

1 **Oxytocin modulates responses to inequity in dogs**

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17 **Abstract**

18 Although several animals respond negatively to inequity, the underlying neurochemistry of the
19 process remains poorly understood. In this study, we tested whether the neuropeptide oxytocin
20 mediates responses to inequitable outcomes in domestic dogs (*Canis familiaris*). Subjects
21 exchanged tokens to receive a food reward in conditions in which the distribution of reward
22 varied. Dogs did respond negatively to inequity, refusing to participate in the test when their
23 partner was rewarded and they were not. Their responses could not be explained merely by
24 frustration, since the presence of a partner being rewarded had a significant effect on their
25 behavior, compared to when the partner was present but not rewarded. Furthermore, after
26 oxytocin intake dogs were less sensitive to the inequitable distribution of reward, performing
27 more successful trials than when administered with placebo. Further, oxytocin treatment also
28 increased dogs' attention towards their partners, and slowed their decision times, but did not
29 affect their affiliation level toward their partners or the experimenter. Together, our findings
30 suggest that oxytocin modulates responses to inequity in dogs by potentially affecting decision-
31 making processes, but not by increasing affiliation.

32 **Keywords**

33 Domestic dogs, inequity aversion, oxytocin, decision latency, affiliation

34

35 **Introduction**

36 Inequity aversion, i.e. negative reactions to unequal outcomes [1], is thought to be a key
37 proximate mechanism in the evolution of cooperation [2, 3]. In order to show inequity aversion,
38 individuals need to be able to compare their own efforts and outcomes with those of others,
39 recognize and evaluate the inequity, and be motivated to react to it [3]. While the responses
40 seem remarkably similar, and they probably rest on the same cognitive mechanisms [4], this
41 phenomenon differs from the well-documented “frustration” effect (or contrast effect, [5]) in
42 that in the former the referent is social – one’s partner’s outcomes – while in the latter the
43 referent is individual – one’s own previous outcomes [2, 6, 7].

44 Decades of research in multiple disciplines have demonstrated that humans show an inclusive
45 sense of fairness across a variety of situations, responding negatively to inequitable outcomes
46 between themselves and another individual [1, 8]. These responses occur not only when subjects
47 receive a lesser value outcome than a social partner (i.e. disadvantageous inequity or first-order
48 inequity aversion, c.f. [2]), but also when they receive a more valuable outcome than a social
49 partner (i.e. advantageous inequity or second order inequity aversion, c.f. [2]). In some cases,
50 even third parties whose payoffs are not affected by inequity are willing to pay a cost in order to
51 punish others for unfair behavior. For instance, in a third-party economic game, third party
52 players evaluate the distribution of resources among two other players and have the option of
53 either doing nothing (i.e. keeping their own endowment for themselves) or spending some of
54 their endowment to punish unfair transactions. In Fehr and Fischbacher’s study [9], almost two-
55 thirds of the third party players punished players whose offer was perceived as unfair (i.e. only a
56 small proportion of the donor’s endowment was shared with the recipient).

57 Humans are not the only species to respond negatively to inequity. Accumulating evidence over
58 the last decade from multiple non-human animal studies indicate that at least some aspects of
59 inequity aversion are present in a wide variety of species and situations [2]. The typical

60 experimental paradigm to test inequity aversion in animals involves pairing two individuals
61 from the same social group and alternately ask them to complete a task in order to obtain a food
62 reward. Variation in the quality of the reward given to each partner, or the amount of effort
63 needed to obtain the rewards, creates the different experimental conditions that will be later
64 compared (e.g. baseline – where both individuals obtain the same reward – vs. inequity – where
65 the subject receives a less preferred reward than the partner) (see [3] for a detailed description of
66 the experimental paradigm). In these controlled experiments, capuchin monkeys (*Sapajus*
67 *apella*; [10, 11]; but see [12]), chimpanzees (*Pan troglodytes*; [13, 14]; but see [15]), macaques
68 (*Macaca fascicularis*; [16]), marmosets (*Callitrix spp.*; [17, 18], but see [19]); domestic dogs
69 (*Canis familiaris*; [20-22]), wolves (*Canis lupus*; [22]), rats (*Rattus norvegicus*; [23]), mice
70 (*Mus spp.*; [24]), and corvids (*Corvus spp.*; [25]), but not squirrel monkeys (*Saimiri spp.*; [19]),
71 owl monkeys (*Aotus spp.*; [19]), kea (*Nestor notabilis*; [26]) or cleaner fish (*Labroides*
72 *dimidiatus*; [27]), seem to have the ability to detect inequity and, like humans, react negatively
73 when they receive less than a partner. Animals in these studies refused a lesser reward and/or
74 stopped participating in the interaction if their partners received better rewards than themselves.

75 While the current animal literature indicates that this behavior is widespread in cooperative
76 species, it also shows that the patterns of inequity aversion vary considerable both across and
77 within species [2, 3]. For instance, in contrast to some species of primates and corvids, which
78 react to differences in the quality of food reward and working effort [3, 25], pet dogs have been
79 shown to respond only to inequity in the presence and absence of a reward [20] (but see [22] for
80 pack-living dogs). Furthermore, there are also striking differences in individuals' sensibility to
81 inequality within species (e.g. capuchin monkeys, see references above) or even within the same
82 population (e.g. chimpanzees, [13, 14]). The observed variability in animal's inequity responses
83 has been attributed in part to differences in cognitive and motivational capacities, demographic
84 variables, relationship quality between interacting partners, or individual's personalities, as well
85 as differences in experimental methodologies [4]. However, patterns are not consistent across

86 studies and there are many other unmeasured factors that may influence animals' responses to
87 unequal outcomes.

88 The majority of studies on inequity aversion in animals have focused on their behavioral
89 responses, and as a consequence very little is known about the neural circuitry and
90 neurochemistry underlying such responses. Human functional neuroimaging investigations have
91 identified brain regions, such as the striatum, the anterior insula, the prefrontal cortex, and the
92 amygdala, that are involved in altruistic, fair and trusting behaviors [8, 28]. There is also
93 correlational and causal evidence from computational and pharmacological interventions
94 showing a functional link between the neurochemical systems, i.e. dopamine, oxytocin,
95 serotonin; and human egalitarian and trusting behaviors [29-31]. In non-human animals,
96 although the involvement of these neurochemical systems in regulating social behavior has been
97 extensively studied [32-34], their effects on prosocial concerns in general and inequity aversion
98 in particular have been largely unexplored. Only one study has examined the effect of oxytocin
99 on inequity responses in non-human primates, reporting no effect, perhaps owing to small
100 sample size (i.e. only the male subsample (N = 4) showed inequity aversion, [17]).

101 The present study uses a pharmacological intervention with a double-blind, within subject,
102 counterbalanced design, to investigate whether oxytocin modulates reactions to unequal
103 outcomes in the domestic dog. Understanding the mechanisms that underlie inequity aversion in
104 animals will help us to understand not only the evolution of the biological bases of human
105 fairness, but also the individual differences in sensibility to inequality observed in many species,
106 including humans. Recent research on dogs has shown that oxytocin promotes social approach
107 and affiliation with familiar partners, increases their attention to social cues, and induces
108 positive expectations on ambivalent outcomes [35-37]. However, the accumulative evidence on
109 oxytocin also shows that its effects on prosocial behavior and cooperation depend on pre-
110 existing social motivations or perceptions, be they pro- or anti-social [38, 39]. That is, when

111 social cues are perceived as “positive” (e.g. support given by a friend) oxytocin seems to
112 increase individuals’ prosocial behaviors and promote adaptive stress responses, but diminish
113 these responses when the social cues are perceived as “negative” (e.g. support given by a
114 stranger) [40]. Thus, we speculated that if oxytocin enhances mainly individuals’ pro-social
115 tendencies or social motivation toward others, the administration of oxytocin should be
116 associated with an increase in dogs’ tolerance to inequity. Conversely, if oxytocin increases
117 mainly the salience of social agents, then a larger sensibility to inequity should emerge after
118 oxytocin administration.

119

120 **Methods**

121 **Ethical Statement**

122 The present study adheres to the Association for the Study of Animal Behaviour (ASAB)
123 guidelines. The experimental protocol was approved by the Ethics Committee of Azabu
124 University (Japan) (No. 130304-2) and the experimental procedure was supervised by members
125 of the Training and Veterinary Departments of the Yokohama Center of the Japan Guide Dogs
126 Association (J.G.D.A.) where the study was conducted.

127 **Subjects**

128 Sixteen Labrador retriever dogs older than 12 mo of age served as subjects of this study
129 [females = 8; male = 8; mean age 1.2 yr. (SE = 0.3)]. All dogs were candidate guide dogs at the
130 Japan Guide Dog Association (JGDA). They were born at the JGDA breeding facility and raised
131 at volunteer puppy raisers’ home until they were approximately one year of age. After that,
132 candidate guide dogs were moved to JGDA Training Center in Yokohama (Japan) where they
133 received their education. At the JGDA facility, dogs were housed in small groups up to four
134 individuals. At the start of the study, all dogs had received the same level of training (i.e. basic
135 obedience training). Genetically unrelated dogs living in the same kennel as the subjects acted

136 as partners during the experimental sessions. Partners were usually subjects themselves in other
137 tests.

138 **Experimental procedure**

139 Tests were conducted at the Yokohama JGDA Center (Japan). In the experimental room
140 (outside the kennel block), the subject and the partner stayed in adjacent testing enclosures (170
141 cm x 170 cm), separated from each other by a panel pet fence. The separation between the bars
142 of the fence was wide enough so dogs could clearly see each other, as well as interact with
143 limited physical contact (e.g. sniffing, licking), but they were not able to reach their partner's
144 rewards. Food rewards were placed in food bowls located next to the middle panel fence so
145 subjects could easily see what their partners received.

146 **Training**

147 Prior to the study, all subjects had been trained to exchange an inedible token (i.e. hard foam
148 cylinders of 10 cm in length and 6.5 cm in diameter) for a food reward (i.e. one piece of dry dog
149 food). The subjects were not restrained and could freely move around the testing area. In order
150 to start an exchange trial, the dog had to be standing up or sitting down in front of the
151 experimenter and looking at her. The experimenter then threw the token into one of the corners
152 of the testing area (approximately 150 cm away from the experimenter) and asked the dog to
153 retrieve it. The dog had 15 seconds to perform the task. During this time, the experimenter,
154 sitting in front of the testing area with her right palm open next to the bowl, asked for the token
155 every 3 seconds. The experimenter avoided any further communication, including eye contact
156 with the dogs. To count as a successful exchange, the dog had to retrieve the token and place it
157 in the experimenter's open palm or right next to it. The experimenter then took the token out of
158 reach from the dog and placed one piece of dry dog food into the bowl. Rewards, held on the
159 experimenter's left hand, were always present and clearly visible to the dogs. If the dog refused
160 to return the token within 15 seconds, the session was terminated. In order to participate in the

161 study, dogs had to meet the criterion of retrieving the token to the experimenter at least 35 times
162 in a row. Only one male dog did not meet this criterion and therefore did not participate in the
163 study. The rest of the dogs achieved this criterion in up to four 20 min sessions.

164 **Testing conditions**

165 Each testing session started with a 24 warm-up trials session (12 trials per individual), in which
166 both dogs received a food reward upon token return. Token exchange and reward delivery
167 followed the same procedure as previously described for the training sessions. The pre-test trials
168 function to ensure that dogs were aware of the experimental procedure in the social setting and
169 that they were motivated to participate in the experiment. Subjects that failed to successfully
170 perform at least 10 out of 12 warm-up trials were not tested on that day.

171 All testing sessions consisted of a single condition. No subject was tested more than once per
172 day, and each dog was tested during the same 2 hour time-block of the day. Each testing session
173 consisted of a series of 60 alternating trials between the partner and the subject, so that each dog
174 received up to 30 trials per session (or until the subject refused to participate), and the partner
175 always performed immediately before the subject. If the dog refused to return the token within
176 15 seconds, the session was terminated. Each subject underwent five different testing conditions
177 (Table 1): equity (EQ), inequity-saline (IN-SL), inequity-oxytocin (IN-OT), social control (SC),
178 and non-social control (NSC). In the EQ condition, both dogs performed the task (i.e. returning
179 the token) and both dogs received the food reward after returning their own token. In both
180 inequity conditions, both the subject and the partner completed the task, but only the partner
181 received a food reward after returning the token. In the SC condition, the subject and the partner
182 performed the task, but neither of them received any food reward after returning their tokens.
183 Finally, in the NSC condition, subjects were tested without a partner and did not receive a
184 reward after completing the task. The rest of the experimental procedures, including the
185 presence of food rewards and experimenter movements, remained the same across conditions.

186 The order of treatment was randomized across dogs and each condition carried out on different
187 days.

188

Treatment	Description
Equity (EQ)	Both dogs received one chow item upon token return
Inequity – saline (IN-SL)	Subject received no food after returning the token while partner received one food item. Experimental session started after subject received a saline intranasal spray
Inequity – oxytocin (IN-OT)	Subject received no food after returning the token while partner received one food item. Experimental session started after subject received an intranasal spray with oxytocin
Social control (SC)	Neither subject nor partner received any food item after returning the token
Nonsocial control (NSC)	Subject received no food after returning the token. Partner was not present

189 Table 1. Treatment names and their descriptions.

190

191 **Oxytocin treatment**

192 Prior to the start of the inequity conditions, dogs received a 40 IU of OT or saline in 100- μ L
193 solution, depending on the testing condition. Similarly, to previous studies on dogs [35, 36], we
194 administered OT to dog subjects using intranasal delivery. The delivery of the spray was

195 performed by a second experimenter who did not participate in the rest of the study. Thus, the
196 experimenter exchanging tokens with the dogs was unaware of which treatment the subjects
197 received. Furthermore, in order to ensure that any difference between the inequity-saline
198 condition and the equity and control conditions was not due to the administration of the spray,
199 dogs also received an intranasal saline spray prior to these conditions. Five to ten minutes after
200 spray intake, dogs underwent the warm-up session, and testing sessions started between 15 to 20
201 min after spray delivery. The oxytocin administration procedures, as well as the timeline of the
202 testing sessions, were based on previous work on the physiological and behavioral effects of
203 exogenous oxytocin on dogs [35, 36]. One male dog that showed aversive reaction to the
204 administration of the spray was dropped from the study. Hence, the total number of dogs that
205 performed all testing conditions was 8 females and 6 males.

206 **Behavioral measures**

207 All sessions were videotaped and coded by observers who did not participate in the study and
208 were blind to the hypothesis. A trial was coded as successful if the dog retrieved the token and
209 placed it on or next to the experimenter's hand. The total number of successful trials per session
210 was coded to see whether the subject refused to cooperate differentially in the various
211 conditions. Latency to return the token was calculated as the time from the start of the trial (i.e.
212 the moment the token left the experimenter's hand) to the moment the dog retrieved the token to
213 the experimenter. Affiliative behaviors, including sniffing, licking, gentle touching with the
214 nose, and play invitations (i.e. play bows), as well as behaviors indicative of distress, such as
215 self-licking, self-scratching, yawning, and vocalizing (e.g. whining), were recorded in an all
216 occurrence sampling. Additionally, we coded the number of times the subject looked at the
217 partner (defined as staring, looking at partner or no clear gaze direction but head frontally
218 oriented to partner for at least 2 s). Twenty percent of the sessions were coded by a second
219 observer to calculate inter-observer reliability. Reliability was high for token return (Cohen's k
220 = 0.97), latency to return the token (Spearman's correlation: $r_s = 0.984$; $p < 0.001$), affiliation to

221 partner ($r_s = 0.948$; $p < 0.001$), affiliation to experimenter ($r_s = 0.858$; $p = 0.001$), distress
222 behaviors ($r_s = 0.842$; $p < 0.001$), and number of looks ($r_s = 0.863$; $p < 0.001$).

223 **Data analysis**

224 To investigate whether the number of successful returns varied according to the experimental
225 condition, we used a Generalized Linear Mixed Model (GLMM) with Poisson error distribution
226 and a log link function. The number of trials that subjects returned the token to the experimenter
227 was set as the response term. Experimental conditions (see Table 1), subject's sex, and their
228 interaction were included as explanatory terms. To examine whether the latency to return the
229 token varied according to the experimental condition, a Linear Mixed Model (LMM) with
230 normal error distribution was used. For this analysis, latency to return the token was \log_{10} -
231 transformed to fit a normal distribution. LMM were also used to examine whether the
232 occurrence of the different behavioral measures was affected by the experimental condition.
233 Analyses were conducted via separate LMM for each variable (i.e. affiliation to partner,
234 affiliation to experimenter, distress behaviors). Additionally, the effect of the experimental
235 condition on the number of times subjects looked to their partners was analyzed via a GLMM
236 with Poisson error distribution and a log link function. The number of looks per session,
237 controlled by the number of trials performed per session, was set as the response term. In all
238 models, experimental condition, subjects' sex and their interaction were entered as fixed terms,
239 and subjects' ID was included as a random term to control for the effect of repeated measures
240 on the distribution of data. A step-down strategy (i.e. fixed factors were removed from the
241 model sequentially) was used and the selection of the models was done using the Akaike's
242 Information Criterion (AIC). We compared the best model with the respective null model,
243 which only contained random effects, by using a likelihood ratio test and considered only
244 significant effects of the individual predictors if the best model explained the variance
245 significantly better than the null model. When an effect of a three-level factor (i.e., treatment)
246 was found, multiple comparisons between the groups were run to determine their relative

247 effects. Finally, to compare whether dogs' behavioral reactions (i.e. latency, self-directed
248 behaviors) at the beginning of each testing session differed from those at the end of the session,
249 the mean value of each behavior for the first four trials was calculated and compared with the
250 mean value of the last four trials using Wilcoxon signed rank tests. All analyses were performed
251 on R version 2.14.1 [41]. All p values are corrected for multiple comparisons.

252

253 **Results**

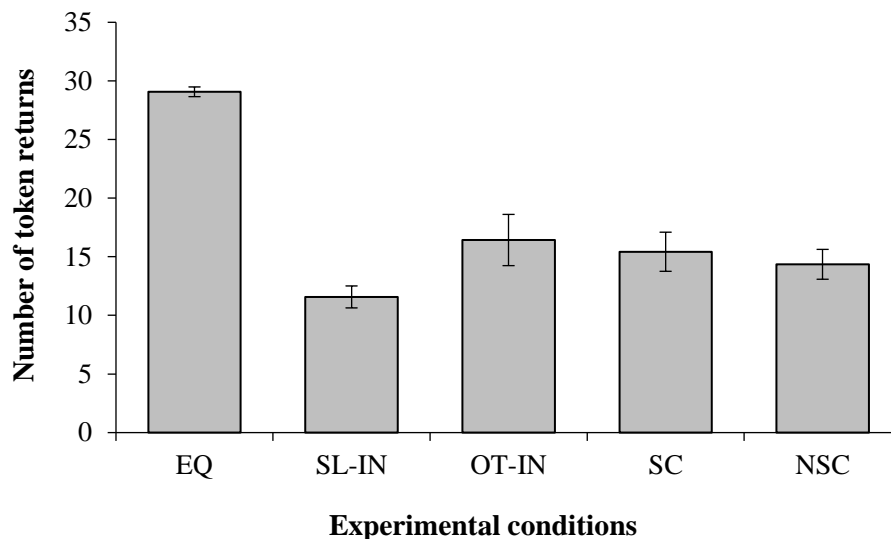
254 **Reactions to inequitable outcomes**

255 We first examined the effects of reward distribution in dogs' performance in the placebo
256 condition. Dogs' token exchange rate (i.e. number of successful trials performed on each
257 session) was significantly affected by testing condition (likelihood ratio test: $\chi^2(4) = 131.5$, $p <$
258 0.001), but not by subject's sex ($\chi^2(1) = 0.531$, $p = 0.466$). A priori planned comparisons
259 revealed that, as expected, absence of reward induced dogs to perform fewer successful trials
260 than when dogs received a reward (EQ vs. IN-SL: glmm: $z = 9.908$, $p < 0.001$; EQ vs. SC:
261 glmm: $z = 7.521$, $p < 0.001$; EQ vs. NSC: glmm: $z = 8.179$, $p < 0.001$; Figure 1). That not
262 receiving a reward increased subjects' frustration until they finally refused to participate was
263 further supported by the results of the analyses of behavioral indicators of distress. Average
264 rates of self-directed behaviors were significantly higher during the four trials prior to refusal
265 than during the first four trials of each session for all conditions but for the EQ condition
266 (Wilcoxon signed rank test: IN-SL: $n = 10$, $z = -2.191$, $p = 0.028$, $r = 0.69$; SC: $n = 12$, $z = -$
267 2.118 , $p = 0.034$, $r = 0.61$; NSC: $n = 10$, $z = -2.803$, $p = 0.005$, $r = 0.88$; EQ: $n = 9$, $W = 22$, $p =$
268 0.177).

269 We then compared whether the presence of a partner receiving a reward, in addition to reward
270 distribution, had any effect on dogs' performance. We found that dogs' token exchange rates
271 were lower in the IN-SL condition than in the social and non-social control sessions, although

272 the latter did not reach statistical significance (glmm: IN-SL vs. SC: $z = -2.765$, $p = 0.015$, IN-
 273 SL vs. NSC: $z = -2.041$, $p = 0.098$; Figure 1). That is, dogs completed fewer trials when the
 274 partner was present and received a reward than when the partner was present but did not receive
 275 a reward. Subjects also tended to perform fewer successful trials when the partner was present
 276 and received a reward than when the partner was not present at all.

277



278

279 Figure 1. Average number of trials in which the subjects returned the token to the experimenter
 280 in the different experimental conditions. Bars represent the mean values, and whiskers the SE.
 281 EQ, equity test; IN-SL, inequity-saline; IN-OT, inequity-oxytocin; SC, social control; NSC,
 282 nonsocial control. For a full description of the experimental conditions see Table 1.

283

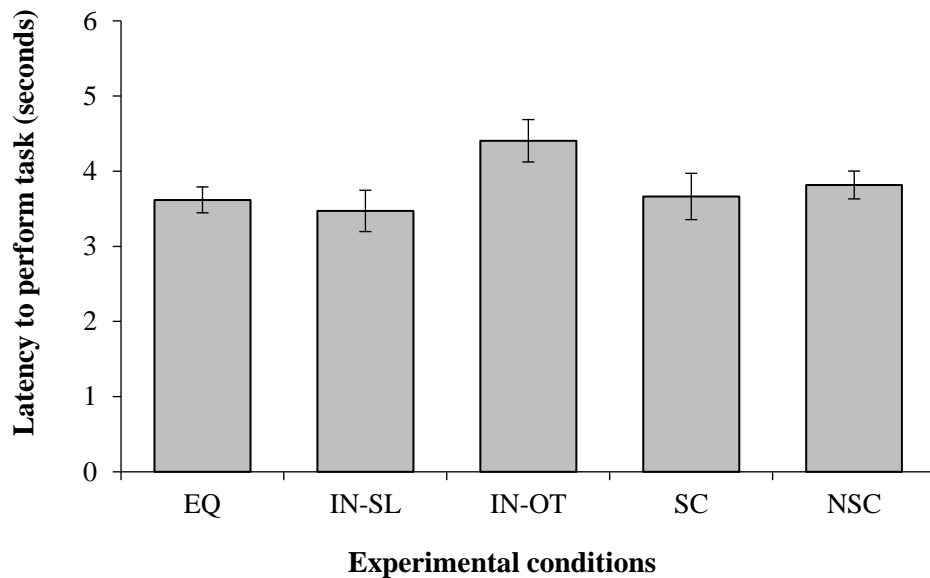
284 While the presence of a partner receiving a reward seems an important factor for refusing to
 285 return the token, it did not have a similar effect on the overall latency to perform the task.
 286 Average latency to return the token was not significantly different between the EQ condition

287 and the IN-SL condition, or between the EQ condition and the control conditions (likelihood
288 ratio test: $\chi^2(4) = 18.814$, $p < 0.001$; EQ vs. IN-SL: lmm: $z = 0.711$, $p = 0.954$; EQ vs. SC: lmm:
289 $z = 0.145$, $p = 0.999$; EQ vs. NSC: lmm: $z = 2.367$, $p = 0.124$; Figure 2). Similarly, dogs did not
290 perform more self-directed behaviors during the EQ condition compared with the IN-SL or
291 control conditions (likelihood ratio test, full vs. null model: $\chi^2(5) = 1.603$, $p = 0.901$).

292 **Effect of oxytocin on inequity aversion**

293 The type of treatment dogs were administered did affect their reactions during the inequity
294 conditions. Specifically, after oxytocin intake dogs completed more successful trials than when
295 sprayed with saline (IN-SL vs. IN-OT: glmm: $z = -3.415$, $p = 0.005$, Figure 1). The positive
296 effect of oxytocin, however, did not overcome their avoidance to the inequitable distribution of
297 rewards, since subjects performed fewer successful trials in the IN-OT condition than in the EQ
298 condition (EQ vs. IN-OT, glmm: $z = 6.915$, $p < 0.001$, Figure 1). We then investigated whether
299 the latency to successfully complete the task varied according to treatment. When dogs were
300 administered OT, they hesitated significantly longer to return the token to the experimenter than
301 when administered saline solution (IN-OT vs. IN-SL: lmm: $z = 3.484$, $p = 0.004$; Figure 2).
302 Moreover, their latencies during the IN-OT condition tended to be longer than during the EQ
303 condition (IN-OT vs. EQ, lmm: $z = 2.773$, $p = 0.044$; Figure 2), suggesting that dogs greatly
304 hesitated to return the token after receiving oxytocin treatment. This hesitation, however, was
305 not accompanied by higher rates of self-directed behaviors (likelihood ratio test, full vs. null
306 model: $\chi^2(5) = 1.603$, $p = 0.901$).

307



308

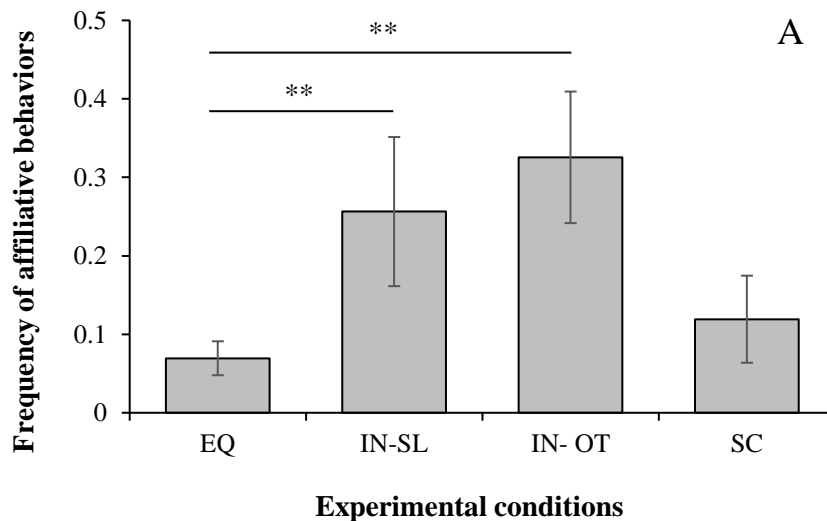
309 Figure 2. Mean average latency (\pm SE) to perform the task according to treatment. EQ, equity
 310 test; IN-SL, inequity-saline; IN-OT, inequity-oxytocin. For a full description of the
 311 experimental conditions see Table 1.

312

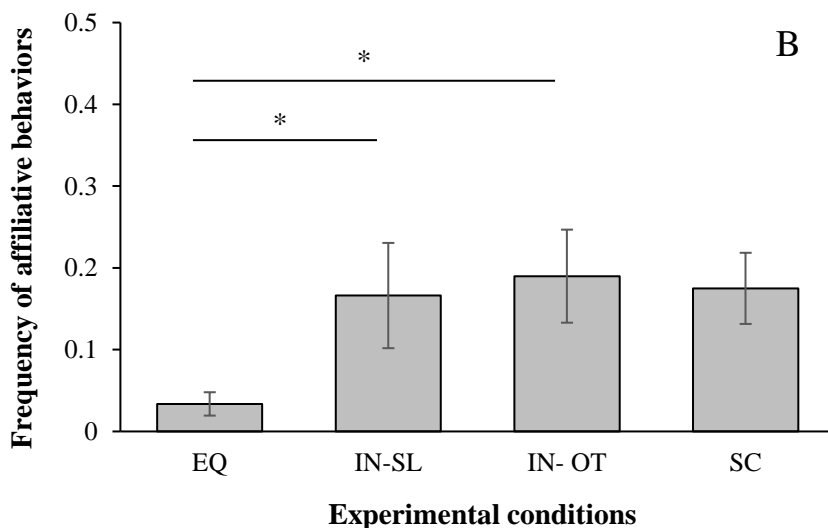
313 **Oxytocin and social behaviors**

314 Previous studies have shown that the administration of external oxytocin enhances dogs'
 315 affiliation tendencies and increases their attention to social cues [35, 36, 42]. Therefore, we
 316 explored whether changes in these responses could mediate the observed differences in task
 317 performance. When analyzing the affiliative behaviors directed to dog partners, we found that
 318 affiliation was affected by testing condition (likelihood ratio test: $\chi^2(3) = 49.474$, $p < 0.001$), but
 319 not by sex (likelihood ratio test: $\chi^2(1) = 1.001$, $p = 0.317$). Independent of the treatment
 320 received, dogs affiliated significantly less often with their partners when both dogs received a
 321 reward, than when only the partner received a reward (IN-OT vs. EQ: lmm: $z = 5.199$, $p <$
 322 0.001 ; IN-SL vs EQ: lmm: $z = 3.383$, $p = 0.004$; Figure 3). We did not find, however, a
 323 significant difference between the two inequity conditions (IN-OT vs. IN-SL: lmm: $z = -1.593$,

324 $p = 0.366$; Figure 3). Similar results were found when we examined the behaviors directed to
 325 the experimenter (testing condition: $\chi^2(4) = 25.7$, $p < 0.001$; sex: $\chi^2(1) = 0.1153$, $p < 0.7342$).
 326 Overall, dogs initiated affiliation towards the experimenter less often during the EQ condition
 327 than during both inequity conditions (IN-OT vs. EQ: lmm: $z = 3.117$, $p = 0.014$; IN-SL vs. EQ:
 328 lmm: $z = 2.524$, $p = 0.027$; Figure 3), while oxytocin treatment was not associated with higher
 329 affiliation levels compared to saline treatment (IN-OT vs. IN-SL: lmm: $z = 0.439$, $p = 0.991$;
 330 Figure 3).



331



332

333 Figure 3. Average frequencies of affiliative behaviors subject dogs directed towards their

334 partners (A) and the experimenter (B) according to treatment. Bars represent the mean values,

335 and whiskers the SE. EQ, equity condition; IN-SL, inequity-saline; IN-OT, inequity-oxytocin.

336 For a full description of the experimental conditions see Table 1. ** $p < 0.01$; * $p < 0.05$

337

338 Finally, we also evaluated how often dog subjects looked at their partners on each experimental

339 condition. Again, testing condition ($\chi^2(3) = 31.184$, $p < 0.001$), but not subject's sex ($\chi^2(1) =$

340 1.001 , $p < 0.316$) had a significant impact on dogs' attention towards their partners, which was

341 higher after oxytocin intake than after saline treatment (IN-OT vs. IN-SL: glmm: $z = 3.420$, $p =$

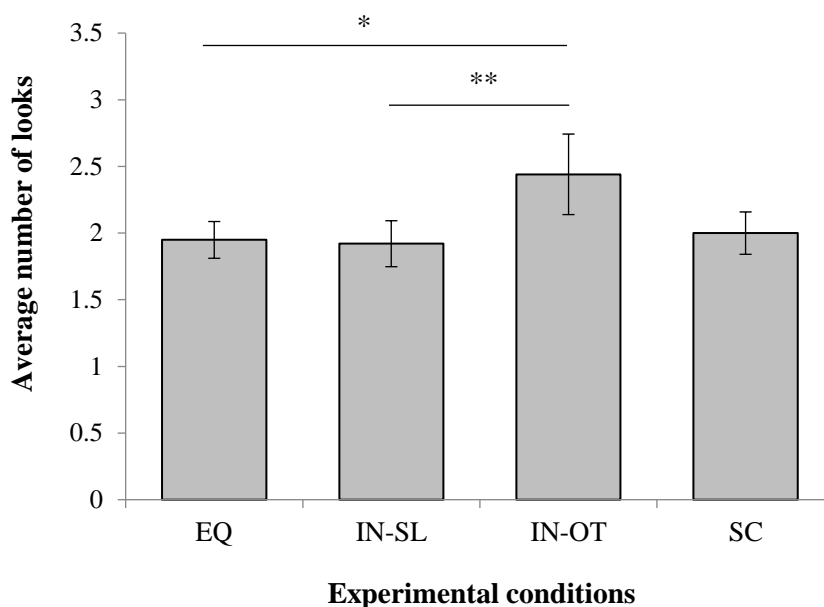
342 0.003 ; Figure 4). Furthermore, dogs also checked their partners more often during the IN-OT

343 condition than during the EQ condition (IN-OT vs. EQ: glmm: $z = 2.982$, $p = 0.014$; Figure 4),

344 while there were no differences between EQ and IN-SL conditions ($z = -.0439$, $p = 0.971$;

345 Figure 4). These results suggest that oxytocin treatment, rather than reward distribution, was

346 associated with an increase in dogs' tendency to look at their partners.



347

348 Figure 4. Average number of times per trial subject dogs looked to their partners according to

349 treatment. Bars represent the mean values, and whiskers the SE. EQ, equity condition; IN-SL,

350 inequity-saline; IN-OT, inequity-oxytocin. For a full description of the experimental conditions
351 see Table 1. ** $p < 0.01$; * $p < 0.05$

352

353 **Discussion**

354 In this study, we investigated whether the neuropeptide oxytocin could modulate inequity
355 responses in the domestic dog. The results of our double-bind, within-subject study reiterate that
356 domestic dogs are averse to disadvantageous inequity and show that oxytocin affects these
357 responses. Dogs paired with a familiar partner showed variation between conditions in their
358 willingness to participate in the task, depending upon whether rewards were the same. Dogs
359 performed fewer successful trials when their partners were rewarded and they themselves were
360 not than when neither of the dogs received a reward. Moreover, dogs also responded differently
361 depending upon whether a partner was present, showing a tendency towards completing fewer
362 successful trials in the inequity condition than in the non-social control (although this trend did
363 not reach statistical significance). Our results, thus, are consistent with previous research
364 showing that dogs are sensitive to the unequal distribution of reward [20-22].

365 In contrast with other species showing inequity aversion, pet dogs seem to be sensitive only to
366 reward distribution (i.e. presence/absence) but not to the quality of the rewards (but see [22] for
367 pack-living dogs). Due to this characteristic, in our experiment the inequity between partners
368 was created by the presence/absence of rewards. Furthermore, all sessions started with warm-up
369 trials in which dog subjects received a reward upon token return. Consequently, it could be
370 argued that not receiving a reward in the inequity condition could be enough to elicit frustration
371 and reduce dogs' willingness to participate in the interaction. There is abundant evidence
372 showing that animals develop expectations about rewards, and that the omission of an expected
373 reward elicits frustration [43, 44]. In fact, subjects' average exchange rate dropped from 29.1
374 successful trials in the EQ condition to only 13.8 successful trials when they did not receive a

375 reward (performance for IN-SL, SC, and NSC averaged). Furthermore, in absence of reward,
376 dogs' distress levels (measured as rates of self-directed behaviors) increased over the course of
377 the experimental session, a tendency that was not observed in the equity condition. However,
378 this frustration effect alone cannot fully explain our results, since dogs responded differently
379 depending on what the partner received, after controlling for their own reward. Overall, subjects
380 performed fewer successful trials when the partner received a reward than when it did not,
381 suggesting that seeing the partner receiving a reward, in addition to not receiving one
382 themselves, increased dogs' frustration. On the contrary, if dogs' responses were only based on
383 the negative expectancy violation, we would not have expected any difference between these
384 conditions. Therefore, these findings stress the importance of the social context in inducing
385 dogs' negative responses, and support previous studies showing that dogs clearly attend to
386 differential reward distribution and exhibit disadvantageous inequity aversion [20, 22, 45].

387 Our study shows previous undescribed effects of oxytocin on animals' responses to inequity
388 aversion. After oxytocin intake, dogs were less sensitive to the unequal distribution of rewards,
389 performing more successful trials than when administered with placebo. Extensive animal
390 research has shown that this neuropeptide is implicated in the regulation of several social
391 behaviors, including pair-bonding, sexual behavior, parental care, or social memory [32, 33,
392 46]. More recent research has also revealed that oxytocin influences prosocial decision making
393 in human and non-human primates, although the valence and magnitude of its effects are highly
394 sensitive to the social context [38, 47]. Aside from this research, only one study has evaluated
395 the effect of oxytocin on inequity aversion in animals. After oxytocin treatment, marmosets did
396 not increase or decrease their preferences for the equity (i.e. both individuals received the same
397 type of reward) or inequity options (i.e. the partner received a more preferred food reward than
398 the subject), suggesting that oxytocin did not influence their inequity aversion [17]. In contrast,
399 we found that oxytocin had a significant effect on dogs' responses when facing unequal
400 distribution of reward, increasing their tolerance towards disadvantageous outcomes.

401 Intriguingly, oxytocin also seems to differently affect prosocial behaviors in these two species.
402 While it reduces both socio-sexual and prosocial behaviors towards strangers in marmosets [48],
403 oxytocin promotes positive social behaviors in domestic dogs [35, 42] (but see [49] and results
404 from this study). Collectively, these findings support the idea that though oxytocin seems to be
405 an important underlying mechanism regulating cooperative associations in mammalian species
406 [32, 33, 46], its effects are not only context dependent, but they can also differ between species
407 in important and distinct ways. Further research on a wider range of species is clearly needed to
408 increase our understanding of the neurobiological bases of inequity aversion.

409 It could be argued that the observed effect of oxytocin on dog's token return rates was due to a
410 reduction in animals' stress levels after oxytocin intake, which in turn would have reduced
411 dog's frustration of not getting a reward, regardless of the social context. Previous studies have
412 shown that oxytocin has behavioral and physiologic anxiolytic effects. For instance, the
413 administration of exogenous oxytocin in humans, non-human primates and rodents attenuates
414 animals' stress responses by lowering the activity of the hypothalamic-pituitary-adrenal axis
415 [50, 51]. While our current study cannot rule out the possibility of a more general effect of
416 oxytocin on frustration, our data on self-directed behaviors show that individuals' distress levels
417 did not differ between inequity conditions, suggesting that our findings cannot be explained by a
418 mere reduction in animal's distress. Further research should explore the degree to which this
419 neuropeptide affects not only individuals' reactions to unequal outcomes, but also other related
420 mechanisms such as contrast effect [5].

421 An unanticipated result was that oxytocin treatment was not associated with higher affiliation
422 levels as compared to saline treatment. This result contrasts with research reporting that
423 oxytocin enhances positive social behaviors in both human and non-human animals, including
424 dogs [46]. However, as discussed above, there is also increasing recognition that oxytocin's
425 effects are sensitive to the social and motivational context, leading to different effects on

426 behavior [38, 47]. For instance, oxytocin-treated marmosets exhibit reduced food-sharing
427 behavior as compared to controls when tested with strangers, but similar levels when tested with
428 pair-mates [48]. Similarly, oxytocin increases affiliation tendencies in dogs when subjects were
429 not asked to perform any task [35], but reduces friendly reactions when facing a negative
430 valenced situation [49], and has no effect when dogs were asked to perform a task ([52], this
431 study). Dogs' affiliation tendencies were, however, affected by reward distribution. Overall,
432 dogs initiated affiliation towards their dog partners and the experimenter less often during the
433 EQ condition than during either inequity conditions. It is possible that dogs directed more
434 affiliation towards their partners when they did not receive a reward in an attempt to increase
435 their partner's tolerance around food resources. We could not, however, test this hypothesis
436 since the experimental setup – with a panel fence between testing enclosures – prevented dogs
437 from reaching each other's rewards.

438 Our analyses also revealed that oxytocin treatment enhanced dogs' attention to their partners, as
439 well as increased their decision latency. These findings are in agreement with previous research
440 showing that oxytocin influences the processing of social information. Exogenous oxytocin
441 enhances attention to facial features and expressions in monkeys, increases social orientation
442 and gaze to the eye region of human faces in dogs, and improves the ability to infer the
443 emotional state of others in humans [38, 46]. Further, oxytocin effects on response time parallel
444 previous research in human and non-human primates reporting that this neuropeptide modulates
445 deliberation times during decision making. For instance, oxytocin slows overall evaluation time
446 for rating faces in humans [53], and prolongs response times associated with reward donation
447 decisions in macaques [54]. These oxytocin-induced changes in reaction time have been
448 interpreted as reflecting internal processes, such as deliberation and control; that occur during
449 active interaction with others [55]. Consistent with this idea, oxytocin receptors are densely
450 localized in brain areas implicated in emotional and social information processing, such as the
451 amygdala, hypothalamus, or nucleus accumbens [56, 57]. Furthermore, evidence from human

452 neuroimaging studies reveals that these brain areas are activated during decision-making tasks
453 involving interaction with other participants, but not during non-social tasks [30].

454 At first glance, higher attention to partners and longer decision times during the inequity-
455 oxytocin condition might seem to conflict with higher tolerance to unequal distribution of
456 rewards. In principle, one would expect that attending more often to what the partner gets would
457 be associated with higher sensibility toward unequal reward distribution. However, it should be
458 noted that we found no differences in reaction time or frequency of looking to partners between
459 the equity and inequity-saline conditions, suggesting that dogs' responses to inequity are not
460 necessarily linked to changes in these behaviors. Furthermore, although longer latency times
461 could be interpreted as lower willingness to participate in the interaction [20], they have also
462 been associated with an increased willingness to behave pro-socially [54]. Thus, it is likely that
463 the observed increase in social attention and decision times after oxytocin treatment reflects
464 oxytocin effects on the processing of social information involved in decision making. Of
465 relevance, recent human studies have highlighted the role of oxytocin on emotional regulation
466 during decision making in social contexts. The activity of the anterior insular cortex, i.e. a brain
467 area involved in the regulation of social emotions [58], is greater when making decisions that
468 may result in betrayal [28], and exogenous oxytocin reduces its activity as well as the negative
469 emotions associated to social betrayal [30]. Therefore, it is possible that oxytocin increases
470 dogs' tolerance to unequal outcomes by reducing, or helping to cope with, the unpleasant
471 arousal associated with knowing that one's partner is obtaining more than oneself.

472 Our study, though, cannot determine the exact mechanisms through which oxytocin affects
473 dogs' reactions to inequity and alternative mechanisms cannot be excluded, including the
474 possibility that the observed changes are a result of the influence of peripheral OT receptors.
475 Although a number of studies have reported behavioral effects of peripheral oxytocin
476 administration in dogs [59], the mechanisms are still unknown, and the evidence showing that

477 oxytocin is able to cross the blood-brain barriers and exert direct effect on the brain is not
478 conclusive [60, 61]. Furthermore, the oxytocinergic system exerts its effects on multiple brain
479 areas, likely interacting with other neurotransmitter systems to influence social cognition and
480 behavior [56, 57]. For instance, it is known that oxytocin enhances reward via dopamine-
481 dependent mesolimbic reward pathways [62], and a functional link between dopamine and pro-
482 social concerns has been described in humans [29], which invites to speculate about a possible
483 interplay of both systems in regulating inequity aversion. Future research combining
484 endocrinological, pharmacological, and neuroimaging methods will be critical in order to shed
485 light on the interaction of neurotransmitters, inequity aversion and cooperation.

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