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

Short title: Manipulative gaze in chimpanzees

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Abstract

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

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

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

Introduction

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

Following gaze is not merely a response to a stimulus, as individuals appear to understand that gaze conveys information; for example, all great apes follow gaze around barriers to a target [Tomasello et al., 1999; Bräuer et al., 2005], and often refer back to the face of a human experimenter after following their gaze to the ceiling where no target was present [Call et al., 1998; Braüer et al., 2005]. Additionally, social gaze may be important for inferring someone's intentions to act, or for conveying one's own intentions [Baron-Cohen, 1995; Santos & Hauser, 1999; Ferrari et al., 2000; Freire et al., 2004; Csibra, 2010; see Rizzolatti & Craighero, 2004 for details on the neurological underpinnings of understanding intention, and Call & Tomasello, 2008 for a review of apes' understanding of intention]. In fact, some great apes have been observed spontaneously using ostensive gaze cues to direct humans' attention [Gómez, 1996; de Waal, 2001], and there is evidence that wild chimpanzees differentially alarm call more towards ignorant bystanders to inform them of the presence of a predator [Crockford et al., 2012; Schel et al., 2013], yet the question remains as to whether chimpanzees use gaze as a cue to deliberately share information with conspecifics [Shepherd, 2010]. Ultimately, understanding someone else's gaze and to what they have visual access aids in attributing what they know or believe [Wimmer et al., 1988; Povinelli et al., 1990; Baron-Cohen, 1991, 1995; Gopnik et al., 1994; Mitchell, 1997; Hare et al., 2000; Hare et al., 2001]. Attributing knowledge or belief to another individual impacts how one predicts how the other will behave in that context [Premack & Woodruff, 1978; Baron-Cohen, 1995; Schmelz et al., 2011].

If chimpanzees are able to use others' gaze as a source of information, then counter-measures to this ability may also have developed. Specifically, chimpanzees may be able to deceive a competitor by omission (averted gaze) or by commission (deliberately gazing at the 'wrong' place). Experimental evidence from primates interacting with human experimenters has shown that subjects can refrain from exposing hidden food to human competitors [Woodruff & Premack, 1979; Mitchell & Anderson, 1997; Anderson et al., 2001; Karg et al., 2015a]. However, they are often only able to do so after many trials, and they generally do not act to cover up exposed food [Karg et al., 2015a]. There is also evidence for primates alerting cooperative humans to the presence of hidden food or tools to access food [Woodruff & Premack, 1979; Call & Tomasello, 1994; Gómez, 1998; Menzel, 1999; Leavens et al., 2004; Zimmerman et al., 2009; Karg et al., 2015a]. While evidence is lacking in non-human primates for finding hidden food in an object choice task when a human experimenter's cooperative gaze is the sole cue [Anderson et al., 1995, 1996; Call & Tomasello, 1998; Peignot & Anderson, 1999; Call et al., 2000; Burkart & Heschl, 2007], chimpanzees are able to recognize what conspecifics do and do not see in food competition situations, and adjust their behavior to take advantage [Hare et al., 2000; Hare et al., 2001], indicating that chimpanzees perform better in the more socio-ecologically relevant context of competition with conspecifics [Hare & Tomasello, 2004]. This evidence suggests that not only do chimpanzees know what others do and do not see, but also that they can use this information strategically in dyadic food competition.

Rich narrative descriptions have reported an escalating tactical arms race between conspecific competitors in the informed forager paradigm, such as how an informed subordinate can act to counter a dominant's exploitation by delaying their approach to the food, or by moving in a different direction [Menzel, 1974; Coussi-Korbel, 1994; Held et al., 2000, 2002; Hare et al., 2001; Hirata & Matsuzawa, 2001; Fujita et al., 2002; Hare et al., 2003; Ducoing & Thierry, 2003, 2004; Bugnyar & Kotrschal, 2004; Schloegl et al., 2008; Amici et al., 2009; Held et al., 2010]. In the seminal paper, Menzel [1974] described how his informed subordinate, Belle, interacted with her competitor, Rock: she sat atop the hidden food and stopped uncovering it in his presence, he pushed her away to steal the food; she stopped short, and he expanded his search area; Belle waited until Rock was looking away before approaching the food, but he turned around; she walked in the opposite direction and doubled back once Rock was distracted; she walked towards a smaller pile of food, and when Rock no longer fell for that trick, Belle began to throw tantrums. Why did Belle behave this way? Did she have insight into the mind of her competitor and strategically devise her tactics to counter Rock's actions? Did she read and react to Rock's movements? Or were her responses learned, from initially coincidental conjunctions? Often, narrative descriptions such as the one of Belle and Rock's interaction are brushed aside as merely anecdotes because they do not systematically attempt to answer the above questions [Bernstein, 1988], but they have real value as a starting point for deeper investigation [de Waal, 1986; Byrne, 1997; Bates & Byrne, 2007]. Using a sensitive instrument, cross correlation [Oram et al., 2001; Hall et al., 2014], to measure the interactions observed, we can pull apart the overall tactic to examine the temporal contingencies between actions and reactions to better describe the behavioral mechanisms underlying tactical deception [Whiten & Byrne, 1988; Byrne & Whiten, 1990].

In this study, we investigated a subordinate's ability to remain one step ahead of the dominant's exploitation; we aimed to validate statistically how chimpanzees use cues during foraging competition. Whereas prior studies have reported the outcomes of foraging competition (i.e., how many pieces of food each competitor ate), our focus was on the behavioral mechanisms underlying these tactics. We therefore examined whether the informed subordinate used visual signals differently when under exploitation pressure from the dominant. We tested two chimpanzees in an informed forager food competition task. In Experiment 1, we hid a highly preferred food item (a banana). We asked whether the dominant would exploit the subordinate's foraging behavior by following her movement and her gaze, and in turn whether the subordinate would tactically deceive the dominant by avoiding gazing towards the hidden banana, in order to counter this exploitation. In Experiment 2, we hid a banana and a moderately preferred cucumber. Chimpanzees can recall and recover hidden food in the order of their preference [Sayers & Menzel, 2012], so we would expect the subordinate to approach the banana first, if she were acting on her preferences. However, if the subordinate had learned over the course of Experiment 1 that the dominant would steal any uncovered food, the subordinate might in principle use cues to recruit her competitor towards the 'decoy' cucumber first. We asked whether the subordinate's behavior would differ when approaching either bait, and if the subordinate would use gaze cues to manipulate (i.e., tactically deceive) the dominant.

Methods

Study site and subjects

We tested two unrelated adult female chimpanzees, from the same social group of 11 individuals at the Yerkes National Primate Research Center field station in Lawrenceville, Georgia, USA. Data were collected from October 2010 to August 2011. Reinette (aged 23) was subordinate to Georgia (30), as determined by dyadic food competitions conducted prior to the experiment. Chimpanzees were housed in an outdoor enclosure (24 x 30 m) with a central climbing structure and had access to indoor spaces (188 m^3). All individuals were fed twice daily with chow, fruit and vegetables, and water was available *ad libitum*. Chimpanzees were not deprived of food or water at any time during the experiment and were not subject to any invasive procedure. The other group members were held indoors during testing, without visual access to the outdoor compound. Research complied with protocols approved by the Institutional Animal Care and Use Committee (IACUC) and adhered to the legal requirements of the United States. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

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

Experiment 1: One Reward

The subordinate and dominant chimpanzees were brought into an indoor testing area, each in an adjacent holding space with visual access between them through a mesh panel (72 x 52 cm). The informed subordinate additionally had visual access into the outdoor enclosure via a Lexan window installed in the hydraulic door. The dominant did not have visual access to the outdoor enclosure, thus remaining ignorant of actions conducted in the enclosure.

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

Experiment 2: Two Unequal Rewards

We chose to test the chimpanzees using cucumber as a moderate-value reward, based on our observations of chimpanzees feeding; bananas were used as high-value rewards. To confirm that their preferences remained consistent and that a chimpanzee had not approached a cucumber before a banana due to a preference for the cucumber, each chimpanzee was individually tested on 10 counterbalanced trials for her preference between banana and cucumber after the completion of Experiment 2. A chimpanzee was individually presented with a small slice of cucumber and a small slice of banana approximately 30 cm apart on a sliding tray; chimpanzees indicated their choice by pointing through the mesh to their preferred item, and were given that item. In the preference test, subordinate Reinette chose 10/10 banana slices, and dominant Georgia chose 9/10 banana slices.

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

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

Data Coding

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

We defined *alternate gaze* as "one chimpanzee looks at the other individual, and then gazes towards the hidden bait for two seconds." We defined any *pause* (in locomotion, in gazing towards the bait, etc.) as a halt in the behavior for five consecutive seconds. In studies on collective movement in primates, it has been shown that when a leader pauses to look back to group-mates, it serves not only to monitor who has joined the movement but also to recruit others to join [Meunier et al., 2007; Sueur and Petit, 2010]. We therefore combined the prior two definitions to operationalize our definition of *recruit* as "one chimpanzee looks at the other individual, and then gazes towards the hidden bait for two seconds, while pausing in her locomotion (for five consecutive seconds)." We defined *approach* as "the chimpanzees are in different quadrants of the enclosure and one individual locomotes towards the other." *Search* was defined as any active food-uncovering behavior (e.g. overturning a barrel, reaching into a tire, etc.) within one body length of defined hiding places.

Statistical Analysis

The behavior (i.e., gaze and movement direction) of each chimpanzee was measured over a period of time, and each individual's actions were compared to those of the other, so as to determine whether the one chimpanzee's actions were contingent on, or occurred in a time-locked pattern relative to, the actions of the other chimpanzee. We used cross correlations, which measure the correlation between two variables as a function in time, to compare the behavior of two chimpanzees [for a detailed explanation of this approach, see Oram et al., 2001; Hall et al., 2014]. In the correlogram figures, the binary behavioral series from one chimpanzee is designated as a referent and the beginning of the series represents $t = 0$. The other behavioral series (the target) is then plotted with time lags relative to the referent; the process is repeated with each new instance of the referent behavior plotted at $t = 0$. Pearson's correlations are calculated for pairs of values at each time lag (ranging from -20 to +20 seconds post-stimulus, that is, before and after the referent behavior is plotted at $t = 0$). Therefore the referent behavior at $t = 0$ should not be considered the "start" of the behavior, but rather "while doing" the behavior [see Fig. 1 in Hall et al., 2014]. The key aspect of this statistic is to demonstrate how closely two actions are linked in time; considering that the data are compiled from all trials within an experiment, any significant outcomes indicate that the data overcome a high threshold of likelihood. Cross correlations were tested against 10,000 random permutations of within-trial data (this within-trial shuffled control is labeled "Noise" in the figures) using –log-likelihood values of *t* tests to calculate significance; significant values were set at $p < 0.05$.

Results

Experiment 1: One Reward

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

Does the Subordinate Withhold Cues from the Dominant?

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

Experiment 2: Two Unequal Rewards

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

Does the Subordinate Recruit the Dominant to the Decoy?

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

Does the Subordinate's Behavior Manipulate the Dominant?

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

Discussion

In both experiments, tactical deceptions functioned to (a) withhold information about the location of the highly preferred banana, or (b) mislead the dominant competitor to the less preferred cucumber. We have previously shown [Hall et al., 2014] that a dominant chimpanzee will modify her search for hidden food by exploiting a subordinate's behavior: in particular, that the dominant is attentive to the subordinate's gaze—whether straight ahead or off-axis from the direction of her body—while the subordinate walks. In the current study, the subordinate learned to avoid this type of competition from the dominant by withholding cues and by approaching the less preferred cucumber first, which speaks to great apes' ability to plan for the immediate future [Mulcahy & Call, 2006; Osvath & Osvath, 2008]. While we expected the subordinate to lead the dominant towards the cucumber, we additionally found an unexpected pattern (alternating gaze between the partner and the cucumber—but not the banana—while pausing) that functioned to recruit the dominant to that location, indicating that chimpanzees are highly flexible in their use of gaze direction and movement to both conceal and *reveal* information to manipulate a foraging partner. Therefore, when the subordinate's recruiting tactic was successful, it proximately functioned to occupy the dominant in a search for a less preferred food, and ultimately functioned to allow the subordinate to retrieve the more preferred banana, without competition.

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

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

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

In Experiment 2, the fact that the subordinate was able to retrieve the banana while the dominant was busy searching for the cucumber could have initially been a coincidence, and subsequently become a learned contingency that she used successfully on trials 11-14 [see Heyes, 1998; Povinelli & Vonk, 2003, 2004 for discussions on 'behavioral rules']. Chimpanzees have difficulty inhibiting themselves in the presence of desired food [Boysen, 1996; Boysen et al., 2001; but see Rosati et al., 2007], so avoiding walking or gazing towards the banana for a few moments might be considered a self-distracting behavior [Evans & Beran, 2007], functioning to prevent the worse outcome of the dominant finding it. An intriguing possibility, however, is that the subordinate may have learned that the dominant partner would exploit her movement and gaze wherever she went [as in Hall et al., 2014], so the subordinate continued on a trajectory away from the hidden banana, and towards the decoy cucumber, in order to deceive her competitor [Güzeldere et al., 2002; Bugnyar & Kotrschal, 2004].

In approaching the cucumber in particular, the subordinate looked at her competitor in an ostensive manner, that is, she looked directly at her partner in order to get her attention [e.g., Senju & Csibra, 2008], and then used her own gaze (head orientation) as a social cue to point towards the location of the cucumber, and was then likely to pause her movement for five seconds. This combined sequence of physical cues functioned to recruit the dominant to that location. The subordinate, however, did not behave this way while approaching the banana. That the subordinate was able to flexibly withhold gazing towards the banana during episodes in which the dominant was exploiting her, yet distinctively point towards the hiding location of the cucumber under similar circumstances, fits Tomasello and Call's [1997] definition of intentional action for reaching her implied goal (here, obtaining the hidden banana). There is good evidence that chimpanzees respond not only to others' behavior but also to their goals or intentions, responding differently to humans that behave as if they are unwilling or unable to provide food [Call et al., 2004], humans that act purposefully or accidentally [Call & Tomasello, 1998; Tomasello & Carpenter, 2005], and by offering help to a human striving for an out of reach item [Warneken et al., 2006; Warneken et al., 2007]. It has been hypothesized that not only is it possible for gaze direction to expose truthful information (such as the location of the hidden bait), but also that gaze can reveal deceptive intent [Freire et al., 2004]; it would therefore behoove the subordinate to judiciously control her gaze direction when the dominant is present.

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

Primates exhibit sophisticated, flexible, and strategic social maneuvering, and are able to predict and manipulate others' behavior in novel situations [Jolly, 1966; Kummer, 1967; Humphrey, 1976; Byrne & Whiten, 1988; Byrne, 1996; Whiten & Byrne, 1997; Dunbar, 1998]. This ability likely arises from lifelong learning and understanding that their own, and others' behavior is influenced by, for example, what is visible [Level 1 perspective taking: Flavell, 1992]. Though the subordinate and the dominant never switched roles in this study, the subordinate may have learned through her own life experiences to infer what was visible to her partner [Karg et al., 2015a], and then manipulated her gaze direction to hide cues from her partner. In particular for chimpanzees and other animals exhibiting a fission-fusion dynamic, differences in access to knowledge exist due to socioecological factors [Aureli et al., 2008], therefore the ability to gain information (or hide it) from others may also have an evolutionary advantage during competitive and cooperative situations [Hall & Brosnan, in press].

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

Acknowledgements

This project was funded by the National Institutes of Health's Office of Research Infrastructure Programs base grant to the Yerkes National Primate Research Center - P51OD011132. Financial support for KH was provided by Janet T. Anderson Trust, Scottish Overseas Research Student Award Scheme, and a University of St Andrews School of Psychology studentship. MWC was supported by the FIRST program (NIH/NIGMS (USA) IRACDA grant number K12 GM000680). We thank Emory University, Living Links, and Yerkes National Primate Research Center, which is fully accredited by the American Association for Accreditation of Laboratory Animal Care. Additional thanks to Victoria Horner and J. Devyn Carter for helpful discussions, and to Andrew Whiten for his support. The authors declare no conflicts of interest.

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

FIGURE 2: Experiment 1: When the Dominant approaches the Subordinate, does the Subordinate stop walking? Referent behavior: dominant walks towards the subordinate from a different quadrant in the enclosure. Target behavior: subordinate stops walking for 5 consecutive seconds. After the dominant walked towards the subordinate from a different quadrant, the subordinate stopped walking more than expected from the within-trial shuffled control (peak at time= +10, r= 0.1799, n= 22; -log-likelihood= 3.8645, $p<0.05$).

FIGURE 3: Experiment 1: when the Subordinate stops walking, does she stop gazing towards the banana? Referent behavior: subordinate stops walking for five consecutive seconds. Target behavior: subordinate stops gazing towards the banana for five consecutive seconds. After the subordinate stops walking for five seconds, she stopped gazing towards the bait for five seconds (peak at time= +2, r= 0.1319, n= 144; –log-likelihood= 3.0490, $p<0.05$).

FIGURE 4: Experiment 2: When the Subordinate alternates gaze between the Dominant and the cucumber, does the Subordinate stop walking? Referent behavior: subordinate looks at the dominant and then gazes towards the cucumber for two seconds. Target behavior: subordinate stops walking for five seconds. After the subordinate alternated her gaze between the dominant and the cucumber, she stopped walking significantly more than expected from the within-trial shuffled control (Peak at time= +11, r= 0.1437, n= 743; –log-likelihood= 8.5099, $p<0.05$).

FIGURE 5: Experiment 2: When the Subordinate alternates gaze between the Dom and the banana, does the Subordinate stop walking? Referent behavior: subordinate looks at the dominant and then gazes towards the banana for two seconds. Target behavior: subordinate stops walking for five seconds. The relationship is no different than expected from the within-trial shuffled control (peak at time= -8, r= 0.0681, n= 888; –log-likelihood=2.3693, *ns*).

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

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

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

Table 1: Trial outcomes for Experiment 1

	Trial																							
Reward	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Banana																								
Sub		✓	✓	✓	✓	✓	✓	✓		✓		✓		✓		✓		✓		✓		✓		✓
Dom	✓								✓		✓		✓		✓		✓		✓		✓		✓	

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.

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

Figure 1

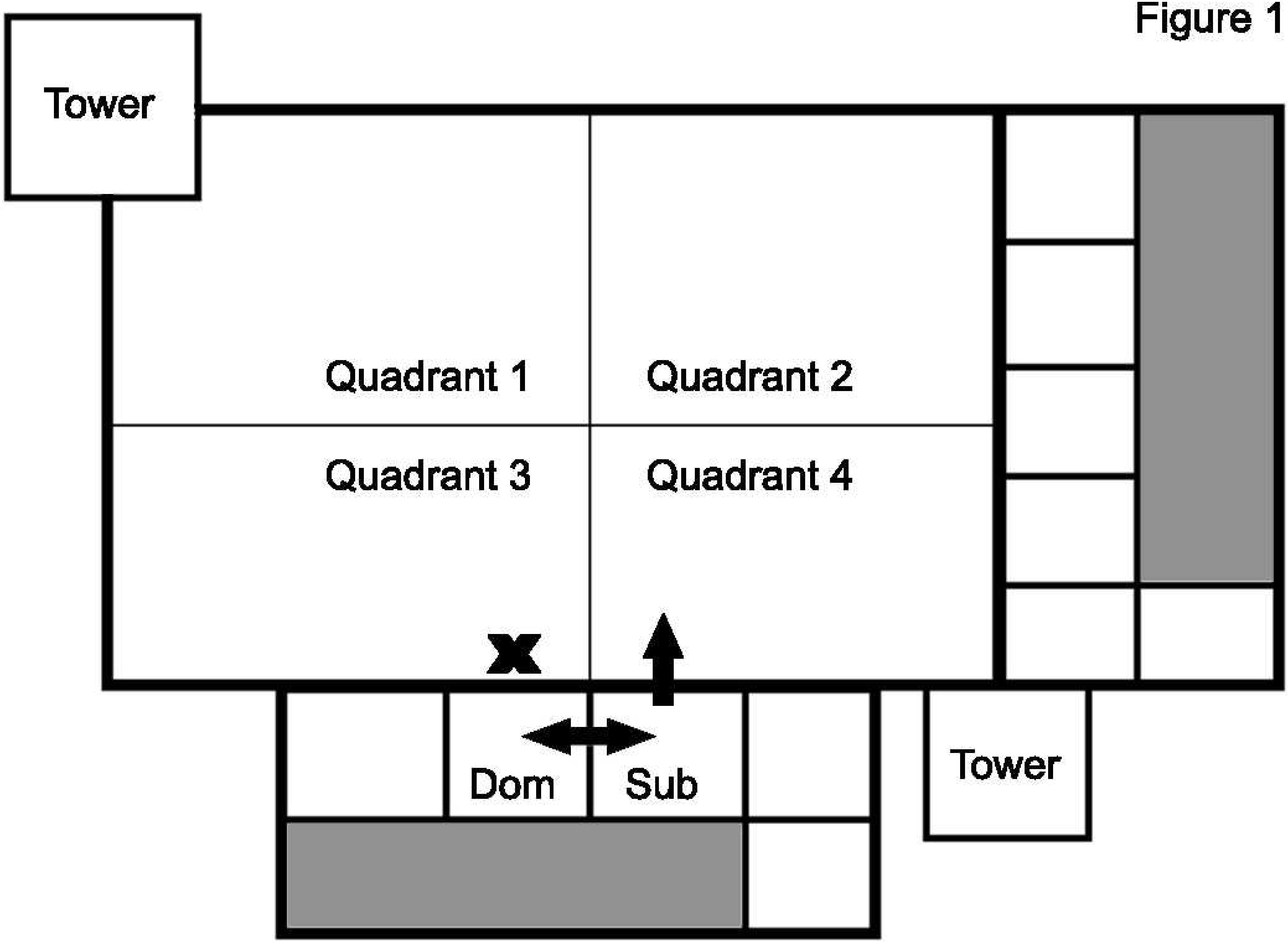
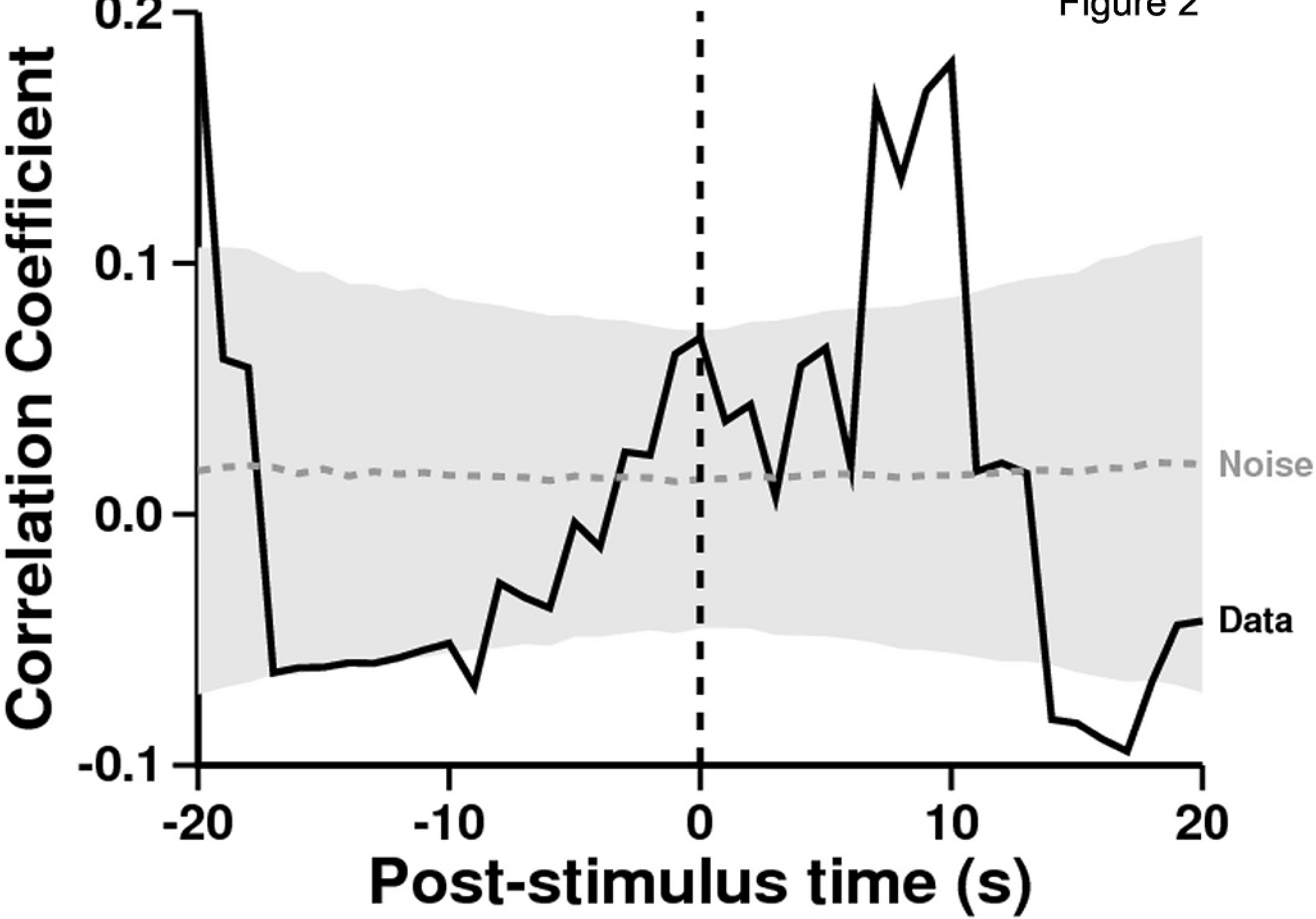

Tower
Quadrant 1
Quadrant 2
Quadrant 3
Quadrant 4
Dom
Sub
Tower

Figure 2


0.2
0.1
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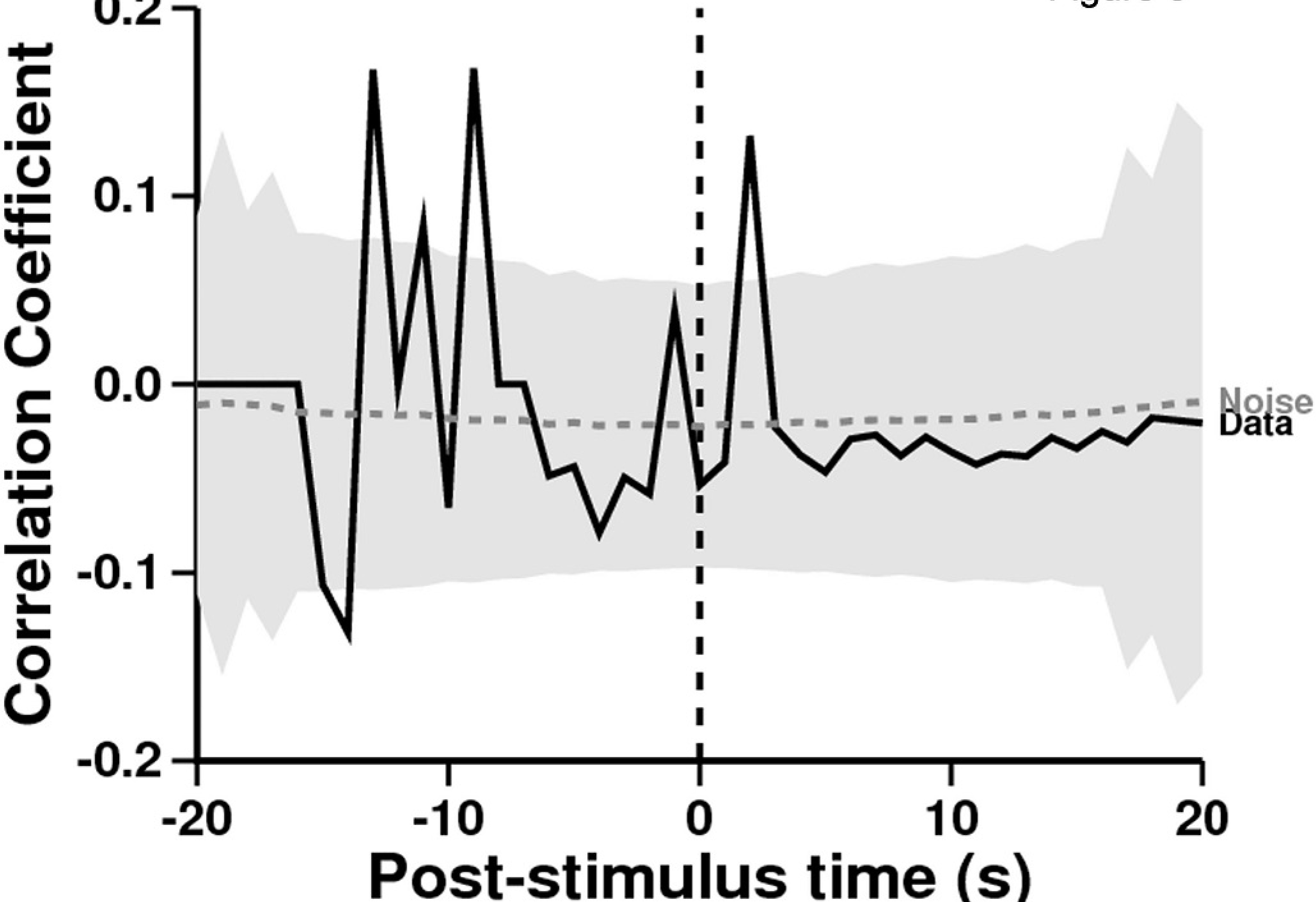
Correlation Coefficient
Noise
Data
-20
-10
0
10
20
Post-stimulus time (s)

Figure 3



0.2
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Correlation Coefficient
-20
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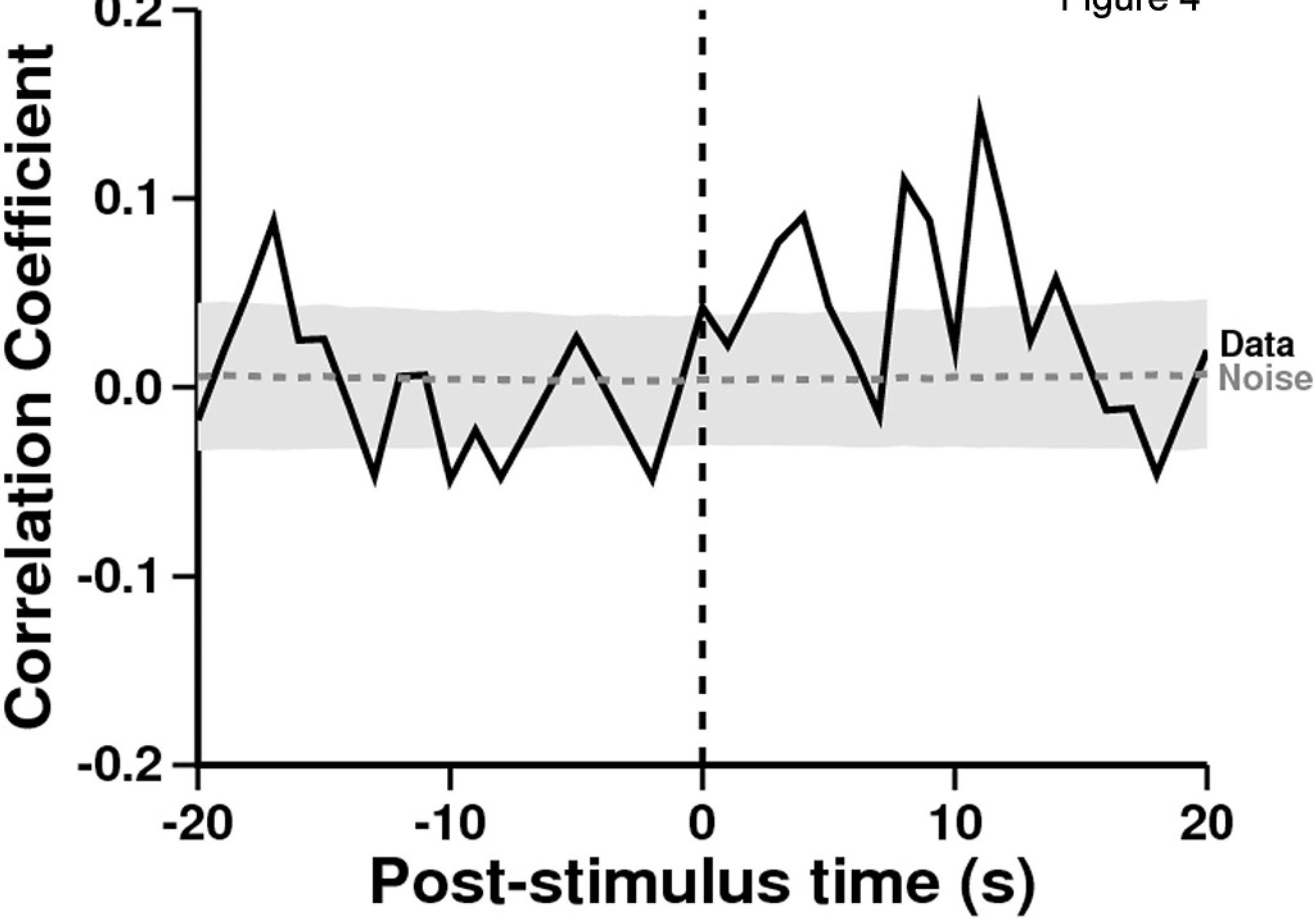
Post-stimulus time (s)
Noise
Data

Figure 4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Correlation Coefficient
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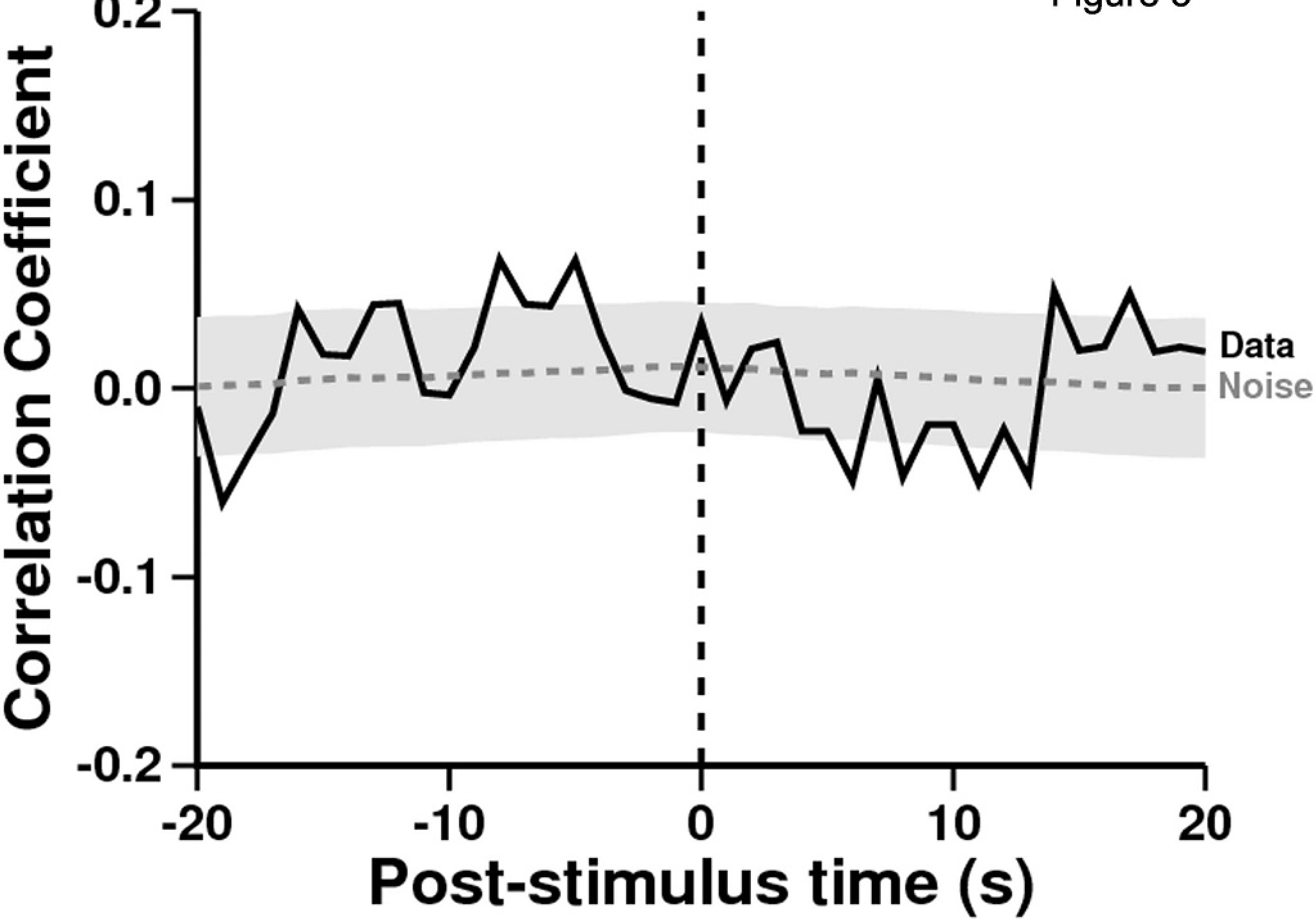
10
20
Post-stimulus time (s)
Data
Noise

Figure 5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Correlation Coefficient
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-10
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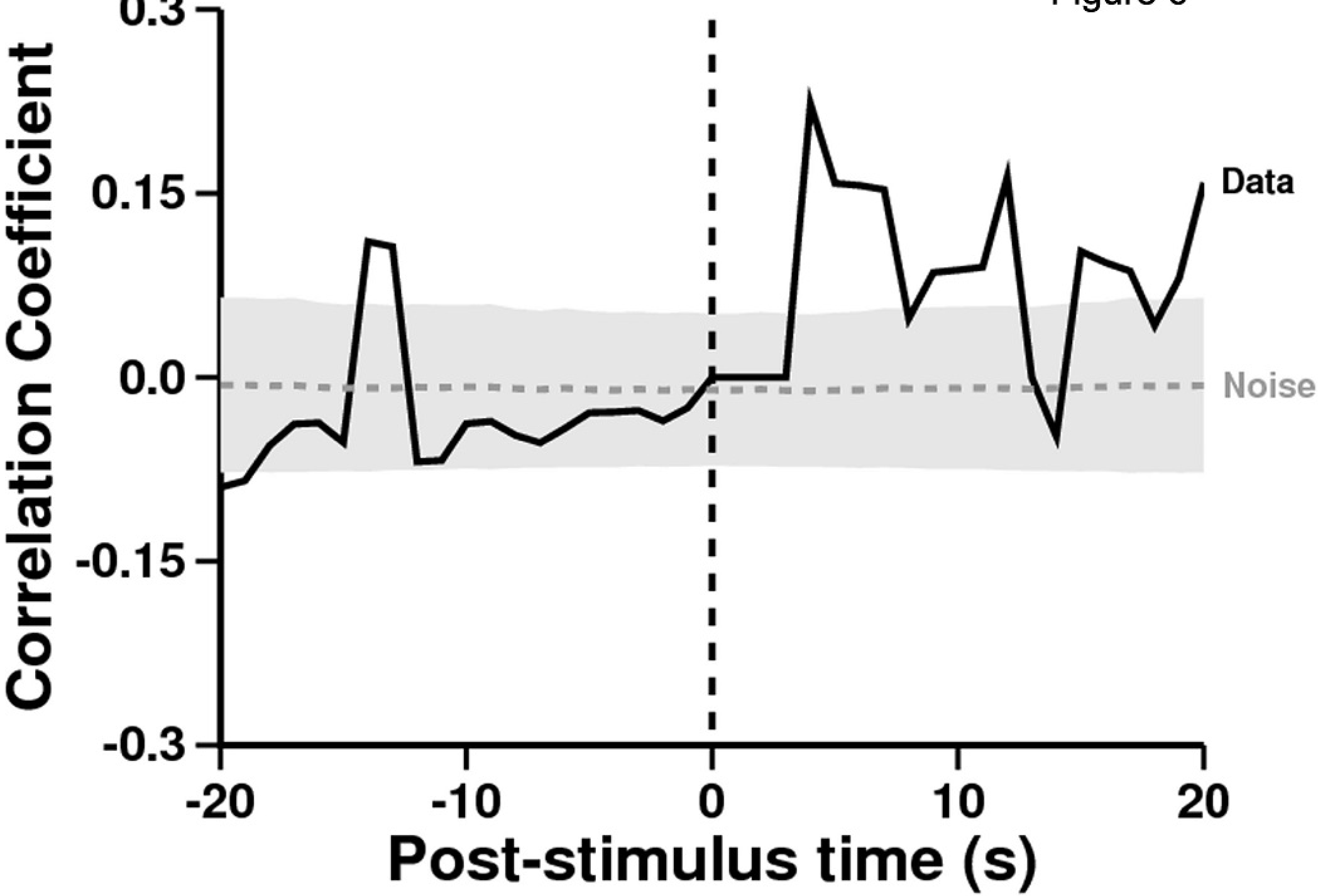
10
20
Post-stimulus time (s)
Data
Noise

Figure 6


0.3
0.15
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Correlation Coefficient
Data
Noise
-20
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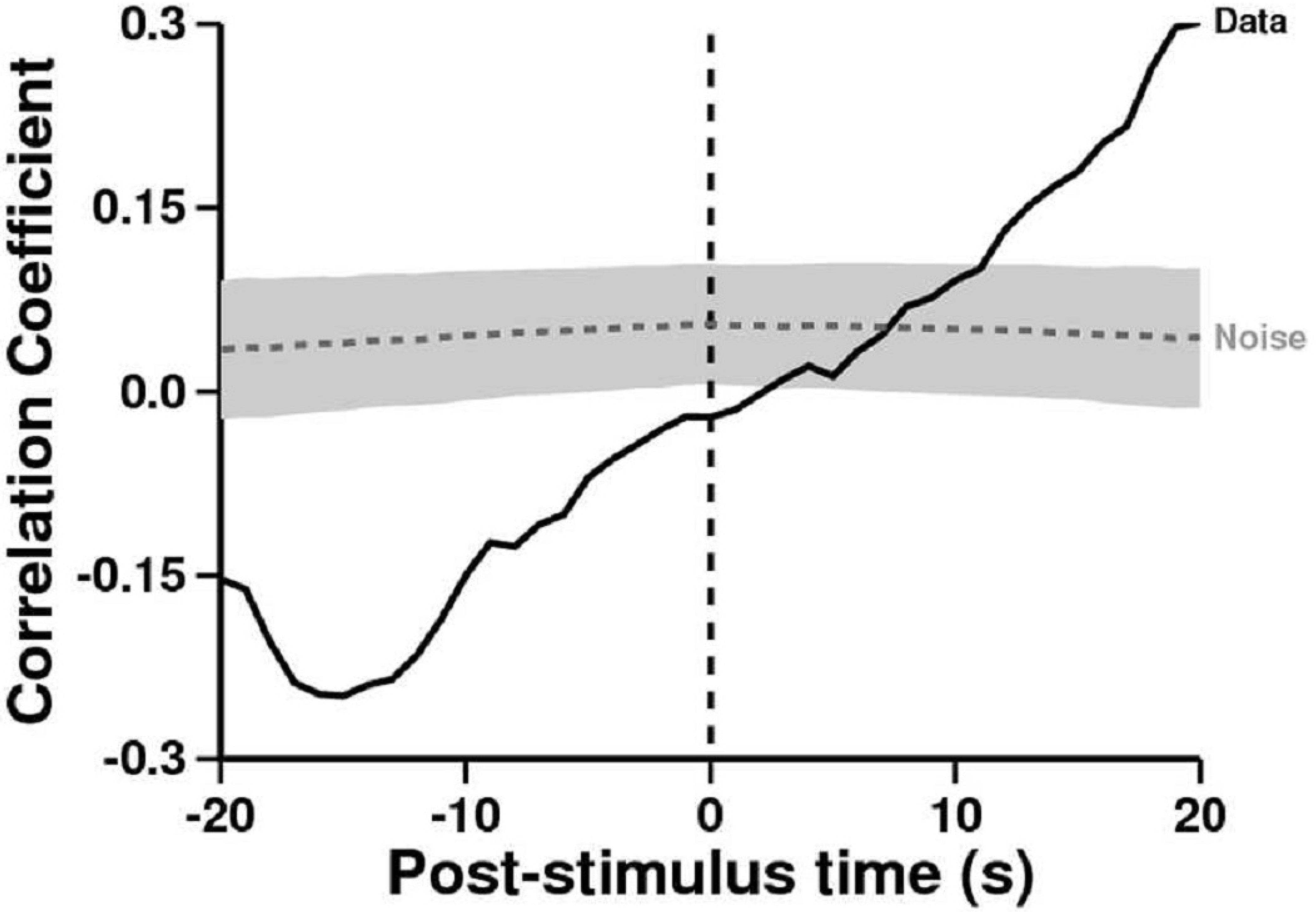
Post-stimulus time (s)

Figure 7



Data
Noise
Correlation Coefficient
0.3
0.15
0.0
-0.15
-0.3
-20
-10
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10
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Post-stimulus time (s)