

# Animal Cognition

## The effect of experience and of dots' density and duration on the detection of coherent motion in dogs --Manuscript Draft--

<b>Manuscript Number:</b>					
<b>Full Title:</b>	The effect of experience and of dots' density and duration on the detection of coherent motion in dogs				
<b>Article Type:</b>	Original Article				
<b>Corresponding Author:</b>	Paolo Mongillo, DVM, PhD Università degli Studi di Padova Dipartimento di Biomedicina Comparata e Alimentazione ITALY				
<b>Corresponding Author Secondary Information:</b>					
<b>Corresponding Author's Institution:</b>	Università degli Studi di Padova Dipartimento di Biomedicina Comparata e Alimentazione				
<b>Corresponding Author's Secondary Institution:</b>					
<b>First Author:</b>	Orsolya Kanizsár, PhD				
<b>First Author Secondary Information:</b>					
<b>Order of Authors:</b>	Orsolya Kanizsár, PhD Paolo Mongillo, DVM, PhD Luca Battaglini, PhD Gianluca Campana, PhD Miina Lööke Lieta Marinelli, DVM, PhD				
<b>Order of Authors Secondary Information:</b>					
<b>Funding Information:</b>	<table border="1"><tr><td>Università degli Studi di Padova (DOR1673431)</td><td>Prof. Lieta Marinelli</td></tr><tr><td>Università degli Studi di Padova (PhD scholarship)</td><td>Dr Orsolya Kanizsár</td></tr></table>	Università degli Studi di Padova (DOR1673431)	Prof. Lieta Marinelli	Università degli Studi di Padova (PhD scholarship)	Dr Orsolya Kanizsár
Università degli Studi di Padova (DOR1673431)	Prof. Lieta Marinelli				
Università degli Studi di Padova (PhD scholarship)	Dr Orsolya Kanizsár				
<b>Abstract:</b>	<p>Knowledge about the mechanisms underlying canine vision is far from being exhaustive, especially that concerning post-retinal elaboration. One aspect that has received little attention is motion perception, and in spite of the common belief that dogs are extremely apt at detecting moving stimuli, there is no scientific support to such assumption. In fact, we recently showed that dogs have higher thresholds than humans for coherent motion detection (Kanizsar et al. 2017). This term refers to the ability of the visual system to perceive several units moving in the same direction, as one, coherently moving global unit. Coherent motion perception is commonly investigated using random dot displays, containing variable proportions of coherently moving dots. Here, we investigated the relative contribution of local and global integration mechanisms to coherent motion perception, and changes in detection thresholds as a result of repeat-ed exposure to the experimental stimuli. Dogs who had been involved in the previous study were administered a conditioned discrimination task, in which we systematically manipulated dot density and duration and, eventually, we re-assessed our subjects' threshold after extensive exposure to the stimuli. Decreasing dot duration impacted on dogs' ac-curacy in detecting coherent motion only at very low duration values, revealing the efficacy of local integration mechanisms. Density impacted on dogs' accuracy in a linear fashion, indicating less efficient global integration. There was limited evidence of improvement in the re-assessment but, with an average threshold at re-assessment of 29%, dogs' ability to detect coherent motion</p>				

	remains much poorer than that of humans.
<b>Suggested Reviewers:</b>	Kun Guo, BSc PhD Reader, University of Lincoln kguo@lincoln.ac.uk Expertise in cognitive neuroscience of vision, including dog motion perception.
	Anna Kis, PhD Magyar Tudomanyos Akademia vargane.kis.anna@ttk.mta.hu The proposed reviewer has experience in dogs' cognition and visual perception
	George Mather, PhD Professor, University of Lincoln gmather@lincoln.ac.uk Professor of Vision Science
<b>Opposed Reviewers:</b>	

[Click here to view linked References](#)

1 **The effect of experience and of dots' density and duration on the detection of coherent motion in dogs**

2

3 Orsolya Kanizsár<sup>a</sup>, Paolo Mongillo<sup>a\*</sup>, Luca Battaglini<sup>b</sup>, Gianluca Campana<sup>b</sup>, Miina Lõoke<sup>c</sup>, Lieta Marinelli<sup>a</sup>

4 <sup>a</sup>Laboratory of Applied Ethology, Department of Comparative Biomedicine and Food Science, University of Padua,

5 Viale dell'Università 16, 35020, Legnaro (PD), Italy. <sup>b</sup>Department of General Psychology, University of Padua, Via

6 Venezia 8, 35131, Padova, Italy <sup>c</sup>Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014,

7 Tartu, Estonia

8

9 \*Corresponding author's email: [paolo.mongillo@unipd.it](mailto:paolo.mongillo@unipd.it) telephone number: +39 049 641862

10

11 ORCID:

12 Orsolya Kanizsar: 0000-0001-7351-7359

13 Paolo Mongillo: 0000-0001-8599-4005

14 Luca Battaglini: 0000-0002-5187-9225

15 Gianluca Campana: 0000-0003-4019-085X

16 Miina Lõoke: 0000-0002-3981-1551

17 Lieta Marinelli: 0000-0003-0609-2172

18

19 **Abstract**

20 Knowledge about the mechanisms underlying canine vision is far from being exhaustive, especially that concerning

21 post-retinal elaboration. One aspect that **has** received little attention is motion perception, and in spite of the common

22 belief that dogs are extremely apt at detecting moving stimuli, there is no scientific support to such assumption. In fact,

23 we recently showed that dogs have higher thresholds than humans for coherent motion detection (Kanizsar et al. 2017).

24 This term refers to the ability of the visual system to perceive several units moving in the same direction, as one, coher-

25 ently moving global unit. Coherent motion perception is commonly investigated using random dot displays, containing

26 variable proportions of coherently moving dots. Here, we investigated the relative contribution of local and global inte-

27 gration mechanisms to coherent motion perception, and changes in detection thresholds as a result of repeated exposure

28 to the experimental stimuli. Dogs who had been involved in the previous study were administered a conditioned dis-

29 crimination task, in which we systematically manipulated dot density and duration and, eventually, we re-assessed our

30 subjects' threshold after extensive exposure to the stimuli. Decreasing dot duration impacted on dogs' accuracy in de-

31 tecting coherent motion only at very low duration values, revealing the efficacy of local integration mechanisms. Den-

32 sity impacted on dogs' accuracy in a linear fashion, indicating less efficient global integration. There was **limited** evi-  
33 dence of improvement in the re-assessment but, with an average threshold at re-assessment of 29%, dogs' ability to de-  
34 tect coherent motion remains much poorer than that of humans.

35

36 **keywords:** coherent motion, dot density, dot lifetime, perceptual learning, dog

37

### 38 **ACKNOWLEDGMENTS**

39 We are very grateful to the student Giulia Madumali Zotti for helping with experiments and to Dr. Carlo Poltronieri for  
40 his technical assistance. The study was funded by the University of Padova (to LM, 2016 - prot. DOR1673431). Dr.

41 Orsolya Kanizár was supported by a PhD grant funded by the University of Padova.

42

43 **INTRODUCTION**

44

45 Dogs make extensive use of visual information, in tasks as simple as recognizing their owner (Mongillo et al. 2017b), to  
46 more cognitively complex activities, such as understanding human communicative signs (reviewed by Kaminsky and  
47 Nitzchener 2013), attentional states (Gácsi et al. 2004; Virányi et al. 2004) and emotions (Albuquerque et al. 2016; Na-  
48 gasawa et al. 2011). Notwithstanding the demonstrated importance of such sensory modality, research on the mecha-  
49 nisms underlying canine vision is far from being exhaustive (Byosiére et al. 2017a). Most of the studies on the topic  
50 focused on the functional properties of eye structures, and their impact on basic characteristics of sight, like acuity, light  
51 sensitivity, and color discrimination. A much smaller number of studies looked at higher level (i.e. post-retinal) visual  
52 elaboration processes, like the perception and the discrimination of object shapes and sizes (e.g. Byosiére et al. 2017b;  
53 Milgram et al. 1994) or the spatial integration of local elements into a global percept (Mongillo et al. 2017a; Pitteri et al.  
54 2014a, b).

55 One aspect that **has** received very little attention is dogs' perception of motion. However, the ability to detect and en-  
56 code information about moving stimuli is likely to be involved in many aspects of the life of a dog. For instance, it  
57 could play a fundamental role in predatory behavior, with its desirable (e.g. for hunting dogs) or undesirable (for dogs  
58 expressing predation as a problematic behavior) consequences. In spite of common belief holding that dogs are ex-  
59 tremely apt at detecting moving stimuli, there is no scientific data supporting such assumption. In fact, to date, the only  
60 study that dealt with dogs' ability to perceive motion, recently conducted by our research group, suggests that the oppo-  
61 site is the case (Kanizsar et al. 2017).

62 In such study, we specifically dealt with dogs' ability to detect coherent motion, that is the ability to perceive several  
63 local units moving with the same direction and speed as a single, coherently moving unit (Braddick 1993; Williams and  
64 Brannan 1994). **According to a widely accepted theory, the perception of coherent motion represents the second of a**  
65 **two-stage motion processing mechanism, whereby higher order neurons integrate the local component of motion ana-**  
66 **lyzed by neurons in the initial stage, providing a global percept (Rust et al. 2006). Such mechanism represents a crucial**  
67 **step to an organisms' ability to extrapolate complex information about relevant stimuli from motion cues (Berental and**  
68 **Pinto 1994; Blanke et al. 2007).** The physiological boundaries of coherent motion perception are commonly investi-  
69 gated via discrimination tasks using random dot displays (Newsome and Pare, 1988), where a given number of dots  
70 moves in the same direction (signal dots), among a number of dots moving in random directions (noise). The smaller  
71 the proportion of signal dots that the subject needs in order to detect the coherent motion, the lower is the individual's  
72 threshold. Using this paradigm, we found that dogs have an average threshold of coherent motion detection of 42%,  
73 considerably higher than the 5% thresholds found in human subjects assessed in the same experimental condition  
74 (Kanizsar et al. 2017), and also higher than thresholds reported for other species, including monkeys (Newsome and

75 Pare 1988), seals (Weiffen et al. 2014) and cats (Huxlin and Pasternak 2004; Rudolph and Pasternak 1996). Thus, dogs'  
76 coherent motion perception abilities seem to be rather poor, not just compared to primates, but even to phylogenetically  
77 closer species.

78 One factor that could have contributed to our dog's high thresholds, is their relatively little experience with the experi-  
79 mental stimuli. It has been widely demonstrated that the performance in many visual tasks improves after experience  
80 with the stimuli. Motion detection tasks make no exception, and improvement in detection thresholds through practice  
81 have been documented in humans, mice, monkeys and seals (Britten et al. 1992; Douglas et al. 2006; Watanabe et al.  
82 2001; Weiffen et al. 2014). The dogs who took part in our previous study were privately owned, and, although they had  
83 received extensive training, their overall exposure to the experimental stimuli was limited if compared to studies em-  
84 ploying animals housed in experimental facilities. It therefore remains a viable hypothesis that thresholds observed in  
85 our dogs did not represent their lower asymptote, and that such thresholds could be improved by giving dogs additional  
86 experience with the stimuli.

87 The thresholds of motion detection are also greatly influenced by the characteristics of the experimental stimuli. For  
88 instance, both a shorter duration (i.e. the amount of a dot remains visible before disappearing and being replaced by an-  
89 other dot elsewhere in the display)<sup>1</sup> and a lower density of dots in the display result in higher thresholds of coherent mo-  
90 tion detection in both human and non-human subjects (Snowden and Kavanagh 2006; Talcott et al. 2000; Weiffen et al.  
91 2014). It is unlikely that changing the duration or dot density used in our previous experiment (Kanizsar et al. 2017)  
92 would improve our dogs' thresholds, since stimuli were designed in order to maximize the dogs' performance and both  
93 parameters were set around the upper range end, in comparison with those used in other studies. Nonetheless, manipu-  
94 lating these parameters would still be useful in the attempt to clarify the relative contribution of different mechanisms to  
95 coherent motion perception (e.g. Bischof et al. 1999). Indeed, there are at least two basic processes through which co-  
96 herent motion detection can be attained, that is the integration of single motion units moving in the same direction  
97 across multiple time frames (local integration), which would be more greatly affected by shorter dots' duration, and the  
98 integration of multiple motion units moving in the same direction, across as few as two subsequent frames (global inte-  
99 gration), which would be more greatly affected by lower dot densities. Although the role of local and global integration,  
100 and their neurophysiological substrates, have been largely addressed in the primate literature, there are substantial dif-  
101 ferences between primates and carnivoran (Aguirre et al. 2007; Djavadian and Harutiunian-Kozak 1983), to suggest that  
102 the mechanisms leading to te detection of coherent motion may differ between these taxa.

103 The experiments described in this paper represent an extension of our previous study (Kanizsar et al. 2017) and were  
104 aimed at investigating the relative contribution of local and global integration mechanisms and the role of experience in

---

<sup>1</sup>In the vision literature this parameter is also called *lifetime*

105 determining dogs' coherent motion detection thresholds. To these aims, the same dogs who took part in our previous  
106 experiment underwent a two-alternative forced choice discrimination task using random dot displays, in which we sys-  
107 tematically varied the dot density or duration. After the dogs completed these tasks we re-assessed the subjects' thresh-  
108 olds using the same testing procedure and parameters as described in Kanizsar et al. (2017), to investigate the effects of  
109 extensive stimulus exposure on dogs' coherent motion detection thresholds.

110

## 111 **MATERIALS AND METHODS**

112

### 113 **Subjects**

114

115 Our sample included five mesocephalic pet dogs, three females (1 Mongrel, 1 Mudi, 1 Siberian Husky) and two males  
116 (1 Cocker Spaniel, 1 Labrador-Poodle Mix), between 3 and 11 years of age. All of these dogs had participated in the  
117 previous study that investigated dogs' thresholds of coherent motion detection (Kanizsar et al. 2017). Dogs belonged to  
118 private owners who participated in the experiments on a voluntary basis. The subjects underwent a veterinary examina-  
119 tion before the enrollment in the experiments to exclude health conditions that would prevent them from participation.  
120 Dogs were selected upon the requirement that they were highly motivated for food and willing to cooperate, while feel-  
121 ing comfortable with being in the laboratory.

122

### 123 **Experimental setting**

124

125 All the experiments took place in the Laboratory of Applied Ethology of the Department of Biomedicine and Food Sci-  
126 ence (University of Padova, Italy). A testing area of 2.5 x 3 m was established in a laboratory room. Stimuli were pre-  
127 sented on two identical monitors (VG248QE, ASUSTeK Computer Inc., Taipei, Taiwan). Their refresh rate was set at  
128 100 Hz, to prevent possible biases on motion detection, due to dogs' higher flicker fusion frequency (Miller and Mur-  
129 phy 1995). Monitors were connected to a PC (Optiplex 960, Dell Inc., Round Rock, Texas, USA). They were placed  
130 side by side at 25 cm from each other. During presentations, the dog viewed the monitors from a distance of 70 cm.  
131 Monitors were attached to height-adjustable stands, so that their height could be set at eye level for each subject.  
132 Presentations were controlled by the experimenter with a Bluetooth® keyboard (K400 Plus, Logitech International  
133 S.A., Lausanne, Switzerland).

134

### 135 **Stimuli**

136

137 All experimental stimuli were created with MATLAB (MATLAB version 7.10.0. Natick, Massachusetts: The Math-  
138 Works Inc., 2010), using features of the Psychtoolbox (Brainard 1997; Pelli 1997). The stimuli were displayed on a  
139 black area of 31.1 cm x 31.1 cm (24.0 x 24.0 deg, from the viewing distance of 70 cm), where white dots with a diame-  
140 ter of 0.16 cm moved **towards the left side of the monitor** at a speed of 19.4 cm/s (15.0 deg/s). For all the training trials  
141 (including those used in the test phases), the positive stimulus was set at a coherence of 80%, i.e. 80% of the dots  
142 moved in the same direction, whereas the remaining 20% moved in random directions. In all **test and training** trials, the  
143 negative stimulus had a coherence level of 0%, that is all of the dots moved in random directions. In training trials, there  
144 was a total of 5000 dots moving in the display, for a density of 5.9 dots/cm<sup>2</sup> (8.7 dots/deg<sup>2</sup>) and dots had a duration of  
145 1000 ms. Dot density, dot duration and the percentage of coherence of the display were manipulated in the test trials of  
146 the respective experiments, for which a detailed description of the stimuli is given below.

147

#### 148 **Training phase and general test procedure**

149

150 Each dog underwent three tests, aimed at assessing respectively the effect of dot duration, dot density and experience on  
151 their coherent motion detection threshold. The latter was defined as the percentage of coherently moving dots in the  
152 positive stimulus at which dogs' accuracy in discriminating such stimulus reached an estimated value of 75%.

153 Prior to each test, dogs underwent a training phase, identical in all respects to the one they had already undergone in the  
154 previous study (Kanizsar et al. 2017). Briefly, such phase consisted in a two-alternative forced choice discrimination  
155 task, where dogs had to discriminate a random dot display with a coherence of 80% (**positive stimulus**), from one with a  
156 coherence of 0%. Training sessions were composed of 20 trials, in each of which dogs were presented with the positive  
157 and negative stimuli, and, after an inspection time of 4 s, they had to choose one of the two stimuli by approaching and  
158 touching one of the two monitors with their snout. **The side of presentation of negative and positive stimuli were ran-**  
159 **domly determined by the software, with the constraint that they were counterbalanced within a session. After touching**  
160 **one of the two monitors, the stimuli disappeared, and dogs were reinforced with food (pieces of sausage of about 1cm<sup>3</sup>)**  
161 **if they chose the positive stimulus; immediately after finishing eating, dogs were called to the starting position and the**  
162 **next trial began. If dogs chose the negative stimulus, they received no reward and after an interval of approximately 7 s**  
163 **they were called back to the starting position for the next trial.** Training was completed when dogs reached a criterion of  
164 90% or better accuracy (i.e. at least 18 correct choices out of 20 trials), in 6 consecutive sessions. In this phase, as well  
165 in the tests, dogs underwent a maximum of 4 sessions per day.

166 In the tests dogs underwent several sessions composed of a certain number of 'training' trials, in which the two stimuli  
167 were identical to those presented in the training phase, and 'test' trials, where the characteristics of the stimuli were ma-



168 nipulated, according to the specifics of each test (described below in detail). The first 4 trials of every session were al-  
169 ways of the training type, serving as a ‘warm-up’, whereas in rest of the session a set number of training and test trials  
170 were intermingled in random order. The side of presentation of the positive stimulus was also randomized and counter-  
171 balanced within each session. **In test trials, dogs were never reinforced regardless of their choice.** The inclusion of train-  
172 ing trials in test sessions was meant to maintain dogs’ motivation throughout, and to allow an assessment of subjects’  
173 discriminative performance during tests; **if a dog failed to maintain a criterion of 85% correct responses in the training**  
174 **trials of the test phase (e.g. more than 2 errors in the 14 training trials), it was sent back to the training phase.**

175

#### 176 **Dot density test**

177

178 This test was meant to investigate whether the manipulation of dots density in the presented displays affected individual  
179 thresholds of coherent motion detection. The test comprised 10 test sessions, each including 14 training trials and 6 test  
180 trials. In the latter, the density of dots in both the positive and negative stimuli was set to one of 3 different levels (8.7  
181 dots/deg<sup>2</sup>, 1.74 dots/deg<sup>2</sup> and 0.17 dots/deg<sup>2</sup>), so that every density level was shown twice per session, and 20 times in  
182 the entire test. **The choice of the density levels was based on the comparative literature and on pilot testing, with the aim**  
183 **of maximizing the sensitivity of the assay.** In test trials, the level of coherence of signal dots in the positive stimulus  
184 was set for each dog to its individual threshold, as resulting from the previous study, where **dot density was set to 8.7**  
185 **dots/deg<sup>2</sup>,** (Kaniszar et al. 2017); the dots’ duration was the same as in the training stimuli (1000 ms).

186

#### 187 **Dot duration test**

188

189 This test was meant to investigate whether the manipulation of dots’ duration affected individual thresholds of coherent  
190 motion detection. The test comprised 10 test sessions, each including 14 training trials and 6 test trials. In the latter, the  
191 duration of dots in both the positive and negative stimuli was set to one of 3 different levels (1000 ms, 200 ms, and 50  
192 ms), so that every duration level was shown twice per session, and 20 times in the entire test. **The choice of the duration**  
193 **levels was based on the comparative literature and on pilot testing, with the aim of maximizing the sensitivity of the**  
194 **assay.** In test trials, the level of coherence of signal dots in the positive stimulus was set for each dog to its individual  
195 threshold, as resulting from the previous study, **where dot duration was set to 1 s** (Kaniszar et al. 2017); the dots’ den-  
196 sity was the same as in the training stimuli (8.7 dots/deg<sup>2</sup>).

197

#### 198 **Re-assessment of coherent motion detection thresholds**

199

200 This test was meant to assess the effects of experience on the thresholds of coherent motion detection of dogs, by re-  
201 peating the assessment procedure that the same dogs had previously undergone (Kanizsar et al. 2017), after having be-  
202 ing exposed to the positive training stimulus in (at least) additional 640 trials since the first threshold assessment. The  
203 interval between the two assessments was on average 2 months.

204 The test consisted of 10 sessions, each composed of 14 training trials and 10 test trials. In the latter, the coherence of the  
205 positive stimulus was varied across 5 different levels (i.e. 60%, 50%, 40%, 30%, and 20% coherently moving signal  
206 dots); each of these levels was shown twice within the same session, and 20 times in the entire test.

207

## 208 **Data collection and statistical Analysis**

209

210 Linear regression analyses were run to find the best model for describing the relationships between the dots density and  
211 duration and the proportion of correct responses, respectively in the dot duration and in the dot density tests. Choice of  
212 the best fitting model was based on visual inspection of the data and on the comparison of the  $R^2$ . After that, a two-tail  
213 one sample t-test was run to determine whether the mean slope of the functions was significantly different from zero,  
214 indicating better ( $> 0$ ) or worse ( $< 0$ ) performance when the independent variable increases.

215 For the re-assessment of coherent motion detection thresholds, data of each dog were fitted with a logistic function by  
216 using the routines provided by Palamedes (Prins and Kingdom 2009), which consider a proportion of correct response  
217 for the level of coherence given by as:

$$218 \quad P(C; \alpha, \beta, \gamma, \lambda) = \gamma + \frac{1 - \gamma - \lambda}{1 + e^{-\beta(C-\alpha)}}$$

219 As the task was a 2-alternative forced-choice, the lower asymptote for guess (*Gamma*) was set to 0.5, while the upper  
220 asymptote (*Lambda*) was fixed by setting the lapse rate (probability of an incorrect response, independent of stimulus  
221 intensity) to 0.02. The parameters *Alpha* and *Beta* were left free. *Alpha* refers to the threshold, i.e. the value along the  
222 abscissa corresponding to the coherence level at which the function attains its steepest point. *Beta* is a discrimination  
223 parameter often referred to as the ‘slope’. Then, a one-tail paired t-test was run for threshold, slope and upper asymp-  
224 tote, regardless the small sample size, in order to investigate whether the parameters differed between the thresholds  
225 assessment performed in Kanizsar et al. (2107) and the re-assessment of the current study.

226 Finally, to determine whether improvements in thresholds after experience depended on the initial performance level,  
227 an analysis of correlations was run between the thresholds reported for each dog by Kanizsar et al. (2017), and the dif-  
228 ference between such threshold and that observed for the same dog in the re-assessment test of the current study.

229

## 230 **RESULTS**

231 All dogs rapidly reached the learning criterion in the training phases preceding each test phase (median N of sessions  
232 needed to reach the learning criterion = 6; min = 6, max = 8). In test sessions, all dogs maintained the criterion of 85%  
233 accuracy in the training trials, thus no dog was retroceded to training once started any of the test phases.

234

235 *Effect of dot density*

236

237 Figure 1 shows the proportion of correct choices as a function of dot density. An optimum way to fit these data is a sim-  
238 ple linear model (see Table 1 for individual *slopes*, *intercepts* and  $R^2$ ). A two-tailed, one-sample t-test showed that the  
239 *slope* of the linear regression was significantly higher than zero ( $t_4 = 3.58$ ,  $P = 0.023$ , Cohen's  $d = 2.58$ ), indicating that  
240 dog's performance linearly improves with increasing dot density.

241

242 *Effect of dot duration*

243

244 Figure 2 shows the proportion of individual correct choices as a function of dot's duration. The dog's performance in-  
245 creases rapidly as the dot duration increases. In four out of five dogs,  $R^2$  is higher than 0.7 (see Table 3). Furthermore, a  
246 two-tails one-sample t-test showed that the slope of the logarithmic regression was significantly higher than zero ( $t_4 =$   
247 4.68,  $P = 0.008$ , Cohen's  $d = 3.3$ ). This indicates that dog's performance increases rapidly as the dot duration increases,  
248 but then it stabilizes for duration above 200 ms.

249

250 *Effect of repeated exposition to the stimuli*

251

252 Figure 3 shows the individual psychometric functions and the proportion of correct choices as a function of coherence,  
253 comparing the results reported in Kanizsar et al. (2017) with those of the re-assessment performed on the same dogs in  
254 the current study. Table 3 shows the *Alpha* (threshold) and *Beta* (slope) parameters for each dog. The mean threshold of  
255 coherent motion detection in dogs in the re-assessment was 29.3%, while the mean slope was 0.06; comparatively, the  
256 mean threshold assessed by Kanizsar et al. (2017) in the same dogs was 42.2%, whereas the mean slope was 0.08. The  
257 difference in thresholds between the two assessments approached significance ( $t_4 = 2.08$ ,  $P = 0.104$ , Cohen's  $d = 1.53$ ) as  
258 well as the difference in slope ( $t_4 = 1.85$ ,  $P = 0.12$ , Cohen's  $d = 0.97$ ). There was a significant correlation between the  
259 threshold observed in the first assessment, and the degree of improvement in the re-assessment ( $r = 0.94$ ,  $P = 0.014$ ), so  
260 that larger improvement was seen in dogs who had initially shown the higher thresholds.

261

262 **DISCUSSION**

263

264 In this study, we assessed dogs' threshold of coherent motion detection as a function of dot density, dot duration and of  
265 the dogs' experience with the experimental stimuli. The results show that dogs' ability to detect coherent motion is neg-  
266 atively affected by dots' duration only at very short duration values, while changes in density impact on dogs' thresh-  
267 olds of motion detection in a linear fashion. Finally, re-assessment of the dogs' thresholds of motion detection after ex-  
268 tensive practice with the experimental stimuli produced variable results within our sample, with indications of improve-  
269 ment.

270 The dogs' ability to detect coherent motion as a function of dots' duration decreased according to a logarithmic curve:  
271 dogs' performance showed only a trivial, if any, decrement when duration was lowered from 1000 to 200 ms, with four  
272 out of five dogs still performing with an accuracy at or above 70%; however, when duration was further reduced to 50  
273 ms, dogs' performance clearly dropped, with accuracy falling below 60% for all dogs. A short duration affects the pos-  
274 sibility to rely on local integration, that is to detect the direction of movement of few, closely-spaced dots, which is a  
275 prerequisite to detect coherent motion. The mechanism has been found to contribute to coherent motion detection in  
276 humans as well as in other animal species, although to a different extent (e.g. Bischof et al. 1999; Talcott et al. 2000;  
277 Weiffen et al. 2014). How do dogs compare to humans or other animal species? Talcott et al. (2000) found that humans'  
278 motion detection improved when duration was increased from 200 ms up to about 900 ms, and remained unchanged  
279 above such values. This would suggest a higher efficiency of local motion integration mechanism in dogs' than in hu-  
280 mans, as our dogs' performance had already reached its asymptote with a dots' duration of 200 ms. However, when  
281 stimuli are presented on a monitor, where the sensation of movement is provided by discrete image changes, the possi-  
282 bility to determine a dot's displacement also depends on the number of frames displayed. In this respect, in Talcott et al.  
283 (2000), the 200 ms and 900 ms conditions contained 4 and 18 frames, values that are respectively much more similar to  
284 our 50 ms (5 frames) and 200 ms (20 frames) conditions than to the 200 and 1000 ms. Thus, if frame number rather  
285 than time is considered, the improvement in performance of our dogs as a function of dots' duration is very similar to  
286 that of humans. Regardless of which of the two parameters is considered, the results indicate that dogs' local integration  
287 mechanisms are at least as efficient as they are in humans, and are therefore unlikely to play a major role in determining  
288 dogs' higher threshold of coherent motion detection. In addition, the efficiency in local integration mechanisms is in  
289 line with dogs' alleged skillfulness in detecting locally moving stimuli, such as a prey moving in the distance (Miller  
290 and Murphy 1995).

291 Our results on local motion integration are less directly comparable to those obtained in other animal species, due to  
292 relevant methodological differences. For instance, Weiffen et al. (2014) assessed a seal's motion detection sensitivity to  
293 varying duration at 125, 250, and 500 ms (frame rates were not provided); across these values, the seals' decrement in

294 threshold appeared to be linear, with no indication of a stabilization. This may suggest that seal's local motion integra-  
295 tion still had space for improvement (i.e. it is less efficient than that of our dogs) but without an assessment of the ani-  
296 mals' sensitivity in a wider range, and considered other differences in the characteristics of the presented stimuli be-  
297 tween the two studies, this remains only a speculative hypothesis.

298 Dogs' ability to detect coherent motion decreased in a linear fashion when dot density was reduced from 8.7 to 0.17  
299 dots/deg<sup>2</sup>, with four of the five dogs performing with < 60% accuracy at the lowest density level. The dependency of  
300 coherent motion detection from dot density is thought to reflect mechanisms of global integration: the higher total num-  
301 ber of dots moving in a consistent direction determines the recruitment of a higher number of low-level motion detec-  
302 tors sensitive to that specific direction, while inhibiting those sensitive to other directions, thereby increasing the possi-  
303 bility to identify a set of coherently moving stimuli as a single entity. Our results indicate progressive improvement in  
304 dogs' reliance on such global integration mechanisms as density increases, at least within the range of densities that we  
305 investigated. By way of comparison, adult humans tested across a range of densities roughly spanning our two highest  
306 levels showed very little improvement in their detection threshold (Talcott et al. 2000) and the seal in the study of  
307 Weiffen et al. (2014) only showed improvement when density was increased up to 0.77 dots/deg<sup>2</sup>, but no further im-  
308 provement with higher density values. Although proper comparisons are hindered by methodological differences, the  
309 results suggest that dogs' global integration mechanisms for motion detection are less efficient than in humans and also  
310 other species; in turn, such lower efficiency in global motion detection may be responsible for the higher thresholds of  
311 coherent motion detection found in dogs.

312 As far as nervous structures are concerned, local integration is thought to rely on low-level direction-sensitive detectors,  
313 found in the primary visual cortex. The sensitivity to a specific direction of local motion units emerges at this level in  
314 both primates (Wurtz and Kandel 2000) and cats (Humphrey and Saul 2002). By contrast, global integration occurs at a  
315 higher level, in specialized areas of the extra-striate cortex. As opposed to primary visual cortex, there is substantial  
316 difference in the neuro-functional organization of these areas between primates, where global motion detection occurs  
317 in the middle-temporal area (Newsome and Pare 1988), and other mammals, such as the cat, where the same processes  
318 occur in the lateral suprasylvian area (Gizzi et al. 1990; Rudolph and Pasternak 1996); although dogs' visual cortex has  
319 not been studied as thoroughly as that of the cat, and no data directly comparable to our results exists in the cat litera-  
320 ture, there seems to be a good degree of correspondence in the neuro-functional organization of these areas between the  
321 two species (Aguirre et al. 2007). Thus, the difference in the functions and organization of these areas between dogs and  
322 primates could be responsible for the different abilities of global integration between dogs and humans. The larger vari-  
323 ability observed in the effect of dot density than duration is also in agreement with the higher-level origin (i.e. further  
324 from sensory origin) of processes that affect dogs' performance.

325 After the extensive exposure to random dots motion displays, dogs' thresholds of coherent motion perception were re-  
326 assessed using the same procedure they underwent earlier (Kanizsar et al. 2017) and dogs' average thresholds passed  
327 from 42% of the first study, to about 29%. The analysis did not result in a significant difference; however, for three out  
328 of the five dogs the improvement seemed to be very clear (>10%); the remaining two dogs showed little change from  
329 the first assessment.

330 This suggests that some of the dogs had not reached their lower asymptote in threshold in the course of the first experi-  
331 ment, but needed further exposition to the stimuli in order to optimize their performance. Similar effects of experience  
332 in improving coherent motion detection have been reported in many other species, including rodents (Douglas et al.  
333 2006), seals (Weiffen et al. 2014), monkeys (Britten et al. 1992) and humans (Sagi 2011). Most likely, such improve-  
334 ment is the result of perceptual learning, a well-known effect often observed in visual tasks, which is believed to reflect  
335 improvement in low-level cortical processes, consequent to extensive exposure to specific stimuli. In the context of  
336 global motion detection, the neurobiological substrate of such improvement has been localized in the middle-temporal  
337 area of primates' brain (Thomson and Liu 2006). The improvement in threshold in our dogs showed some inter-individ-  
338 ual variability, and their degree of improvement was correlated to the threshold observed in the first test, so that dogs  
339 with the highest detection thresholds, also showed the largest improvement in the present study. Both variability in the  
340 degree of perceptual learning and its dependency on the initial performance have been observed before in visual tasks in  
341 humans and are consistent with perceptual learning processes (Doshier and Lu 2005; Fahle and Henke-Fahle 1996).  
342 The difference in average threshold between the first assessment and that done in the present did not reach statistical  
343 significance; however, considered the small number of subjects and the extent of the improvement observed in some of  
344 them, it seems sensible to conclude that experience had an effect in improving detection thresholds. In spite of such im-  
345 provement, final thresholds for all dogs were still markedly higher than those observed in humans in our first experi-  
346 ment.

347

## 348 **Conclusions**

349

350 This study confirms our previous findings that dogs coherent motion perception is less efficient than that of humans, and  
351 suggests that the source of such differences is to be found in dogs' less efficient global integration mechanisms. By  
352 contrast, dogs' local motion integration seems to be highly efficient, possibly more than the corresponding mechanism in  
353 humans. These findings bear on some relevant practical aspects. For instance, it would be important to determine how  
354 the mechanisms of motion detection contribute to prey drive, or whether the efficiency of dogs' local motion integration  
355 mechanisms allows them to be particularly good at spotting movements in the distance, as it was earlier suggested.

356 The study also shows that the performance of dogs in motion detection tasks can be improved through perceptual learning,  
357 although the presence and the extent of such improvement are variable, with larger improvements seen in subjects with  
358 the worst initial performance. In any case, such improvement is not sufficient to bring dogs' thresholds near the level of  
359 human ones. Whether dogs' poor ability to detect coherent motion extends to other aspects of motion detection (for  
360 instance, the ability to detect minimum amounts of global motion) remains an aspect to be addressed by future studies.

361

## 362 COMPLIANCE WITH ETHICAL STANDARDS

363 None of the authors of this paper has any financial or personal relationship with other people or organizations which  
364 might inappropriately influence or bias its content.

365 All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

366

367

## 368 REFERENCES

369

- 370 1. Albuquerque N, Guo K, Wilkinson A, Savalli C, Otta E, Mills D (2016) Dogs recognize dog and human emo-  
371 tions. *Biol Lett* 12: 20150883. [https://doi.org/ 10.1098/rsbl.2015.0883](https://doi.org/10.1098/rsbl.2015.0883)
- 372 2. Aguirre GK, Komáromy AM, Cideciyan AV, Brainard DH, Aleman TS, Roman AJ, Avants BB, Gee JC, Kor-  
373 czykowski M, Hauswirth WW, Acland GM (2007) Canine and human visual cortex intact and responsive de-  
374 spite early retinal blindness from RPE65 mutation. *Plos Med* 4:e230. <https://doi.org/10.1371/jour->  
375 [nal.pmed.0040230](https://doi.org/10.1371/journal.pmed.0040230)
- 376 3. Bertenthal BI, Pinto J. (1994). Global processing of biological motions. *Psychol Sci* 5:221–225. doi:  
377 [10.1111/j.1467-9280.1994.tb00504.x](https://doi.org/10.1111/j.1467-9280.1994.tb00504.x)
- 378 4. Bischof WF, Reid SL, Wylie DR, Spetch ML (1999) Perception of coherent motion in random dot displays by  
379 pigeons and humans. *Percept Psychophys* 61:1089-1101. <https://doi.org/10.3758/BF03207616>
- 380 5. Blanke O, Brooks A, Mercier M, Spinelli L, Adriani M, Lavanchy L, Safran AB, Landis T (2007) Distinct  
381 mechanisms of form-from-motion perception in human extrastriate cortex. *Neuropsychol* 45:644-653.  
382 <https://doi.org/10.1016/j.neuropsychologia.2006.07.019>.
- 383 6. Braddick O (1993) Segmentation vs integration in visual motion processing. *Trends Neurosci* 16:263-268.  
384 [https://doi.org/10.1016/0166-2236\(93\)90179-P](https://doi.org/10.1016/0166-2236(93)90179-P)
- 385 7. Brainard DH (1997) The psychophysics toolbox. *Spat Vision* 10:433-436.
- 386 8. Britten KH, Shadlen MN, Newsome WT, Movshon J (1992) The analysis of visual motion: a comparison of  
387 neuronal and psychophysical performance. *J Neurosci* 12:4745-4765.

- 388 9. Byosiere SE, Chouinard PA, Howell TJ, Bennett PC (2017a) What do dogs (*Canis familiaris*) see? A review of  
389 vision in dogs and implications for cognition research. *Psychon Bull Rev* 1-16. [https://doi.org/10.3758/s13423-](https://doi.org/10.3758/s13423-017-1404-7)  
390 017-1404-7
- 391 10. Byosiere SE, Feng LC, Chouinard PA, Howell TJ, Bennett PC (2017b) Relational concept learning in domestic  
392 dogs: Performance on a two-choice size discrimination task generalises to novel stimuli. *Behav Process*  
393 145:93-101. <https://doi.org/10.1016/j.beproc.2017.10.009>
- 394 11. Djavadian RL, Harutiunian-Kozak BA (1987) Retinotopic organization of the lateral suprasylvian area of the  
395 cat. *Acta Neurobiol Exp* 43:251-262.
- 396 12. Doshier BA, Lu ZL (2005) Perceptual learning in clear displays optimizes perceptual expertise: Learning the  
397 limiting process. *Proc Natl Acad Sci USA* 102:5286-5290. <https://doi.org/10.1073/pnas.0500492102>
- 398 13. Douglas RM, Neve A, Quittenbaum JP, Alam NM, Prusky GT (2006) Perception of visual motion coherence  
399 by rats and mice. *Vision Res* 46:2842-2847. <https://doi.org/10.1016/j.visres.2006.02.025>
- 400 14. Fahle M, Henkle-Fahle S (1996) Interobserver variance in perceptual performance and learning. *Invest Ophth*  
401 *Vis Sci* 37:869-877.
- 402 15. Gácsi M, Miklósi Á, Varga O, Topál J, Csányi V (2004) Are readers of our face readers of our minds? Dogs  
403 (*Canis familiaris*) show situation-dependent recognition of human's attention. *Anim Cogn* 7:144-153.  
404 <https://doi.org/10.1007/s10071-003-0205-8>
- 405 16. Gizzi MS, Katz E, Movshon JA (1990) Spatial and temporal analysis by neurons in the representation of the  
406 central visual field in the cat's lateral suprasylvian visual cortex. *Visual Neurosci* 5:463-468.  
407 <https://doi.org/10.1017/S0952523800000584>
- 408 17. Humphrey AL, Saul AB (2002) The emergence of direction selectivity in cat primary visual cortex. In: Payne  
409 B, Peters A (ed) *The Cat Primary Visual Cortex*. Academic Press, London, pp 343-386
- 410 18. Huxlin KR, Pasternak T (2004) Training-induced recovery of visual motion perception after extrastriate cortical  
411 damage in the adult cat. *Cereb Cortex* 14:81-90. <https://doi.org/10.1093/cercor/bhg106>
- 412 19. Kaminski J, Nitzschner M (2013) Do dogs get the point? A review of dog-human communication ability.  
413 *Learn Motiv* 44:294-302. <https://doi.org/10.1016/j.lmot.2013.05.001>
- 414 20. Kanizsar O, Mongillo P, Battaglini L, Campagna G, Marinelli L (2017) Dogs are not better than humans at  
415 detecting coherent motion. *Sci Rep-UK* 7:11259. <https://doi.org/10.1038/s41598-017-11864-z>
- 416 21. Milgram NW, Head E, Weiner E, Thomas E (1994) Cognitive functions and aging in the dog: acquisition of  
417 nonspatial visual tasks. *Behav Neurosci* 108:57. <http://dx.doi.org/10.1037/0735-7044.108.1.57>
- 418 22. Miller PE, Murphy CJ (1995) Vision in dogs. *J Am Vet Med Assoc* 15:1623-1634.



- 419 23. Mongillo P, Pitteri E, Sambugaro P, Carnier P, Marinelli L (2017a) Global bias reliability in dogs (*Canis fa-*  
420 *miliaris*). *Anim Cogn* 20:257-265. <https://doi.org/10.1007/s10071-016-1044-8>
- 421 24. Mongillo P, Scandurra A, Kramer RSS, Marinelli L (2017b) Recognition of human faces by dogs (*Canis*  
422 *familiaris*) requires visibility of head contour. *Anim Cogn* 20:881-890. <https://doi.org/10.1007/s10071-017->  
423 1108-4
- 424 25. Nagasawa M, Murai K, Mogi K, Kikusui T (2011) Dogs can discriminate human smiling faces from blank ex-  
425 pressions. *Anim Cogn* 14:525-533. <https://doi.org/10.1007/s10071-011-0386-5>
- 426 26. Newsome WT, Pare BT (1988) A selective impairment of motion perception following lesions of the middle  
427 temporal visual area (MT). *J Neurosci* 8:2201-2211.
- 428 27. Pelli DG (1997) The VideoToolbox software for visual psychophysics: Transforming numbers into movies.  
429 *Spat Vis* 10:437-442. <https://doi.org/10.1163/156856897X00366>
- 430 28. Pitteri E, Mongillo P, Carnier P, Marinelli L (2014a) Hierarchical stimulus processing by dogs (*Canis famil-*  
431 *iaris*). *Anim Cogn* 17:869-877. <https://doi.org/10.1007/s10071-013-0720-1>
- 432 29. Pitteri E, Mongillo P, Carnier P, Marinelli L, Huber L (2014b) Part-based and configural processing of  
433 owner's face in dogs. *PlosONE* 9:e108176. <https://doi.org/10.1371/journal.pone.0108176>
- 434 30. Prins N, Kingdom FAA (2009) Palamedes: Matlab routines for analyzing psychophysical data. <http://www.pal->  
435 [amedestoolbox.org](http://www.palamedestoolbox.org).
- 436 31. Rudolph KK, Pasternak T (1996) Lesions in cat lateral suprasylvian cortex affect the perception of complex  
437 motion. *Cereb Cortex* 6:814-822. <https://doi.org/10.1093/cercor/6.6.814>
- 438 32. Rust NC, Mante V, Simoncelli EP, Movshon JA (2006). How MT cells analyze the motion of visual patterns.  
439 *Nat Neurosci* 9:1421.
- 440 33. Sagi D (2011) Perceptual learning in vision research. *Vision Res* 51:1552-1566.  
441 <https://doi.org/10.1016/j.visres.2010.10.019>
- 442 34. Snowden RJ, Kavanagh E (2006) Motion perception in the ageing visual system: minimum motion, motion  
443 coherence, and speed discrimination thresholds. *Perception* 35:9-24. <https://doi.org/10.1068/p5399>
- 444 35. Talcott JB, Hansen PC, Assoku EL, Stein JF (2000) Visual motion sensitivity in dyslexia: evidence for tem-  
445 poral and energy integration deficits. *Neuropsychologia* 38:935-943. <https://doi.org/10.1016/S0028->  
446 3932(00)00020-8
- 447 36. Thompson B, Liu Z (2006) Learning motion discrimination with suppressed and un-suppressed MT. *Vision*  
448 *Res* 46:2110-2121. <https://doi.org/10.1016/j.visres.2006.01.005>
- 449 37. Virányi Z, Topál J, Gácsi M, Miklósi Á, Csányi V (2004) Dogs respond appropriately to cues of humans' at-  
450 tentional focus. *Behav Process* 66:161-172. <https://doi.org/10.1016/j.beproc.2004.01.012>
- 451  
452

- 453 38. Watanabe T, Nanez JE, Sasaki Y (2001) Perceptual learning without perception. *Nature* 413:844-847.  
454 <https://doi.org/10.1038/35101601>
- 455 39. Weiffen M, Mauck B, Dehnhardt G, Hanke FD (2014) Sensitivity of a harbor seal (*Phoca vitulina*) to coherent  
456 visual motion in random dot displays. *Springerplus*. 3:688. <https://doi.org/10.1186/2193-1801-3-688>
- 457 40. Williams D, Brannan, J (1994) Spatial integration of local motion signals. In: Smith A, Snowden R (ed) *Visual*  
458 *Detection of Motion*. Academic Press, London, pp 291-303
- 459 41. Wurtz RH, Kandel ER (2000) Perception of motion, depth and form. In: Kandel ER, Schwartz JH, Jessel TM  
460 (ed) *Principles of Neural Science*, 4th edn. McGraw-Hill, New York, pp 548-571.  
461

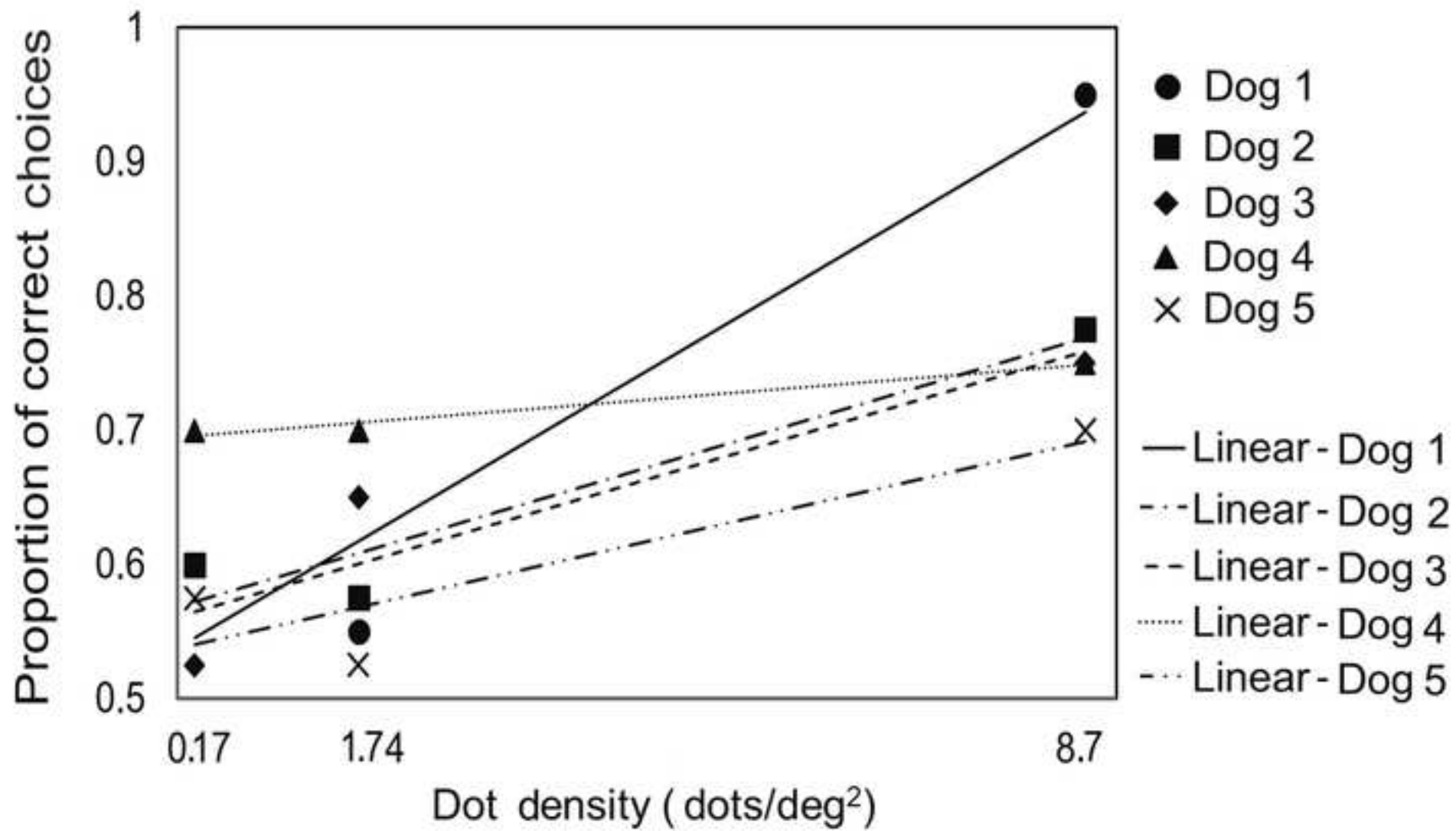
462 **Figure 1.** Dot density test: proportion of correct choices performed by each dog as a function of dot density. Symbols  
463 indicate the proportion of correct choices; lines represent the linear regression of the data of each subject.

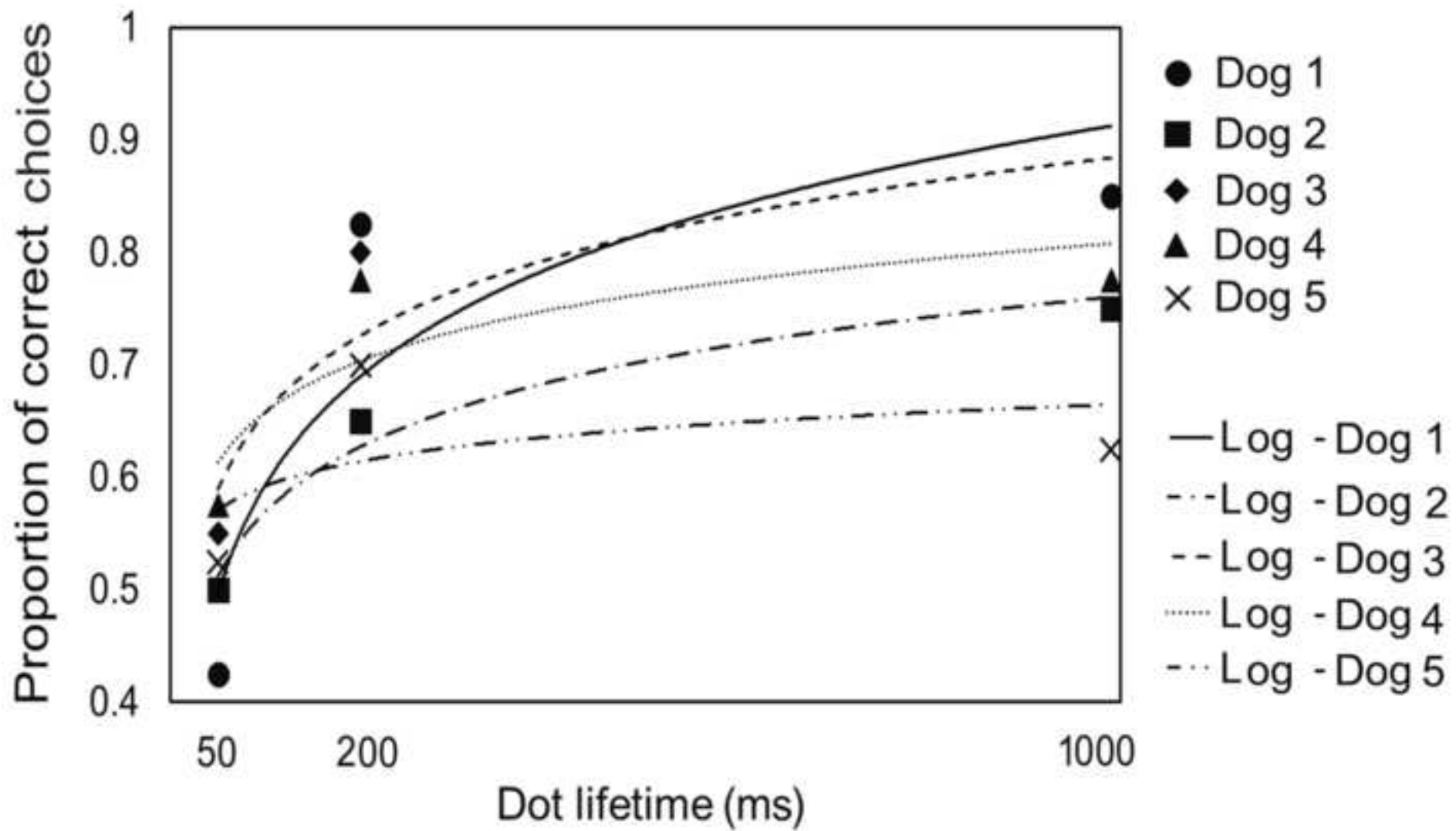
464

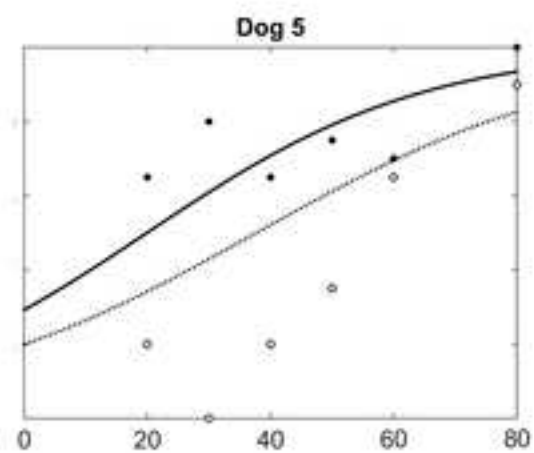
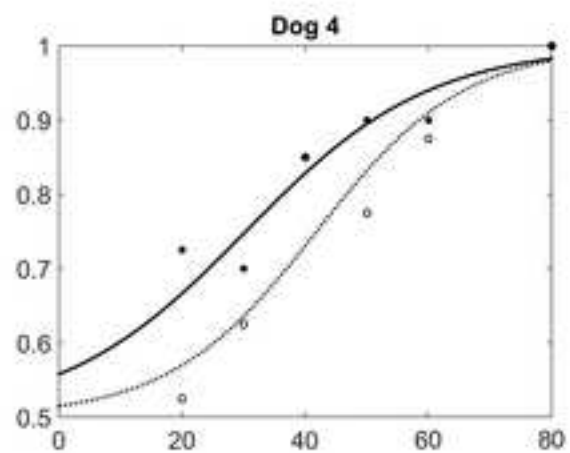
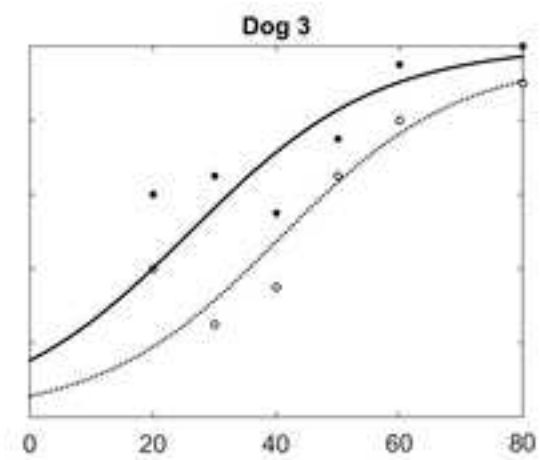
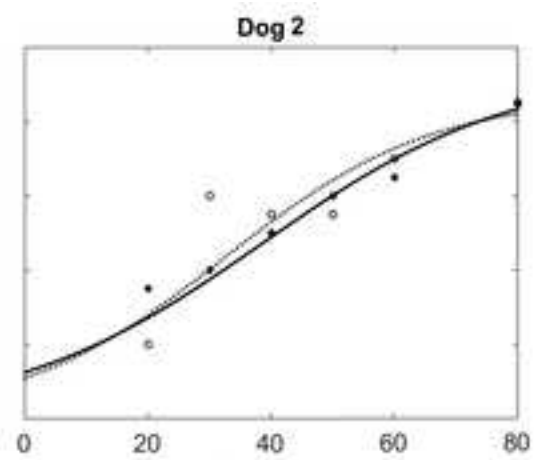
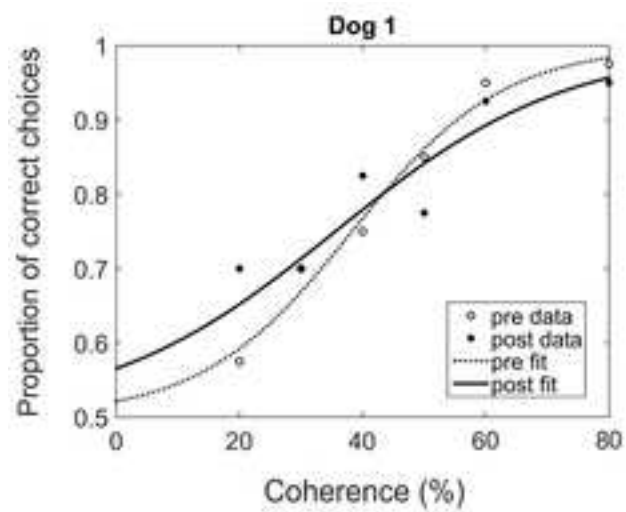
465 **Figure 2.** Dot duration test: proportion of correct choices performed by each dog as a function of dot's duration. Sym-  
466 bols are indicating the proportion of correct choices while lines represent the linear regression of the data of each sub-  
467 ject.

468

469 **Figure 3.** Psychometric curves and proportion of correct choices as a function of coherence, assessed in Kanizsar et al.  
470 (2017) (dotted line, empty circles) and in present study (black line, filled circles) on the same five dogs.







1 **Table 1.** Dot density test: values of *slope*, *intercept* and  $R^2$  of the linear regression of the data of each of the  
2 five dogs.

	<i>Slope</i>	<i>Intercept</i>	$R^2$
Dog 1	0.046	0.46	0.92
Dog 2	0.023	0.57	0.92
Dog 3	0.023	0.56	0.83
Dog 4	0.006	0.69	0.97
Dog 5	0.018	0.54	0.81

3

1 **Table 2.** Dot lifetime test: values of *slope*, *intercept* and  $R^2$  of the linear regression of the data of each of the  
2 five dogs.

3

	<i>Slope</i>	<i>intercept</i>	$R^2$
Dog 1	0.14	0.91	0.75
Dog 2	0.08	0.76	0.97
Dog 3	0.09	0.88	0.84
Dog 4	0.06	0.81	0.71
Dog 5	0.03	0.66	0.28

4



1 **Table 3.** Values of the *Alpha* (threshold) and *Beta* (slope) parameters for each of the five dogs in the first  
2 assessment (Kanizsar et al., 2017) and in the current study's re-assessment

3  
4

	<i>Alpha</i>	<i>Beta</i>	<i>Alpha</i>	<i>Beta</i>
	<i>1<sup>st</sup> assessment</i>	<i>1<sup>st</sup> assessment</i>	<i>re-assessment</i>	<i>re-assessment</i>
Dog 1	37.6	0.095	33.72	0.058
Dog 2	37.4	0.048	39.42	0.048
Dog 3	40.5	0.068	24.19	0.069
Dog 4	41.8	0.086	29.42	0.075
Dog 5	53.9	0.104	19.63	0.05

5  
6  
7



Click here to access/download  
**Supplementary Material**  
Response to reviewers.docx





Click here to access/download  
**Supplementary Material**  
Cover Letter\_200518.docx

