ($N = 6, Mdn z = 1.89$), Mann-Whitney $U = 34.5, p = .05$,
457 shown in Figure 6a. Dogs scored significantly higher on *ipsilateral* ($N = 188, Mdn z = 1.00$)
458 than on *contralateral* ($N = 95, Mdn z = 0.00$) pointing cues, shown in Figure 6b. This shows
459 that lateral cue features can differentially affect different species' performance.

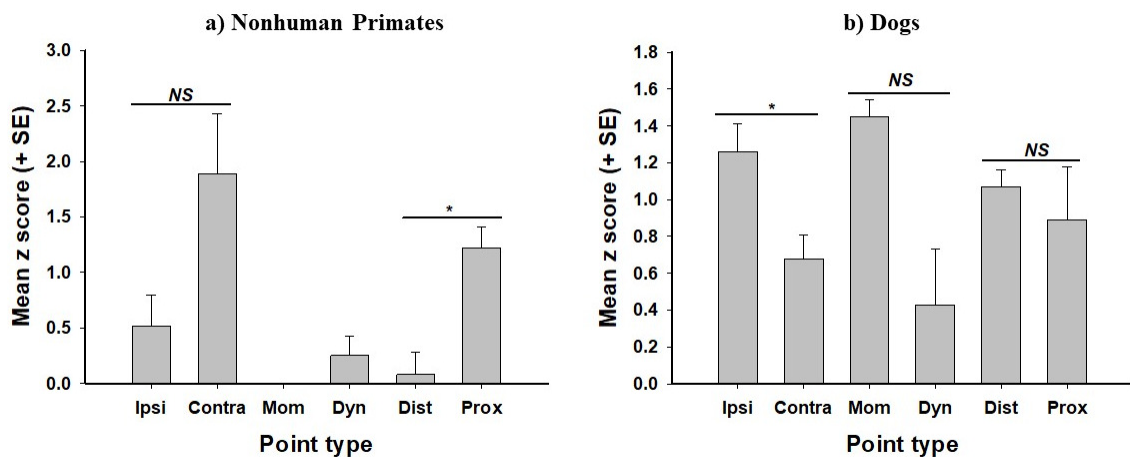
460 Figure 5b shows the percentage of the different temporal cue types presented to
461 nonhuman primates and dogs. There was a significant difference across taxa in temporal cue
462 properties, with 4% of cues presented to nonhuman primates being static, 7% momentary and
463 90% dynamic, compared with 1% static for dogs, 45% momentary and 42% dynamic, Kruskal-
464 type according to a) lateral features b) temporal features and c) distance features of the cue.
465 Wallis $\chi^2(2, N = 2105) = 195.48, p < .001, r = .30$. This demonstrates that there are also
466 systematic differences in the temporal properties of cue types presented to nonhuman primates
467 and dogs, with a bias towards dynamic pointing for nonhuman primates. There were
468 insufficient data to analyse performance differences between the three point types for
469 nonhuman primates (see Figure 6a), and there was no significant difference in performance on
470 *dynamic* ($N = 46, Mdn z = 0.57$) and *momentary* ($N = 378, Mdn z = 0.89$) pointing cues within

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



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

473



474 **Figure 6.** The mean z scores and standard errors for a) nonhuman primates and b) dogs on the
 475 different pointing cue types. Ipsi = *ipsilateral*; Contra = *contralateral*; Dyn = *dynamic*; Mom =
 476 *momentary*; Dist = *distal*; Prox = *proximal*. * denotes significant at $p < .05$. NS = not
 477 significant. Please note difference in scale ranges for the Z-score.

478

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

485 higher on *proximal* ($N = 54$, $Mdn z = 0.90$) than on *distal* ($N = 20$, $Mdn z = 0.00$) pointing cues,
486 Mann Whitney $U = 309.50$, $p = .005$ (Figure 6a). Within dogs, there was no significant
487 difference in performance between *distal* ($N = 375$, $Mdn z = 1.07$) and *proximal* ($N = 43$, $Mdn z$
488 $= 0.63$) pointing cues, Mann-Whitney $U = 7441.00$, $p = .406$ (Figure 6b). This demonstrates
489 that, for nonhuman primates, there are performance differences associated with the distance
490 properties of the cue being presented.

491

492 **Multiple conditions**

493 Four hundred and two subjects took part in studies in which they were presented with
494 multiple cue types. Individual performance data were available for 210 of these subjects. There
495 were insufficient data to conduct statistically robust comparisons of performance according to
496 level of human experience. Analyses were possible, however, for comparisons of performance
497 according to cue type. Nonhuman primates scored higher when tested with *distal* cues (mean z
498 $= 2.47$, $SD = 1.62$) than with *proximal* cues (mean $z = 0.75$, $SD = 1.62$), ($Z = -3.01$, $p = .003$).
499 Dogs, in contrast, performed better when tested with *proximal* (mean $z = 3.90$, $SD = 0.62$)
500 rather than *distal* cues (mean $z = 0.51$, $SD = 2.59$), ($Z = -2.37$, $p = .018$). With regard to
501 temporal properties of cues, nonhuman primates scored higher when tested with *dynamic*
502 (mean $z = 1.07$, $SD = 0.93$) rather than *momentary* (mean $z = 0.05$, $SD = 1.09$) cues, ($Z = -2.58$,
503 $p = .010$). This was also the case for dogs (*dynamic* mean $z = 2.33$, $SD = 1.50$; *momentary*
504 mean $z = 0.80$, $SD = 1.75$), ($Z = -2.94$, $p = .003$). This shows that both temporal and distance
505 properties of pointing cues may affect individual performances, and that there may be different
506 processes at play in terms of their effects depending on taxonomic group. There were
507 insufficient data to analyse performance for *static*, *ipsilateral* and *contralateral* pointing cues.

508

509 **Inter-object distance**

510 Further procedural differences were found with respect to the inter-object distance
511 between containers. Dogs ($Mdn = 155.0$ cm) were tested with significantly greater inter-object
512 distances than nonhuman primates ($Mdn = 58.0$ cm), (Mann-Whitney $U = 4917.5$, $z = -27.99$, p
513 $<.001$), demonstrating a bias towards greater distances between the containers for dogs than for
514 nonhuman primates, congruent with Mulcahy and Hedge's (2012) findings. Analyses of the
515 relationship between inter-object distance and performance by species found significant
516 correlations between these inter-object distance and cue types, although with different patterns
517 between the two species. For dogs, *ipsilateral*: significant positive correlation ($r_s(155) = .17$, p
518 $= .032$), *contralateral*: significant positive correlation ($r_s(19) = .75$, $p < .001$), *static*:
519 insufficient data, *momentary*: significant positive correlation: ($r_s(269) = .23$, $p < .001$),
520 *dynamic*: no significant correlation ($r_s(46) = -.17$, $p = .261$), *distal*: significant positive
521 correlation ($r_s(299) = .319$, $p < .001$), and for *proximal*: insufficient data. For nonhuman
522 primates, *ipsilateral*: significant negative correlation ($r_s(24) = -.64$, $p = .001$), *contralateral*:
523 insufficient data, *static*: insufficient data, *momentary*: insufficient data, *dynamic*: no significant
524 correlation ($r_s(27) = -.04$, $p = .836$), *distal*: insufficient data, and for *proximal*: no significant
525 correlation ($r_s(41) = -.214$, $p = .180$). Thus, for dogs, increasing inter-object distance correlates
526 positively with performance in the face of cues that are characteristic of past research with this
527 species (*ipsilateral*, *momentary*, *distal* points—see Figure 5). In contrast, for nonhuman
528 primates, sample sizes are generally too small to invoke confidence—the only significant
529 correlation was a negative correlation between inter-object distance and performance with
530 *ipsilateral* cues, which are not the most characteristic cues used in studies with nonhuman
531 primates (Figure 5a).

532

533

Discussion

534 Our results highlight the procedural and methodological factors that can influence a

535 subject's performance on the OCT and demonstrate that the trend in the existing literature to
536 compare across these two taxonomic groups without considering these factors greatly reduces
537 the legitimacy of findings. First, it is clear from the results that experiential history with
538 humans can influence an individual's ability in the comprehension of pointing cues. This
539 supports the results of Udell and colleagues (Udell, Dorey & Wynne, 2008; Udell et al., 2012),
540 Lyn and her colleagues (Lyn, 2010; Lyn, Russell & Hopkins, 2010), and numerous others (e.g.,
541 Bard, Bakeman, Boysen, & Leavens, 2014; Call & Tomasello, 1994; Hopkins, Russell,
542 McIntyre, & Leavens, 2013; Pedersen, Segerdahl, & Fields, 2009; Scheel, Shaw, & Gardner,
543 2016) who suggested that exposure to humans and immersion in their environment is a key
544 factor in the development of the comprehension of human communicative cues. As shown in
545 Figure 2, the nonhuman primate subjects in the existing literature come from a wide variety of
546 rearing backgrounds, with only 6% of subjects being enculturated and the majority being
547 nursery-raised or mother-reared in captivity. When this is compared with the dogs' rearing
548 history data, it is clear that the vast majority of dogs are sampled from a pet background. Those
549 who had more impoverished backgrounds in terms of human experience--for example, stray,
550 shelter and free ranging dogs--demonstrated lower success rates on the OCT (e.g., Udell, Dorey
551 & Wynne, 2008; Udell, Dorey & Wynne, 2010). Thus, to make generalisations about the
552 relative abilities of species without considering their experiential backgrounds (e.g. Herrmann
553 et al., 2007; Kirchhofer et al., 2012) and, furthermore, to base theories of species' evolutionary
554 histories on results from such studies (e.g. Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006;
555 Hare & Tomasello, 2005) is not warranted, due to the pervading imbalance in task-relevant
556 pre-experimental experience between dogs and nonhuman primates. Moreover, enculturated
557 apes significantly outperform institutionalized apes when they are directly compared (Lyn et
558 al., 2010; Russell, Lyn, Schaeffer, & Hopkins, 2011). Contemporary claims to the effect that
559 dogs have greater social awareness than nonhuman primates are, thus, not supported by

560 compelling experimental evidence.

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

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

585 Finally, the differences found in the distances between the containers in the testing
586 paradigm support Mulcahy and colleagues' (Mulcahy & Call, 2009; Mulcahy & Hedge, 2012)
587 assertions that nonhuman primates tend to be tested with a central version of the task, whereas
588 dogs are tested with a more peripheral version. The authors suggest that placing containers
589 close together and within the direct line of vision of the subject can lead to the salience of the
590 containers distracting the subjects' attention from the cue being presented. Alternatively, it may
591 be that placing the containers further apart signifies an additional cost to make a choice, and, as
592 such, there is an increase in the attention afforded the cues by the subject. The positive
593 correlations found in the current review, between inter-object distance and performance on
594 several cue types provide support for these hypotheses and further evidence that inter-species
595 comparisons without regard for procedural factors such as these is neither appropriate nor
596 scientifically sound.

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

607 First, as advocated by Bard and Leavens (2014), researchers could establish
608 performance parameters across the full range of rearing histories within a species. With respect
609 to human experience, there is a large range of variation in the familiarity that individual animal

610 subjects will have with human communicative conventions, and this is true both of dogs and
611 nonhuman primates. Previous direct comparisons within species, across different levels of
612 exposure to human communicative conventions, have revealed that subjects that have had more
613 intensive exposure to humans perform systematically better than conspecifics raised in greater
614 isolation from humans on a variety of tasks, including the OCT (Bard et al., 2014; Call &
615 Tomasello, 1994; Lyn et al., 2010; Russell et al., 2011). These studies reveal that because these
616 organisms are developmentally responsive to quality and quantity of human contact, therefore
617 no systematic performance difference between species—on the OCT or any other such assay—
618 can be rationally attributed to evolutionary, as opposed to developmental factors. Consideration
619 of rearing history differences will, therefore, significantly improve the sophistication of
620 interpretations of these differences, as exemplified by Call and Tomasello (1994) and the
621 researchers who have followed them in considering the effects of human exposure on cognitive
622 development within species. In the fullness of time, as population parameters emerge from
623 more individual studies, then the degrees of responsiveness of different taxa to human exposure
624 will permit comparisons of these presumably different performance curves across species. The
625 essential point is that comparative psychologists cannot legitimately continue to assume that
626 pre-experimental developmental experience is irrelevant to performance.

627 A second promising approach to comparing across species is to directly manipulate the
628 task-relevant experiences of representatives of different taxa through explicit training regimens
629 (Leavens & Racine, 2009; Leavens et al., 2017). The ability to use others' deictic cues is a
630 developmental milestone in our species (Butterworth, 2001), and it is clear that human children
631 display this ability to use communicative cues only after many months of intensive exposure to
632 cultural environments characterized by frequent referential signalling, both verbally and non-
633 verbally. There is no reason, in principle, that human children could not learn to use these
634 communicative cues in these reference-intensive environments, notwithstanding that many

635 contemporary researchers have elected to interpret this developmental milestone as evidence
636 for human-unique cognitive abilities (for discussion, see, e.g., Leavens, 2018; Moore &
637 Corkum, 1994; Triesch, Teuscher, Deák, & Carlson, 2006). Thus, a promising corrective
638 approach is to intensively train animals to use referential cues; if representatives of a species
639 are incapable of learning to use these cues even after months of intensive training to use the
640 cue, then one might reasonably conclude that the species has an inherent difficulty
641 understanding these cues. If, on the other hand, such representatives can acquire the ability to
642 use directional cues, then this serves as a clear demonstration that a learning pathway exists for
643 this species to the use of human-given cues to object location. This approach can ameliorate the
644 deficiencies in pre-experimental learning opportunities that exist in the environments of some
645 captive animals (e.g., Bard & Leavens, 2014; Udell et al., 2012).

646 In conclusion, the current review builds on existing criticisms of the current state of the
647 OCT literature to further demonstrate that methodological and procedural confounds limit the
648 validity of the results of many studies. Moreover, we found examples, within each group,
649 where it was clear that certain methodological factors (e.g., cue type) were correlated with
650 performance; this pattern of findings strongly argues against theoretical interpretations of
651 previously published group differences between dogs and nonhuman primates as evidence for
652 inherent differences in cognitive capabilities (*contra*, e.g., Hare & Tomasello, 2004, 2005;
653 Kirchoffer et al., 2012); we think this pattern also provides a significant challenge to the
654 Domestication Hypothesis, the idea that dogs' performances on the OCT are better explained
655 with reference to their selective histories, as opposed to their ontogenetic experiences (Hare &
656 Tomasello, 2005). To the contrary, our analysis supports numerous previous reports that the
657 use of experimenter-given cues to find hidden objects is well within the competencies of
658 nonhumans, when they are treated pre-experimentally and experimentally like human children
659 or like domesticated animals (e.g., Lyn et al., 2010; Russell et al., 2011; Thomas, Murphy, Pitt,

660 Rivers, & Leavens, 2008; Udell et al., 2012); these findings are consistent with the Lived
661 Experiences model, the idea that organisms adapt, ontogenetically, to the specific ecological
662 features of their rearing environments, promulgated by, Bard and colleagues (e.g. Bard &
663 Leavens, 2014). To put this another way, based on this pattern of evidence, it is not necessary
664 to invoke human cognitive specializations to account for the ability to follow referential cues.
665 In order to gain a more comprehensive understanding of the abilities of different taxonomic
666 groups to understand human communicative cues, it is necessary for further research that
667 controls for the abovementioned factors to be conducted. We recommend that a series of
668 systematic experiments in which these variables are manipulated is required. This should begin
669 by manipulating such variables with human infant participants, such that the effect of, for
670 example, barriers or pointing cues can be established in this ‘enculturated’ sample, and then to
671 broaden the samples of species, maintaining consistency throughout and ensuring that
672 comparisons are only made across truly comparable groups. In addition, our analysis
673 demonstrates that much greater consideration needs to be given to ontogenetic influences on
674 behaviour, rather than the pervasive reliance on phylogenetic explanations that prevails in the
675 literature (Bard & Leavens, 2014; Leavens et al., 2017). Consistent with Udell and colleagues
676 (Udell, Dorey & Wynne, 2008a, 2008b, 2010) we argue that, prior to asserting reductionist
677 interpretations that assume that individuals’ behaviour is solely a function of their evolutionary
678 history, their individual learning experiences must be taken into account.
679

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Supplementary Materials

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Table S1. Authors and dates of publication; subject species, with sample size shown in parentheses; and cuing conditions of studies for which

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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>

(2013)^b

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1098 Notes: ^a Denotes studies for which only life history data was available. ^b Denotes studies for which life history and individual performance data
1099 were available (except Bräuer et al., 2006, where performance data were only available for dogs and Itakura and Tanaka, 1998, where
1100 performance data were only available for orangutans).

1101 *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

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