

1 **Chimpanzee uses manipulative gaze cues to conceal and reveal information to**
2 **foraging competitor**

3 **Short title: Manipulative gaze in chimpanzees**

4 Katie Hall^{a, b, c*}, Mike W. Oram^b, Matthew W. Campbell^{c, d}, Timothy M. Eppley^{c, e},
5 Richard W. Byrne^b, and Frans B.M. de Waal^c

6

7 ^a Chicago Zoological Society – Brookfield Zoo, 3300 Golf Road, Brookfield, IL 60513,
8 United States of America

9 ^b School of Psychology, University of St Andrews, St Mary’s College, South Street, St
10 Andrews, Fife, KY169JP, United Kingdom

11 ^c Living Links, Yerkes National Primate Research Center, Emory University, 2409 Taylor
12 Lane, Lawrenceville, Georgia, 30329, United States of America

13 ^d California State University, Channel Islands, One University Drive, Camarillo, CA
14 93012, United States of America

15 ^e Department of Anthropology, University of Texas at Austin, 2201 Speedway Stop
16 C3200, Austin, TX 78712, United States of America

17

18 * Corresponding author

19 Chicago Zoological Society—Brookfield Zoo

20 3300 Golf Road

21 Brookfield, Illinois 60513 USA

22 Tel: +1 (708) 688-8414

23 Email: KatieHallPhD@gmail.com

24 **Abstract**

25 Tactical deception has been widely reported in primates on a functional basis, but details
26 of behavioral mechanisms are usually unspecified. We tested a pair of chimpanzees (*Pan*
27 *troglodytes*) in the informed forager paradigm, in which the subordinate saw the location
28 of hidden food and the dominant did not. We employed cross-correlations to examine
29 temporal contingencies between chimpanzees' behavior: specifically how the direction of
30 the subordinate's gaze and movement functioned to manipulate the dominant's searching
31 behavior through two tactics, withholding and misleading information. In Experiment 1,
32 not only did the informed subordinate tend to stop walking towards a single high value
33 food, but she also refrained from gazing towards it, thus withholding potentially revealing
34 cues from her searching competitor. In a second experiment, in which a moderate value
35 food was hidden in addition to the high value food, whenever the subordinate alternated
36 her gaze between the dominant and the moderate value food, she often paused walking
37 for 5 seconds; this frequently recruited the dominant to the inferior food, functioning as a
38 'decoy'. The subordinate flexibly concealed and revealed gaze towards a goal, which
39 suggests that not only can chimpanzees use visual cues to make predictions about
40 behavior, but also that chimpanzees may understand that other individuals can exploit
41 their gaze direction. These results substantiate descriptive reports of how chimpanzees
42 use gaze to manipulate others, and to our knowledge are the first quantitative data to
43 identify behavioral mechanisms of tactical deception.

44

45 **Keywords:** tactical deception; Machiavellian intelligence; gaze following; informed
46 forager paradigm; *Pan troglodytes*

47

48 **Research Highlights:** Cross correlations show a subordinate chimpanzee tactically
49 deceived a dominant by not gazing towards a valuable food (withholding), and recruiting
50 to a ‘decoy’ food (misleading). Chimpanzees understand that others can exploit their gaze
51 direction.

52

53 **Introduction**

54 Competition for food is a common occurrence among animals. To compete
55 successfully, individuals have several options, including observing the behavior of others
56 in order to gain information from them about the location of a food patch or how to
57 process a particular food item. Like other species of non-human primate, chimpanzees
58 have been found to follow the gaze of their conspecifics [Tomasello et al., 1998; Hattori
59 et al., 2010; Hall et al., 2014; Kano & Call, 2014] and that of human experimenters
60 [Itakura, 1996; Povinelli & Eddy, 1996; Call et al., 1998; Itakura & Tanaka, 1998;
61 Povinelli et al., 1999; Tomasello et al., 2001; Leavens et al., 2004], even in the absence
62 of head movement cues [for reviews, see Tomasello et al., 2003; Call & Tomasello, 2008;
63 Whiten, 2013]. Chimpanzees (*Pan troglodytes*) can use others’ gaze direction to gain
64 information about their attentional states and their focus of interest [Emery, 2000]: for
65 example, the presence of food or predators, and social interactions between others [Hare
66 et al., 2000; Itakura, 2004; Schloegl et al., 2007; Zuberbühler, 2008; Rosati & Hare,
67 2009].

68 Following gaze is not merely a response to a stimulus, as individuals appear to
69 understand that gaze conveys information; for example, all great apes follow gaze around

70 barriers to a target [Tomasello et al., 1999; Bräuer et al., 2005], and often refer back to
71 the face of a human experimenter after following their gaze to the ceiling where no target
72 was present [Call et al., 1998; Braüer et al., 2005]. Additionally, social gaze may be
73 important for inferring someone's intentions to act, or for conveying one's own intentions
74 [Baron-Cohen, 1995; Santos & Hauser, 1999; Ferrari et al., 2000; Freire et al., 2004;
75 Csibra, 2010; see Rizzolatti & Craighero, 2004 for details on the neurological
76 underpinnings of understanding intention, and Call & Tomasello, 2008 for a review of
77 apes' understanding of intention]. In fact, some great apes have been observed
78 spontaneously using ostensive gaze cues to direct humans' attention [Gómez, 1996; de
79 Waal, 2001], and there is evidence that wild chimpanzees differentially alarm call more
80 towards ignorant bystanders to inform them of the presence of a predator [Crockford et
81 al., 2012; Schel et al., 2013], yet the question remains as to whether chimpanzees use
82 gaze as a cue to deliberately share information with conspecifics [Shepherd, 2010].
83 Ultimately, understanding someone else's gaze and to what they have visual access aids
84 in attributing what they know or believe [Wimmer et al., 1988; Povinelli et al., 1990;
85 Baron-Cohen, 1991, 1995; Gopnik et al., 1994; Mitchell, 1997; Hare et al., 2000; Hare et
86 al., 2001]. Attributing knowledge or belief to another individual impacts how one
87 predicts how the other will behave in that context [Premack & Woodruff, 1978; Baron-
88 Cohen, 1995; Schmelz et al., 2011].

89 If chimpanzees are able to use others' gaze as a source of information, then
90 counter-measures to this ability may also have developed. Specifically, chimpanzees may
91 be able to deceive a competitor by omission (averted gaze) or by commission
92 (deliberately gazing at the 'wrong' place). Experimental evidence from primates

93 interacting with human experimenters has shown that subjects can refrain from exposing
94 hidden food to human competitors [Woodruff & Premack, 1979; Mitchell & Anderson,
95 1997; Anderson et al., 2001; Karg et al., 2015a]. However, they are often only able to do
96 so after many trials, and they generally do not act to cover up exposed food [Karg et al.,
97 2015a]. There is also evidence for primates alerting cooperative humans to the presence
98 of hidden food or tools to access food [Woodruff & Premack, 1979; Call & Tomasello,
99 1994; Gómez, 1998; Menzel, 1999; Leavens et al., 2004; Zimmerman et al., 2009; Karg
100 et al., 2015a]. While evidence is lacking in non-human primates for finding hidden food
101 in an object choice task when a human experimenter's cooperative gaze is the sole cue
102 [Anderson et al., 1995, 1996; Call & Tomasello, 1998; Peignot & Anderson, 1999; Call
103 et al., 2000; Burkart & Heschl, 2007], chimpanzees are able to recognize what
104 conspecifics do and do not see in food competition situations, and adjust their behavior to
105 take advantage [Hare et al., 2000; Hare et al., 2001], indicating that chimpanzees perform
106 better in the more socio-ecologically relevant context of competition with conspecifics
107 [Hare & Tomasello, 2004]. This evidence suggests that not only do chimpanzees know
108 what others do and do not see, but also that they can use this information strategically in
109 dyadic food competition.

110 Rich narrative descriptions have reported an escalating tactical arms race between
111 conspecific competitors in the informed forager paradigm, such as how an informed
112 subordinate can act to counter a dominant's exploitation by delaying their approach to the
113 food, or by moving in a different direction [Menzel, 1974; Coussi-Korbel, 1994; Held et
114 al., 2000, 2002; Hare et al., 2001; Hirata & Matsuzawa, 2001; Fujita et al., 2002; Hare et
115 al., 2003; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al.,

116 2008; Amici et al., 2009; Held et al., 2010]. In the seminal paper, Menzel [1974]
117 described how his informed subordinate, Belle, interacted with her competitor, Rock: she
118 sat atop the hidden food and stopped uncovering it in his presence, he pushed her away to
119 steal the food; she stopped short, and he expanded his search area; Belle waited until
120 Rock was looking away before approaching the food, but he turned around; she walked in
121 the opposite direction and doubled back once Rock was distracted; she walked towards a
122 smaller pile of food, and when Rock no longer fell for that trick, Belle began to throw
123 tantrums. Why did Belle behave this way? Did she have insight into the mind of her
124 competitor and strategically devise her tactics to counter Rock's actions? Did she read
125 and react to Rock's movements? Or were her responses learned, from initially
126 coincidental conjunctions? Often, narrative descriptions such as the one of Belle and
127 Rock's interaction are brushed aside as merely anecdotes because they do not
128 systematically attempt to answer the above questions [Bernstein, 1988], but they have
129 real value as a starting point for deeper investigation [de Waal, 1986; Byrne, 1997; Bates
130 & Byrne, 2007]. Using a sensitive instrument, cross correlation [Oram et al., 2001; Hall
131 et al., 2014], to measure the interactions observed, we can pull apart the overall tactic to
132 examine the temporal contingencies between actions and reactions to better describe the
133 behavioral mechanisms underlying tactical deception [Whiten & Byrne, 1988; Byrne &
134 Whiten, 1990].

135 In this study, we investigated a subordinate's ability to remain one step ahead of
136 the dominant's exploitation; we aimed to validate statistically how chimpanzees use cues
137 during foraging competition. Whereas prior studies have reported the outcomes of
138 foraging competition (i.e., how many pieces of food each competitor ate), our focus was

139 on the behavioral mechanisms underlying these tactics. We therefore examined whether
140 the informed subordinate used visual signals differently when under exploitation pressure
141 from the dominant. We tested two chimpanzees in an informed forager food competition
142 task. In Experiment 1, we hid a highly preferred food item (a banana). We asked whether
143 the dominant would exploit the subordinate's foraging behavior by following her
144 movement and her gaze, and in turn whether the subordinate would tactically deceive the
145 dominant by avoiding gazing towards the hidden banana, in order to counter this
146 exploitation. In Experiment 2, we hid a banana and a moderately preferred cucumber.
147 Chimpanzees can recall and recover hidden food in the order of their preference [Sayers
148 & Menzel, 2012], so we would expect the subordinate to approach the banana first, if she
149 were acting on her preferences. However, if the subordinate had learned over the course
150 of Experiment 1 that the dominant would steal any uncovered food, the subordinate might
151 in principle use cues to recruit her competitor towards the 'decoy' cucumber first. We
152 asked whether the subordinate's behavior would differ when approaching either bait, and
153 if the subordinate would use gaze cues to manipulate (i.e., tactically deceive) the
154 dominant.

155

156 **Methods**

157 *Study site and subjects*

158 We tested two unrelated adult female chimpanzees, from the same social group of
159 11 individuals at the Yerkes National Primate Research Center field station in
160 Lawrenceville, Georgia, USA. Data were collected from October 2010 to August 2011.
161 Reinette (aged 23) was subordinate to Georgia (30), as determined by dyadic food

162 competitions conducted prior to the experiment. Chimpanzees were housed in an outdoor
163 enclosure (24 x 30 m) with a central climbing structure and had access to indoor spaces
164 (188 m³). All individuals were fed twice daily with chow, fruit and vegetables, and water
165 was available *ad libitum*. Chimpanzees were not deprived of food or water at any time
166 during the experiment and were not subject to any invasive procedure. The other group
167 members were held indoors during testing, without visual access to the outdoor
168 compound. Research complied with protocols approved by the Institutional Animal Care
169 and Use Committee (IACUC) and adhered to the legal requirements of the United States.
170 The research adhered to the American Society of Primatologists (ASP) Principles for the
171 Ethical Treatment of Non Human Primates.

172 For coding purposes, we defined the boundaries of four approximately equal
173 quadrants (Q1, Q2, Q3, Q4) in the outdoor enclosure, each with four hiding places in or
174 under enrichment items such as tires, barrels, and kegs (Figure 1). The baiting schedule
175 cycled through the four quadrants in a counterbalanced order. Each trial was video
176 recorded using cameras (Panasonic PV-GS320, Sony DCR-HC52, Canon Vixia HF100)
177 placed at opposite angles over the enclosure.

178

179 *Experiment 1: One Reward*

180 The subordinate and dominant chimpanzees were brought into an indoor testing
181 area, each in an adjacent holding space with visual access between them through a mesh
182 panel (72 x 52 cm). The informed subordinate additionally had visual access into the
183 outdoor enclosure via a Lexan window installed in the hydraulic door. The dominant did

184 not have visual access to the outdoor enclosure, thus remaining ignorant of actions
185 conducted in the enclosure.

186 Once the outdoor enclosure was void of chimpanzees, the experimenter entered,
187 and attracted the subordinate's attention through the Lexan window. The experimenter
188 hid the banana in one of 16 pre-determined hiding locations while the subordinate
189 watched. An observer remained in the indoor testing area and confirmed that the
190 subordinate watched the baiting procedure. After baiting, the experimenter left the
191 enclosure and ascended an observation tower in order to control one of two video
192 recorders covering all the space within the outdoor compound. Once in position, the
193 dominant and then the subordinate were released into the enclosure, with a delay of
194 approximately three seconds between the hydraulic doors opening fully, to prevent the
195 subordinate from finding the food before the dominant had a chance to search. The
196 experimenter video recorded the trials from a tower. The pair was tested in 24 trials. A
197 more detailed description of this experimental set-up can be found in Hall *et al.* [2014].

198

199 *Experiment 2: Two Unequal Rewards*

200 We chose to test the chimpanzees using cucumber as a moderate-value reward,
201 based on our observations of chimpanzees feeding; bananas were used as high-value
202 rewards. To confirm that their preferences remained consistent and that a chimpanzee had
203 not approached a cucumber before a banana due to a preference for the cucumber, each
204 chimpanzee was individually tested on 10 counterbalanced trials for her preference
205 between banana and cucumber after the completion of Experiment 2. A chimpanzee was
206 individually presented with a small slice of cucumber and a small slice of banana

207 approximately 30 cm apart on a sliding tray; chimpanzees indicated their choice by
208 pointing through the mesh to their preferred item, and were given that item. In the
209 preference test, subordinate Reinette chose 10/10 banana slices, and dominant Georgia
210 chose 9/10 banana slices.

211 The chimpanzees were held in the same adjacent cages as in Experiment 1: the
212 subordinate with visual access to the outdoor enclosure, the dominant without. Two
213 experimenters entered the outdoor enclosure. The first experimenter hid the cucumber in
214 one of the 16 pre-determined hiding locations as the subordinate subject watched. As
215 soon as the cucumber was placed, the second experimenter then hid the banana in a
216 different pre-determined location in view of the subordinate chimpanzee. A third
217 experimenter remained inside with the chimpanzees and confirmed that the subordinate
218 watched the baiting procedure. The experimenters then left the enclosure and ascended
219 the observation towers to activate the video recorders. At this point, both chimpanzees
220 were released into the enclosure. The pair was tested in 20 trials.

221 Similar to Experiment 1, the baiting schedule cycled through the four quadrants in
222 a counterbalanced order with only one item hidden in a quadrant. Additionally, no two
223 items were hidden together on the left (Q1, Q3) or the right (Q2, Q4) side of the
224 enclosure because of the possibility that a chimpanzee would find the food closer to her
225 starting position first, regardless of her preference. Placing one food item on the left half
226 of the enclosure and one item on the right also allowed for approaches to be coded with
227 minimal ambiguity as to which item the chimpanzee was walking toward.

228

229 *Data Coding*

230 All videos were coded for chimpanzees' movement and gaze direction using
231 Noldus Observer XT 9 software [Noldus Information Technology, Inc., Wageningen,
232 Netherlands]. State variables were recorded in 1-second intervals using instantaneous
233 sampling, and point variables were recorded using all-occurrence sampling [Altmann,
234 1974]. We coded state variables including the direction of movement or gaze relative to
235 the location of the competitor (toward/away), the hidden food item(s) (toward/away), and
236 the defined quadrants of the enclosure (1-4). Gaze direction was coded based on the
237 direction of head position. We coded point variables including *change direction* and *seize*
238 *food*. We recorded which chimpanzee ate the food(s) in each trial; a trial was ended after
239 all available food items were consumed, or after five minutes of recording, whichever
240 came first.

241 We defined *alternate gaze* as “one chimpanzee looks at the other individual, and
242 then gazes towards the hidden bait for two seconds.” We defined any *pause* (in
243 locomotion, in gazing towards the bait, etc.) as a halt in the behavior for five consecutive
244 seconds. In studies on collective movement in primates, it has been shown that when a
245 leader pauses to look back to group-mates, it serves not only to monitor who has joined
246 the movement but also to recruit others to join [Meunier *et al.*, 2007; Sueur and Petit,
247 2010]. We therefore combined the prior two definitions to operationalize our definition of
248 *recruit* as “one chimpanzee looks at the other individual, and then gazes towards the
249 hidden bait for two seconds, while pausing in her locomotion (for five consecutive
250 seconds).” We defined *approach* as “the chimpanzees are in different quadrants of the
251 enclosure and one individual locomotes towards the other.” *Search* was defined as any

252 active food-uncovering behavior (e.g. overturning a barrel, reaching into a tire, etc.)
253 within one body length of defined hiding places.

254

255 *Statistical Analysis*

256 The behavior (i.e., gaze and movement direction) of each chimpanzee was
257 measured over a period of time, and each individual's actions were compared to those of
258 the other, so as to determine whether the one chimpanzee's actions were contingent on, or
259 occurred in a time-locked pattern relative to, the actions of the other chimpanzee. We
260 used cross correlations, which measure the correlation between two variables as a
261 function in time, to compare the behavior of two chimpanzees [for a detailed explanation
262 of this approach, see Oram *et al.*, 2001; Hall *et al.*, 2014]. In the correlogram figures, the
263 binary behavioral series from one chimpanzee is designated as a referent and the
264 beginning of the series represents $t = 0$. The other behavioral series (the target) is then
265 plotted with time lags relative to the referent; the process is repeated with each new
266 instance of the referent behavior plotted at $t = 0$. Pearson's correlations are calculated for
267 pairs of values at each time lag (ranging from -20 to +20 seconds post-stimulus, that is,
268 before and after the referent behavior is plotted at $t = 0$). Therefore the referent behavior
269 at $t = 0$ should not be considered the "start" of the behavior, but rather "while doing" the
270 behavior [see Fig. 1 in Hall *et al.*, 2014]. The key aspect of this statistic is to demonstrate
271 how closely two actions are linked in time; considering that the data are compiled from
272 all trials within an experiment, any significant outcomes indicate that the data overcome a
273 high threshold of likelihood. Cross correlations were tested against 10,000 random
274 permutations of within-trial data (this within-trial shuffled control is labeled "Noise" in

275 the figures) using $-\log$ -likelihood values of t tests to calculate significance; significant
276 values were set at $p < 0.05$.

277

278 **Results**

279 *Experiment 1: One Reward*

280 Over the course of Experiment 1, the dominant gained a banana from the
281 subordinate (i.e., by rushing to the location of the hidden food when the subordinate was
282 actively searching) on nine out of 24 trials (37.5%), indicating considerable exploitation
283 pressure. During the first half of the experiment, the subordinate retrieved almost all of
284 the bananas, but then the dominant gained one on every other trial until the end of the
285 experiment (Table 1).

286

287 *Does the Subordinate Withhold Cues from the Dominant?*

288 One of the ways in which the dominant exploited the subordinate's knowledge
289 was to follow her and steal food from the hiding location once the subordinate had
290 uncovered it. We asked whether the subordinate was able to withhold any cues that could
291 reveal the location of the hidden food to the dominant. In response to the dominant
292 directly approaching her, the subordinate was likely to pause walking for five consecutive
293 seconds (Fig. 2). Additionally, when the subordinate stopped walking for five seconds,
294 she was slightly more likely to stop gazing towards the banana for five seconds than
295 expected by chance (Fig. 3). Put simply, when the dominant approached her, the
296 subordinate stopped walking and gazing in the direction of the hidden banana.

297

298 *Experiment 2: Two Unequal Rewards*

299 During the first experiment, the dominant had learned to follow the subordinate
300 around the enclosure, and she continued to do so throughout the second experiment,
301 despite the subordinate's apparent attempts to deflect her. The subordinate obtained
302 slightly fewer than half of the rewards in Experiment 2: 8 bananas and 9 cucumbers
303 (42.5% of total rewards); the dominant competitor gained 11 bananas and 9 cucumbers
304 (50% of total) (Table 2). One banana (trial 10) and two cucumbers (trials 4 and 7) were
305 not picked up within the allotted five minutes. The subordinate approached the cucumber
306 first on trials 1, 6, 8, 11, 12, 13, 17, and 20, and the dominant took the cucumber on half
307 of those trials (6, 12, 17, 20).

308

309 *Does the Subordinate Recruit the Dominant to the Decoy?*

310 We asked whether the subordinate approached the less preferred cucumber in a
311 different manner from the banana. The subordinate alternated her gaze between the
312 dominant partner and whichever hidden food she approached, but when the subordinate
313 alternated gaze between the dominant and the cucumber, she often paused walking for
314 five seconds (we defined this gaze alternation coupled with a movement pause as a
315 *recruit*, see Methods section) without immediately uncovering the food (Fig. 4). On the
316 other hand, the subordinate was less likely to pause her movement while alternating her
317 gaze between her competitor and the banana (Fig. 5), instead attempting to reach the
318 banana before her competitor, sometimes by running. The subordinate approached the
319 two baits differently: by pausing and alternating gaze with her ignorant competitor, she

320 may have revealed the location of the cucumber to her, whereas she moved swiftly to
321 retrieve the banana.

322

323 *Does the Subordinate's Behavior Manipulate the Dominant?*

324 In addition to manipulative tactics throughout the two experiments, on four
325 consecutive trials (11-14) in Experiment 2, the subordinate used the same tactic
326 successfully: she walked towards and *recruited* towards the cucumber, and then while the
327 dominant was searching at that location, the subordinate moved toward the location of the
328 banana, unaccompanied by the dominant. We therefore evaluated the proximate success
329 of the subordinate's *recruit*, showing that this behavior caused the dominant to search in
330 the area (Fig. 6; includes data from all 20 trials). Finally, we evaluated the ultimate
331 success of the subordinate's *recruit*, finding (a) that prior to the dominant searching for
332 the cucumber, the subordinate did not walk towards the banana and (b) that the
333 subordinate tended to move towards the hidden banana while the dominant was busy
334 searching at the site of the cucumber (Fig. 7; includes data from all 20 trials). When the
335 subordinate paused and gazed towards the cucumber, the dominant became occupied in a
336 search in that area, allowing the subordinate to retrieve the banana without the dominant
337 following her.

338

339 **Discussion**

340 In both experiments, tactical deceptions functioned to (a) withhold information
341 about the location of the highly preferred banana, or (b) mislead the dominant competitor
342 to the less preferred cucumber. We have previously shown [Hall *et al.*, 2014] that a

343 dominant chimpanzee will modify her search for hidden food by exploiting a
344 subordinate's behavior: in particular, that the dominant is attentive to the subordinate's
345 gaze—whether straight ahead or off-axis from the direction of her body—while the
346 subordinate walks. In the current study, the subordinate learned to avoid this type of
347 competition from the dominant by withholding cues and by approaching the less
348 preferred cucumber first, which speaks to great apes' ability to plan for the immediate
349 future [Mulcahy & Call, 2006; Osvath & Osvath, 2008]. While we expected the
350 subordinate to lead the dominant towards the cucumber, we additionally found an
351 unexpected pattern (alternating gaze between the partner and the cucumber—but not the
352 banana—while pausing) that functioned to recruit the dominant to that location,
353 indicating that chimpanzees are highly flexible in their use of gaze direction and
354 movement to both conceal and *reveal* information to manipulate a foraging partner.
355 Therefore, when the subordinate's recruiting tactic was successful, it proximately
356 functioned to occupy the dominant in a search for a less preferred food, and ultimately
357 functioned to allow the subordinate to retrieve the more preferred banana, without
358 competition.

359 Our study provides empirical evidence that chimpanzees are able to use gaze and
360 movement cues to reveal information to a conspecific foraging competitor as a
361 manipulative, and ultimately deceptive tactic. The results provide rigorous statistical
362 demonstration of specific behavioral mechanisms underlying foraging competition,
363 adding validation to other published observations [Menzel, 1974; Byrne & Whiten, 1990;
364 Coussi-Korbel, 1994; Held et al., 2000, 2002; Hare et al., 2001; Hirata & Matsuzawa,
365 2001; Fujita et al., 2002; Hare et al., 2003; Ducoing & Thierry, 2003, 2004; Bugnyar &

366 Kotrschal, 2004; Schloegl et al., 2008; Amici et al., 2009; Held et al., 2010; Wheeler &
367 Hammerschmidt, 2013]. Though we are limited in the conclusions we can draw based on
368 the behavior of a single pair, repeated trials between the same pair allow us to focus on
369 how animals interact during a naturalistic foraging problem and how they adjust their
370 tactics over time.

371 It is plausible that the subordinate chimpanzee in this study might have stopped
372 walking towards the banana in Experiment 1, or paused near the cucumber in Experiment
373 2, in order to avoid approaching a monopolizable food item in the presence of the
374 dominant [Held et al., 2002; Bräuer et al., 2007; Amici et al., 2009]. The subordinate's
375 behavior, however, cannot be attributed to the 'evil-eye hypothesis' [Kaminski et al.,
376 2008] because the dominant was not shown the location of either food item. Though on
377 the surface, the subordinate's movement cue (or lack thereof) was similar in these two
378 scenarios, her gaze cues were very different between the two baits: she avoided gazing
379 towards the banana while pausing in Experiment 1, and alternated her gaze between the
380 dominant and the cucumber (but not the banana) while pausing in Experiment 2. This
381 subtle behavioral difference suggests that chimpanzees may be aware that other
382 individuals can exploit their gaze direction.

383 In Experiment 2, the fact that the subordinate was able to retrieve the banana
384 while the dominant was busy searching for the cucumber could have initially been a
385 coincidence, and subsequently become a learned contingency that she used successfully
386 on trials 11-14 [see Heyes, 1998; Povinelli & Vonk, 2003, 2004 for discussions on
387 'behavioral rules']. Chimpanzees have difficulty inhibiting themselves in the presence of
388 desired food [Boysen, 1996; Boysen et al., 2001; but see Rosati et al., 2007], so avoiding

389 walking or gazing towards the banana for a few moments might be considered a self-
390 distracting behavior [Evans & Beran, 2007], functioning to prevent the worse outcome of
391 the dominant finding it. An intriguing possibility, however, is that the subordinate may
392 have learned that the dominant partner would exploit her movement and gaze wherever
393 she went [as in Hall *et al.*, 2014], so the subordinate continued on a trajectory away from
394 the hidden banana, and towards the decoy cucumber, in order to deceive her competitor
395 [Güzeldere *et al.*, 2002; Bugnyar & Kotrschal, 2004].

396 In approaching the cucumber in particular, the subordinate looked at her
397 competitor in an ostensive manner, that is, she looked directly at her partner in order to
398 get her attention [e.g., Senju & Csibra, 2008], and then used her own gaze (head
399 orientation) as a social cue to point towards the location of the cucumber, and was then
400 likely to pause her movement for five seconds. This combined sequence of physical cues
401 functioned to recruit the dominant to that location. The subordinate, however, did not
402 behave this way while approaching the banana. That the subordinate was able to flexibly
403 withhold gazing towards the banana during episodes in which the dominant was
404 exploiting her, yet distinctively point towards the hiding location of the cucumber under
405 similar circumstances, fits Tomasello and Call's [1997] definition of intentional action
406 for reaching her implied goal (here, obtaining the hidden banana). There is good evidence
407 that chimpanzees respond not only to others' behavior but also to their goals or
408 intentions, responding differently to humans that behave as if they are unwilling or
409 unable to provide food [Call *et al.*, 2004], humans that act purposefully or accidentally
410 [Call & Tomasello, 1998; Tomasello & Carpenter, 2005], and by offering help to a
411 human striving for an out of reach item [Warneken *et al.*, 2006; Warneken *et al.*, 2007]. It

412 has been hypothesized that not only is it possible for gaze direction to expose truthful
413 information (such as the location of the hidden bait), but also that gaze can reveal
414 deceptive intent [Freire et al., 2004]; it would therefore behoove the subordinate to
415 judiciously control her gaze direction when the dominant is present.

416 Though it would be difficult to falsify an explanation using behavioral rules, such
417 as “wait to retrieve food until competitor’s line of vision to the food is obstructed by a
418 barrier,” for this flexible and strategic maneuvering [Seed and Tomasello, 2010], it would
419 be equally difficult to demonstrate experimental evidence of mental state representation,
420 such as “I know the dominant is ignorant about the food,” precisely because both
421 explanations require observing another individual’s behavior in context [Whiten, 1996].
422 However, post-hoc behavioral explanations are rarely predictive of future behavior
423 [Byrne & Bates, 2006], especially in novel situations, in the same way that an
424 explanation by mental state attribution is. Whereas proponents of either explanation
425 (behavioral or mental state) may argue that the others’ explanation over-complicates the
426 issue [Heyes, 1998; Povinelli & Vonk, 2003, 2004; Byrne & Bates, 2006; Penn &
427 Povinelli, 2007], others argue for a middle ground or alternative explanation [Tomasello
428 & Call, 1997; Hare et al., 2001; Tomasello et al., 2003; Call & Tomasello, 2005; see
429 Whiten, 1996, 2013 for an explanation of intervening variables, and Martin & Santos,
430 2016, for a hypothesis of awareness relations]: in which chimpanzees have developed
431 intelligent problem solving strategies for some physical and social problems, but fall
432 short of attributing certain mental states to one another, such as false beliefs.

433 Primates exhibit sophisticated, flexible, and strategic social maneuvering, and are
434 able to predict and manipulate others’ behavior in novel situations [Jolly, 1966; Kummer,

435 1967; Humphrey, 1976; Byrne & Whiten, 1988; Byrne, 1996; Whiten & Byrne, 1997;
436 Dunbar, 1998]. This ability likely arises from lifelong learning and understanding that
437 their own, and others' behavior is influenced by, for example, what is visible [Level 1
438 perspective taking: Flavell, 1992]. Though the subordinate and the dominant never
439 switched roles in this study, the subordinate may have learned through her own life
440 experiences to infer what was visible to her partner [Karg *et al.*, 2015a], and then
441 manipulated her gaze direction to hide cues from her partner. In particular for
442 chimpanzees and other animals exhibiting a fission-fusion dynamic, differences in access
443 to knowledge exist due to socioecological factors [Aureli *et al.*, 2008], therefore the
444 ability to gain information (or hide it) from others may also have an evolutionary
445 advantage during competitive and cooperative situations [Hall & Brosnan, *in press*].

446 We have focused on demonstrating the behavioral contingencies between
447 individuals in a foraging competition, that is, *how* chimpanzees gain knowledge from
448 conspecifics, rather than *what* they know—whether they know a rule, a mental state, or
449 something in between. The tactical deceptions observed in this study suggest that the
450 subordinate chimpanzee may be aware that the dominant can exploit her gaze cues, so
451 she flexibly and strategically adjusted her gaze as a counter-measure, in an intentional
452 manner.

453

454 **Acknowledgements**

455 This project was funded by the National Institutes of Health's Office of Research
456 Infrastructure Programs base grant to the Yerkes National Primate Research Center -
457 P51OD011132. Financial support for KH was provided by Janet T. Anderson Trust,

458 Scottish Overseas Research Student Award Scheme, and a University of St Andrews
459 School of Psychology studentship. MWC was supported by the FIRST program
460 (NIH/NIGMS (USA) IRACDA grant number K12 GM000680). We thank Emory
461 University, Living Links, and Yerkes National Primate Research Center, which is fully
462 accredited by the American Association for Accreditation of Laboratory Animal Care.
463 Additional thanks to Victoria Horner and J. Devyn Carter for helpful discussions, and to
464 Andrew Whiten for his support. The authors declare no conflicts of interest.

465

466 **References**

467 Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:
468 227-266.

469

470 Amici, F., Aureli, F., Visalberghi, E., Call, J. 2009. Spider monkeys (*Ateles geoffroyi*)
471 and capuchin monkeys (*Cebus apella*) follow gaze around barriers: evidence for
472 perspective taking?. *Journal of Comparative Psychology*, 123: 368-374.

473

474 Anderson, J. R., Kuroshima, H., Kuwahata, H., Fujita, K., Vick, S. J. 2001. Training
475 squirrel monkeys (*Saimiri sciureus*) to deceive: acquisition and analysis of behavior
476 toward cooperative and competitive trainers. *Journal of Comparative Psychology*, 115:
477 282-293.

478

- 479 Anderson, J. R., Montant, M., Schmitt, D. 1996. Rhesus monkeys fail to use gaze
480 direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*,
481 37: 47-55.
- 482
- 483 Anderson, J. R., Sallaberry, P., Barbier, H. 1995. Use of experimenter-given cues during
484 object-choice tasks by capuchin monkeys. *Animal Behaviour*, 49: 201-208.
- 485
- 486 Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., ... &
487 Holekamp, K. 2008. Fission-fusion dynamics. *Current Anthropology*, 49: 627-654.
- 488
- 489 Baron-Cohen, S. 1991. Precursors to a Theory of Mind: understanding attention in others.
490 In Whiten, A. (Ed.) *Natural Theories of Mind: evolution, development and simulation of*
491 *everyday mindreading*, Blackwell: Cambridge, pp 233-251.
- 492
- 493 Baron-Cohen, S. 1995. *Mindblindness: an essay on autism and Theory of Mind*,
494 Cambridge: MIT Press.
- 495
- 496 Bates, L. A., Byrne, R. W. 2007. Creative or created: using anecdotes to investigate
497 animal cognition. *Methods*, 42: 12-21.
- 498
- 499 Bernstein, I.S. 1988. Metaphor, cognitive belief, and science [Peer commentary on
500 "Tactical deception in primates" by Whiten A, Byrne RW]. *Behavioral and Brain*
501 *Sciences* 11:233–273.

502

503 Boysen, S. T. 1996. "More is less": the elicitation of rule-governed resource distribution
504 in chimpanzees. In Russon, A.E., Bard, K.A., Parker, S.T. (Eds.). *Reaching into thought:
505 the minds of the great apes*. Cambridge: Cambridge University Press, 177-189.

506

507 Boysen, S. T., Berntson, G. G., Mukobi, K. L. 2001. Size matters: impact of item size and
508 quantity on array choice by chimpanzees (*Pan troglodytes*). *Journal of Comparative
509 Psychology*, 115: 106-110.

510

511 Bräuer, J., Call, J., Tomasello, M. 2005. All great ape species follow gaze to distant
512 locations and around barriers. *Journal of Comparative Psychology*, 119: 145-154.

513

514 Bräuer, J., Call, J., Tomasello, M. 2007. Chimpanzees really know what others can see in
515 a competitive situation. *Animals Cognition* 10: 439-448.

516

517 Bugnyar, T., Kotrschal, K. 2004. Leading a conspecific away from food in ravens
518 (*Corvus corax*)? *Animal Cognition*, 7: 69-76.

519

520 Burkart, J. M., Heschl, A. 2007. Understanding visual access in common marmosets,
521 *Callithrix jacchus*: perspective taking or behavior reading?. *Animal Behaviour*, 73: 457-
522 469.

523

524 Byrne, R. W. 1996. Machiavellian intelligence. *Evolutionary Anthropology* 5: 135-143.

525

- 526 Byrne, R. W. 1997. What's the use of anecdotes? Attempts to distinguish psychological
527 mechanisms in primate tactical deception. In Mitchell, R.W., Thompson, N.S., Lyn
528 Miles, H. (Eds). *Anthropomorphism, Anecdotes, and Animals*. New York: State
529 University of New York Press, pp. 134-150.
- 530
- 531 Byrne, R.W., Bates, L.A. 2006. What are animals cognitive? *Current Biology* 16: R445-
532 R448.
- 533
- 534 Byrne, R.W., Whiten, A. 1988. Machiavellian intelligence: social expertise and the
535 evolution of intellect in monkeys, apes and humans. New York: Oxford University Press.
- 536
- 537 Byrne, R.W., Whiten, A. 1990. Tactical deception in primates: the 1990 database.
538 *Primate Report*, Whole Volume 27, pp.1-101.
- 539
- 540 Call, J., Agnetta, B., Tomasello, M. 2000. Cues that chimpanzees do and do not use to
541 find hidden objects. *Animal Cognition*, 3: 23-34.
- 542
- 543 Call, J., Hare, B., Carpenter, M., Tomasello, M. 2004. 'Unwilling' versus 'unable':
544 chimpanzees' understanding of human intentional action. *Developmental science*, 7: 488-
545 498.
- 546
- 547 Call, J., Hare, B. A., Tomasello, M. 1998. Chimpanzee gaze following in an object-
548 choice task. *Animal Cognition*, 1: 89-99.

549

550 Call, J., Tomasello, M. 1994. Production and comprehension of referential pointing by
551 orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 108: 307-317.

552

553 Call, J., Tomasello, M. 1998. Distinguishing intentional from accidental actions in
554 orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*) and human children
555 (*Homo sapiens*). *Journal of Comparative Psychology*, 112: 192-206.

556

557 Call, J., Tomasello, M. 2005. What chimpanzees know about seeing revisited: an
558 explanation of the third kind. In Eilan, N., Hoerl, C., McCormack, T., Roessler, J. (Eds.),
559 *Joint attention: communication and other minds*. Oxford: Clarendon Press, pp. 45-64.

560

561 Call, J., Tomasello, M. 2008. Does the chimpanzee have a theory of mind? 30 years later.
562 *Trends in Cognitive Sciences*, 12: 187-192.

563

564 Coussi-Korbel, S. 1994. Learning to outwit a competitor in mangabeys (*Cercocebus*
565 *torquatus torquatus*). *Journal of Comparative Psychology*, 108: 164-171.

566

567 Crockford, C., Wittig, R. M., Mundry, R., Zuberbühler, K. 2012. Wild chimpanzees
568 inform ignorant group members of danger. *Current Biology*, 22: 142-146.

569

570 Csibra, G. 2010. Recognizing communicative intentions in infancy. *Mind & Language*,
571 25: 141-168.

572

573 de Waal, F.B.M. 1986. Deception in the natural communication of chimpanzees. In:
574 Mitchell, R.W., Thompson, N.S. (eds), *Deception: human and nonhuman deceit*, pp. 221-
575 244. Albany: SUNY Press.

576

577 de Waal, F.B.M. 2001. Pointing primates: sharing knowledge...without language. The
578 Chronicle of Higher Education, 47: B7-B9.

579

580 Ducoing, A.M., Thierry, B. 2003. Withholding information in semifree-ranging tonkean
581 macaques (*Macaca tonkeana*). Journal of Comparative Psychology, 117: 67-75.

582

583 Ducoing, A.M., Thierry, B. 2004. Following and joining the informed individual in
584 semifree-ranging tonkean macaques (*Macaca tonkeana*). Journal of Comparative
585 Psychology, 118: 413-420.

586

587 Dunbar, R.I.M. 1998. The social brain hypothesis. Evolutionary Anthropology 6: 178-
588 190.

589

590 Emery, N.J. 2000. The eyes have it: the neuroethology, function and evolution of social
591 gaze. Neuroscience & Biobehavioral Reviews, 24: 581-604.

592

593 Evans, T. A., Beran, M. J. 2007. Chimpanzees use self-distraction to cope with
594 impulsivity. Biology Letters, 3: 599-602.

595

596 Flavell, J. H. 1992. Perspectives on perspective taking. In Beilin, H., Pufall, P.B. (Eds.).
597 *Piaget's theory: prospects and possibilities*. Hillsdale, New Jersey: L. Erlbaum, pp. 107–
598 139.

599

600 Freire, A., Eskritt, M., Lee, K. 2004. Are eyes windows to a deceiver's soul? Children's
601 use of another's eye gaze cues in a deceptive situation. *Developmental Psychology* 40:
602 1093-1104.

603

604 Gómez, J. C. 1996. Ostensive behavior in great apes: the role of eye contact. In Russon,
605 A.E., Bard, K.A., Parker, S.T. (Eds.). *Reaching into thought: the minds of the great apes*.
606 Cambridge: Cambridge University Press, pp. 131-151.

607

608 Gómez, J. C. 1998. Assessing Theory of Mind with nonverbal procedures: problems with
609 training methods and an alternative "key" procedure. *Behavioral and Brain Sciences*, 21:
610 119-120.

611

612 Gopnik, A., Slaughter, V., Meltzoff, A. 1994. Changing your views: how understanding
613 visual perception can lead to a new theory of the mind. In Lewis, C., Mitchell, P. (Eds.).
614 *Children's early understanding of mind: origins and development*. London: Psychology
615 Press, pp. 157-181.

616

- 617 Güzeldere, G., Nahmias, E., Deaner, R. 2002. Darwin's continuum and the building
618 blocks of deception. In: Bekoff, M., Allen, C., Burghardt, G.M. (Eds.), *The cognitive*
619 *animal: empirical and theoretical perspectives on animal cognition*. Cambridge: MIT
620 Press, pp 353-362.
- 621
- 622 Hall, K., Brosnan, S.F. In press. Cooperation and deception in primates. *Infant Behavior*
623 *and Development*.
- 624
- 625 Hall, K., Oram, M.W., Campbell, M.W., Eppley, T.M., Byrne, R.W., de Waal, F.B.M.
626 2014. Using cross correlations to investigate how chimpanzees (*Pan troglodytes*) use
627 conspecific gaze cues to extract and exploit information in a foraging competition.
628 *American Journal of Primatology* 76: 932-941.
- 629
- 630 Hare, B., Addessi, E., Call, J., Tomasello, M., Visalberghi, E. 2003. Do capuchin
631 monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behavior*,
632 65: 131-142.
- 633
- 634 Hare, B., Call, J., Agnetta, B., Tomasello, M. 2000. Chimpanzees know what
635 conspecifics do and do not see. *Animal Behavior*, 59: 771-785.
- 636
- 637 Hare, B., Call, J., Tomasello, M. 2001. Do chimpanzees know what conspecifics know?
638 *Animal Behavior*, 61: 139-151.
- 639

- 640 Hare, B., Tomasello, M. 2004. Chimpanzees are more skillful in competitive than in
641 cooperative cognitive tasks. *Animal Behaviour*, 68: 571-581.
- 642
- 643 Hattori, Y., F. Kano, M. Tomonaga. 2010. Differential sensitivity to conspecific and
644 allospecific cues in chimpanzees and humans: a comparative eye-tracking study. *Biology*
645 *Letters*, doi: 10.1098/rsbl.2010.0120.
- 646
- 647 Held, S., Mendl, M., Devereux, C., Byrne, R.W. 2000. Social tactics of pigs in a
648 competitive foraging task: the 'informed forager' paradigm. *Animal Behavior*, 59: 569-
649 576.
- 650
- 651 Held, S., Mendl, M., Devereux, C., Byrne, R.W. 2002. Foraging pigs alter their behavior
652 in response to exploitation. *Animal Behavior*, 64: 157-165.
- 653
- 654 Held, S., Byrne, R.W., Jones, S., Murphy, E., Friel, M., Mendl, M.T. 2010. Domestic
655 pigs, *Sus scrofa*, adjust their foraging behavior to whom they are foraging with. *Animal*
656 *Behavior*, 79: 857-862.
- 657
- 658 Heyes, C. M. 1998. Theory of Mind in nonhuman primates. *Behavioral and Brain*
659 *Sciences*, 21: 101-114.
- 660
- 661 Hirata, S., Matsuzawa, T. 2001. Tactics to obtain a hidden food item in chimpanzee pairs
662 (*Pan troglodytes*). *Animal Cognition*, 4: 285-295.

663

664 Humphrey, N.K. 1976. The social function of intellect. In: Bateson, P. P. G., Hinde, R.A.
665 (Eds.). *Growing points in ethology*. Cambridge University Press, Cambridge, pp. 451-
666 479.

667

668 Itakura, S. 1996. An exploratory study of gaze- monitoring in nonhuman primates.
669 Japanese Psychological Research, 38: 174-180.

670

671 Itakura, S. 2004. Gaze- following and joint visual attention in nonhuman animals.
672 Japanese Psychological Research, 46: 216-226.

673

674 Itakura, S., Tanaka, M. 1998. Use of experimenter-given cues during object-choice tasks
675 by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants
676 (*Homo sapiens*). Journal of Comparative Psychology, 112: 119-126.

677

678 Jolly, A. 1966. Lemur social behavior and primate intelligence. Science, 153: 501-506.

679

680 Kaminski, J., Call, J., Tomasello, M. 2008. Chimpanzees know what others know, but not
681 what they believe. Cognition, 109: 224-234.

682

683 Kano, F., Call, J. 2014. Cross-species variation in gaze following and conspecific
684 preference among great apes, human infants and adults. Animal Behaviour, 91: 137-150.

685

- 686 Karg, K., Schmelz, M., Call, J., Tomasello, M. 2015a. Chimpanzees strategically
687 manipulate what others can see. *Animal Cognition*, 18: 1069-1076.
688
- 689 Karg, K., Schmelz, M., Call, J., Tomasello, M. 2015b. The goggles experiment: can
690 chimpanzees use self-experience to infer what a competitor can see?. *Animal Behaviour*,
691 105: 211-221.
692
- 693 Kummer, H. 1967. Tripartite relations in hamadryas baboons. In Altmann, S.A. (Ed.),
694 *Social communication among primates*. Chicago: University of Chicago Press, pp. 63-71.
695
- 696 Martin, A., Santos, L. R. 2016. What cognitive representations support primate Theory of
697 Mind?. *Trends in Cognitive Sciences*, 20: 375-382.
698
- 699 Menzel, C. R. 1999. Unprompted recall and reporting of hidden objects by a chimpanzee
700 (*Pan troglodytes*) after extended delays. *Journal of Comparative Psychology*, 113: 426-
701 434.
702
- 703 Menzel, E.W. 1974. A group of young chimpanzees in a one-acre field. In Schrier, A.M.,
704 Stollnitz, F. (Eds.) *Behavior of nonhuman primates*. San Diego: Academic Press, pp 83-
705 153.
706
- 707 Meunier, H., Deneubourg, J., Petit, O. 2007. How many for dinner? Recruitment and
708 monitoring by glances in capuchins. *Primates*, 49: 26-31.

709

710 Mitchell, P. 1997. *Introduction to Theory of Mind. Children, autism, and apes*. London:

711 Arnold.

712

713 Mitchell, R. W., Anderson, J. R. 1997. Pointing, withholding information, and deception

714 in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111: 351-361.

715

716 Mulcahy, N. J., Call, J. 2006. Apes save tools for future use. *Science*, 312: 1038-1040.

717

718 Noldus, L. P. J. J. 1996. *The Observer, Version 9.0*. Wageningen, The Netherlands:

719 Noldus Information Technology.

720

721 Oram, M. W., Hatsopoulos, N. G., Richmond, B. J., Donoghue, J. P. 2001. Excess

722 synchrony in motor cortical neurons provides redundant direction information with that

723 from coarse temporal measures. *Journal of Neurophysiology*, 86: 1700-1716.

724

725 Osvath, M., Osvath, H. 2008. Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo*726 *abelii*) forethought: self-control and pre-experience in the face of future tool use. *Animal*727 *Cognition*, 11: 661-674.

728

729 Peignot, P., Anderson, J. R. 1999. Use of experimenter-given manual and facial cues by

730 gorillas (*Gorilla gorilla*) in an object-choice task. *Journal of Comparative Psychology*,

731 113: 253-260.

732

733 Penn, D.C., Povinelli, D.J. 2007. On the lack of evidence that non-human animals
734 possess anything remotely resembling a “theory of mind.” *Philosophical Transactions of*
735 *the Royal Society of London B: Biological Sciences* 362: 731-744.

736

737 Povinelli, D. J., Bierschwale, D. T., Cech, C. G. 1999. Comprehension of seeing as a
738 referential act in young children, but not juvenile chimpanzees. *British Journal of*
739 *Developmental Psychology*, 17: 37-60.

740

741 Povinelli, D.J., Nelson, K.E., Boysen, S.T. 1990. Inferences about guessing and knowing
742 by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 104: 203-210.

743

744 Povinelli, D.J., Eddy, T.J. 1996. Factors influencing young chimpanzees' (*Pan*
745 *troglodytes*) recognition of attention. *Journal of Comparative Psychology*, 110: 336-345.

746

747 Povinelli, D. J., Vonk, J. 2003. Chimpanzee minds: suspiciously human?. *Trends in*
748 *Cognitive Sciences*, 7: 157-160.

749

750 Povinelli, D. J., Vonk, J. 2004. We don't need a microscope to explore the chimpanzee's
751 mind. *Mind & Language*, 19: 1-28.

752

753 Premack, D., Woodruff, G. 1978. Does the chimpanzee have a theory of mind?
754 *Behavioural and Brain Sciences*, 1: 515-526.

755

756 Rizzolatti, G., Craighero, L. 2004. The mirror-neuron system. *Annual Review of*
757 *Neuroscience*, 27: 169-192.

758

759 Rosati, A. G., Stevens, J. R., Hare, B., Hauser, M. D. 2007. The evolutionary origins of
760 human patience: temporal preferences in chimpanzees, bonobos, and human adults.
761 *Current Biology*, 17: 1663-1668.

762

763 Rosati, A.G., Hare, B. 2009. Looking past the model species: diversity in gaze-following
764 skills across primates. *Current Opinion in Neurobiology*, 19: 45-51.

765

766 Santos, L. R., Hauser, M. D. 1999. How monkeys see the eyes: cotton-top tamarins'
767 reaction to changes in visual attention and action. *Animal Cognition*, 2: 131-139.

768

769 Sayers, K., Menzel, C. R. 2012. Memory and foraging theory: chimpanzee utilization of
770 optimality heuristics in the rank-order recovery of hidden foods. *Animal Behaviour*, 84:
771 795-803.

772

773 Schel, A.M., Townsend, S.W., Machanda, Z, Zuberbühler, K., Slocombe, K.E. 2013.
774 Chimpanzee alarm-call production meets key criteria for intentionality. *PLoS ONE* 8:
775 e76674. doi:10.1371/journal.pone.0076674

776

- 777 Schloegl, C., Kotrschal, K., Bugnyar, T. 2007. Gaze following in common ravens,
778 *Corvus corax*: ontogeny and habituation. *Animal Behaviour*, 74: 769-778.
779
- 780 Schloegl, C., Kotrschal, K., Bugnyar, T. 2008. Modifying the object-choice task: is the
781 way you look important for ravens? *Behavioural Processes*, 77: 61-65.
782
- 783 Schmelz, M., Call, J., Tomasello, M. 2011. Chimpanzees know that others make
784 inferences. *Proceedings of the National Academy of Sciences* 108: 3077-3079.
785
- 786 Seed, A., Tomasello, M. 2010. Primate cognition. *Topics in Cognitive Science* 2: 407-
787 419.
788
- 789 Senju, A., Csibra, G. 2008. Gaze following in human infants depends on communicative
790 signals. *Current Biology*, 18: 668-671.
791
- 792 Shepherd, S. V. 2010. Following gaze: gaze-following behavior as a window into social
793 cognition. *Frontiers in Integrative Neuroscience*, 4: 1-13.
794
- 795 Sueur, C., Petit, O. 2010. Signals use by leaders in *Macaca tonkeana* and *Macaca*
796 *mulatta*: group-mate recruitment and behavior monitoring. *Animal Cognition*, 13: 239-
797 248.
798
- 799 Tomasello, M., Call, J. 1997. *Primate Cognition*. Oxford: Oxford University Press.

800

801 Tomasello, M., Call, J., Hare, B. 1998. Five primate species follow the visual gaze of
802 conspecifics. *Animal Behaviour*, 55: 1063-1069.

803

804 Tomasello, M., Call, J., Hare, B. 2003. Chimpanzees understand psychological states—the
805 question is which ones and to what extent. *Trends in Cognitive Sciences*, 7: 153-156.

806

807 Tomasello, M., Carpenter, M. 2005. Intention-reading and imitative learning. In Hurley,
808 S. (Ed.), *From neuroscience to social science*. Cambridge, MA: The MIT Press, pp. 133-
809 148.

810

811 Tomasello, M., Hare, B., Agnetta, B. 1999. Chimpanzees, *Pan troglodytes*, follow gaze
812 direction geometrically. *Animal Behaviour*, 58: 769-777.

813

814 Warneken, F., Chen, F., Tomasello, M. 2006. Cooperative activities in young children
815 and chimpanzees. *Child Development*, 77: 640–663.

816

817 Warneken, F., Hare, B., Melis, A. P., Hanus, D., Tomasello, M. 2007. Spontaneous
818 altruism by chimpanzees and young children. *PLoS Biology*, 5: e184.

819

820 Wheeler, B. C., Hammerschmidt, K. 2013. Proximate factors underpinning receiver
821 responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it
822 counterdeception? *American Journal of Primatology*, 75: 715-725.

823

824 Whiten, A. 1996. When does smart behaviour-reading become mind-reading?. In
825 Carruthers, P., Smith, P.K. (Eds.), *Theories of theories of mind*. Cambridge: Cambridge
826 University Press, pp. 277-292.

827

828 Whiten, A. 2013. Humans are not alone in computing how others see the world. *Animal*
829 *Behaviour*, 86: 213-221.

830

831 Whiten, A., Byrne, R.W. 1988. Tactical deception in primates. *Behavioral and Brain*
832 *Sciences* 11: 233-273.

833

834 Whiten, A. Byrne, R.W. 1997. *Machiavellian Intelligence II: extensions and evaluations*.
835 Cambridge: Cambridge University Press.

836

837 Wimmer, H., Hogrefe, G-J., Perner, J. 1988. Children's understanding of informational
838 access as a source of knowledge. *Child Development*, 59: 386-396.

839

840 Woodruff, G., Premack, D. 1979. Intentional communication in the chimpanzee: the
841 development of deception. *Cognition*, 7: 333-362.

842

843 Zimmermann, F., Zemke, F., Call, J., Gómez, J. C. 2009. Orangutans (*Pongo pygmaeus*)
844 and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Animal*
845 *Cognition*, 12: 347-358.

846

847 Zuberbühler, K. 2008. Gaze Following. *Current Biology*, 18: R453-R455.

848

849 FIGURE 1: Diagram of chimpanzees' living areas and outdoor enclosure with Quadrants
850 1-4 labelled (not to scale). Arrows represent visual access during the baiting procedure,
851 and the "X" represents no visual access during the baiting procedure.

852

853 FIGURE 2: Experiment 1: When the Dominant approaches the Subordinate, does the
854 Subordinate stop walking? Referent behavior: dominant walks towards the subordinate
855 from a different quadrant in the enclosure. Target behavior: subordinate stops walking for
856 5 consecutive seconds. After the dominant walked towards the subordinate from a
857 different quadrant, the subordinate stopped walking more than expected from the within-
858 trial shuffled control (peak at time= +10, $r = 0.1799$, $n = 22$; $-\log$ -
859 $p < 0.05$).

860

861 FIGURE 3: Experiment 1: when the Subordinate stops walking, does she stop gazing
862 towards the banana? Referent behavior: subordinate stops walking for five consecutive
863 seconds. Target behavior: subordinate stops gazing towards the banana for five
864 consecutive seconds. After the subordinate stops walking for five seconds, she stopped
865 gazing towards the bait for five seconds (peak at time= +2, $r = 0.1319$, $n = 144$; $-\log$ -
866 $p < 0.05$).

867

868 FIGURE 4: Experiment 2: When the Subordinate alternates gaze between the Dominant
869 and the cucumber, does the Subordinate stop walking? Referent behavior: subordinate
870 looks at the dominant and then gazes towards the cucumber for two seconds. Target
871 behavior: subordinate stops walking for five seconds. After the subordinate alternated her
872 gaze between the dominant and the cucumber, she stopped walking significantly more
873 than expected from the within-trial shuffled control (Peak at time= +11, $r = 0.1437$, $n =$
874 743 ; $-\log$ - $p < 0.05$).

875

876 FIGURE 5: Experiment 2: When the Subordinate alternates gaze between the Dom and
877 the banana, does the Subordinate stop walking? Referent behavior: subordinate looks at
878 the dominant and then gazes towards the banana for two seconds. Target behavior:
879 subordinate stops walking for five seconds. The relationship is no different than expected
880 from the within-trial shuffled control (peak at time= -8, $r = 0.0681$, $n = 888$; $-\log$ -
881 $p < 0.05$).

882

883 FIGURE 6: Experiment 2: When the Subordinate recruits towards the cucumber, does the
884 Dominant search for it? Referent behavior: subordinate looks at the dominant and then
885 gazes towards the cucumber for two seconds, and subordinate stops walking for five
886 seconds. Target behavior: dominant searches for the cucumber. After the subordinate
887 recruits the dominant to the cucumber, the dominant searches for the cucumber

888 significantly more than expected from the within-trial shuffled control (peak at time= +4,
889 $r= 0.2230$, $n= 175$; $-\log\text{-likelihood}= 8.1650$, $p<0.05$).

890 FIGURE 7: Experiment 2: When the Dominant searches for the cucumber, does the
891 Subordinate walk towards the banana? Referent behavior: dominant searches for the
892 cucumber. Target behavior: subordinate walks towards the banana. After the dominant
893 begins to search for the cucumber, the subordinate walks towards the banana significantly
894 more than expected from the within-trial shuffled control (peak at time= +20, $r= 0.3012$,
895 $n= 285$; $-\log\text{-likelihood}= 11.5386$, $p<0.05$).

Table 2: Trial outcomes for Experiment 2. Note that no cucumber was obtained on trials 4 or 7, and no banana was obtained on trial 10.

	<u>Trial</u>																			
Reward	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<u>Cucumber</u>																				
Sub	✓	✓	✓		✓			✓			✓		✓					✓	✓	
Dom						✓			✓	✓		✓		✓	✓	✓	✓			✓
<u>Banana</u>																				
Sub						✓			✓		✓	✓	✓	✓			✓		✓	
Dom	✓	✓	✓	✓	✓		✓	✓							✓	✓		✓		✓

Figure 1

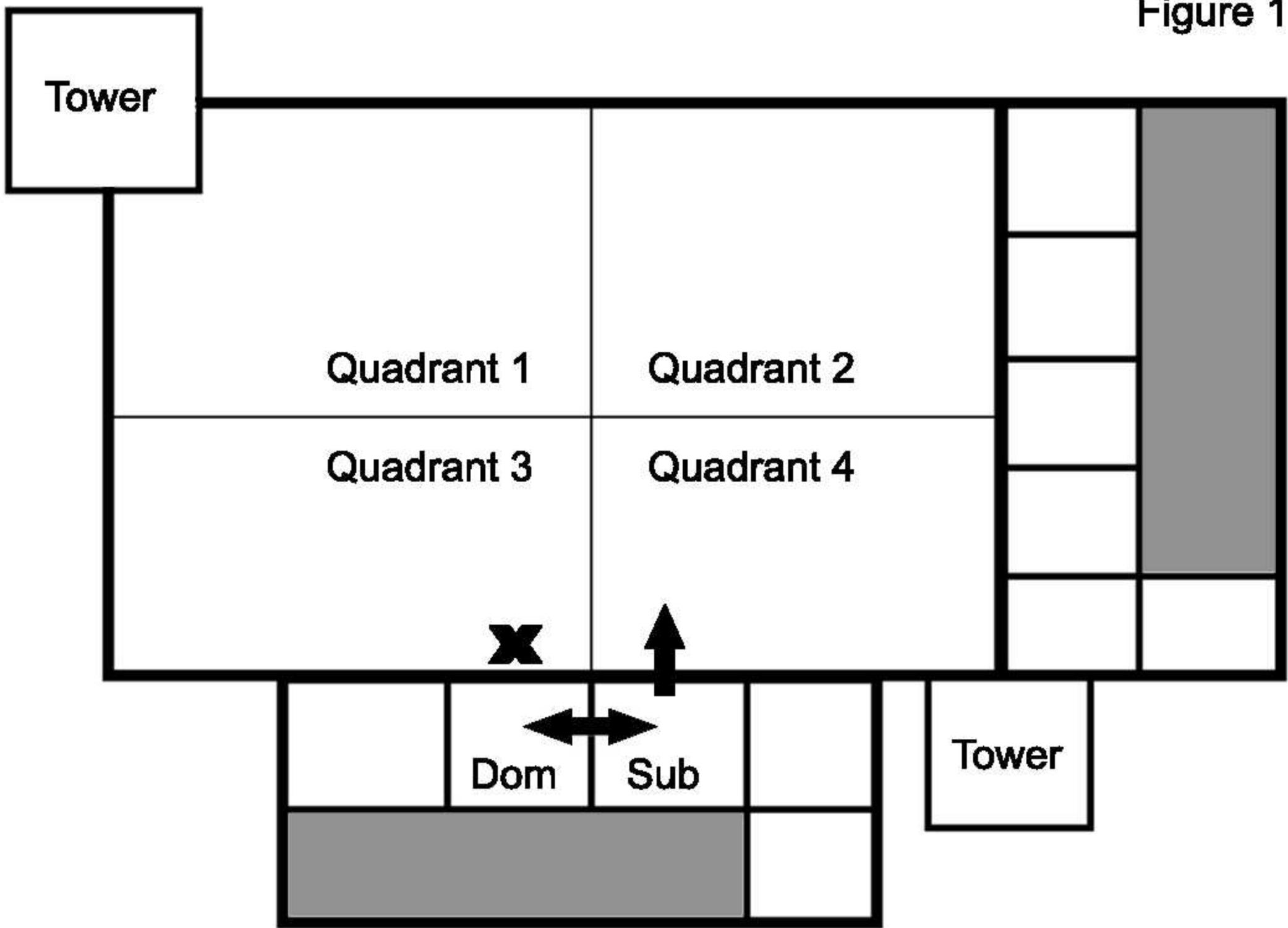


Figure 2

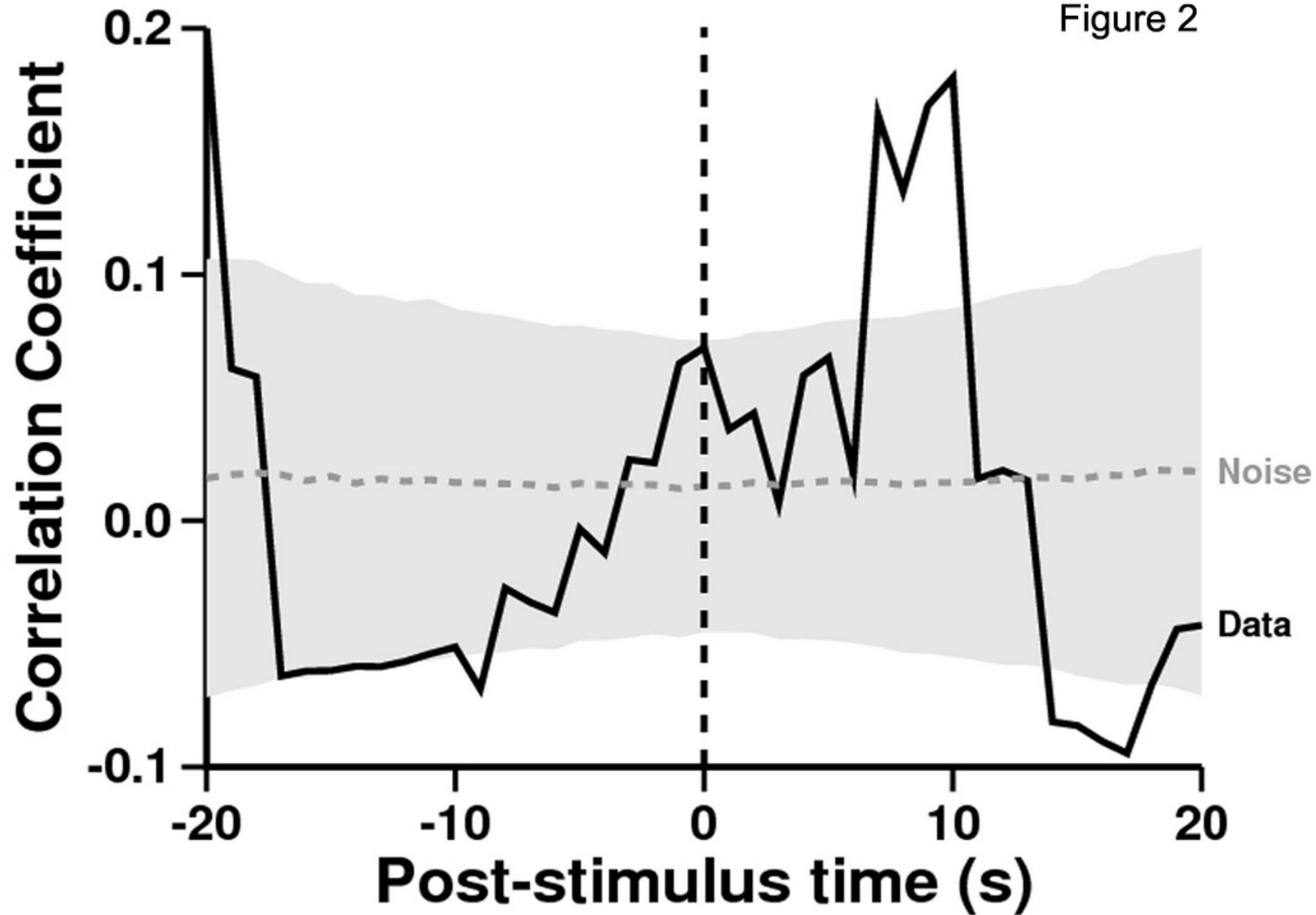


Figure 3

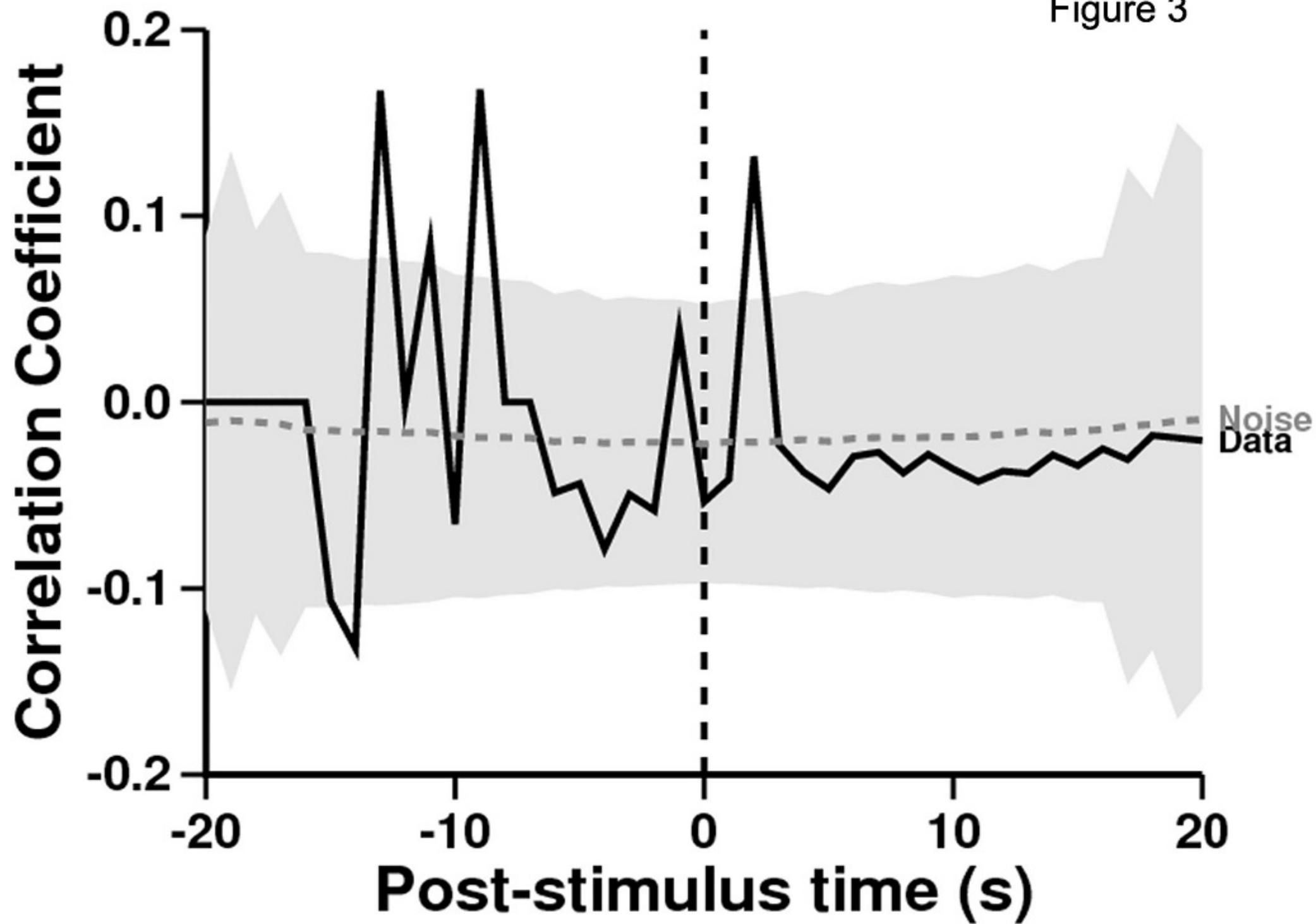


Figure 4

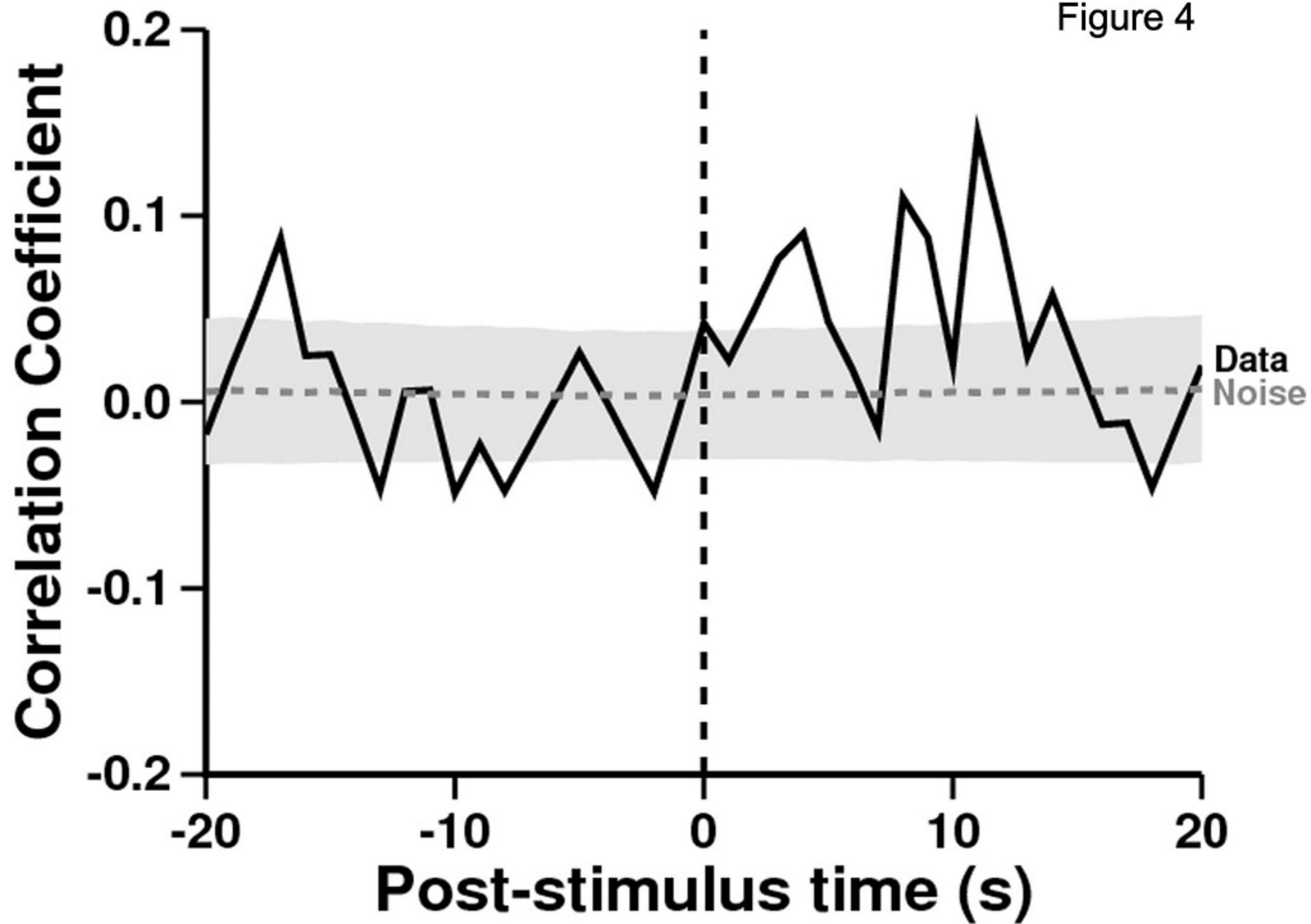


Figure 5

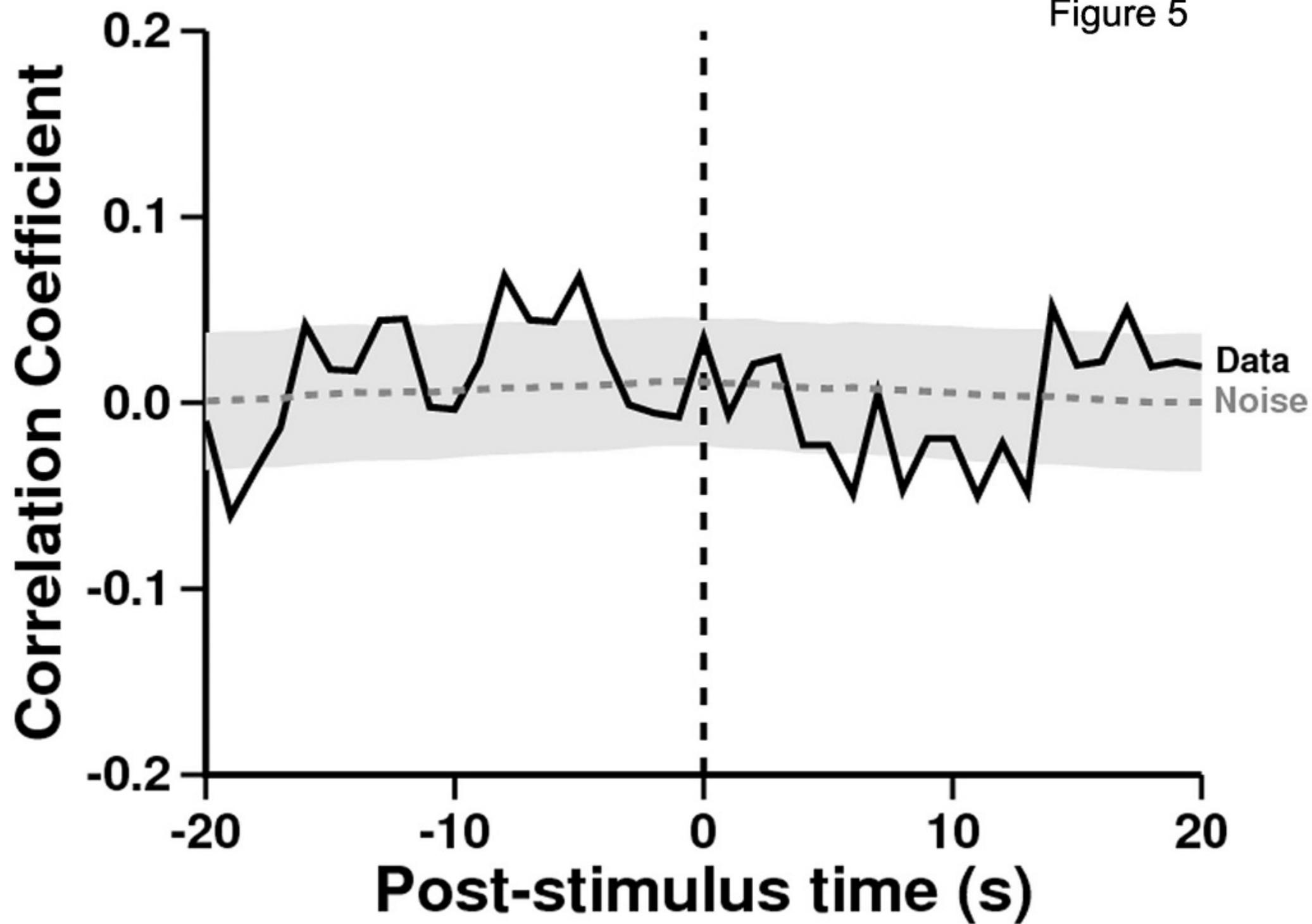


Figure 6

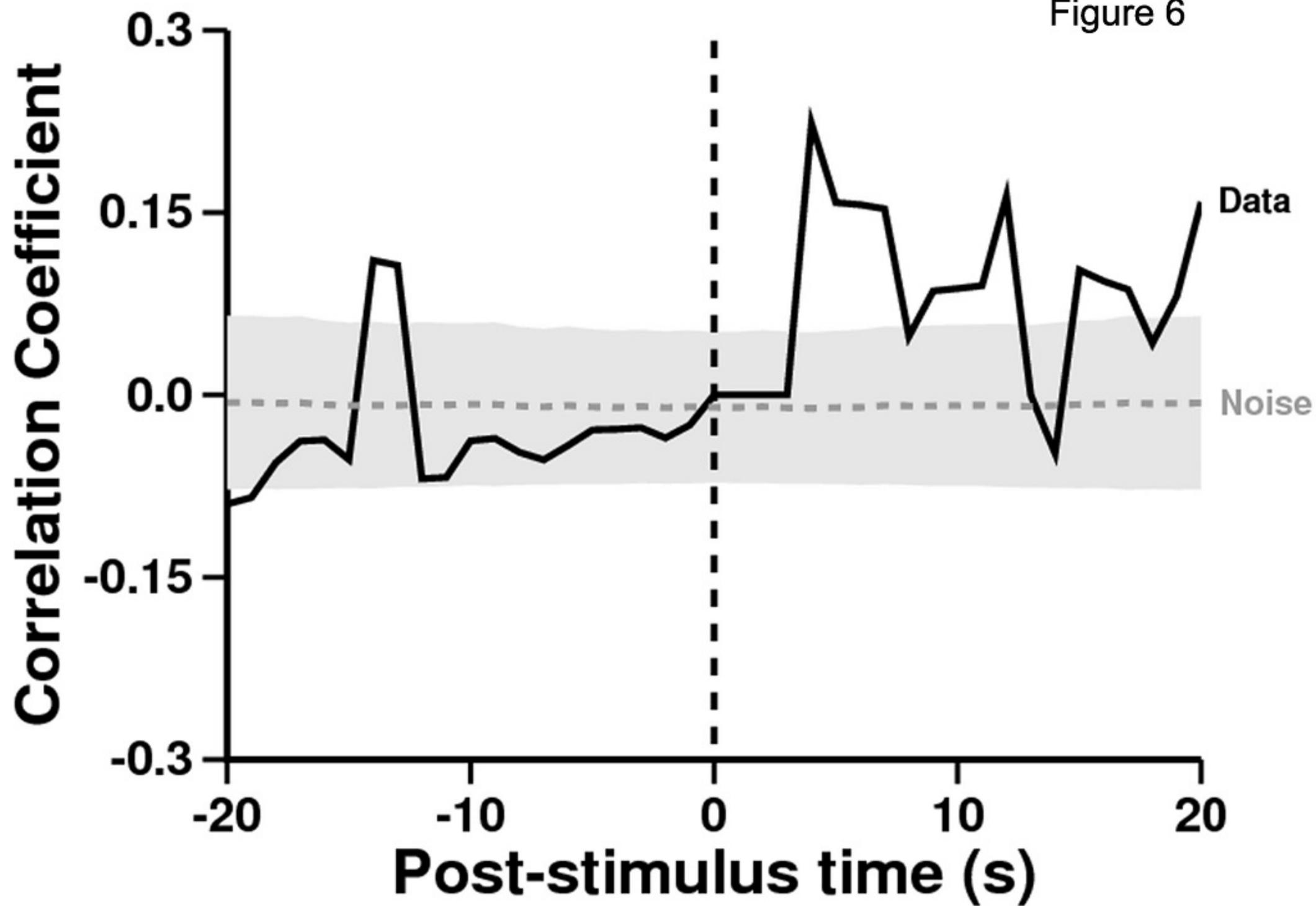


Figure 7

