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Partner Coordination in Relation to Reward Cost on a Computerized Task in a Social Group of Rhesus Monkeys (*Macaca mulatta*)

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An abstract of
A dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

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We manipulated how monkeys were rewarded at two interconnected touch-screen computer kiosks continuously available in their home enclosure to provide less expensive rewards (FR1) when two monkeys participated together at the kiosks and more expensive (FR10), or no, rewards when monkeys participated alone. Our goal was to determine if rhesus monkeys can learn the contingency between a partner's participation at an adjacent kiosk and reward outcome. We examined whether monkeys' partnered behavior (two monkeys working at the kiosks) increased when partnered trials, where two monkeys were logged-in and working at the kiosks at the same time, were rewarded on FR1, and solo trials, where only one monkey was logged-in and working, were rewarded on FR10 or not at all. We also examined how the monkeys engaged in partnered behavior during these conditions to determine the extent to which they learned the contingency. 14 young rhesus monkeys were given voluntary access to the computer kiosks and freedom of partner choice. Monkeys significantly increased partnered behavior during conditions when partnered trials produced less expensive rewards than conditions when partnered and solo trial rewards did not differ. Certain types of partnered behavior, such as participating at the kiosks within close temporal proximity of a partner after refraining from solo participation, were also significantly higher when partnered trials were less expensive. Rhesus monkeys are able to learn the contingency between a partner's participation and reward outcome, and actively adjust their behavior to maximize rewards using this contingency.

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Introduction

Psychologists, philosophers, theologians, and neuroscientists have long struggled with the question of what makes humans, or the human mind, unique. A common argument is that humans have a superior capacity for self-awareness and social cognition; humans can understand others' intentions and emotional states and empathize with others (Decety & Jackson, 2004). Humans can behave prosocially and, some would argue, altruistically: performing acts at great cost to oneself for the benefit of another individual (Silk & House, 2011). These prosocial behaviors are not necessarily linked to reproductive success and are seemingly not limited to kin (Silk & House, 2011). Attempts to identify ultimate and proximate explanations of these complex social behaviors have resulted in research exploring if, to what extent, and under what circumstances nonhuman animals demonstrate the same capacities (Mendres & de Waal, 2000).

Investigating what nonhuman animals understand about intention and if they are self-aware is difficult; paradigms are designed to elicit specific behavior which could indicate a capacity for such abilities, but attributing intention or awareness to observable behavior is not always possible (Albiach-Serrano, 2015). An important first step to understanding if nonhumans share these attributes with humans is to identify what cognitive mechanisms would be required and then experimentally determine which mechanisms are present in other species.

Cooperation is one such complex behavior that has been frequently studied in nonhumans (Smith, 2014). Evidence of cooperative acts in nature are widely documented, but how and why animals cooperate is still up for debate (Mendres & de Waal, 2000; Albiach-Serrano, 2015). Experimental paradigms have been designed to elicit cooperative behavior in a laboratory setting and make conclusions about what subjects understand about the cooperative task, the role of a partner, and the intentions of a partner (Albiach-Serrano, 2015). However, interpretations of what the animals understand vary, and if their performance is in fact indicative of an understanding of intention is unclear (Albiach-Serrano, 2015). Additionally, failures to cooperate in experimental settings are seen as an absence of the required mechanisms for cooperation or an inability to perform intentional cooperation, when these failures may result from issues with the experimental design (Molesti & Majolo, 2015). In order to answer if a species can cooperate, it is important to 1) design an experiment in which that species can succeed if they do possess the capacity to do so and 2) start with an examination of known cognitive mechanisms required for cooperation before leaping to conclusions about intention or self-awareness. Such an approach would paint a more accurate picture of what mechanisms are shared across species and could act as a platform for future research to incrementally assess mechanisms required for intention and understanding to further elucidate what differences exist between species. The purpose of this study was to examine if rhesus monkeys possess cognitive mechanisms required for cooperation to add to the literature examining what capacities for cooperation rhesus monkeys possess.

Defining and Assessing Cooperation

The definition used for examinations of cooperation in nonhumans is two or more individuals coordinating action to achieve, or attempt to achieve, a common goal (Albiach-Serrano, 2015; Boesch & Boesch, 1989; Goodall, 1986). Examples of cooperative behavior in a natural setting have been used to propose levels that correspond to underlying mechanisms required for intentional cooperation, which requires that an individual possesses the ability to understand the goals and intentions of others (Boesch & Boesch, 1989; Drea, 2006).

Boesch and Boesch (1989) used examples of cooperative group hunting in chimpanzees to define four levels of cooperation, with increasing levels of complexity in organization and action: similarity, synchrony, coordination, and collaboration. The first level, similarity, was defined as all individuals concentrating similar actions on the same goal, without adjusting to one another (Boesch & Boesch, 1989). Synchrony was defined as each individual concentrating similar actions on the same goal while also relating actions in time with each other (Boesch & Boesch, 1989). Coordination involves concentrating similar actions on the same goal while relating actions both in time and in space to each other (Boesch & Boesch, 1989). The final level, collaboration, was defined as two individuals performing different yet complementary actions on the same goal (Boesch & Boesch, 1989).

In a methodological review of cooperation studies, Albiach-Serrano (2015) proposed an operational definition of cooperation and its levels that combined some of the aspects put forth by Boesch and Boesch (1989) and further clarified the cognitive mechanisms underlying cooperation. According to Albiach-Serrano (2015), cooperation occurs when a problem can be solved with simultaneous or sequential, similar or complementary actions of individuals, with a focus on the type of stimuli eliciting cooperative behavior as a means of identifying the level of complexity. This definition included five levels, which differed based on factors such as similarity, synchrony, and coordination, but also included aspects of intentionality and understanding the role of a partner (Albiach-Serrano, 2015). In this model, the first level is independent cooperation, or when individuals share similarity but are not attending to each other's actions (Albiach-Serrano, 2015). Presence-dependent cooperation is exhibited in situations where an individual is more likely to act in another's presence, and action-dependent cooperation is defined as individuals being more likely to act when another performs a particular action (Albiach-Serrano, 2015). Form-dependent cooperation, or coordination, involves two or more individuals coordinating actions, incorporating the synchrony and coordination levels proposed by Boesch and Boesch (1989) (Albiach-Serrano, 2015). The last level of cooperation in Albiach-Serrano's model is intentional cooperation, which incorporates an understanding of a partner's goals and intentions, as well as where the partner's attention is directed (2015).

In both examples, cooperation can be broken down into distinct levels reflecting the complexity of coordination involved. Levels like those proposed by Boesch & Boesch (1989) and Albiach-Serrano (2015) have been used as a rubric for assessing cooperative behavior to determine what capacities exist for cooperation in nonhuman species. Experiments have been designed which incorporate methods to determine if collaboration or intentional cooperation is possible. However, it is difficult to assess what nonhuman animals understand about the role that a partner plays during cooperation, or what cooperation is, without the convenience of language. Frequency of partnered behavior, context of partnered behavior, and withholding participation in tasks until another individual is present have been used as evidence for cooperation like the intentional cooperation or collaboration described by Boesch and Boesch (1989) and Albiach-Serrano (2015). However, it is possible that these types of performance do not indicate anything about understanding or intention, but rather reflect a learned contingency between a partner and a successful outcome, and the changes in partnered behavior observed occur when individuals alter their behavior whether or not cues to participate are available. This does not negate the importance of this evidence; being able to use a partner as a cue for participation is a necessary mechanism for higher levels of cooperation. Learning such a contingency is required for understanding what contexts provide opportunities for cooperation, thus influencing when and how individuals cooperate. Experimental examinations of cooperation in a variety of nonhuman species designed to assess the capacity for these levels of cooperation are described below.

A commonly used paradigm to examine cooperation in an experimental setting is a variation of the rope-pulling task designed by Crawford (1937). In this experiment, a heavy platform was placed outside of an enclosure, with two pieces of food placed out of reach on top of the platform. To reach the food, the platform needed to be simultaneously pulled closer to the cage by the two individuals. The platform was too heavy for one individual to pull alone, so simultaneous, coordinated pulling by two chimpanzees was required to gain access to the food. Crawford (1937) observed chimpanzees coordinate their actions to pull the platform toward their enclosure and successfully access the food rewards. Crawford (1937) also described observations of what appeared to be recruitment behavior: when one individual became seemingly disinterested in the task, the chimpanzee still at work displayed behavior toward the other that looked as if his participation was being recruited, eventually getting him to return to the task. This recruitment behavior has been cited as evidence that these chimpanzees understood the role that a partner plays in a cooperative task and were capable of adjusting their actions in coordination with the intentions of the other individual and, as such, demonstrate intentional cooperation. Descriptions of behavior like that in Crawford (1937) are compelling, but anecdotal. This does not negate the possibility that the recruitment behavior observed did indicate some kind of understanding of the partner's intentions, but it does provide evidence that experience with a cooperative setting and learning the contingencies between a partner and a reward outcome may be a necessary first step in successful cooperation.

In 1943, Warden and Galt used Crawford's approach to examine cooperation in three species of monkey: four cebus monkeys, three rhesus macaques, and two sooty mangabeys. The monkeys were trained to pull platforms of various weights with a rope, and then placed in a cooperative test similar to the one described in Crawford (1937). The monkeys did not show any coordinated pulling in the first test phase (Warden & Galt, 1943). Monkeys were then trained to simultaneously pull ropes that were attached to two separate, lighter boxes, and the monkeys were able to successfully pull in synchrony with an adjacent monkey (Warden & Galt, 1943). However, in the cooperative test where they needed to coordinate rope pulling to pull one shared heavy box toward them to obtain a food reward, the monkeys did not successfully coordinate pulling. When describing their performance, Warden and Galt (1943) mentioned that if one monkey pulled alone, the second monkey would not start pulling until the box started to budge. This was taken as a failure to cooperate, but could reflect a lack of motivation. Perhaps the monkeys in this task did not want to exert the effort required to move the heavy box unless it appeared to be moveable.

Many variations of this rope-pulling task have been carried out on a variety of species, with added manipulations to better control what subjects learned about the task. In one experiment, chimpanzees were given a rope-pulling task similar to Crawford (1937), but the rope was situated in such a way that if pulled by one individual, the entire rope would come loose and the reward would remain out of reach (Hirata & Fuwa, 2007). In this experiment, the chimpanzees were trained to manipulate the rope in solo situations before completing the cooperative task. After extensive training, the chimpanzees were able to coordinate to pull the rope and successfully obtain the food reward (Hirata & Fuwa, 2007).

In addition to chimpanzees and the three previously mentioned monkey species, this rope-pulling paradigm has been used to assess cooperation in capuchins, cotton-top tamarins, hyenas, rooks, and elephants, among others, to varying degrees of success and interpretation. In a rope-pulling cooperative experiment, capuchin monkeys did not preferentially pull when a partner was present, leading the authors to conclude that any signs of cooperation on this task were accidental successes (Chalmeau & Visalberghi, 1997; Visalberghi, Quarantotti, & Tranchida, 2000). However, Mendres and de Waal (2000) reported successful coordination between capuchins, with more rope pulls in the presence of a partner than when alone. This was described as evidence that the capuchins understood the role of the partner, thus demonstrating intentional cooperation (Mendres & de Waal, 2000). Cotton-top tamarins given a handle-pulling task to receive a food reward were able to successfully coordinate action to receive rewards and also alter behavior based on the presence or absence of a partner (Cronin, Kurian, & Snowdon, 2005). Seed, Clayton, and Emery (2008) investigated if rooks could solve a cooperative rope-pulling task and not only were they successful, but the tolerance level between individuals in a pair influenced performance such that more tolerant relationships were more successful (Seed, Clayton, & Emery, 2008). In one manipulation, one rook was introduced to the apparatus before a partner was available. In this delayed access scenario, the rooks did not hesitate to pull, leading the authors to conclude that they lacked understanding of the necessity of a partner (Seed, Clayton, & Emery, 2008). Hyenas, cooperatively hunting carnivores in the wild, successfully coordinated action in a laboratory setting to solve tasks that modeled group hunting situations (Drea & Carter, 2009). The hyenas also appeared to alter behavior based on the experience level of another individual, suggesting an ability to monitor the actions of a partner (Drea & Carter, 2009). Plotnik, Suphachoksahakun, and de Waal (2011) adapted the rope-pulling paradigm for investigating cooperation in Asian elephants. The authors reported that the elephants successfully coordinated to pull the rope and receive a reward, and that elephants would wait to manipulate and pull the rope until both partners were present (Plotnik, Suphachoksahakun, & de Waal, 2011).

One commonality across these studies is using waiting to participate as evidence of intentional cooperation. The argument is as follows: if an individual understands that a partner is required to receive a reward and the role that the partner plays in that task, then the individual should not engage with the task until the partner is present. Thus, when they wait to perform until joined by a partner, the conclusion is made that they are capable of intentional cooperation. As mentioned previously, this behavior does not necessarily indicate that the individual understands or knows the intentions of the partner or that they share a common goal with the partner. It is possible that this waiting behavior is a reflection of a learned association between the presence of a partner and successful task completion, but this learned association supports the idea that the framework required for understanding a cooperative context exists in these species.

Cooperation in Rhesus Monkeys

There are relatively few studies of cooperation in rhesus monkeys that assess cooperation in the same way as has been done in other species. This gap in the literature may reflect social differences between rhesus monkeys and species often used in cooperation experiments. Many of the species that are chosen for cooperative experiments are selected because they demonstrate some sort of species-specific cooperative behavior in the wild. As mentioned previously, chimpanzees are cooperative hunters (Boesche & Boesche, 1989). Capuchins are a socially tolerant species, with evidence of food sharing after cooperative hunting in the wild (de Waal & Davis, 2003). Cotton-top tamarins are cooperative breeders; both parents share the burden of rearing young (Snowdon, 1996). Captive rooks have been observed creating and maintaining alliances in which food sharing and support in agonistic incidents are common (Seed, Clayton, & Emery, 2008). Hyenas are cooperative hunters (Holekamp, Sakai, & Lundrigan, 2007), and elephants reportedly show cooperation in the wild through allomothering and protective coalitions (Plotnik, Suphachoksahakun, & de Waal, 2011).

Documented evidence of cooperation in rhesus monkeys typically refers to cooperation that occurs during or after agonistic interaction, but these types of coordinated action are well documented. Rhesus monkeys are categorized as a despotic species because of their high levels of harsh competition and low levels of tolerance for non-kin (Silk, 1982). de Waal and Yoshihara (1983) examined the post-conflict behavior of rhesus monkeys and found that after agonistic incidents opponents had an increased likelihood of approaching and contacting one another. This likeliness to approach increased when the bond between the two individuals was strong, such as between individuals within a matriline (de Waal & Yoshihara, 1983). The formation of coalitions during agonistic interactions has been well documented in rhesus macaques. More specifically, female rhesus macaques form coalitions while protecting or supporting maternal kin (Kaplan, 1977), even in high-risk situations when they are acting against higher-ranking individuals (Bernstein & Ehardt, 1985; Datta, 1983; Kaplan, 1977). Male rhesus monkeys living on Cayo Santiago were observed forming coalitions to overpower and displace higher ranking males in their social group (Higham & Maestripieri, 2010).

Not only do rhesus monkeys coordinate action with coalitions to support one another during fights, but this support seems to be reciprocal. Reciprocal agonistic interventions in chimpanzees, rhesus macaques, and stumptail macaques were investigated by de Waal and Luttrell (1988). In all three species, significant levels of reciprocity were observed for pro interventions; a pro intervention was defined as one in which individual A and individual C are engaged in a fight and individual B supports individual A (de Waal & Luttrell, 1988). Although there was a stronger correlation between providing and receiving support in chimpanzees, that rhesus macaques demonstrated any level of reciprocity could suggest an understanding of an acquisition of mutual benefits. The authors suggest that these data support the idea that all three species, including rhesus macaques, are capable of maintaining mental records of when and from whom they received support and then are able to use that information to alter their behavior to behave reciprocally (de Waal & Luttrell, 1988).

Experimental investigations of cooperation in rhesus monkeys are relatively rare. One of the few cooperative experiments similar to those discussed earlier conducted on rhesus macaques was in 1992 by Petit, Desportes, and Thierry. The authors observed if Tonkean and rhesus macaques were able to coordinate action to move heavy stones in order to receive hidden food rewards. Tonkean macaques demonstrated some success in moving the stone to obtain a food reward, but individual actions were more common than joint actions of two individuals and did not appear to show any synchrony (Petit, Desportes, & Thierry, 1992). Instances of rhesus monkeys coordinating action to move a stone only occurred twice, and each time this behavior was displayed by the same pair of individuals (Petit, Desportes, & Thierry, 1992). Interestingly, the two successful rhesus individuals were a male/female consort pair, suggesting that in situations of high tolerance the rhesus monkeys were able to successfully coordinate action.

Molesti and Majolo (2015) documented successful coordination of wild barbary macaques on a rope-pulling task, a species closely related to rhesus, when given the opportunity to choose a partner. The monkeys were allowed to choose when to interact with the apparatus and with whom to work (Molesti & Majolo, 2015). High levels of tolerance and the relationship between two partners impacted successful completion of the task (Molesti & Majolo, 2015). That barbary macaques are capable of coordinating action on a rope-pulling task suggests that this mechanism would also be present in rhesus monkeys, and that designing an experiment where the social context can allow for partnered behavior to occur is imperative for successful coordination.

In a controlled laboratory study, Brosnan, Wilson, and Beran (2012) examined the role of information in coordination decision making in rhesus monkeys. In this study, the authors used the “Assurance Game,” a task in which reward outcomes are based on the choices of two partners. There are three possible choice scenarios which lead to different distributions of rewards: both individuals choose stag, resulting in an equal, large reward distribution to each partner, both individuals choose hare, resulting in an equal, low reward distribution to each partner, and one individual chooses stag while the other chooses hare, which only provides a low reward to the hare player (Brosnan, Wilson, & Beran, 2012). In some conditions the monkeys could see the choice that the partner monkey selected and in others the choices were not visible (Brosnan, Wilson, & Beran, 2012). Regardless of whether or not the partner’s choice was made visible, pairs of rhesus monkeys were able to coordinate and both choose the stag option, resulting in the largest reward payoff for each monkey. This success on a coordinated-decision making game suggests that rhesus monkeys are able to learn to coordinate behaviors for mutual benefit. The authors hypothesized that the rhesus monkeys were capable of reaching this decision to optimize mutual benefit through an associative mechanism; they were able to learn what strategy had the highest probability of a high reward outcome.

Rhesus monkey social behavior and structure may make it difficult for cooperation experiments like those previously described to accurately assess the level of cooperation that the monkeys can express. Their low levels of tolerance may preclude them from engaging in coordination with another individual if the relationship between the two does not warrant such behavior. A study design which allows the rhesus monkeys freedom to partner with individuals within their social group may result in a different expression of coordination than previously recorded. Similarly, the limited research on rhesus macaque cooperation in a laboratory setting typically involves adult monkeys. It is possible that juvenile monkeys would have higher levels of tolerance with a wider net of individuals as a result of their differences in social behavior (Liao, Sosa, Wu, & Zhang, 2017). Social network analysis has revealed that the number of social partners that rhesus monkeys have decreases with age, and that juvenile monkeys have more diversified social networks (Liao, Sosa, Wu, & Zhang, 2017). Additionally, juvenile and subadult rhesus monkeys are more likely than adults to initiate affiliative play interactions (Liao, Sosa, Wu, & Zhang, 2017). This seems to indicate a potential for performance in cooperation tests to differ based on age. If juvenile monkeys have a broader, more diverse social network of potential partners and are more likely to initiate affiliative play, then it is possible that they would be more likely to successfully coordinate with a wider variety of partners than adult monkeys.

As Brosnan, Wilson, and Beran (2012) demonstrated, it is apparent that monkeys are capable of coordinating decisions, or at least learning patterns, to optimize rewards and obtain a mutual benefit during computerized tests. This suggests that monkeys are capable of altering behavior to maximize reward outcomes. It is possible, then, to build upon this research and examine in what contexts rhesus are capable of coordinating action to maximize rewards.

Current Study

The current study was designed to examine if rhesus monkeys could learn to use a partner as a discriminant cue for reward and examine if monkeys could coordinate participation with a partner to maximize rewards. As mentioned previously, the ability to learn the contingency between a partner and a successful outcome is an important mechanism underlying cooperation, and partner coordination demonstrates a level of cooperation preceding intentional cooperation. Although previous studies in other species have attempted to examine intentional cooperation, the goal of this study was to first and foremost address if monkeys could demonstrate successful coordination after learning the contingency between a partner and reward. Experiments examining cooperation in rhesus monkeys are rare, and a goal of this study was to add to the existing literature documenting if rhesus monkeys possess underlying cognitive mechanisms required for cooperation.

The current study employed an experimental design which allowed participation of individuals in all age groups, provided free partner choice, and required coordination of participation to obtain rewards. An interconnected, two-touch-screen computer kiosk system was mounted in the home enclosure of a mixed-age, mixed-sex social group of rhesus macaques. Removing animals from their home enclosures can induce significant stress, potentially altering performance (Washburn & Rumbaugh, 1991), and it has been well documented that monkeys are capable of voluntarily participating in computerized tasks available in their home enclosures (Andrews & Rosenblum, 1994; Gazes, Brown, Basile, & Hampton, 2012; Gazes, Lutz, Meyer, Hassett, & Hampton, 2019; Hassett, 2011). Such paradigms where animals are tested in their home groups improve ecological validity and provide enrichment for the subjects (Drea & Wallen, 1999; Drea, 2006; Fagot & Paleressompoulle, 2009). Voluntary participation and freedom of partner choice were used to allow monkeys to choose when, and with whom, to work, potentially increasing their abilities to learn the contingency between a partner and reward. Reward outcomes were manipulated to encourage partner coordination. In some conditions, rewards were less expensive, or required fewer trials to obtain a reward, if two monkeys worked at the kiosks at the same time, and in others, rewards were only available if two monkeys worked at the same time.

Previous research has shown that younger monkeys are more likely to interact with computer kiosks available in a home enclosure than older monkeys, perhaps as a result of viewing participating at the kiosks as a form of play (Hasset, 2011). It was hypothesized that if younger monkeys are more likely to interact with the kiosks and have more diversified and broad social networks (Liao, Sosa, Wu, & Zhang, 2017), then they would be tolerant of another monkey engaging with the kiosks at the same time and interact with the kiosks often enough to learn to use a second, or partner, monkey as a cue.

It was hypothesized that monkeys would be able to learn to use a partner as a discriminant cue for reward. Rhesus monkeys have demonstrated the ability to learn reward contingencies in a variety of cognitive tasks (Visco-Comandini, Ferrari-Toniolo, Satta, Papazachariadis, Gupta, Nalbant, & Battaglia-Mayer, 2015; Evans, Perdue, Parrish, & Beran, 2014). In the current study, the contingency that monkeys were required to learn involved a social cue. It was possible that low levels of tolerance between individuals could 1) deter monkeys from working together at the kiosks frequently enough to learn the contingency between a partner and reward or 2) influence what monkeys attend to while at the kiosks, impacting their ability to learn what contextual cues contribute to a successful outcome. In order to address these concerns, monkeys were given continuous access during the day to the kiosks and were not limited in the number of trials they could complete. This freedom in when to participate was designed to provide ample opportunities to the monkeys to participate when the social context could allow partnering.

If monkeys are capable of learning the contingency between a partner and a reward, then an increase in partnered behavior would be expected when partnered participation resulted in better rewards than solo participation. Additionally, if this contingency was learned, then a decrease in solo participation would be expected when trials were only rewarded for partnered behavior. As there was no limit to the number of trials a monkey could complete in a day, just assessing an increase in partnered behavior would not necessarily indicate anything about the learned contingency, but rather reflect higher participation when less expensive rewards could be obtained. Therefore, it was important to address how partnered behavior changed in relation to solo behavior.

If monkeys are capable of using a partner as a cue for participation and coordinating participation at the kiosks, then it was expected that there would be observable differences in how monkeys engaged in partnered behavior when rewards were less expensive when partnering than when participating alone. Specifically, it was expected that monkeys would increase their participation at the kiosks within close temporal proximity of a partner; two monkeys would being to work at the kiosks within a short timeframe of one another in conditions when partnered behavior was required for less expensive rewards.

Methods

Study Design Overview

In order to assess if rhesus macaques are capable of coordinating action to obtain food rewards when given autonomy over partner choice, a touch-screen computer kiosk system was developed to allow subjects to voluntarily participate with other individuals in the social group in which these subjects were housed. Subjects that successfully completed training to interact with the kiosks and participate at different fixed-reward ratios were advanced to a series of experiments in which coordinated action with a partner influenced the rewards received. This project was completed under an approved Institutional Animal Care and Use protocol.

Subjects

Subjects were rhesus macaques socially housed in a large, outdoor enclosure (30m x 30m) with attached heated and cooled indoor housing at the Yerkes National Primate Research Center in Lawrenceville, Georgia, which is fully accredited by the American Association for the Accreditation of Laboratory Animal Care. Water is accessible in both the indoor and outdoor areas, and the monkeys have continuous access to food pellets (Purina Mills, St. Louis, MO) via four automated feeders attached to the outdoor enclosure. Monkeys can access these automated feeders with passive radio-frequency identification (RfID) tags implanted in each wrist, which also allow them access to the computer kiosk system. The monkeys receive a daily supplement of either a fruit or vegetable in the mid-afternoon, and enrichment is provided daily in the form of cardboard boxes, butcher paper smeared with yogurt, or food foraging toys.

Sixty-nine macaques live in this socially naturalistic, mixed-age and mixed-sex group, ranging in age from newborn to 20 years. During this study, the group consisted of 35 adult females and their offspring and two adult breeder males. All subjects above 6 months of age had RfID tags implanted in each wrist (see implantation procedures below), allowing them access to the automated feeders as well as this kiosk system. Individuals older than six months all had previous experience working at the kiosks prior to the start of data collection for this study.

Initially, all 46 monkeys with RfID tags at the onset of data collection were eligible to participate. As training progressed, access to the kiosks was limited to a subset of individuals that successfully passed specific (see below) training stages. During the experimental test of partner coordination, 18 individuals initially had access to the kiosks. Three adult females who advanced to the experimental test of partner coordination ceased participation within the first week and were thus no longer allowed to access the kiosks and were dropped from the study. One subject was removed from the group midway through testing for colony management reasons and was excluded from analysis, leaving 14 subjects (see Table 1 for subject demographics).

Behavioral observations of agonistic interactions between animals by research and colony management staff were used to determine the social rank of each matriline. Each monkey within a matriline was assigned the matrilineal rank as their social rank.

RfID Tag Implantation

Subjects were implanted with RfID microchips (12.5mm, 134.2 kHz ISO, Datamars Inc., Youngstown, OH) using sterile 12 gauge needles with disposable single-use plunger-style implanters. This procedure was carried out by trained research personnel while the animals were sedated with an intramuscular injection of Ketamine at 10mg/kg during routine veterinarian-led physical exams. One unique RfID microchip with a 15-digit code for identification was implanted in each wrist of the animal.

Apparatus and Materials

Two inter-connected, touch-screen computer kiosks were mounted along the edge of the outdoor housing area of the social group (Figure 1) behind a window of 1.3cm-thick clear polycarbonate resin. The monkeys had a clear view of both kiosks but had physical access limited to a single touch-screen and reward pellet cup accessible through an armhole cut in the polycarbonate at each kiosk. These holes were centered approximately 15cm in front of each touch-screen. Each armhole was encircled by one RfID antenna 14cm in diameter, and the armholes had a maximum opening of 5cm. The two kiosks were within visual and auditory range of one another, but separated so that one monkey could not manipulate both kiosks at once or touch a monkey at another kiosk. A small metal perch (60cm) was attached to the interior of the compound wall right below each armhole, allowing access to each touch-screen. The perches were separated by a 125cm gap preventing subjects from walking from one kiosk to the other.

Each kiosk contained a NEMA 4 15" capacitive touch screen monitor (Vartech Systems Inc., Baton Rouge, LA), mounted in a cutout of a large weather-proof enclosure (McMaster Carr, Elmherst, IL). Each touch screen was connected by a VGA cable for video and serial-to-USB converter for "mouse" input to a low-power netbook running the Windows 7 (Microsoft, Redmond, WA) operating system and a java-based platform program with a suite of pre-set cognitive tasks developed by Patrick Ulam (2014, 2018). An automatic pellet dispenser (Med Associates Inc., Georgia, Vermont) was connected to a programmable logic controller (PLC) to allow input and output connections via a serial-to-USB converted connection to each netbook. Rewards were 94mg, grain-based, banana flavored pellets (Bio-serv, Frenchtown, NJ). The RfID antennae were custom built and connected to modified iMax Black Label RfID readers (Datamars Inc., Youngstown, OH). These readers were modified to identify RfID tags every 300ms. Each of these connections was mapped to a COM port using the Windows Device Manager within the netbooks. The two netbooks communicated via an Ethernet cable housed in a weather-proof conduit connected to each kiosk. Through this connection, settings could be designated in the software to alter reward outcomes based on participation at the two kiosks. The netbooks were remotely accessible using the TeamViewer (TeamViewer Inc., Tampa, FL) software, and all data backed up to an onsite server. A small thermostat and fan were also housed in each kiosk box to prevent overheating, and generic loud-speakers were connected to the netbooks to provide audio feedback to animals participating at the kiosks.

Apparatus Exploration

In order to garner interest in both kiosks on the first day that they were made available, small amounts of peanut butter were smeared on the touch-screens at each kiosk. This only occurred on the first day to demonstrate to the monkeys that the kiosks were active and that interacting with the touch-screens could provide food rewards.

Data Collection Timeline

Data for this study were collected between October 1st, 2018 and October 9th, 2019. Kiosks were available from 7:00AM until 8:00PM every day that data were collected. Monkeys were not limited to a set number of trials, and could work on a kiosk whenever one was available.

Experimental Design

Software overview

Although interconnected, the two kiosks were independent so that two monkeys could work at a kiosk at the same time, at their own pace, at different stages of training. The java-based platform program allowed the experimenter to design specific experimental tasks and what was presented to the monkey on the screen, as well as control under what conditions rewards were dispensed. Data were stored in a database specified by a configuration file in the software and accessed via MYSQL (Oracle Corp., Redwood City, CA). Monkeys could be assigned to different types of tasks on any given day at one or both of the kiosks. When a monkey placed an arm through the armhole, the RfID antenna detected the unique tag code and transmitted that code via the RfID reader to the kiosk program, which retrieved information from the database to present the assigned trial type to the monkey. Two repeated readings of the same 15-digit RfID code were required to start a trial to ensure correct identification.

Additionally, each kiosk was color-coded, to provide information that certain cues were unique to a specific kiosk. One kiosk was designated the “blue” kiosk, and the second the “green” kiosk. When the kiosks were on and available for testing, the background of the screen was white with a colored border. At the “blue” kiosk, the border was always blue, and at the “green” kiosk, the border was always green. The stimuli presented during trials were also color coded in the same manner.

There are several aspects of trial presentation that are consistent throughout the study, regardless of trial type. Upon “logging-in” to the kiosks via the RfID antenna, the white background with a colored border would disappear and a trial would be presented. If a trial was completed successfully, a bright yellow screen would flash for 500ms and a high-tone “woo-hoo” would play from the speakers as a reward pellet was dispensed. If no touch was registered or if a tag other than the initial tag read was detected within 10,000ms of a log-in, the trial was aborted and the screen turned purple for 3,000ms. If an incorrect touch was made, the trial was also aborted and the screen turned purple for 3,000ms.

Kiosk training

Subjects first needed to be trained to interact with the kiosks to receive rewards. Kiosk training included three stages: “screen touch”, “long screen touch”, and “square touch.” During the screen touch stage, the stimulus presented was a colored background. At the “blue” kiosk, the background would turn blue, and at the “green” kiosk, the background would turn green. A touch at any location on the screen for any amount of time would result in a correct trial outcome. Monkeys needed to complete 25 screen touch trials to advance to the long touch stage of screen touch training. During the first set of long screen touch trials, monkeys were required to touch the screen for 100ms to complete a correct trial. After 25 consecutive successful trials, the time of the screen touch was increased to 200ms in order to receive a pellet reward. After 25 consecutive successful 200ms trials, monkeys advanced to the square touch task, which was the task used for the rest of the study. The stimulus in these trials was no longer a colored background, but a 160 pixels x 160 pixels square that appeared in one of 16 possible locations (Figure 2) that were randomly generated for each trial. The squares were color coded for each kiosk, such that the "blue" kiosk displayed a blue square and the "green" kiosk displayed a green square. To complete a correct trial, the monkey needed to touch the square for at least 200ms. Subjects could advance after successfully completing 80 of 100 consecutive square touch trials. After monkeys successfully completed square touch training, their testing schedules were designed to prevent them from working at one kiosk for more than 50 trials at a time, to expose them to both the "green" and "blue" kiosks through forced alternation. After 50 trials at one kiosk were completed, access to that kiosk would be denied. The monkeys would be required to have their next log in at the neighbor kiosk to receive rewards, and access to the first kiosk would not return until after 50 trials were completed at the neighbor kiosk. After two weeks in this stage, the experimental design was changed. Monkeys were no longer forced to switch in order to advance, but any monkey who had not completed more than 65% of their previous trials at a single kiosk could advance, ensuring that subjects had experience at both kiosks. This was done to ensure that the participants in the final phase were exposed to the colored stimuli at both kiosks. Square touch trials were used in the remaining phases of this study. Reference Figures 3 and 4 for graphical representations of screen touch and square touch training trials.

Fixed-ratio reward training

After kiosk training, subjects needed to gain experience receiving rewards at different fixed-ratio reward schedules so that reward outcomes could be manipulated in future trials to incentivize partnered behavior. In all previous trials, the monkeys would receive one reward pellet for each correct trial completed. Upon advancing to this phase, monkeys were placed on an FR2 schedule and incrementally advanced to an FR10 schedule. Monkeys were required to complete 100 trials at each increment before moving on to the next FR. Subjects who stopped participation for five days in a row during this phase were dropped from the study and no longer eligible to participate.

Partner coordination

The goal of this study was to determine if monkeys were capable of changing their behavior, in the form of kiosk participation, as a function of whether or not another monkey was working at the adjacent kiosk. Reward ratios were manipulated over the course of seven conditions as well as the ability to obtain rewards based on whether or not two monkeys were logged in and working at the kiosks within 30 seconds of each other. Subjects completed square touch trials in each condition. These conditions are outlined in Table 2 and are described in detail below.

Each square-touch task constituted a trial. Solo trials were defined as trials during which one monkey was participating at one kiosk with no monkey logged in at the adjacent kiosk. Partnered trials were defined as two monkeys logged-in to the kiosks within 30 seconds of one another. Thus, a partnered trial started once two monkeys were logged in to the kiosks at the same time. Trials prior to a second log-in were categorized as solo trials, and any trials that occurred when no second log-in was detected within 30 seconds were solo trials. Two types of partnered trials were analyzed: partnered trials with dual activation and partnered trials without dual activation. Partnered trials with dual activation referred to partnered trials that occurred after neither monkey had been participating at the kiosks for 5 minutes prior to the first partnered trial recorded. Partnered trials without dual activation were partnered trials that occurred after one monkey had been completing solo trials within 5 minutes prior to partnered trials. Reference Figure 5 for a graphical representation of what occurred on the screen when two log-ins were detected.

The monkeys experienced 7 different conditions during which reward outcomes were manipulated. There were 4 conditions during which solo and partnered trials did not differ in rewards, and 3 conditions during which partnered trials were rewarded after a single successful trial, compared to solo trials which required 10 successful trials for a reward. The first condition was a continuation of the types of trials monkeys had experienced during fixed-reward ratio training: both solo and partnered trials were rewarded on FR10. This condition was designed to measure how frequently two monkeys worked together at the kiosks when they had no prior experience with being rewarded for partnered trials and thus no incentive to partner. Partnering under this condition is an estimate of the random partnering rate. There were two more conditions (3 and 6) with the same FR10 reward outcome as in Condition 1, spaced out through testing to determine if partnered behavior persisted even when partnered trials were no longer rewarded preferentially. The final condition that monkeys experienced (Condition 7) rewarded both solo and partnered trials on FR1 to determine how frequently partnered trials were completed when both solo and partnered trials were rewarded on each trial, as a measure of how frequently monkeys partner when all trials are inexpensive.

The three conditions during which partnered trials produced rewards at a lower cost than solo trials were designed to assess if monkeys increased their participation in partnered trials when partnered trials produced better and cheaper rewards. During the first two conditions where partnered trial rewards were less expensive than solo rewards, a secondary color cue was presented to the monkey during partnered trials (Figure 5). Thus, the monkeys had three cues that a partnered trial had a different outcome than a solo trial: a monkey logged-in at the adjacent kiosk, a color cue on the screen, and cheaper rewards. This secondary color cue was removed for the last condition (Condition 5) where partnered trials produced rewards while solo trials did not. The conditions are described as follows:

Condition 1 – reward by trial type: solo: FR10, partnered: FR10

The first condition lasted 14 days and was a repeat of the final trials monkeys completed in the fixed-reward ratio training. At this point, monkeys had no experience with ever receiving different rewards for working at the kiosk when a partner was present. Partnered behavior during this condition acted as a measure of the probability that monkeys would partner at the kiosks by chance as a result of living in a social group and having access to two active kiosks. All trials were rewarded on FR10, and there was no difference in presentation of trials or reward cues between partnered and solo trials. Conditions where rewards were less expensive for partnered trials than solo trials were compared to Condition 1 to determine if partnered behavior occurred with incentive more frequently than would be expected by chance.

Condition 2 – reward by trial type: solo: FR10, partnered: FR1, secondary color cue

Condition 2 was designed to determine if the monkeys would increase how frequently they completed partnered trials when those trials were rewarded after less effort although solo trials were still rewarded. If partnered trials increased during this condition and were significantly more frequent than in Condition 1, then it would suggest that the monkeys were partnering more frequently than expected by chance, possibly by using a partner as a discriminant cue for a better reward schedule. Additionally, if there was an increase in partnered trials with dual activation, it would suggest that the monkeys were altering how and when they chose to interact with the kiosks based on the availability of a partner. Monkeys were rewarded on an FR10 schedule for solo trials, but when a log-in was detected at the adjacent kiosk, the schedule immediately switched to FR1 for both monkeys at both kiosks. The FR1 schedule maintained for the duration of partnered trials, and when the system no longer detected log-ins at both kiosks, a lone monkey continuing to participate would immediately return to an FR10 schedule.

When a second log-in was detected, the reward presentation on the screen contained an additional component (Figure 5). Whereas for previous correct trials the screen would flash bright yellow and a “woo-hoo” sound would play when a pellet was dispensed, for these correct partnered trials a secondary color cue was presented. This secondary color cue matched the color of the screen at the adjacent kiosk; monkeys at the “blue” kiosk saw the screen flash bright green for 250ms and monkeys at the “green” kiosk saw the screen flash bright blue for 250ms. This cue was presented prior to the yellow screen. The purpose of this secondary color cue was to further differentiate partnered trial rewards from solo trial rewards, and increase the salience of the context of a partnered trial. As all subjects had experience at both kiosks, the goal was to build upon the color associations that they may have developed for each kiosk to add an extra cue that a monkey was working at the adjacent kiosk. Condition 2 lasted for 28 days.

Condition 3 – reward by trial type: solo: FR10, partnered: FR10

After Condition 2, all trials were again rewarded on FR10 for 14 days. This condition was used to assess if monkeys would continue to engage in partnered trials without incentive to determine if an increase in other conditions was a result of a learned contingency between partner and reward. If partnered trials persisted, then it was possible that the monkeys did not associate a partner monkey with the change in reward outcome. If partnered trials decreased, or extinguished, then it would indicate that the monkeys understood the contingency between another monkey's presence and the increased rewards. The secondary color cue was removed during this condition, and there was no trial presentation or reward outcome difference between solo and partnered trials.

Condition 4 – reward by trial type: solo: no reward, partnered: FR1, secondary color cue

In order to determine if monkeys learned that the key factor to receiving better rewards was the presence of a partner, a condition was created which consisted of trials for which subjects were only rewarded for partnered trials. Subjects could still complete trials when alone at a kiosk, but they received no reward pellets. If the ratio between partnered trials and solo trials completed shifted, such that the majority of trials completed were partnered trials, it would indicate that the monkeys learned the relationship between a partner and reward. Additionally, if there was an increase in partnered trials with dual activation, meaning neither monkey was completing solo trials for an extended period of time prior to completing partnered trials, then it would indicate that the monkeys were altering how they were interacting with the kiosks based on the availability of a partner, potentially coordinating behavior with another individual in order to obtain rewards. When two log-ins were detected, the rewards would immediately begin to dispense at an FR1 schedule and maintain that schedule for the duration of partnered trials. When a second log-in was no longer detected by the system, rewards would cease to be dispensed. As in Condition 2, the secondary color cue was presented prior to the yellow flash when partnered trials occurred. Subjects were exposed to Condition 4 trials for 35 days.

Condition 5 – reward by trial type: solo: no reward, partnered: FR1, no secondary color cue

In order to determine if the monkeys were using the partner as a cue for the increased reward or if they were only attending to the secondary color cue provided during the reward presentation, the secondary reward cue, or the flash of color of the partner's kiosk, was eliminated in Condition 5. Solo trials and partnered trials during this condition were presented identically, and the only cue for receiving rewards was a partner at the adjacent kiosk. As in Condition 4, only partnered trials were rewarded, and rewards were dispensed on an FR1 schedule. However, in this condition, the secondary color cue was removed. Thus, on correct trials, subjects only saw the bright yellow flash; no secondary color cue was presented. As in Condition 4, monkeys could still participate in solo trials but no rewards were dispensed at any time for solo trials. This condition lasted 35 days.

Condition 6 – reward by trial type: solo: FR10, partnered: FR10

To determine if the monkeys would continue to complete partnered trials even in the absence of increased rewards, a third iteration of trials for which monkeys were placed on FR10 with no distinction between partnered and solo trials was tested. It was possible that after the extended experience completing partnered trials during Conditions 4 and 5 (if they completed partnered trials), the monkeys would continue to partner even without incentive. If partnered trials did not decrease during this condition, then it would be possible that the monkeys were not fully using a partner as a discriminant cue, and perhaps were just increasing overall interaction with the kiosks to receive more rewards through trial and error. If the partnered trials decreased and solo trials increased, it would indicate that the monkeys had learned that a partner was no longer required for higher rewards, suggesting that they had made that association in the previous conditions. Monkeys remained on Condition 6 for 7 days.

Condition 7 – reward by trial type: solo: FR1, partnered: FR1

In all previous conditions, solo trials were rewarded on an FR10 schedule. In order to determine if the availability of less expensive rewards increased the frequency of concurrent work (when partnering was not required to receive rewards), the final condition placed monkeys on an FR1 schedule regardless of trial type. If monkeys performed partnered trials and partnered trials with dual activation at the same levels during this condition as in the three conditions where partnered trial rewards were less expensive than solo trial rewards, it would suggest that they were not using a partner as a discriminant cue, but increasing kiosk interaction in order to maximize rewards. If partnered trials and partnered trials with dual activation decreased in this condition, it would indicate that the monkeys had learned that a partner was no longer required to receive a reward, thus demonstrating that the association between partner and reward had been made during previous conditions. As in Conditions 5 and 6, there were no computer cues indicating a difference between partnered and solo trials. This condition lasted 7 days.

Data Extraction and Analysis

Data collected for each trial included the task type (e.g. screen touch or square touch), trial location ("green" or "blue"), monkey identification code, date and time (hr:min:s) of the trial, the trial outcome (success or aborted), if two log-ins were detected at the two kiosks, if a reward was dispensed, and if the trial resulted in the monkey advancing to a new stage of testing.

A number of dependent measures were calculated to understand how partnered and solo participation changed based on reward outcome manipulation. To determine if increases in partnered trials could be attributed to overall increases in activity at the kiosks, the average total trials completed by monkey by day were calculated and compared across conditions. Average partnered trials, solo trials, partnered trials with dual activation, and partnered trials without dual activation by monkey by day were also calculated and compared across conditions to detect any changes in the frequency of these trial types due to reward outcome manipulation.

To further assess how monkeys changed kiosk behavior based on reward outcome, proportions of partnered trials out of total trials, partnered trials with dual activation out of total partnered trials, and partnered trials without dual activation out of total partnered trials were calculated and compared across conditions. By analyzing proportions, it is possible to observe if monkeys engaged in more partnered trials than solo trials when partnered trials were incentivized and to account for any potential impact of increased total trials completed in observed increases in partnered trial frequency.

In addition to trials completed, bouts, or sessions of partnered trials were analyzed to determine if monkeys increased the frequency with which they initiated partnered trials when partnered trials resulted in more frequent rewards. "Partnered bouts" were defined as consecutive partnered trials completed by the same two individuals when partnered trials occurred after at least one monkey in a dyad had not worked at a kiosk for five minutes or more prior. Bouts would continue as long as no other individuals interacted with the kiosk and neither monkey ceased participation at the kiosks for five minutes or more. "Partnered bouts with dual activation" were defined as partnered trials that occurred after neither monkey had been working at a kiosk for five minutes and logged-in to the kiosks within 30 seconds of one another. "Partnered bouts without dual activation" were defined as partnered trials that occurred after one monkey had been completing solo trials and was joined by a partner at the adjacent kiosk. By analyzing bouts, it is possible to determine if increased partnered trial frequency was a result of an increased engagement in participating at the kiosks with a partner, or maintaining participation when rewards were distributed on FR1. If no increase in partnered bouts occurred during conditions when partnered trials were rewarded differently, it could suggest that any increase in partnered trials observed in the data could have been due to monkeys receiving frequent rewards and staying at the kiosks as long as those rewards continued to be dispensed. The average number of solo bouts that ended in partnered trails was also calculated and compared across condition to further examine if subjects were using an active, available partner as a cue to participate. Additionally, the average number of solo trials completed prior to a partnered bout without dual activation was calculated and compared to determine if monkeys were completing fewer solo trials prior to being joined by a partner when partnered trials produced cheaper rewards. The average duration, in seconds, of each bout type was also calculated and analyzed across conditions. If durations of bouts increased during conditions where partnered trials were incentivized (Condition 2, Condition 4, and Condition 5), then it would suggest that the monkeys were not increasing active engagement in partnered trials but participating in partnered trials as a result of maximizing rewards when rewards were readily available.

In order to determine if monkeys were relying on the secondary color cue, the proportion of partnered trials out of total trials for the last three days of Condition 4 (solo: no reward, partnered: FR1, secondary color cue) and the first three days of Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) were compared. If a decrease in proportion of partnered trials was detected in Condition 5, it would suggest that the monkeys' performance was impacted by the removal of the secondary color cue and that they were not relying on the log-in of a partner monkey as a cue for more frequent rewards.

Repeated measures analysis of variance (ANOVA) was calculated on all dependent measures to determine if any main effects of condition on partnered behavior were present. For all analyses of variance, if any violations of Mauchley's test for sphericity were found, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. Any significant mean differences were further examined with Bonferroni pairwise comparisons. Effect sizes for ANOVA were calculated using eta squared and Cohen's *d* was calculated to report effect sizes for pairwise comparisons. Critical values were calculated using the Bonferroni-Holm method to correct for multiple comparisons. A criterion of $p < 0.05$ was set for statistical significance for all statistical tests, and all tests were carried out using IBM SPSS 25 (IBM Corp., Armonk, NY).

The proportions of partnered trials completed by each monkey in Condition 1, which indicates the rate at which monkeys partner by chance, and the key conditions during which partnered trials were incentivized (Condition 2, Condition 4, and Condition 5) were calculated and plotted to examine if there appeared to be any differences between individuals.

Partner pairs, or dyads, were identified and the total number of partnered trials completed with a specific partner as well as the percentage of partnered trials completed with a specific partner out of total partnered trials completed by each monkey were calculated. Dyads that completed partnered trials with dual activation during Condition 5 and the percentage and total number of partnered trials completed with a specific partner for each monkey were also examined. This was done to examine if there appeared to be any unique dyads that seemed to partner more frequently with one another, and if partnered trials only occurred between individuals in the same family.

Results

Overall Descriptive Data

54,494 trials were completed by the 14 final subjects over the course of 351 days of data collection between October 1st, 2018 and October 9th, 2019. Number of trials completed by a single individual ranged from 2,926 to 4,436 trials (*M* = 3,892.43, *SD* = 505.39; *Mdn* = 3,999).

Condition Effects

Reward outcomes were manipulated over the course of seven conditions (Table 2) to determine if monkeys could learn to use a partner at the adjacent kiosk as a cue for reward. Solo and partnered participation were analyzed in a variety of contexts to elucidate how these behaviors changed by condition.

Mean trial types across conditions (Appendix)

It was predicted that more partnered trials would occur under conditions where partnered trial rewards were less expensive than solo trial rewards. However, because mean values of trial type are sensitive to how many trials a monkey performed, they do not provide the best test of this hypothesis. The mean values for trial type are presented in the appendix for completeness, but are not the primary measure for assessing the effect of conditions on partnered trials. They are briefly summarized here. Mean solo trials and mean partnered trials were compared across condition (Appendix Figures 3 and 4), and revealed that partnered trials were most frequent in conditions where partnered trial rewards were less expensive than solo rewards, and lowest when partnered trials were not rewarded differently than solo trials. However, because these measures are sensitive to how many total trials were performed these data cannot resolve whether the monkeys were cuing on a partner for reward or if the availability of rewards on an FR1 increased kiosk participation, thus incidentally increasing by chance. In order to assess if the increase in partnered trials reflected a learned contingency between partner and reward, analysis used the proportion of partnered trials completed out of total trials for subsequent comparisons which corrects for total trials.

Similarly, average partnered trials with dual activation and average partnered trials without dual activation have the same drawback as described for mean partnered trials and thus are presented in the appendix and are briefly summarized here. The findings were similar in that those conditions where better rewards were obtained with partnered trials had the highest mean of partnered trials with dual activation (Appendix Figure 5). However, no clear pattern in mean partnered trials without dual approach was observed (Appendix Figure 6). It is difficult to make conclusions about these measures as they do not account for changes in overall participation at the kiosks. Additionally, there are several factors which contribute to a more comprehensive picture of what occurs with partnered trials without dual approach that are discussed below.

Proportion of partnered trials

A key part of determining if monkeys could learn to use a partner as a discriminant cue for less expensive rewards was to determine if they increased the proportion of trials with which they worked at the kiosks with a partner when those trials were rewarded on FR1 schedules when solo trials were either still rewarded on FR10 or not at all. During Condition 1 (solo: FR10, partnered: FR10), monkeys had no prior experience with receiving a different reward outcome for participating in a partnered trial. Therefore, the proportion of partnered trials out of total trials during Condition 1 is a measure of the chance probability that two monkeys would work concurrently at the kiosks when partnered trials are not incentivized. If proportions of partnered trials out of total trials for the three conditions where partnered trials were rewarded differently

(Condition 2, Condition 4, and Condition 5) differed significantly from Condition 1, then it would indicate that the monkeys were partnering more than would be expected by chance.

Analysis of variance revealed a main effect of condition on mean proportion of partnered trials out of total trials $F(2.153, 27.99) = 19.59$, $p < 0.001$, $\eta_p = 0.60$, where the proportion of partnered trials was significantly higher in conditions where partnered behavior was rewarded more frequently (Figure 6). As predicted, the proportion of partnered trials was significantly higher in conditions when partnered trial rewards were less expensive than in Condition 1. Condition 2 (solo: FR10, partnered: FR1, secondary color cue), Condition 4 (solo: no reward, partnered: FR1, secondary color cue), and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly higher proportions of partnered trials than Condition 1 (solo: FR10, partnered: FR10): $p = 0.034$, $d = 0.11$, 95% CI [-0.51, -0.01], $p < 0.001$, $d = 1.61$, 95% CI [-0.83, -0.27], and $p < 0.001$, $d = 2.22$, 95% CI [-0.90, -0.34]), respectively. Interestingly, Condition 2 (solo: FR10, partnered FR1, secondary color cue), Condition 4 (solo: no reward, partnered: FR1, secondary color cue), and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) did not have significantly higher proportions of partnered trials than Condition 3 (solo: FR10, partnered FR10). Condition 3 immediately followed the first condition where partnered trials were incentivized. This lack of a significant difference between incentivized conditions and Condition 3 suggests that the monkeys may have not fully developed the association between a partner and a reward, such that they continued to partner even when those trials were not rewarded differently. This is supported by the finding that Condition 4 (solo: no reward, partnered: FR1, secondary color cue) and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue), the two conditions where solo trials were never rewarded, had significantly higher proportions of partnered trials than Condition 6 (solo: FR10, partnered: FR10), and Condition 7 (solo: FR1, partnered: FR1), the final two conditions during which partnered trials were not rewarded preferentially, suggesting that the monkeys were able to learn the contingency between a partner and a reward, thus altering their behavior at the kiosks (Conditions 4 vs. 6: $p = 0.002$, $d = 1.51$, 95% CI [0.11, 0.53], Conditions 4 vs. 7: $p = 0.001$, $d = 1.65$, 95% CI [0.17, 0.71]; Conditions 5 vs. 6: FR10: $p < 0.001$, $d = 1.91$, 95% CI [0.18, 0.59], Conditions 5 vs. 7: $p < 0.001$, $d = 1.93$, 95% CI [0.24, 0.77]).

It is also important to note that although rewards were less expensive for partnered trials than solo trials in Condition 2 (solo: FR10, partnered: FR1, secondary color cue), the proportion of partnered trials was not as high as in Condition 4 and Condition 5, where solo trials were no longer rewarded at all. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly lower proportions of partnered trials than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 0.08$, 95% CI [-0.41, -0.17]) and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 4.42$, 95% CI [-0.44, -0.28].

Proportion of partnered trials with dual activation

The proportion of partnered trials out of total trials allows for the examination of whether or not the rate of partnering increases during certain conditions. In order to determine if monkeys change how they engage with the kiosks when partnered trials are incentivized, it is important to assess the interval between both partners activating the kiosks after neither monkey was active. By looking at the proportion of partnered trials with dual activation out of total partnered trials, it is possible to infer if monkeys interact with the kiosks more when a partner is readily available. An increase in the proportion of partnered trials with dual activation would provide additional evidence that the monkeys are using a partner as a cue for reward. As with the proportion of partnered trials overall, the proportion of partnered trials with dual activation in

Condition 1 serves as a measure of the chance probability that two monkeys will log-in to the kiosks within close temporal proximity to each other. If the proportions of partnered trials with dual activation are higher in conditions where partnered trial rewards are less expensive than solo trial rewards, it would suggest that the monkeys are participating in this type of partnered behavior more than would be expected by chance.

The mean proportion of partnered trials with dual activation out of total partnered trials also varied significantly by condition F(1.57, 20.48) = 15.24, $p < 0.001$, $\eta_p = 0.54$ (Figure 7). Again, proportions were higher in conditions where partnered trials were incentivized than in conditions where solo and partnered trials were rewarded the same. Proportions were significantly higher in Condition 4 (solo: no reward, partnered: FR1, secondary color cue) than in conditions where solo and partnered trials were rewarded the same: Condition 1 (solo: FR10, partnered: FR10) $p = 0.014$, $d = 1.74$, 95% CI [0.04, 0.43]; Condition 3 (solo: FR10, partnered FR10) $p = 0.032$, $d = 1.46$, 95% CI [0.01, 0.39]; Condition 6 (solo: FR10, partnered: FR10) $p = 0.046$, $d = 1.15$, 95% CI [0.01, 0.33]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly higher proportions than all conditions where successful solo and partnered trials received the same rewards: Condition 1 (solo: FR10, partnered: FR10) $p = 0.009$, $d = 1.84$, 95% CI [0.05, 0.47]; Condition 3 (solo: FR10, partnered: FR10) $p = 0.017$, $d = 1.57$, 95% CI [0.03, 0.42]; Condition 6 (solo: FR10, partnered: FR10) $p = 0.014$, $d = 1.27$, 95% CI [0.03, 0.36]; Condition 7 (solo: FR1, partnered: FR1) $p = 0.026$, $d = 1.41$, 95% CI [0.02, 0.39].

Again it appears that the proportion of partnered trials with dual activation increased with experience and were more prevalent when solo trials were not rewarded at all. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly lower proportions of partnered trials with dual activation than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p = 0.026$, $d = 0.92$, 95% CI [-0.26, -0.01] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.015$, $d = 1.05$, 95% CI [-0.30, -0.02]. This increase in partnered trials with dual activation further supports the hypothesis that the monkeys were able to learn to use a partner as a cue for reward and were interacting with the kiosks more when a partner was available during conditions where partnered trials were incentivized.

Proportion of partnered trials without dual activation

Partnered trials without dual activation are partnered trials that occur after one monkey has been participating in solo trials and is joined by a partner monkey at the adjacent kiosk. The presence of a monkey at a kiosk could signal to other monkeys that better rewards are available, thus cuing the monkeys to interact with the kiosks and partner with the monkey already at the kiosk.

Repeated measures ANOVA revealed a main effect of condition on the mean proportion of partnered trials without dual activation out of total partnered trials $F(2.34, 30.41) = 15.37$, $p < 0.001$, $\eta_p = 0.54$ (Figure 8). While Condition 4 (solo: no reward, partnered: FR1, secondary color cue) and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had higher proportions of partnered trials without dual activation than Conditions 1 and 3 (both - solo: FR10, partnered: FR10), Condition 7 (solo: FR1, partnered: FR1) showed the highest proportions of partnered trials without dual approach across all conditions, including all three conditions where partnered trials were rewarded on FR1 and solo trials on FR10. Condition 2 (solo: FR10, partnered: FR1, secondary color cue), Condition 4 (solo: no reward, partnered: FR1, secondary color cue), and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly lower proportions than Condition 7 (solo: FR1, partnered: FR1): $p < 0.001$, $d =$

1.38, 95% CI [-0.44, -0.11], p = 0.008, d = 1.63, 95% CI [-0.44, -0.05], and p = 0.003, d = 1.61, 95% CI [-0.39, -0.07], respectively. Condition 7 also showed significantly higher total trials completed than Conditions 2, 3, 4, 5, and 6 (Appendix Figure 1), suggesting that these higher levels of partnered trials without dual approach during Condition 7 could be attributed to an overall increase in participation at the kiosks because of the FR1 reward schedules, which resulted in increased partnering by chance.

Partnered bouts

Thus far, the measures analyzed have dealt with the proportion of partnered trials completed. As a result, increases in the number of partnered trials completed could result from monkeys experiencing a less expensive FR schedule and maintaining kiosk participation for longer periods of time to maximize rewards. To determine if the increase in partnered trials observed in partner-incentivized or partnered-only conditions was due to a higher number of trials completed in one kiosk session, partnered bouts were analyzed. A partnered bout began when two monkeys were logged in, or two unique RfID tags were detected, within 30 seconds of one another, kick-starting a series of partnered trials as long as those two tags continued to be read. Partnered bouts include bouts that occurred after one monkey completed solo trials and when two monkeys had a break in participation for 5 minutes prior and activated the kiosks within 30 seconds of one another. By analyzing bouts, or "sessions" of kiosk participation, it is possible to observe if monkeys were increasing length of time spent at kiosks or the frequency with which they chose to work at the kiosks with a partner.

A main effect of condition on mean partnered bouts per day was observed $F(1.69, 22.01) = 19.54$, $p < 0.001$, $\eta_p = 0.60$ (Figure 9). As expected, partnered bouts were more frequent in conditions where partnered trials were better rewarded than solo trials. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly more partnered bouts per day than Condition 1 (solo: FR10, partnered: FR10) $p = 0.025$, $d = 1.10$, 95% CI [0.26, 5.76] and Condition 6 (solo: FR10, partnered: FR10) $p = 0.028$, $d = 1.09$, 95% CI [0.18, 4.55]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more bouts per day than Condition 1 (solo: FR10, partnered: FR10) $p = 0.002$, $d = 1.48$, 95% CI [1.72, 8.99], Condition 3 (solo: FR10, partnered: FR10) $p = 0.003$, $d = 1.41$, 95% CI [1.44, 8.57], Condition 6 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.54$, 95% CI [1.65, 7.78], and Condition 7 (solo: FR1, partnered: FR1) $p = 0.006$, $d = 1.32$, 95% CI [0.82, 6.04]. Similarly, Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly more partnered bouts per day than Condition 1 (solo: FR10, partnered: FR10) $p = 0.00$, $d = 1.27$, 95% CI [1.27, 10.76], Condition 3 (solo: FR10, partnered: FR10) $p = 0.01$, $d = 1.23$, 95% CI [1.05, 10.28], Condition 6 (solo: FR10, partnered: FR10) $p = 0.007$, $d = 1.30$, 95% CI [1.21, 9.52], and Condition 7 (solo: FR1, partnered: FR1) $p = 0.02$, $d = 1.14$, 95% CI [0.47, 7.69]. That there is not only an increase in trials completed but also an increase in kiosk bouts, or sessions, indicates that the partnered behavior observed was not simply a result of monkeys completing more trials during one session as a result of reward maximization.

Partnered bouts with dual activation

Partnered bouts with dual activation were defined as bouts where two monkeys logged-in to the kiosks within 30 seconds of one another after neither monkey had been working at the kiosks for 5 minutes prior. These partnered bouts can be used to assess if monkeys increased the number of times they engaged with the kiosks when a partner was readily available. If an increase in the number of partnered bouts with dual activation exists in conditions where partnered trials are better rewarded, it would support the idea that monkeys were using a partner as a cue for reward.

A main effect of condition on mean partnered bouts with dual activation per day was observed $F(1.28, 16.65) = 14.53$, $p = 0.001$, $\eta_p = 0.53$ (Figure 10). Consistent with findings thus far, there were more partnered bouts with dual activation per day during Condition 4 (solo: no reward, partnered: FR1, secondary color cue) and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) than in conditions where partnered trials were not rewarded differently than solo trials. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more partnered bouts of this type per day than Condition 1 (solo: FR10, partnered: FR10) $p = 0.028$, $d = 1.09$, 95% CI [0.12, 2.99], Condition 3 (solo: FR10, partnered: FR10) $p = 0.027$, $d = 1.09$, 95% CI [0.12, 2.91], Condition 6 (solo: FR10, partnered: FR10) $p = 0.033$, $d = 1.06$, 95% CI [0.08, 2.81], and Condition 7 (solo: FR1, partnered: FR1) $p = 0.049$, $d = 1.01$, 95% CI [0.01, 2.74]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) also had more partnered bouts with dual activation per day than Condition 1 (solo: FR10, partnered: FR10) $p = 0.039$, $d = 1.04$, 95% CI [0.05, 3.04], Condition 3 (solo: FR10, partnered FR10) $p = 0.04$, $d = 1.04$, 95% CI [0.04, 2.97], and Condition 6 (solo: FR10, partnered: FR10) $p = 0.043$, $d = 1.03$, 95% CI [0.03, 2.84]. Monkeys appeared to increase partnered bouts with dual activation more in Condition 4 and Condition 5, where no solo trials were rewarded, than in Condition 2, where solo trials were still rewarded on FR10. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly fewer partnered bouts with dual activation than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p = 0.03$, $d = 1.08$, 95% CI [-2.43, -0.08] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.046$, $d = 1.02$, 95% CI [-2.48, -0.01].

Partnered bouts without dual activation

Partnered bouts without dual activation include bouts where one monkey was already working at the kiosk and was joined by a partner who had not been working for 5 minutes prior. Similar to partnered bouts with dual activation, an increase in partnered bouts without dual activation also indicates that the monkeys were using a partner as a cue for reward: if one monkey is already participating at the kiosks, and if the monkeys learned that a partner is required for more frequent rewards, an already participating monkey would act as a cue for reward availability. An increase in partnered bouts without dual activation greater than what was observed during Condition 1 would suggest that the monkeys were engaging in this type of partnered bout more than would be observed by chance. This measure is sensitive to how frequently monkeys interact with the kiosks when the kiosks are in high demand, however. For example, in Condition 7 monkeys are exposed to FR1 schedules for both solo and partnered trials for the first time since kiosk training. These reward schedules may increase kiosk participation overall, thus increasing the likelihood that two monkeys would work at the kiosk at the same time as a result of two monkeys attempting to complete solo trials. To fully understand what partnered bouts without dual activation reveal about their learned contingency between partner and reward, several additional factors were examined and are described in detail in the next two sections.

There was a main effect of condition on mean partnered bouts without dual activation per day $F(2.29, 29.70) = 10.51$, $p < 0.001$, $\eta_p = 0.45$ (Figure 11). Similar to what was found with the proportion of partnered trials without dual activation, there are more partnered bouts without dual activation during conditions where partnered trials were incentivized (Condition 2, Condition 4, and Condition 5) than in conditions where partnered and solo trials were not rewarded differently (Condition1, Condition 3, and Condition 6). There were significantly more partnered bouts without dual activation in Condition 2 (solo: FR10, partnered: FR1, secondary color cue) than in Condition 1 (solo: FR10, partnered: FR10) $p = 0.006$, $d = 1.31$, 95% CI [0.44, 3.35], Condition 3 (solo: FR10, partnered: FR10) $p = 0.033$, $d = 1.06$, 95% CI [0.09, 3.16], and Condition 6 (solo: FR10, partnered: FR10) $p = 0.013$, $d = 1.20$, 95% CI [0.28, 3.09]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) showed significantly more partnered bouts than Condition 1 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.56$, 95% CI [0.80, 3.69], Condition 3 (solo: FR10, partnered: FR10) $p = 0.005$, $d = 1.35$, 95% CI [0.51, 3.45], and Condition 6 (solo: FR10, partnered: FR10) $p = 0.004$, $d = 1.37$, 95% CI [0.55, 3.52]. There were significantly more partnered bouts without dual activation in Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) than Condition 1 (solo: FR10, partnered: FR10) $p = 0.003$, $d = 1.40$, 95% CI [0.39, 2.97], Condition 3 (solo: FR10, partnered: FR10) $p = 0.018$, $d = 1.15$, 95% CI [0.19, 2.73], and Condition 6 (solo: FR10, partnered: FR10) $p = 0.015$, $d = 1.07$, 95% CI [0.23, 2.80]. No significant differences in partnered bouts without dual activation were detected between Condition 7 and any other condition, when the kiosks were seemingly in higher demand due to FR1 schedules for all trials.

Average solo trials completed prior to partnered bouts without dual activation

Examining the number of solo trials that one monkey completes prior to being joined by a partner for a bout without dual activation is integral to determining if monkeys are behaving in a way that indicates they are using an active monkey at the kiosks as a cue for reward. These solo trials were defined as trials completed at first log-in to a kiosk after a break in participation for 5 minutes or more that persisted until a partner monkey joined at the adjacent kiosk. This is essentially a measure of how long the cue is present before a partner joins.

The average number of solo trials that preceded a partnered bout without dual activation per monkey per day was calculated and compared across conditions. A main effect of condition on mean solo trials was observed $F(2.98, 38.69) = 101.91$, $p < 0.001$, $\eta_p = 0.89$ (Figure 12). Monkeys completed more solo trials prior to being joined by a partner for a partnered bout without dual activation during conditions where partnered trials were not incentivized than in conditions when partnered trials were incentivized. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had fewer solo trials pre-partnered bouts without dual activation than Condition 1 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 3.12$, 95% CI [-9.82, -4.75], Condition 3 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 2.57$, 95% CI [-9.16, -4.42], Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 2.26$, 95% CI [-8.03, -2.54], and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 3.70$, 95% CI [-11.37, -5.06]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly fewer solo trials pre-partnered bouts without dual activation than Condition 1 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 5.18$, 95% CI [-15.11, -8.03], Condition 3 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 4.35$, 95% CI [-15.20, -6.95], Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 4.93$, 95% CI [-11.89, -7.25], and Condition 7 (solo: FR1, partnered FR1) $p < 0.001$, $d = 5.89$, 95% CI [-15.99, -9.00]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly fewer solo trials pre-partnered bouts without dual activation than Condition 1 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 6.40$, 95% CI [-16.03, -10.54], Condition 3 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 5.31$, 95% CI [-16.20, -9.37], Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 6.42$, 95% CI [-13.79, -8.78], and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 7.26$, 95% CI [-17.01, -11.42].

The average number of solo trials that a monkey was able to complete prior to being joined by a partner for a bout of partnered trials without dual activation decreased with experience. The mean solo trials pre-partnered bout without dual activation was significantly higher in Condition 2 (solo: FR10, partnered: FR1, secondary color cue) than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 2.88$, 95% CI [2.01, 6.57] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 4.84$, 95% CI [4.24, 7.76]. Additionally, Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more solo trials pre-partnered bouts than did Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.003$, $d = 1.68$, 95% CI [0.50, 2.93].

These data do not reflect an extinction of solo trials, although a decrease in the average number of solo trials completed by monkey by day was detected in Condition 2, Condition 4, and Condition 5 (Appendix Figure 3). It is impossible to determine what motivated the monkey completing solo trials to do so when partnered trials were better rewarded or when solo trials were not rewarded at all. What these data do show, however, is that the number of trials that a solo monkey completes before being joined by a partner monkey is significantly lower in conditions where partnered trials are better rewarded than the FR10 in Condition 1, which acts as a measure of how many solo trials preceded partnered bouts as a result of monkeys working at the kiosks in a social group, and the three other conditions where solo and partnered trials were not rewarded differently. These data indicate that monkeys are joining an available partner sooner when partnering results in less expensive rewards, potentially using the monkey at a kiosk as a cue for reward availability and frequency, thus motivating them to interact with the kiosks when a partner is available and participating at a kiosk.

Proportion of solo bouts that end in partnered trials

If monkeys are using active, available partners as cues for participation, then an increase in solo bouts ending in partnered trials greater than that observed in Condition 1 would be expected in conditions where rewards are less expensive for partnered trials than solo trials.

A main effect of condition on the proportion of solo bouts that end in partnered trials was observed $F(3.39, 44.04) = 187.33$, $p < 0.001$, $\eta_p = 0.94$ (Figure 13). Proportions were highest in Condition 4 and Condition 5, where partnered trials were rewarded on FR1 and solo trials not at all, and they were significantly higher in Condition 4 and Condition 5 than in conditions where solo trials and partnered trials were not rewarded differently. Additionally, the proportions of solo bouts that end in partnered trials increased with experience; proportions were higher in Condition 5 than Condition 4, and higher in Condition 4 than in Condition 2. Conditions 2 (solo: FR10, partnered: FR1, secondary color cue), 4 (solo: no reward, partnered: FR1, secondary color cue), and 5 (solo: no reward, partnered: FR1, no secondary color cue) had higher proportions of solo bouts ending in partnered trials than Condition 1 (solo: FR10, partnered: FR10): $p = 0.006$, $d = 1.91$, 95% CI [0.05, 0.38], $p < 0.001$, $d = 7.50$, 95% CI [0.53, 0.78], and $p < 0.001$, $d = 10.95$, 95% CI [0.69, 0.91], respectively. Conditions 4 (solo: no reward, partnered: FR1, secondary color cue) and 5 (solo: no reward, partnered: FR1, no secondary color cue) proportions were significantly higher than Condition 3 (solo: FR10, partnered: FR10): $p < 0.001$, $d = 5.02$, 95% CI [0.42, 0.70], $p < 0.001$, $d = 7.03$, 95% CI [0.59, 0.82], respectively. Conditions 4 and 5 also had significantly higher proportions than Condition 6 (solo: FR10, partnered: FR10): $p < 0.001$, $d = 4.70$, 95% CI [0.40, 0.66], $p < 0.001$, $d = 6.66$, 95% CI [0.54, 0.81] and Condition 7 (solo: FR1, partnered: FR1): $p < 0.001$, $d = 6.34$, 95% CI [0.47, 0.70], $p < 0.001$, $d = 9.32$, 95% CI [0.62, 0.85]. The high proportions of solo bouts that end in partnered trials during conditions 4 and 5 suggests that monkeys were using the presence of a monkey active at a kiosk as a cue for reward, as monkeys joined a solo participant more during these conditions than in Condition 1, which acts as a measure of how frequently this would occur by chance, and the other three conditions where solo and partnered trials do not differ in reward outcome.

Condition 2 (solo: FR10, partnered: FR1, secondary color cue), the first condition during which partnered trials were incentivized, had significantly lower proportions of solo bouts ending in partnered trials than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 3.21$, 95% CI [-0.56, -0.32] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 4.59$, 95% CI [-0.69, -0.49]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly lower proportions than Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.003$, $d = 1.32$, 95% CI [-0.26, -0.04]. These data suggest that as monkeys gained experience with the different reward outcomes for partnered trials, their ability to use an already participating monkey as a cue for reward improved.

Duration of partnered bouts

To further assess if increased partnered behavior resulted from monkeys continuing to participate at the kiosks for long periods of time when rewards were distributed on FR1 rather than using a partner as a cue for reward, the durations of partnered bouts were compared across condition. There was a main effect condition on the mean duration (seconds) of partnered bouts $F(6, 78) = 4.04$, $p = 0.001$, $\eta_p = 0.24$ (Figure 14). However, pairwise comparisons revealed no significant mean differences in duration between conditions. These data suggest that the monkeys were not participating in long sessions of partnered trials to maximize rewards after realizing rewards were distributed on FR1, and that the increase in partnered trials that was observed can be attributed to an increase in partnered behavior and not an increase in the amount of time spent at the kiosks while partnering occurred.

Duration of partnered bouts with dual activation

It is important to also examine the duration of partnered bouts with dual activation to determine if an increase in partnered trials with dual activation resulted from longer periods of interacting with the kiosks as soon as cheaper rewards were available rather than an active engagement in partnered behavior.

There was a main effect of condition on duration of partnered bouts with dual activation $F(3.18, 41.34) = 4.08$, $p = 0.011$, $\eta_p = 0.24$ (Figure 15). Condition 1 (solo: FR10, partnered: FR10) had significantly shorter bouts than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p = 0.006$, $d = 1.31$, 95% CI [-111.49, -14.52] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.006$, $d = 1.30$, 95% CI [-118.45, -15.41]. However, no significant differences were detected between conditions 4 and 5 and any other condition, or between Condition 7 (solo: FR1, partnered: FR1) and other conditions. These longer durations in conditions 4 and 5 compared to Condition 1 may indicate that monkeys continue to participate once they are able to receive rewards on an FR1 schedule. It is possible that these longer durations in conditions 4 and 5 reflect an increased motivation to maximize rewards after exerting effort to participate when a partner was available. Because there is no partner requirement in Condition 7 to receive rewards on an FR1 schedule, the monkeys do not need to attend to participating when a partner is available. That partnered bout durations do not differ significantly between Condition 7 and Condition 1 suggest that reward outcome may not be the driving factor in partnered bout duration, but rather reflect an increased motivation to maximize rewards when opportunities to receive rewards are less frequent when only partnered trials are rewarded.

Duration of partnered bouts without dual activation

The duration of partnered bouts without dual activation was also compared across conditions to determine if an increase in partnered trials without dual activation resulted from longer periods of time interacting with the kiosks when rewards were more readily available rather than using a monkey as a cue for reward and actively engaging in partnered trials.

There was no main effect of condition on the duration of partnered bouts without dual activation $F(3.89, 50.62) = 1.82$, $p = 0.14$, $\eta_p = 0.12$ (Figure 16). These data further support the idea that an increase in partnered behavior was not a direct result of monkeys maintaining participation at the kiosks for long periods of time when receiving better rewards. If the monkeys were not using a partner as a cue for reward but rather maintaining kiosk participation as soon as rewards were distributed for every trial, then it would be expected that partnered bouts without dual activation would be longer during conditions when partnered trials were rewarded on FR1. These data do not support this possibility.

Removing the secondary color cue

A secondary color cue was used during reward presentation in Condition 2 and Condition 4 to increase the salience of partnered trial reward outcomes and to provide more information to the monkeys that partnered trials were different than solo trials. This secondary color cue was removed in Condition 5 to determine if monkeys were relying on the secondary color cue or using the presence of a partner monkey as a cue to obtain better rewards. In order to determine the impact of removing the secondary color cue on participation in partnered trials, the last three days of Condition 4 (solo: no reward, partnered: FR1, secondary color cue) and the first three days of Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) were compared to determine if there was any decline in partnered trials as a result of the removal of the color cue.

No main effect of day on proportion of partnered trials was found $F(5, 65) = 0.81$, $p = 0.551$, $\eta_p = 0.06$ (Figure 17). There appeared to be no significant change in the proportion of partnered trials out of total trials when the secondary color cue was removed. In fact, although not significantly different, the mean proportion of partnered trials during the first 3 days of Condition 5, after the secondary color cue was removed, was higher, though not significantly so, than during the last 3 days of Condition 4. These data indicate that not only were the monkeys not affected by the removal of the secondary color cue, but suggest that they had likely been relying on the partner as a cue for reward and not the secondary color cue. It is possible that they used both cues, but performance was unaffected by removing one of the cues.

Performance by individual

Analyses thus far have considered overall group performance. Variation in mean performance likely reflects individual differences in performance. Total trials (partnered and solo) completed by an individual ranged from 1,814 to 3,366 (M = 2,789, SD = 503.41, M_{ed} = 2,902.5). Across all conditions, partnered trials completed by an individual ranged from 306 to 1,891 (M = 1,222, SD = 657.43, M_{ed} = 1,323). Seven individuals completed more than 1,000 partnered trials over the course of the study and four individuals completed fewer than 500 partnered trials total. The proportions of partnered trials out of total trials completed for each individual during Condition 1, which acts as a measure of the chance probability that a monkey will partner when there is no incentive and no prior experience with incentives for partnered behavior, and Condition 2, Condition 4, and Condition 5, the key conditions where partnered trials were rewarded differently than solo trials, are depicted in Figure 18. Beginning in

Condition 2, individual differences in performance are evident. Two individuals did not partner at all during Condition 2, and three individuals did not demonstrate any change in proportion of partnered trials from Condition 1 to Condition 2. While these individuals showed an increase in the proportion of partnered trials during Condition 4 and Condition 5, they still only partnered at or below 50% of the time. While this increase in partnered trials is important, the data suggest that they may not have completely learned the association between a partner monkey and a reward. That approximately half of their trials completed are solo trials, even when solo trials are not rewarded (Condition 4 and Condition 5), suggests that these individuals may have either not developed a strong association between a partner monkey and reward, or that the motivation driving kiosk participation may have less to do with the ability to obtain food rewards and possibly more with reward gained from simply interacting with the kiosks. By contrast, there are seven individuals who, by Condition 5, are partnering at or above 80% of the time. These seven individuals showed the highest level of partnering the first time that partnering resulted in FR1 rewards (Condition 2). These monkeys may have developed a stronger contingency between partner and reward, or may be more motivated to obtain food reward motivated than the poorer performing subjects.

Dyads

There were a total of 48 unique monkey pairs that participated in partnered trials at least once during the study. The number of partners that one monkey had ranged from 2 to 11 (M = 6.43, M_{dn} = 7.00). Partnerships did not appear to be limited to kin, as one of the most prolific partnerships included males from two different matrilines. Figure 19 displays the dyads as well as the percentage of partnered trials completed with each partner for each individual, as well as the total partnered trials completed with each individual. Due to sample size and the composition of the group, it was not possible to analyze whether sex, age, or rank influenced success or the formation of partnerships.

To examine what dyads formed to complete partnered trials with dual activation after monkeys had received extensive experience with better reward outcomes for partnered trials, dyads that completed partnered trials with dual activation during Condition 5 were examined. A total of 16 unique monkey pairs participated in partnered trials with dual activation during Condition 5, with the number of partners a monkey had ranging from 1 to 4 (M = 2.36, M_{dn} = 2.00). Figure 20 displays the dyads as well as the percentage of partnered trials with dual activation completed with each partner for each individual, and the total partnered trials with dual activation completed with each individual during Condition 5.

Discussion

In this study, the rewards that rhesus monkeys received for computer tasks at adjacent, interconnected kiosks were manipulated such that monkeys could receive cheaper rewards (FR1) for partnered trials than for solo trials (FR10), or only receive rewards for partnered trials. These reward outcome manipulations were designed to assess if monkeys would alter their participation at the kiosks to maximize rewards by using a partner monkey as a cue that less expensive rewards were available. The results support the notion that monkeys learned that under some conditions a monkey at a kiosk was a cue that FR1 rewards were available, resulting in the monkeys coordinating their behavior with the other monkey at the kiosk. This is evidence that monkeys exhibit a fundamental mechanism necessary for cooperation, namely coordinating behavior to obtain a common goal. The case, however is not clear cut and there are other possible interpretations of the findings that may suggest that these results do not reflect aspects of cooperation. Some reflection on the study and the findings is necessary to interpret these data.

The first condition (Condition 1) rewarded monkeys on FR10 for both solo and partnered trials, and the software was configured to provide no computer cues to the monkeys that solo and partnered trials differed in rewards. Condition 1 measured the likelihood that two monkeys would partner by chance because they live in a social group and have continuous access to two kiosks. Partnered behavior in Condition 1 was compared to the other conditions where partnered and solo rewards differed, to determine if partnering observed when rewards were manipulated differed from chance. There was an increase in the average number of partnered trials completed by monkeys during conditions where partnered trials received less expensive rewards than solo trials (Conditions 2, 4, and 5) when compared to four conditions where solo and partnered trials produced the same rewards. It is difficult to determine if this increase in partnered trials should be attributed to the monkeys using a partner as a discriminant cue for availability of cheap rewards, or if the monkeys increased kiosk participation to maximize rewards (Appendix Figure 4).

Analysis of the proportion of total trials that were partnered trials revealed that the increase in partnered trials did not result from an overall increase in participation (Figure 6). If monkeys were completing more partnered trials because they were interacting with the kiosks more frequently when cheaper rewards were available, then the proportion of partnered trials completed should remain constant across conditions. As shown in Figure 6, the proportion of partnered trials was significantly higher in conditions when such trials produced inexpensive rewards (FR1); Condition 2 (solo: FR10, partnered: FR1), Condition 4 (solo: no reward, partnered: FR1, secondary color cue), and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) compared to Condition 1 (solo: FR10, partnered: FR10). Similarly, Condition 4 and Condition 5, where only partnered trials were rewarded, had significantly higher proportions of partnered trials than did Condition 6 (solo: FR10, partnered: FR10) or Condition 7 (solo: FR1, partnered: FR1). That Conditions 2, 4, and 5 did not differ significantly from Condition 3 (solo: FR10, partnered: FR10) may reflect that monkeys did not fully learn the contingency between a partner and cheaper rewards during Condition 2, as they continued to partner although partnered trials were no longer better rewarded than were solo trials. It is important to note that while the difference between Conditions 4 and 5 and Condition 3 was not significant, there was an increase in the proportion of partnered trials completed in Conditions 4 and 5 compared to Condition 3, with large effects (d = 1.05, d = 1.34, respectively). However, if the lack of a significant difference resulted from difficulty learning the contingency between partner and cheap rewards, experience with Conditions 4 and 5 appeared to solidify the relationship, as demonstrated by the significant decrease in proportion of partnered trials during Condition 6 and Condition 7, the two final conditions where solo and partnered trials were rewarded the same. It appears as if monkeys learned that rewards no longer differed for solo and partnered trials in these final two conditions, and that partnering was no longer necessary to maximize rewards. It is also possible that individual differences in performance contributed to this overall lack of a significant difference between Conditions 4 and 5 and Condition 3 (discussed below).

Proportions of partnered trials provide valuable information about how partnered behavior changed when reward outcomes were manipulated, but it is possible that the increase in partnered trials could have resulted from monkeys maximizing rewards when rewards were distributed on FR1, rather than monkeys actively changing partnering behavior. A monkey could have approached a kiosk while an adjacent monkey was working, and the change to FR1 motivated monkeys to maintain participation at the kiosks for long periods of time in order to maximize rewards. To assess if this was the case, the average number of partnered bouts, or sessions of partnered trials, was analyzed. By looking specifically at bouts, it is possible to ascertain how frequently monkeys began participating in partnered trials to better understand if an increase in partnered behavior was due to longer periods of kiosk participation or an actual increase in working at the kiosks with a partner. The monkeys in this group were never food-restricted and had continuous access to the kiosks during the day. There was also no limit to the total number of trials that one monkey could complete during a day. As a result, it is possible that the monkeys were less motivated to sit and work for multiple rewards for long periods of time, affecting the length of time spent at the kiosks during one session. Testing took place in their home environment, and the nature of that environment likely determines bout length more than the type of reward they are receiving. Analysis of the average number (Figure 9) and duration (Figure 14) of partnered bouts across conditions demonstrates that monkeys were creating partnered situations more frequently in conditions where more partnered trials were completed as opposed to increasing the length of time spent at the kiosks after initial activation. The average number of partnered bouts was significantly higher in Conditions 2 (solo: FR10, partnered: FR1, secondary color cue), 4 (solo: FR10, partnered: FR1, secondary color cue), and 5 (solo: FR10, partnered: FR1, no secondary color cue) than Condition 1 (solo: FR10, partnered: FR10), which acts as the probability of engaging in partnered bouts without incentive. Additionally, Conditions 4 (solo: no reward, partnered: FR1, secondary color cue) and 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly more partnered bouts than the three other conditions where partnered trials and solo trials produced the same rewards. The duration of partnered bouts did not differ by condition, demonstrating that monkeys were not maximizing rewards by completing longer bouts of partnered trials when cheaper rewards were available. These data demonstrate that monkeys were actively partnering more rather than passively completing partnered trials when cheaper rewards were available.

Reward outcomes significantly affected not only overall partnered behavior, but also the types of partnered behavior monkeys engaged in. Partnered trials with dual activation are important as they measure how monkeys engage in kiosk participation in close temporal proximity to a partner. This closeness in initial kiosk activation could result from monkeys choosing to interact with the kiosks when a partner is readily available thus indicating that the monkeys learned that a partner was required for better rewards. The proportion of total trials that were partnered trials with dual activation was higher in Conditions 4 and 5, the two conditions where only partnered trials were rewarded, than in Conditions 1, 3, 6, and 7, where partnered and solo trials resulted in the same reward outcome (Figure 7). The average number of partnered bouts with dual activation also changed across conditions, with more partnered bouts with dual activation in Conditions 4 and 5 (where only partnered trials were rewarded) than in Conditions 1, 3, and 6 (Figure 10). There were significantly more partnered bouts with dual activation in Condition 4 than Condition 7, with a large effect (d = 1.01), the final condition where all trials were rewarded on FR1, but no significant difference was detected between Condition 5 and Condition 7. However, although not statistically significant, the effect size for the comparison between Condition 5 and Condition 7 was also large (d = 1.31). That monkeys increased their engagement in partnered trials and bouts with dual activation when rewards were dependent upon partnering suggests that the monkeys use a partner as a cue for inexpensive rewards.

There were a number of factors of interest associated with partnered trials without dual activation. Partnered trials without dual activation could reveal whether or not a monkey can use an available partner as a cue to log-in and receive rewards, as one monkey already interacting with a kiosk provides information to the monkeys that partnering is possible. The same pattern that was observed with partnered trials and partnered trials with dual activation was not observed in partnered trials without dual activation. Condition 7, the last condition where all trials, regardless of type, were rewarded on FR1, had a significantly greater proportion of partnered trials without dual activation than any other condition (Figure 8). Condition 7 was the first time since kiosk training that the monkeys received rewards for solo trials on FR1. This availability of cheap rewards for all trials likely increased participation at the kiosks, as indicated by the increase in total trials completed in Condition 7 (Appendix). This increased participation also increases the probability of chance partnering when partnering is not necessary.

Although the proportion of partnered trials without dual approach was higher in Condition 7, there were several other aspects to these trials that demonstrate differences between what was observed in Condition 7 and conditions where partnered trials were required for cheap rewards. By examining solo behavior that immediately preceded partnered bouts without dual activation, it is possible to observe if monkeys were using a solo participant as a cue to participate. If monkeys viewed a solo worker as an available partner, and a cue to participate, in conditions where rewards were cheaper for partnered trials than solo trials, then fewer solo trials performed prior to being joined by a partner would be expected. The average number of solo trials completed by one monkey before being joined by a partner for a partnered bout without dual activation was significantly lower in Conditions 4 and 5 (solo: no reward, partnered: FR1) than all conditions where partnered and solo rewards were the same (Figure 12). Additionally, Condition 2 (solo: FR10, partnered: FR1) had significantly fewer solo trials preceding partnered bouts without dual activation than Conditions 1, 3, and 6 (solo: FR10, partnered: FR10). These data suggest that subjects in the compound were using an active monkey at the kiosks as a cue to participate. It is also interesting that experience appears to influence when monkeys joined an already active partner at the kiosks: Condition 2 had significantly more solo trials preceding partnered bouts without dual activation than Conditions 4 and 5, and Condition 4 had significantly more solo trials preceding partnered bouts without dual activation than did Condition 5, suggesting a learning curve where monkeys became better at recognizing the monkey at a kiosk as a cue that better rewards were available if they activated the open kiosk. It seems unlikely that this reflected chance partnering as the proportion of partnering was much greater than one would expect by chance.

Analysis of the proportion of solo bouts that ended with a partner joining the already active monkey at the kiosks out of total solo bouts completed revealed that monkeys significantly increased the rate at which they joined an active monkey at the kiosks in conditions where partnered trial rewards were less expensive than solo trial rewards. Conditions 4 and 5 (solo: no reward, partnered: FR1) had significantly higher proportions of solo bouts ending in partnered trials than all conditions where partnered and solo rewards were the same (Conditions 1, 3, 6, and 7). In fact, proportion of solo bouts ending in partnered trials in Condition 5, the last condition where partnered trials were rewarded and solo trials were not, was above 0.80 (Figure 13). The majority of solo bouts ended not because a monkey ceased participating in solo trials but because a partner monkey joined at the other kiosk.. While this does not demonstrate anything about the monkey initially completing the solo trials, it does suggest that the joining monkey was using the solo monkey as a cue to work at the kiosks. The proportion of solo bouts ending in partnered trials was significantly lower in Condition 7 than in Conditions 4 and 5, with fewer than 20% of solo bouts ending in partnered trials. It is not surprising that Condition 7 showed the highest levels of partnered bouts without dual approach but different patterns of solo trials preceding partnered trials. The FR1 schedules for both solo and partnered trials likely increased activity at the kiosks and motivation to complete solo trials. Partnered trials without dual approach arguably require the least amount of coordination between partners. The onus for partnering falls on the monkey who joins. It is possible that the initial, solo monkey begins to work at the kiosks as a way to encourage participation by a partner, but it is impossible to determine the monkey's motivation with these data. This is why assessing the solo trials that precede partnered trials without dual approach is important to understand what might be the motivation of the joining monkey. Fewer solo trials in Conditions 4 and 5 suggests that the joining monkey recognized the active solo monkey as a signal that the situation at the kiosks would result in obtaining rewards (Conditions 4 and 5) or cheaper rewards (Condition 2). More solo trials preceding partnered trials without dual activation in Condition 7 demonstrate that the joining monkeys are not using an active monkey as a cue to participate, or at least that cue is not as strong. Again, assessing motivation is difficult, but one could argue that it is possible the monkeys are not as eager to activate the kiosks when a partner is already working during Condition 7, because they understand that the partner's activity is, in this context, unrelated to the rewards they will be able to receive. Thus, while partnered trials without dual approach increase in Condition 7, solo bouts that do *not* end in partnered trials are more prevalent.

The increase in partnered behavior in conditions where partnered trials resulted in cheaper rewards, and the absence of an effect when the secondary color cue was removed in Condition 5 supports the idea that the monkeys were using the participation of a partner as a cue and not relying on what occurred on the computer screen. That the monkeys were using a partner as a cue for participation suggests that they were demonstrating a level of cooperation above independent cooperation. To learn this contingency and demonstrate the partnering observed, monkeys would have needed to attend to the presence and active participation of a partner monkey and adjust their participation accordingly. According to the levels of cooperation proposed by Albiach-Serrano (2015), these data seem to demonstrate that monkeys are capable of coordination, or form-dependent cooperation. The monkeys are adjusting their actions (kiosk participation) to those of others in time and space (Albiach-Serrano, 2015). In order to make any conclusions about intentional cooperation, as defined by Albiach-Serrano (2015), behavioral observations are necessary. Communication between subjects prior to dual activation, or recruitment by a monkey at the kiosks to solicit a partner may have existed, but we do not have this behavioral data, and the kiosk data cannot demonstrate such an effect.

The overall data reveals patterns of partnered behavior supporting the hypothesis that monkeys learn to use a partner as a cue to participate at the kiosks and receive rewards. It is possible that some monkeys were able to learn this contingency better than others. Figure 18 shows the individual data on the proportion of partnered trials in Condition 1, the measure of the probability that this behavior would occur without incentive, and Conditions 2, 4, and 5, where partnered trials resulted in better reward outcomes than did solo trials. While individuals showed similar patterns of partnering during Condition 1, beginning in Condition 2 there are observable differences between individuals. Two individuals did not partner at all during Condition 2, although partnered trials were rewarded on FR1 while solo trials remained on FR10. For these two individuals, the complete absence of partnering during Condition 2 may reflect the tolerance and motivation, or lack thereof, that they had to work with a partner. Seven individuals drastically increased their proportion of partnered trials during Condition 2. These seven individuals also maintained higher proportions of partnered trials during Conditions 4 and 5 than the other subjects, with proportions above 0.90 for 5 subjects. The highest proportion of partnered trials recorded in Condition 5 was 0.96. For comparison, the proportions of partnered trials completed in conditions 1, 3, 6, and 7 were 0.03, 0.14, 0.10, and 0.16, respectively. It is apparent that some individuals were able to learn a strong contingency between a partner and reward and coordinate participation to maximize rewards, resulting in such drastic differences in partnered behavior between conditions.

It could be argued that when solo trials were not rewarded monkeys would quickly cease participating at the kiosks. However, the monkeys have had extensive experience with completing trials on FR10 reward schedules, suggesting that a cessation in solo trials resulting from a lack of reward would not happen immediately and some solo trials would still occur. If they were simply making attempts at the kiosks and quitting when rewards were not dispensed, higher proportions of solo trials out of total trials completed would still be expected. That there were individuals completing, on average, more than 90% of their trials with a partner strongly suggests that these subjects were able to use a partner as a cue for reward. However, for monkeys who were continuing to participate in solo trials more than 50% of the time during Condition 5, the same conclusion cannot be drawn. There was a stark contrast between the lowest and highest proportion of partnered trials completed in Condition 5. The mean proportion of partnered trials completed by monkey Qz, the individual with the lowest mean proportion of partnered trials, was 0.27, and as mentioned previously, the highest was monkey Id at 0.96. It seems unlikely that Qz learned the same contingency, or learned it to the same extent, as did Id. The same could be concluded for all monkeys who participated less than 50% of the time during Condition 5. This means that 50% of the trials that they completed during Conditions 4 and 5 resulted in no rewards. While it is possible that they were rewarded by simply interacting with the kiosks as a form of play behavior, it is more likely that they did not learn the contingency between partner and reward. The 50% of trials that were partnered may have produced enough rewards to keep them participating, but does suggest that they did not fully learn the contingency that predicted better rewards.

While the sample size in this study did not allow for analysis of rank, age, and sex effects on partnered participation, it is interesting to note that the only two individuals from the lowest ranked group that participated in this study, Oe and Ve, had relatively low mean proportions of partnered trials in Condition 5 (0.46 and 0.54, respectively). In a large study assessing participation and performance at multiple touch-screen computer kiosks located in the home enclosure of a social group of rhesus monkeys, Gazes, Lutz, Meyer, Hassett, and Hampton (2019) found that low-ranking individuals seemed to engage in concurrent work at the kiosks less frequently than high ranking individuals. This could result from displacements by higher ranking individuals at the kiosks, as the kiosks act as a resource in the compound, or an avoidance of the kiosks when higher ranking individuals are present. Again, although the sample size is too small to determine what rank effects existed in this study, it is possible that the low proportions of partnering demonstrated by Oe and Ve could be linked to their rank in the group.

Learning history possibly explains these differences in partnered participation between individuals. Seven individuals completed more than 1,000 partnered trials over the course of the study; three of those individuals completing more than 1,800. By contrast, seven completed 945 or fewer partnered trials, with 306 as the lowest number of partnered trials completed by an individual. This smaller number of partnered trials completed over the course of 140 days may not have provided enough experience to learn the contingency between partner and reward. These monkeys also live in a complex social environment. While working at the kiosks, the monkeys are still exposed to a wide variety of distractions from other animals in the group, Yerkes personnel in the area, and anything occurring within or near the compound. Distractions could disrupt participation or prevent monkeys from attending to the context of a partnered trial enough to learn that reward outcomes are dependent on a partner whose arm is through the antenna arm hole and working at the adjacent kiosk. This may be of particular importance to low-ranking animals, who may need to be more vigilant at the kiosks, as the kiosks act as a coveted resource in the group. The two lowest-ranked monkeys worked with each other a majority of the time (Figure 19), which could be due to the level of tolerance between individuals in the same family, or because a low-ranked individual is more likely to work if the adjacent kiosk is not occupied by a higher-ranked monkey. These two individuals completed 881 and 908 partnered trials over the course of the study, with both completing over 80% of their partnered trials with the other. Drea (1999) assessed monkeys' performance on color discrimination tasks and found that when low-ranked animals were tested in a mixed-rank group, they "played dumb" and were not successful at a task that they could perform when not in the presence of higher-ranked individuals. It is possible that the two lowest-ranked individuals in this study could demonstrate more partnering in a context where higher-ranked individuals are removed, or when more low-ranked individuals are available for partnerships. A larger sample size with more representation from different matrilines would help answer this question.

Overall, a large number of dyads were observed over the course of the study, and the number of total partners that one monkey worked with across conditions varied widely. Five dyads completed over 1,000 partnered trials across the 7 conditions. These high frequencies of partnering between two individuals suggests that monkeys may have developed a preference for specific partners. Interestingly, one of these high partnering dyads consisted of two males from different matrilines, suggesting that partnerships, or the tolerance to partner with another individual, was not limited to kin.

Dyads that completed partnered trials with dual activation in Condition 5, after monkeys had extensive experience with varied reward outcomes based on partner participation, were examined. There were fewer dyads and numbers of partners that individual monkeys had during Condition 5 on partnered trials with dual activation, suggesting that monkeys engaged in this type of partnered behavior with a smaller pool of partners. That there are fewer dyads that participated in partnered trials with dual activation during Condition 5, after extensive experience with different reward outcomes for partnered trials, may indicate that monkeys chose partners to work with. Monkeys may have been coordinating with specific partners for partnered trials with dual activation during Condition 5 as opposed to simply using a monkey who appears available to work at the kiosk as a cue to participate. If monkeys were using any available monkey as a cue to interact with the kiosks, then more dyad combinations and more partners per individual would be expected. However, these data suggest that it is possible that monkeys only engaged in partnered trials with dual activation with partners they knew were reliable and would perform. They may also have selected individuals with whom they had a strong relationship. Unfortunately, we do not have any data on social interactions of these monkeys away from the kiosks. These data might provide evidence that monkeys were actually selecting social partners to participate in the kiosk tasks.

In summary, these data support the hypothesis that rhesus macaques living in a socially naturalistic group learn to use a partner monkey as a cue to participate at the kiosks to receive rewards when given the freedom to choose when and with whom to partner. The differences in the types of partnered behavior exhibited in this study based on reward condition indicate that the monkeys could successfully alter how they partnered in order to receive rewards by using the availability of a partner as a discriminant cue. To understand if monkeys are capable of more complex levels of coordination, or even intentional cooperation, further experimental manipulations and observational data are required.

As mentioned previously, an individual “waiting” to participate until a partner is available in coordinated rope-pulling tasks has been cited as evidence that the subjects understood that a partner was required to complete the task, and thus demonstrated a form of intentional cooperation (Albiach-Serrano, 2015; Plotnik, Suphachoksahakun, & de Waal, 2011). However, it is quite possible that this “waiting” behavior described in coordinated rope-pulling experiments more aptly demonstrates that the individuals learned the contingency between partner and reward, and when a partner was not available, the individuals were not cued to engage with the apparatus. While this study cannot conclude that the rhesus monkeys “waited” to participate until a partner was available, there was a significant increase in participation at the kiosks by two monkeys in close temporal proximity of one another during conditions when a partner was required to receive a reward. Observational data is required to determine what, if any, communication happened prior to partnered trials, as well as if any recruitment behavior occurred. Examining recruitment behavior and communication between partners could help elucidate what the monkeys understand about the context of the coordination task. Additionally, the number of solo trials completed by one monkey prior to being joined by a partner decreased significantly during conditions where a partner was required for reward, suggesting that the monkeys were able to use an active, available partner as a cue to interact with the kiosks. This learned contingency and the adjustment of participation based on that of a partner monkey demonstrates that the monkeys are capable of coordination, or form-dependent cooperation, by adjusting their participation based on the participation of a partner within time and space. These results could therefore be used as a basis for developing future cooperative tasks through which more complex levels of coordination, and perhaps "intentional" cooperation, can be tested.

It seems as if rhesus monkeys' failures to coordinate with a partner in other partner coordination experiments are not indicative of an inability to coordinate but rather an artifact of the experimental design, social context, and the age of the subjects. In this study, monkeys were able to volunteer to participate in these touch-screen computer tasks. As training progressed, fewer older individuals participated and eventually the sample consisted of monkeys aged 4 and younger. As mentioned previously, younger individuals have more diversified social networks and demonstrate higher levels of tolerance with individuals outside of their matriline (Liao, Sosa, Wu, & Zhang, 2017). It was not surprising that these young subjects in this study were able to tolerate working at the kiosks next to a partner and then develop the association between partner and reward. This is not to say that older individuals are incapable of learning such a contingency, but that testing needs to incorporate a social context that would allow older monkeys to partner frequently enough to learn the contingency. That monkeys paired with certain partners more often than others suggests that freedom of partner choice is important; the patterns of partnered behavior in this study might not have been observed if two monkeys were artificially paired together in a laboratory setting. Failure to coordinate in previous experiments may have been more indicative of a failure to choose to coordinate with certain animals rather than an incapacity to do so. Future investigations of coordination in rhesus macaques need to incorporate freedom of partner choice.

The square-touch tasks used in all conditions is a simple task and one that monkeys readily learn. Introducing more difficult tasks, where monkeys have to coordinate what stimuli they select in order to receive maximum rewards, could provide more insight into the circumstances during which monkeys are capable of coordinating with a partner as well as how complex this coordination can be (Brosnan, Wilson, & Beran, 2012). Additionally, adding complexity to the task would provide an opportunity to assess complementary behavior, a level of coordination higher than what could be assessed in this study. Because the square-touch task is easily completed by monkeys, it is difficult to assess exactly whether some dyads of monkeys are more successful than others, or if monkeys make judgments about the "quality" of the partner before engaging in coordination. The monkeys had extensive training and experience with square-touch tasks and were rarely unsuccessful at completing the task. Utilizing more difficult tasks could result in monkeys having more success at the kiosks with some partners than others, based on the partner's performance, and therefore change how and with whom monkeys approach to work at the kiosks.

Although there were observable changes in solo participation at the kiosks based on reward outcome, solo trials never fully extinguished. It is difficult to determine if this continued participation in solo trials is indicative of a failure to fully learn the contingency between a partner and reward, because interacting with the kiosks could act as a form of enrichment on its own. It is possible that some of the monkeys learned a contingency that was not fully accurate; the actual mechanism behind monkeys receiving better rewards during partnered trials involves not only the presence of an adjacent monkey at the kiosk, but also their arm through the antenna arm hole so that the RfID tag can be read while they complete trials on the touch-screen computer. If that RfID tag is not detected, then trials are not treated as partnered, and rewards are dispensed as if solo participation were occurring. The kiosks are within close visual and auditory range of one another, but it is possible that monkeys were not attending to the action of the partner monkey but rather their presence. As a monkey needs to be present to have an arm through the antenna, presence may have been more salient than what the partner monkey was doing. Observational data could provide important details about what activity at the kiosks looks like when trials are not being completed to determine if monkeys were completing solo trials when a monkey was sitting on the perch at the adjacent kiosk, perhaps mistaking it as a context for partner coordination. However, the data for partnered trials with dual activation and how solo trials change prior to partnered trials without dual activation indicate that it is not the presence of a monkey that is the most salient cue, but rather the availability of a partner and their active participation that seems to be influencing partnered behavior.

As mentioned previously, these monkeys were never food restricted and had continuous access to food pellets through automated feeders in their home enclosure. The automated feeders use the same RfID technology as the kiosks to identify individuals and distribute rewards. It is possible that these monkeys are not significantly motivated by small food rewards, but are motivated to "play" at the kiosks. Manipulating the kiosks during solo trials still results in colorful flashes on the screen and auditory cues, which can be engaging for the monkeys. Future manipulations could be added which prevent the monkeys from interacting with the kiosks at all if a partner is not present, thus taking away the opportunity to "play" at the kiosks without a partner. This, combined with observational data to determine if monkeys attempt to interact with the kiosks or sit at the apparatus until joined by a partner, will allow more conclusions to be drawn about the strength of the learned contingency between partner and the ability to operate the apparatus.

It is not surprising that rhesus monkeys are capable of learning to use a partner as a cue to participate and receive rewards; rhesus monkeys have been successful in a wide variety of complex cognitive tasks which require them to learn different reward contingencies. Rhesus monkeys also live in complex social groups; that they are capable of using a social cue to alter behavior is expected. However, their failures to coordinate in experiments designed to assess cooperation and their despotic nature have resulted in a lack of an understanding of what levels of partner coordination they can achieve, producing a gap in the literature of where rhesus monkeys fall with other species with regards to their capacities to cooperate. The evidence provided here that rhesus monkeys are capable of using a partner monkey as a discriminant cue can act as a basis upon which other coordination experiments can be built to better understand if, and how, rhesus monkeys cooperate.

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Table 1

Demographics: sex, age and social rank of the study's subjects

Monkey	**Sex**	**Age**	**Rank**
Kw	M	1	1
Mn	F	1	1
Dl	F	1	1
Qf	F	1	1
Id	F	3	1
Zc	F	3	1
Ry	F	2	1
Qz	F	2	1
Ar	M	1	2
Zd	F	4	2
Pl	M	1	2
Ki	M	2	2
Oe	F	1	4
Ve	M	1	4

Table 2

Experimental conditions with reward schedule.

Condition	Solo Reward	Partnered Reward	Secondary Color Cue?	Duration (Days)
1	FR10	FR10	No	14
2	FR10	FR1	Yes	28
3	FR10	FR10	No	14
4	None	FR1	Yes	35
5	None	FR1	No	35
6	FR10	FR10	No	7
7	FR1	FR1	No	7

Note [This table lists the seven conditions that monkeys experienced, the reward schedule for solo and partnered trials, whether a secondary color cue was presented during partnered trials, and the number of trials each condition lasted.]

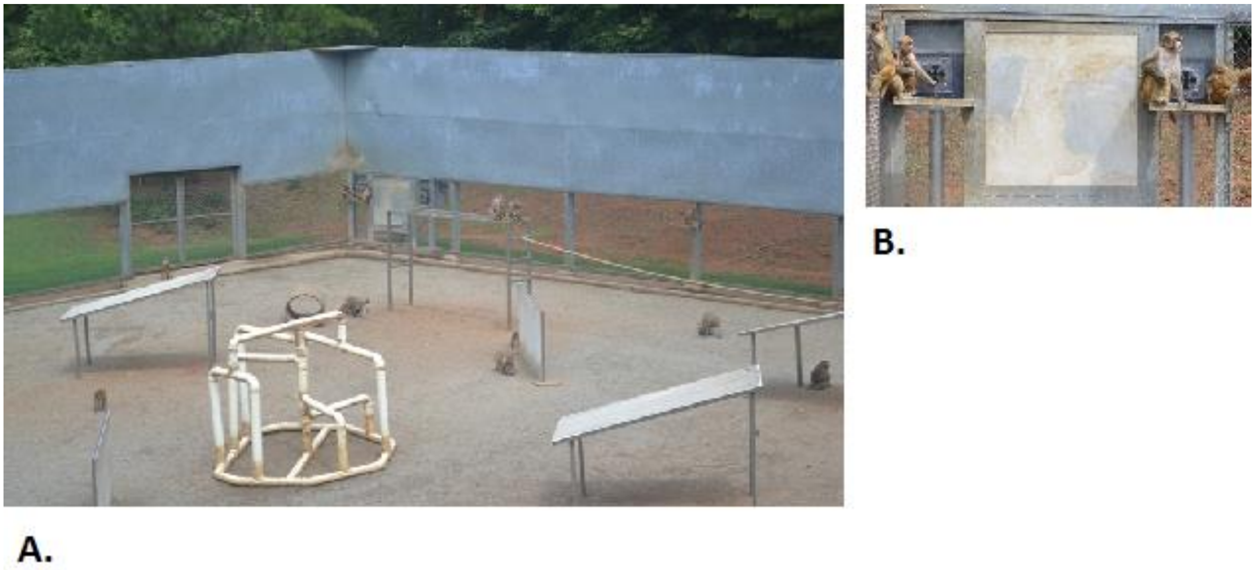


Figure 1. A) An overhead view of the enclosure. The kiosk system is located in the back left corner. B) The two kiosk system from a monkey's viewpoint within the enclosure

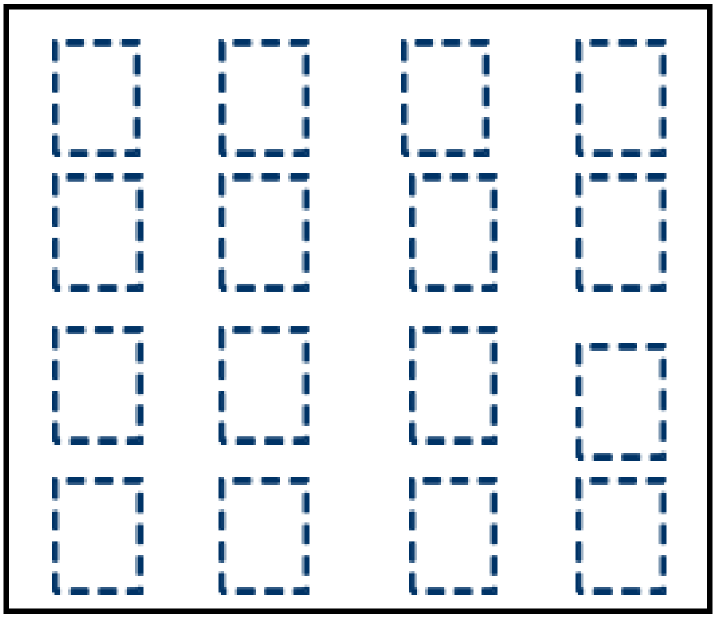


Figure 2. The dotted-lined squares represent the 16 possible locations that the square could be presented during all square-touch trials.

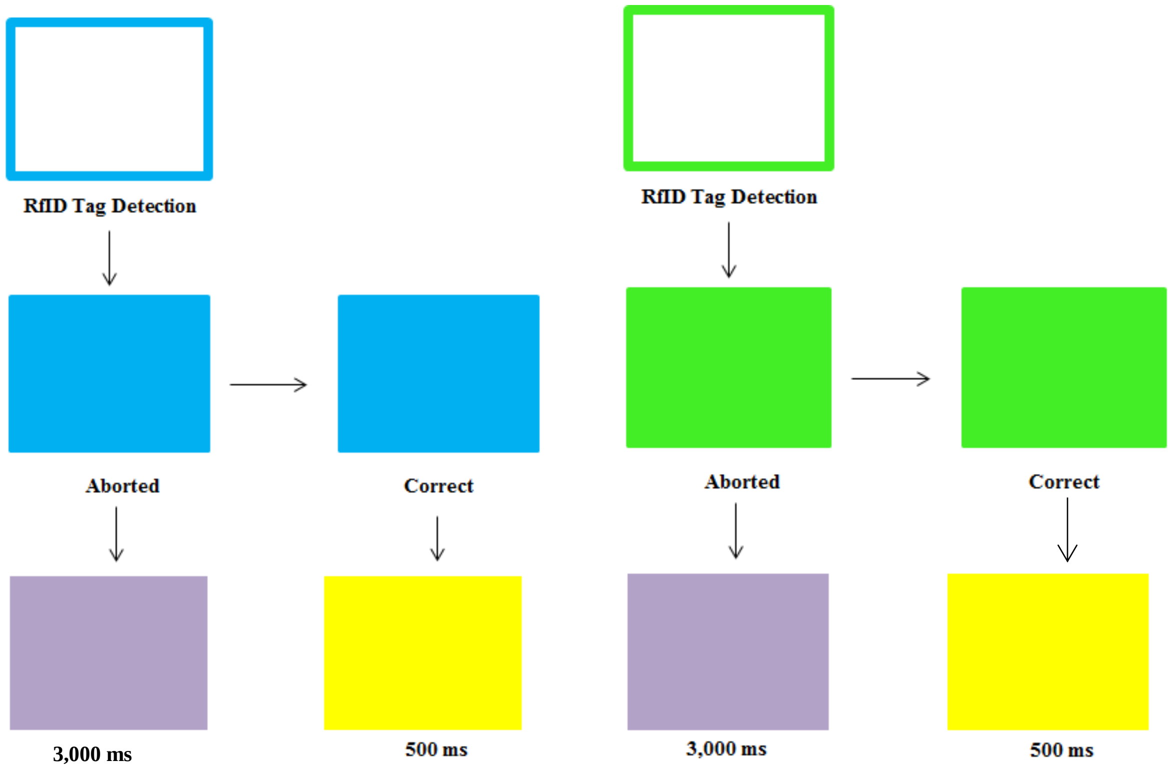


Figure 3. Presentation of screen-touch trials during the kiosk training phase at the "blue" (left) and "green" (right) kiosks. After RfID tag detection, the colored screen was presented. During the first screen touch trials, any touch to the screen within 10,000ms resulted in a correct outcome and the screen flashed yellow for 500ms as a pellet was dispensed. If no touch was detected, the trial was aborted and a purple screen was presented for 3,000ms. During long screen touch trials, a touch needed to be registered for 100ms and 200ms.

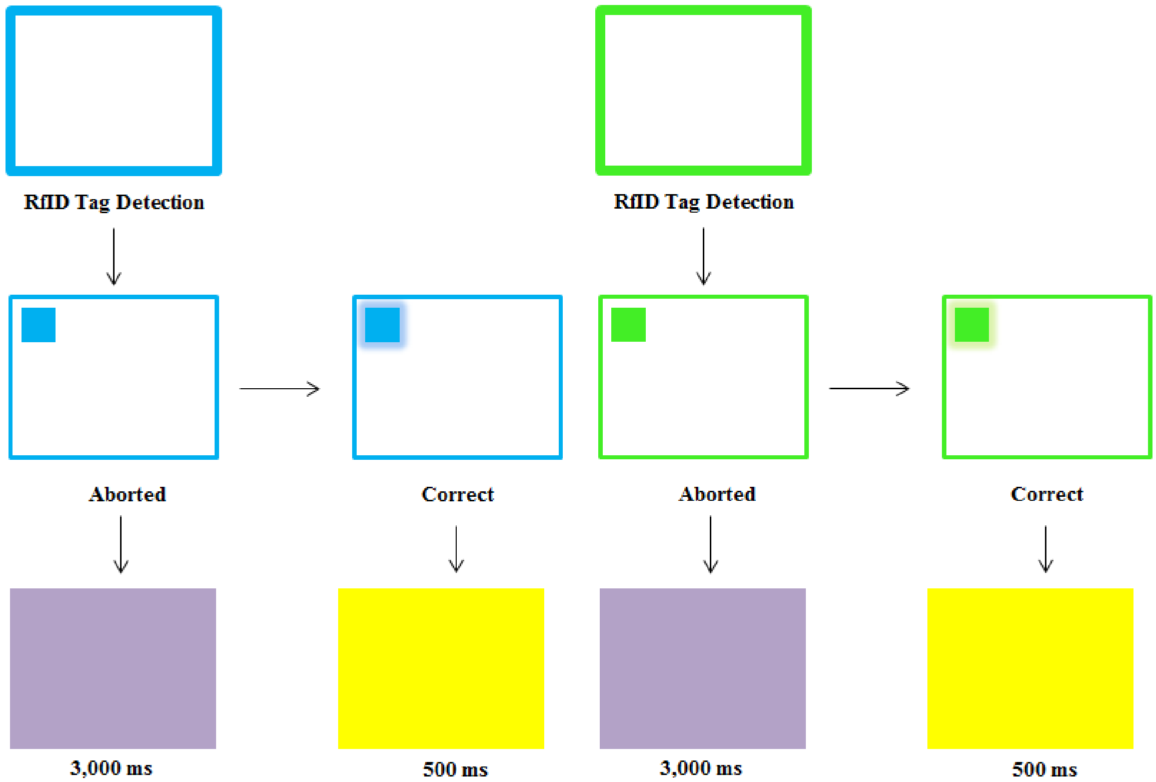


Figure 4. Presentation of square-touch trials at the "blue" (left) and "green" (right) kiosks. If a 200ms touch was registered within 10,000ms of RfID tag detection, the screen would flash yellow as a pellet was dispensed. If no touch was registered or if a touch anywhere on the screen other than the square was detected, the trial was aborted and the screen flashed purple for 3,000ms.

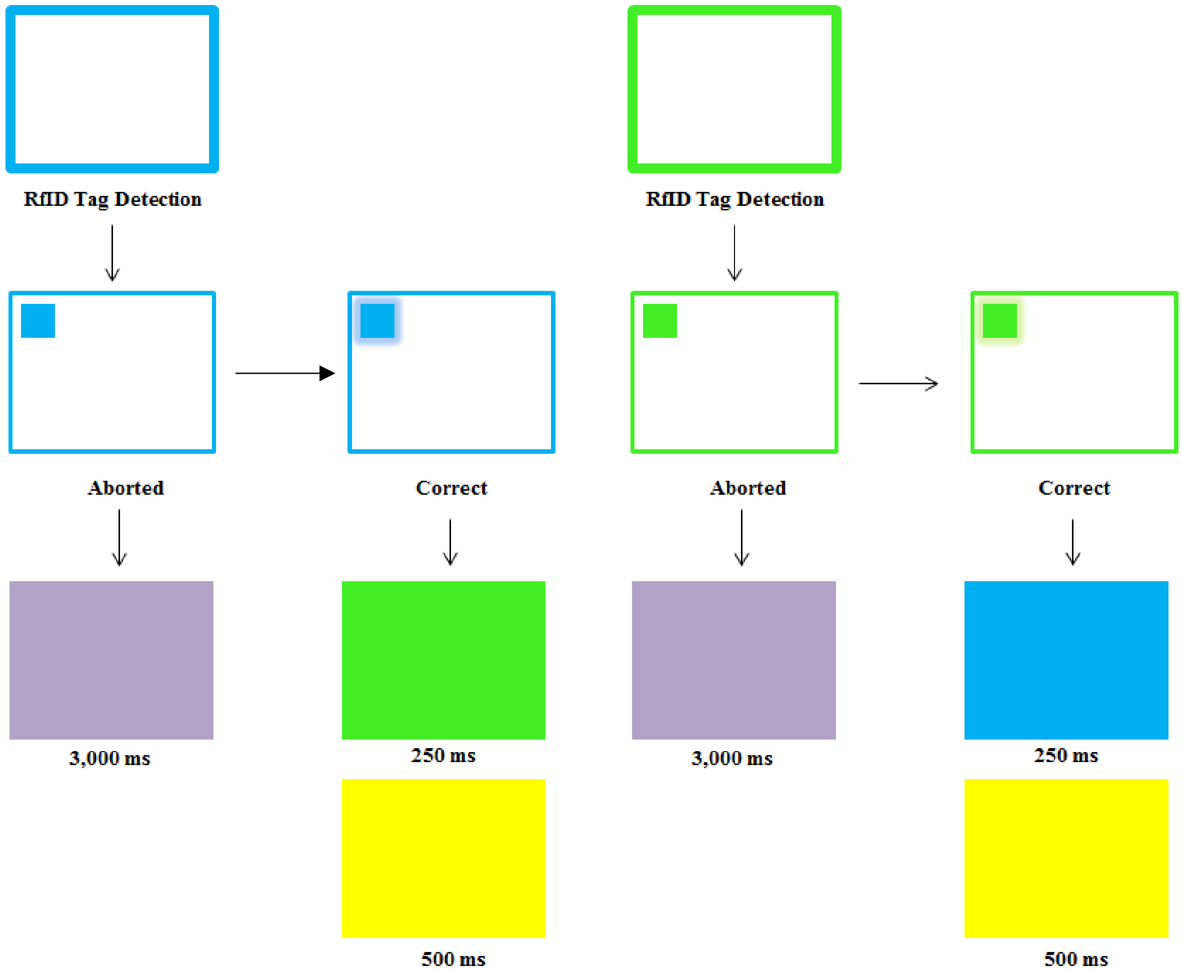


Figure 5. Presentation of the secondary reward cue at the "blue" kiosk (left) and the "green" kiosk (right). If a synced trial was detected, the screen would flash the color of the adjacent kiosk for 250ms immediately before the presentation of the standard yellow reward screen.

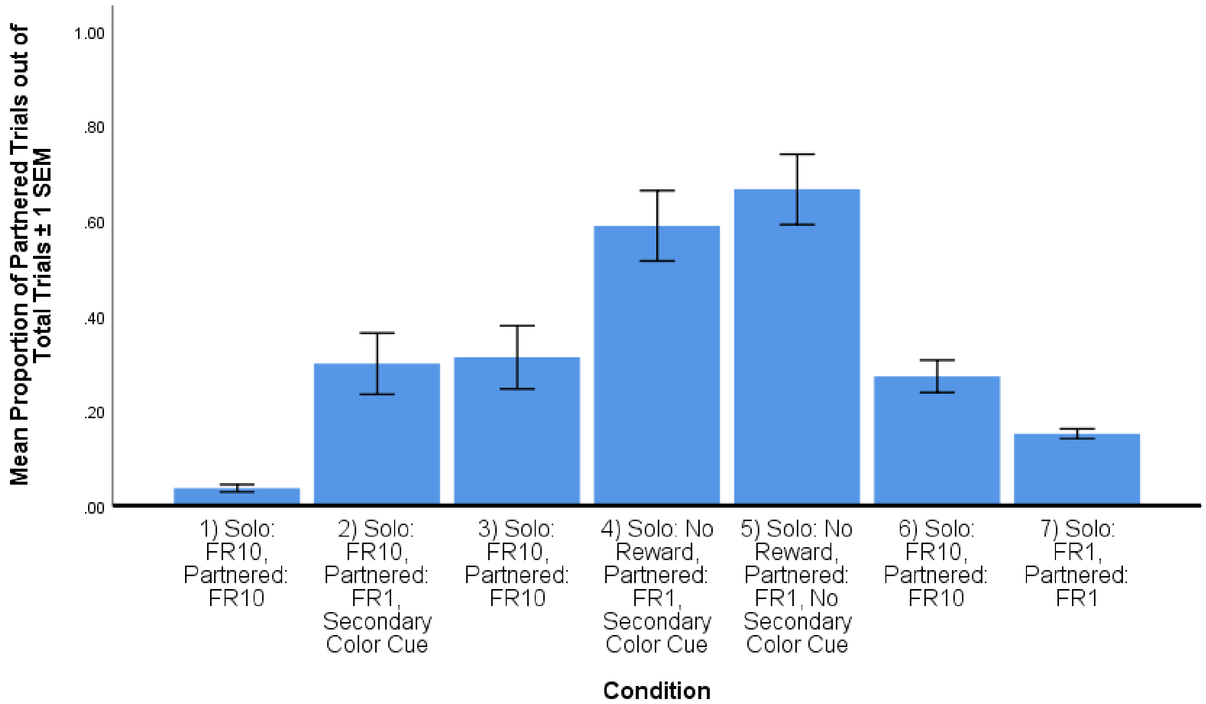


Figure 6. Mean proportion of partnered trials out of total trials completed ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***p***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 2	0.034	0.11	-0.51	-0.01
1 vs. 4	< 0.001	1.61	-0.83	-0.27
1 vs. 5	< 0.001	3.33	-0.90	-0.34
1 vs. 6	< 0.001	2.56	-0.37	-0.10
1 vs. 7	< 0.001	3.41	-0.17	-0.06
2 vs. 4	< 0.001	0.08	-0.41	-0.17
2 vs. 5	< 0.001	4.42	-0.44	-0.28
4 vs. 6	0.002	1.51	0.11	0.53
4 vs. 7	0.001	1.65	0.17	0.71
5 vs. 6	< 0.001	1.91	0.18	0.59
5 vs. 7	< 0.001	1.93	0.24	0.77

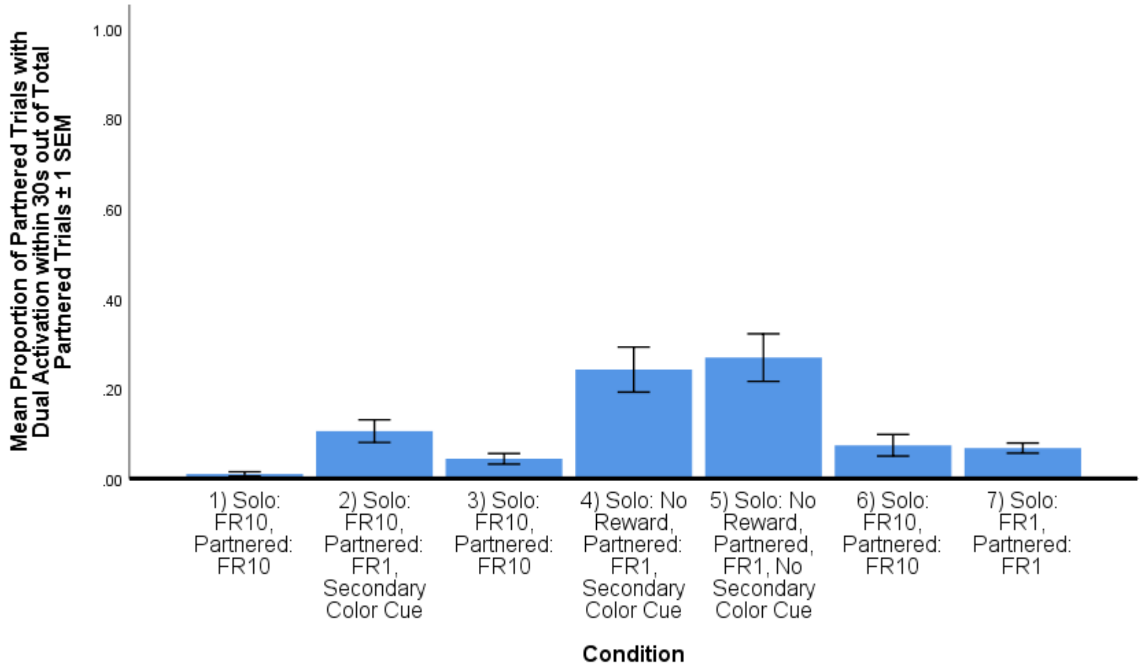


Figure 7. Mean proportion of partnered trials with dual activation within 30 seconds out of total partnered trials ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***p***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 4	0.014	1.74	-0.43	-0.04
1 vs. 5	0.009	1.84	-0.47	-0.05
1 vs. 7	0.015	1.77	-0.11	-0.01
2 vs. 4	0.026	0.92	-0.26	-0.01
2 vs. 5	0.015	1.05	-0.30	-0.02
3 vs. 4	0.032	1.46	-0.39	-0.01
3 vs. 5	0.017	1.57	-0.42	-0.03
4 vs. 6	0.046	1.15	0.01	0.33
5 vs. 6	0.014	1.27	0.03	0.36
5 vs. 7	0.026	1.41	0.02	0.39

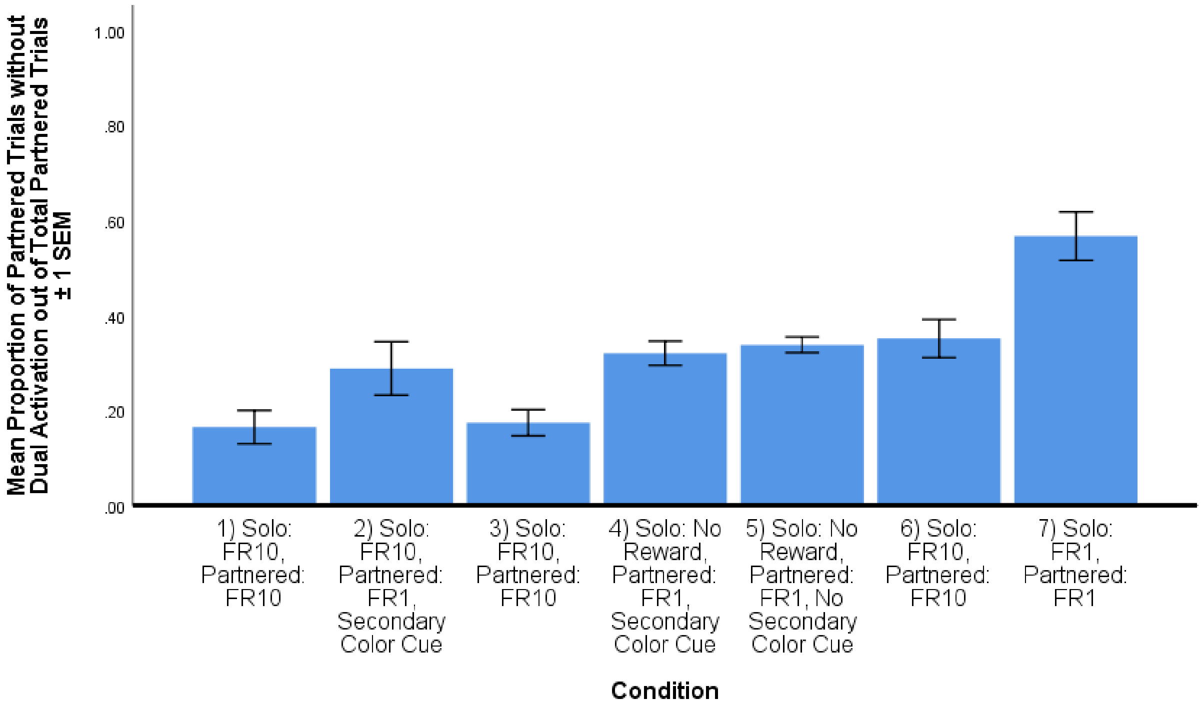


Figure 8. Mean proportion of partnered trials without dual activation out of total partnered trials ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***p***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 4	0.036	1.36	-0.30	-0.01
1 vs. 5	0.01	1.70	-0.31	-0.03
1 vs. 7	0.002	2.45	-0.68	-0.12
2 vs. 7	< 0.001	1.38	-0.44	-0.11
3 vs. 4	0.003	1.47	-0.25	-0.04
3 vs. 5	0.007	1.93	-0.29	-0.04
3 vs. 6	0.018	1.38	-0.44	-0.02
3 vs. 7	< 0.001	2.55	-0.60	-0.19
4 vs. 7	0.008	1.63	-0.44	-0.02
5 vs. 7	0.003	1.61	-0.39	-0.07
6 vs. 7	0.001	1.25	-0.36	-0.08

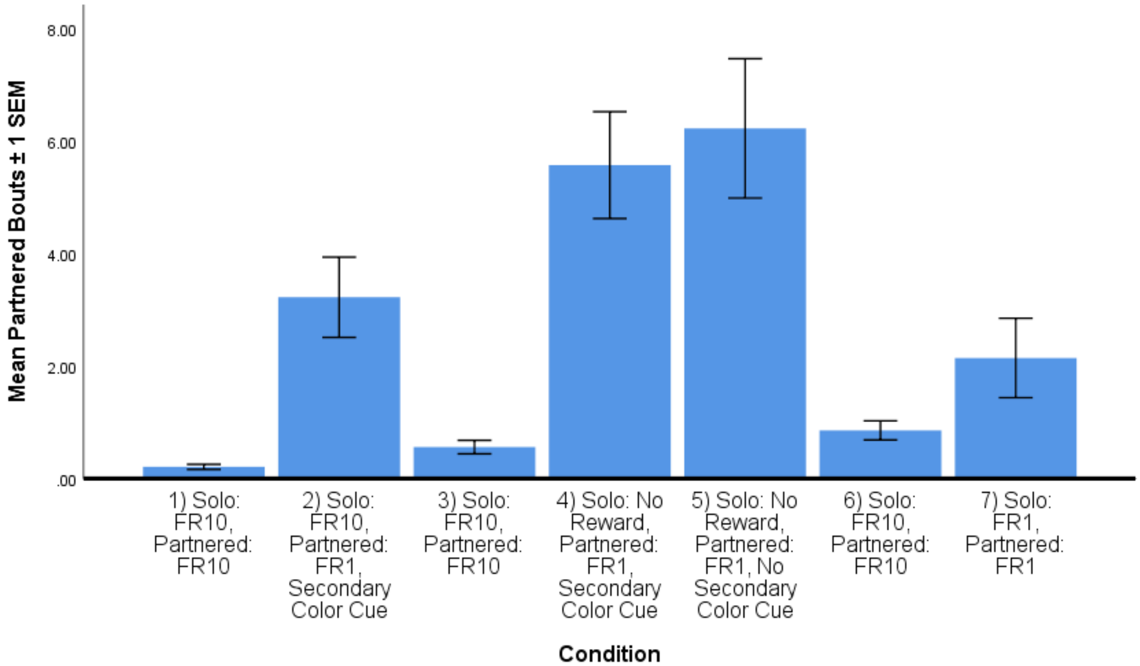


Figure 9. Mean partnered bouts per day ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***p***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 2	0.025	1.10	-5.76	-0.26
1 vs. 4	0.002	1.48	-8.99	-1.72
1 vs. 5	0.008	1.27	-10.76	-1.27
2 vs. 6	0.028	1.09	0.18	4.55
3 vs. 4	0.003	1.41	-8.57	-1.44
3 vs. 5	0.010	1.23	-10.28	-1.05
4 vs. 6	0.001	1.54	1.65	7.78
4 vs. 7	0.006	1.32	0.82	6.04
5 vs. 6	0.007	1.30	1.21	9.52
5 vs. 7	0.020	1.14	0.47	7.69

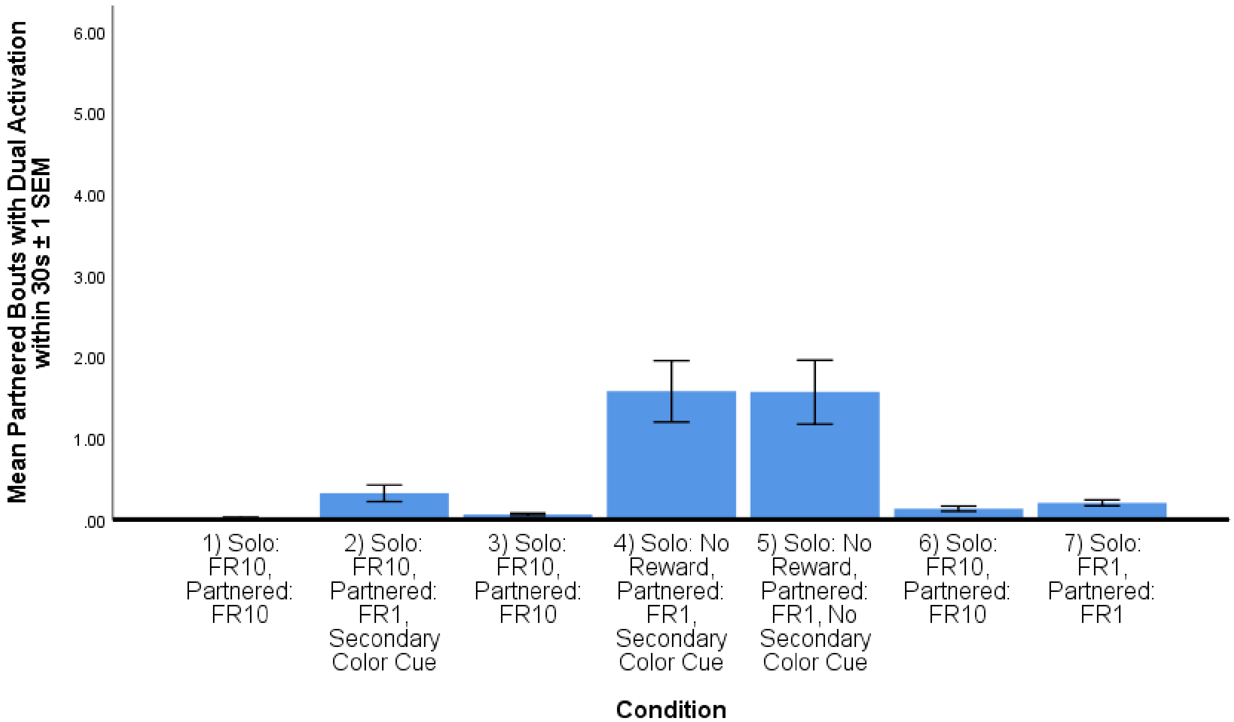


Figure 10. Mean partnered bouts with dual activation within 30 seconds per day ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***p***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 4	0.028	1.09	-2.99	-0.12
1 vs. 5	0.039	1.04	-3.04	-0.05
1 vs. 7	0.005	1.35	-0.32	-0.05
2 vs. 4	0.030	1.08	-2.43	-0.08
2 vs. 5	0.046	1.02	-2.48	-0.01
3 vs. 4	0.027	1.09	-2.91	-0.12
3 vs. 5	0.040	1.04	-2.97	-0.04
4 vs. 6	0.033	1.06	0.08	2.81
4 vs. 7	0.049	1.01	0.01	2.74
5 vs. 6	0.043	1.03	0.03	2.84

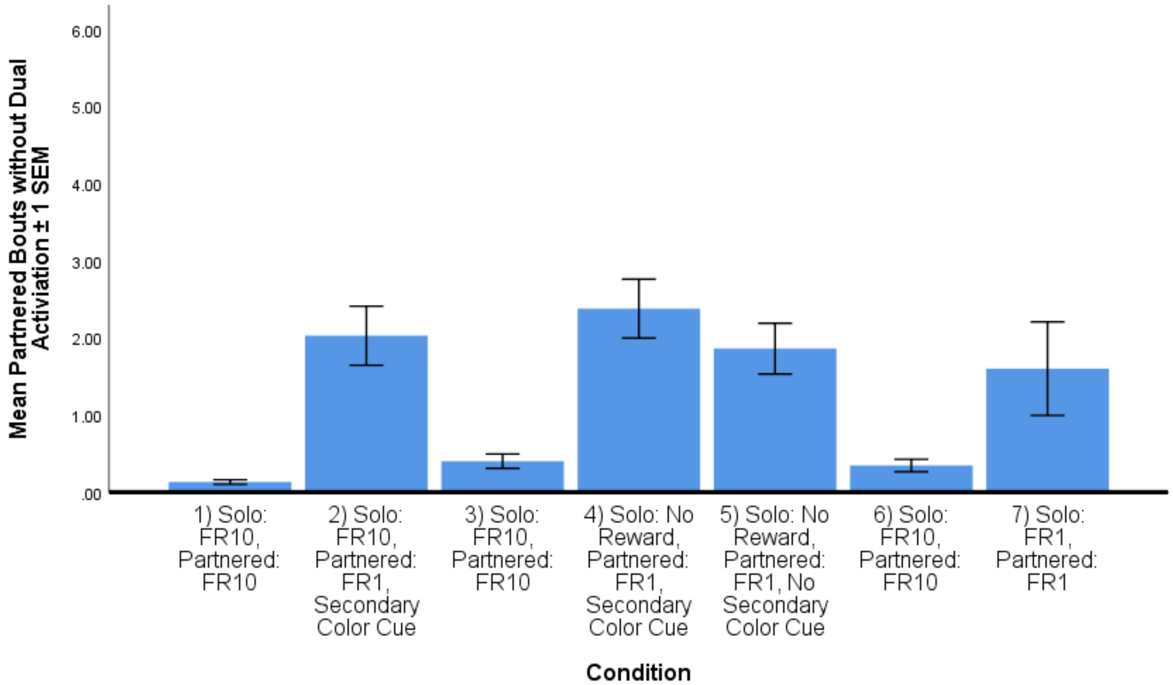


Figure 11. Mean partnered bouts without dual activation per day ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***p***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 2	0.006	1.31	-3.35	-0.44
1 vs. 4	0.001	1.56	-3.69	-0.80
1 vs. 5	0.003	1.40	-2.97	-0.49
2 vs. 3	0.033	1.06	0.09	3.16
2 vs. 6	0.013	1.20	0.28	3.09
3 vs. 4	0.005	1.35	-3.45	-0.51
3 vs. 5	0.018	1.15	-2.73	-0.19
4 vs. 6	0.004	1.37	0.55	3.52
5 vs. 6	0.015	1.07	0.23	2.80

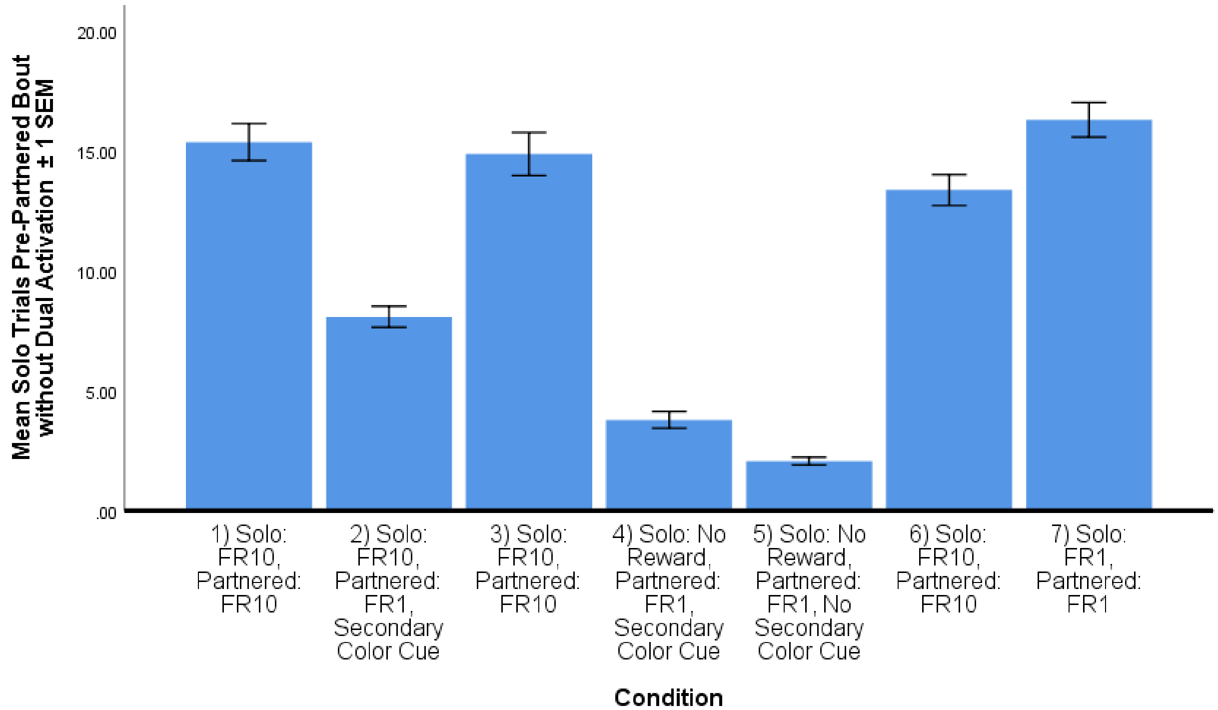


Figure 12. Mean solo trials completed by one monkey before being joined by a partner ± 1 SEM. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***P***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 2	< 0.001	3.12	4.74	9.82
1 vs. 4	< 0.001	5.18	8.03	15.11
1 vs. 5	< 0.001	6.40	10.54	16.03
2 vs. 3	< 0.001	2.57	-9.16	-4.42
2 vs. 4	< 0.001	2.88	2.01	6.57
2 vs. 5	< 0.001	4.84	4.24	7.76
2 vs. 6	< 0.001	2.26	-8.03	-2.54
2 vs. 7	< 0.001	3.70	-11.37	-5.06
3 vs. 4	< 0.001	4.35	6.95	15.20
3 vs. 5	< 0.001	5.31	9.34	16.20
4 vs. 5	0.003	1.68	0.50	2.93
4 vs. 6	< 0.001	4.93	-11.89	-7.25
5 vs. 6	< 0.001	6.42	-13.79	-8.78
5 vs. 7	< 0.001	7.26	-17.91	-11.42

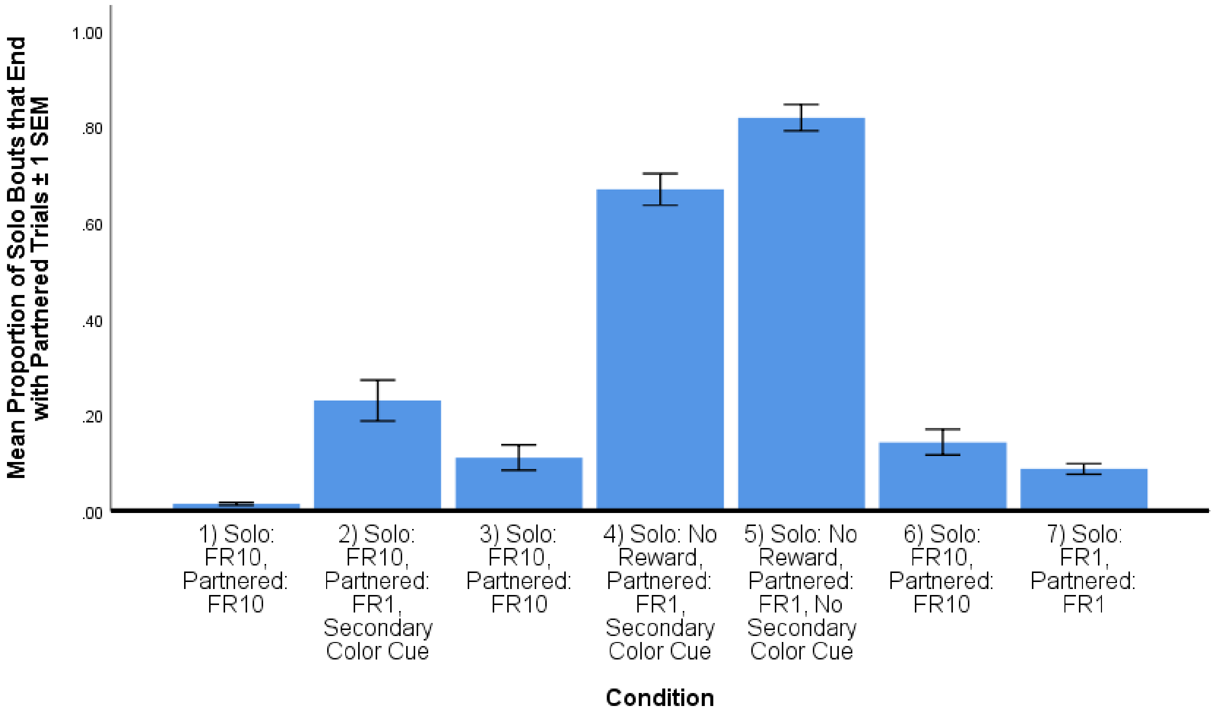


Figure 13. Mean proportion of solo bouts that end with a partner monkey joining the solo participant to complete partnered trials ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	*P*	*d*	95% CI Lower Limit	95% CI Upper Limit
1 vs. 2	0.006	1.91	-0.38	-0.05
1 vs. 4	< 0.001	7.50	-0.78	-0.53
1 vs. 5	< 0.001	10.95	-0.91	-0.69
1 vs. 6	0.008	1.81	-0.23	-0.03
1 vs. 7	< 0.001	2.38	-0.11	-0.04
2 vs. 4	< 0.001	3.21	-0.56	-0.32
2 vs. 5	< 0.001	4.59	-0.69	-0.49
3 vs. 4	< 0.001	5.02	-0.70	-0.42
3 vs. 5	< 0.001	7.03	-0.82	-0.59
4 vs. 5	0.003	1.32	-0.26	-0.04
4 vs. 6	< 0.001	4.70	0.40	0.66
4 vs. 7	< 0.001	6.34	0.47	0.70
5 vs. 6	< 0.001	6.66	0.54	0.81
5 vs. 7	< 0.001	9.32	0.62	0.85

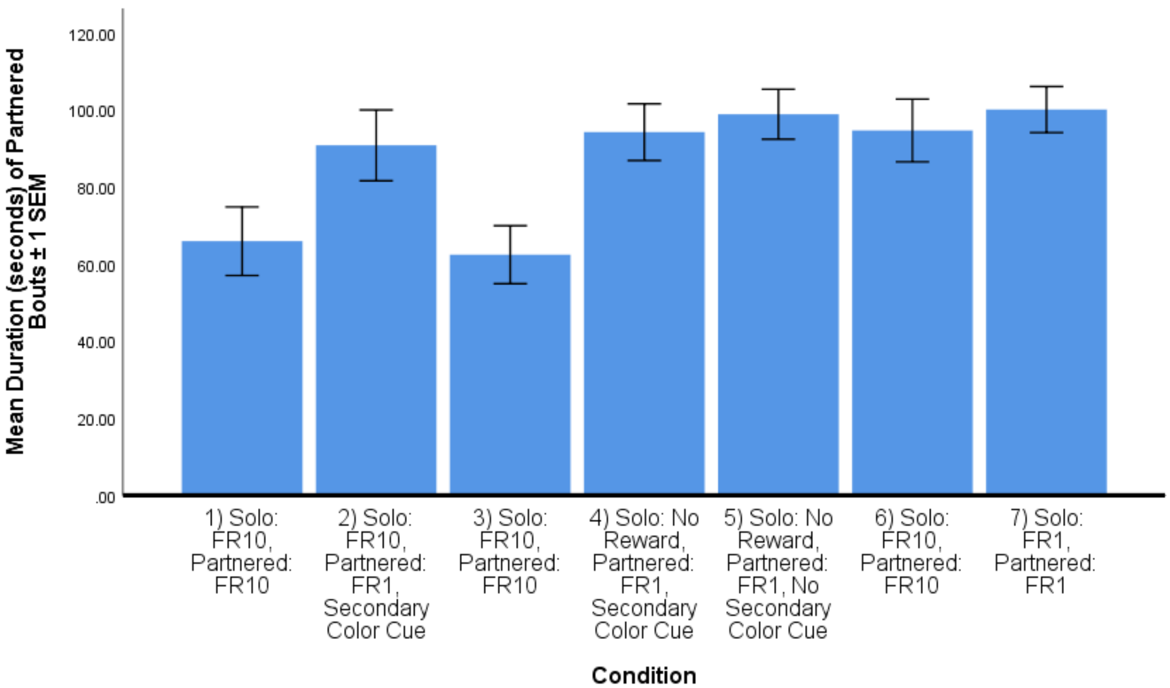


Figure 14. Mean duration (seconds) of partnered bouts ±1 SEM by condition. No significant mean differences were detected.

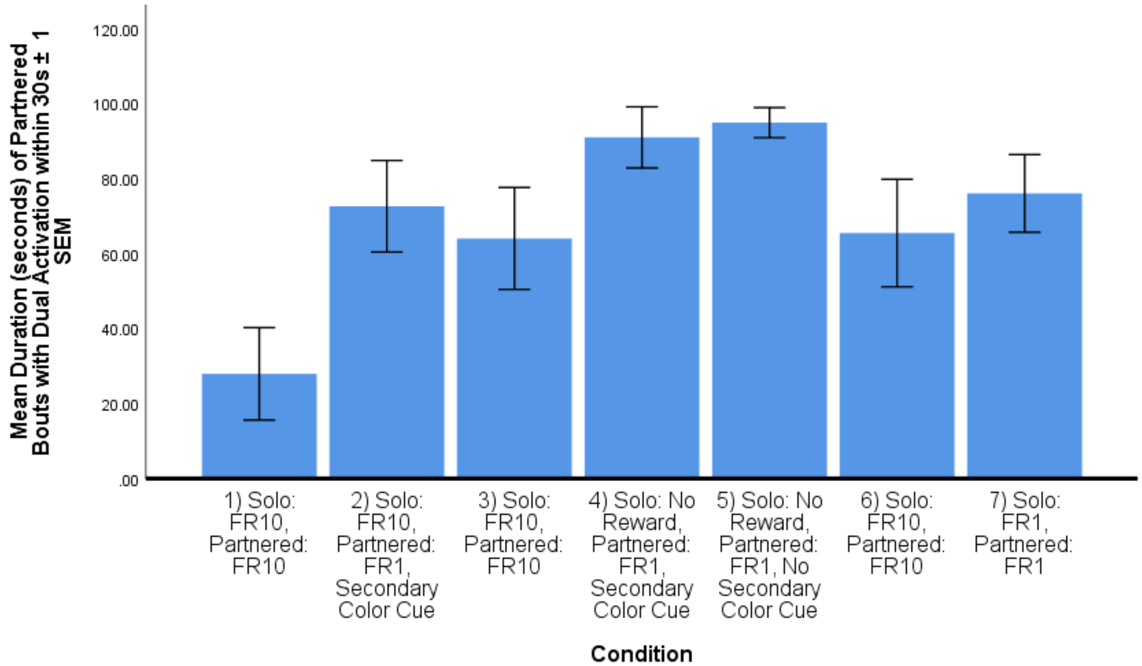


Figure 15. Mean duration (seconds) of partnered bouts with dual activation within 30 seconds ± 1 SEM by condition. Significant mean differences are listed below. Any comparisons that resulted in nonsignificant differences are not listed.

Comparison	***P***	***d***	**95% CI Lower Limit**	**95% CI Upper Limit**
1 vs. 4	0.006	1.31	-111.49	-14.52
1 vs. 5	0.006	1.30	-118.45	-15.41

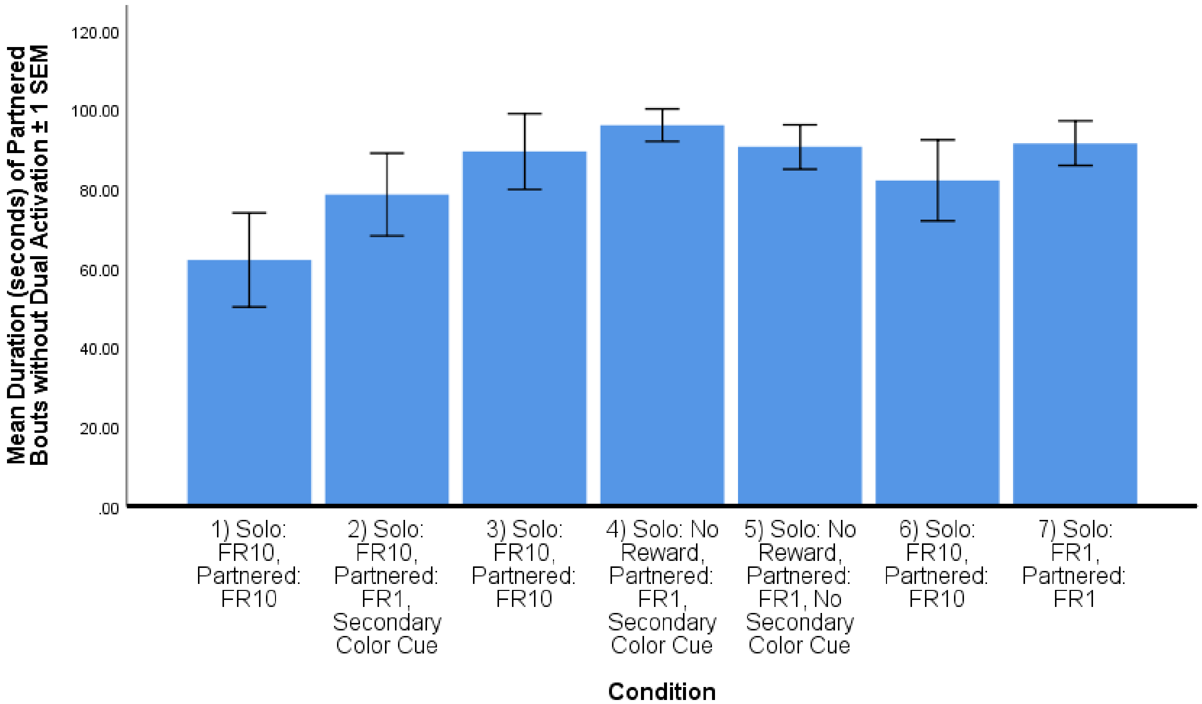


Figure 16. Mean duration (seconds) of partnered bouts without dual activation ± 1 SEM by condition. No significant mean differences were detected.

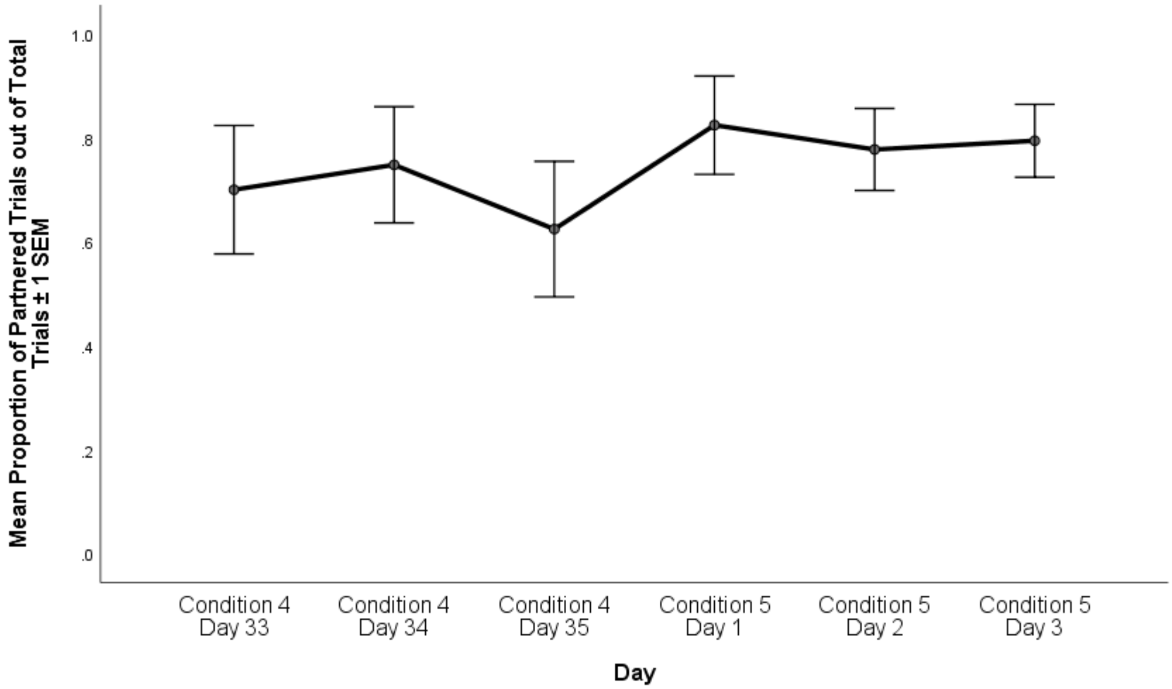


Figure 17. Mean proportion of partnered trials out of total trials ± 1 SEM for the last three days of Condition 4 and the first 3 days of Condition 5. No significant mean differences were detected.

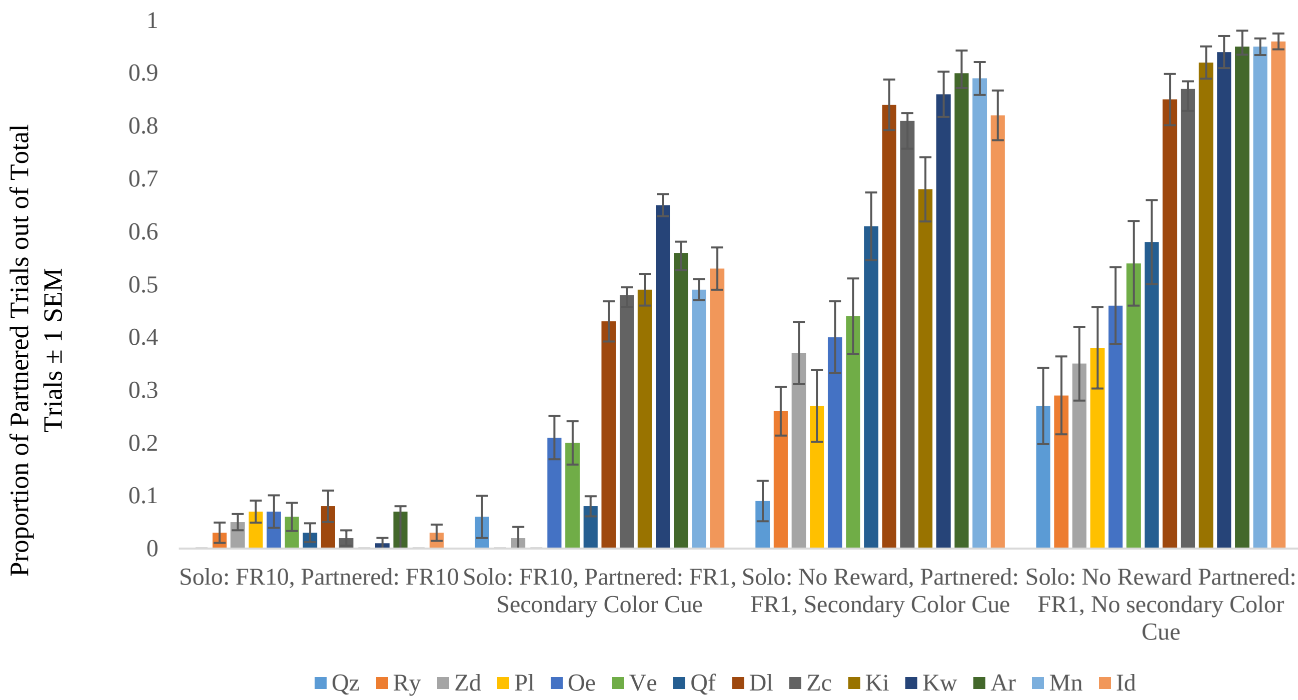


Figure 18. Individual means of proportion of partnered trials in Condition 1 (solo: FR10, partnered: FR10), Condition 2 (solo: FR10, partnered: FR1, secondary color cue), Condition 4 (solo: no reward, partnered: FR1, secondary color cue), and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) ± 1 SEM.

	Ar (M, 2)	Dl (F, 1)	Id (F, 1)	Ki (M, 1)	Kw (M, 1)	Mn (F, 1)	Zc (F, 1)	Oe (F, 4)	Pl (M, 2)	Qf (F, 1)	Qz (F, 1)	Ry (F, 1)	Ve (M, 4)	Zd (F, 2)
Ar (M, 2)		4.36%	2.85%	7.87%	57.62%	20.60%	1.17%					5.36%		0.17%
Dl (F, 1)	10.16%		8.98%	5.08%	3.91%	30.08%	14.84%		10.55%	8.59%	3.91%	1.17%		2.73%
Id (F, 1)	6.64%	8.98%		4.69%	3.16%	5.47%	58.17%		3.13%	7.42%				2.34%
Ki (M, 1)	16.32%	4.51%	4.17%		53.13%	12.15%	5.21%		0.69%		0.69%			3.13%
Kw (M, 1)	55.57%	1.62%	5.49%	24.72%		10.99%	0.65%			0.97%				
Mn (F, 1)	35.45%	22.19%	4.03%	10.09%	19.60%		5.19%			2.31%		1.15%		
Zc (F, 1)	2.86%	15.51%	64.08%	6.12%	1.63%	7.35%				2.45%				
Oe (F, 4)												7.76%	81.90%	10.34%
Pl (M, 2)		50.94%	15.09%	3.77%						9.43%				20.75%
Qf (F, 1)		3.40%	26.29%		9.38%	12.50%	9.38%		7.81%		3.13%	3.13%	21.88%	3.13%
Qz (F, 1)		83.33%		11.90%						4.70%				
Ry (F, 1)	57.14%	5.36%				7.14%		12.27%		3.80%				14.29%
Ve (M, 4)								87.16%		12.84%				
Zd (F, 2)	2.17%	15.22%	13.04%	19.57%				24.16%	19.71%	4.20%		1.93%		

	Ar (M, 2)	Dl (F, 1)	Id (F, 1)	Ki (M, 1)	Kw (M, 1)	Mn (F, 1)	Zc (F, 1)	Oe (F, 4)	Pl (M, 2)	Qf (F, 1)	Qz (F, 1)	Ry (F, 1)	Ve (M, 4)	Zd (F, 2)
Ar (M, 2)		80	52	144	1056	377	21					98		3
Dl (F, 1)	173		153	86	66	511	252		179	146	66	20		46
Id (F, 1)	126	170		89	60	103	1100		59	140				44
Ki (M, 1)	307	85	78		1000	229	98		13		13			59
Kw (M, 1)	1007	29	100	448		199	12			18				
Mn (F, 1)	668	418	76	190	369		98			43		22		
Zc (F, 1)	51	277	1143	109	29	131				44				
Oe (F, 4)												70	744	94
Pl (M, 2)		186	55	14						35				76
Qf (F, 1)		32	248		89	118	89		74		30	30	207	30
Qz (F, 1)		255		36						14				
Ry (F, 1)	254	24				32		55		17				64
Ve (M, 4)								768		113				
Zd (F, 2)	10	72	61	92				114	93	20		9		

Figure 19. This figure displays the partnered dyads that were observed during this study. Monkeys are listed on the left, and potential partners listed on top, with their sex and family rank in parentheses. The percentage of partnered trials completed with a specific partner (top) and the total trials completed with a specific partner (bottom) are listed. The color map transitions from green-yellow-red and indicates the strength of the dyad, with red indicating the highest level of partnership with a particular monkey.

	Ar (M, 2)	Dl (F, 1)	Id (F, 1)	Ki (M, 1)	Kw (M, 1)	Mn (F, 1)	Zc (F, 1)	Oe (F, 4)	Pl (M, 2)	Qf (F, 1)	Qz (F, 1)	Ry (F, 1)	Ve (M, 4)	Zd (F, 2)
Ar (M, 2)				18.40%	61.60%	15.00%	5.00%							
Dl (F, 1)					8.89%	64.11%	19.00%		8.00%					
Id (F, 1)							92.45%		7.55%					
Ki (M, 1)	85.00%				15.00%									
Kw (M, 1)	84.00%	1.05%		14.90%										
Mn (F, 1)	40.70%	25.93%			25.93%		7.41%							
Zc (F, 1)	8.00%	18.31%	72.59%			1.10%								
Oe (F, 4)													100.00%	
Pl (M, 2)		38.51%	61.49%											
Qf (F, 1)											42.17%			57.83%
Qz (F, 1)										100.00%				
Ry (F, 1)														100.00%
Ve (M, 4)								100.00%						
Zd (F, 2)										63.14%		36.86%		

	Ar (M, 2)	Dl (F, 1)	Id (F, 1)	Ki (M, 1)	Kw (M, 1)	Mn (F, 1)	Zc (F, 1)	Oe (F, 4)	Pl (M, 2)	Qf (F, 1)	Qz (F, 1)	Ry (F, 1)	Ve (M, 4)	Zd (F, 2)
Ar (M, 2)				45	150	37	12							
Dl (F, 1)					18	130	38		16					
Id (F, 1)							286		23					
Ki (M, 1)	325				57									
Kw (M, 1)	241	3		43										
Mn (F, 1)	115	73			73		21							
Zc (F, 1)	20	46	184			3								
Oe (F, 4)													45	
Pl (M, 2)		9	15											
Qf (F, 1)											50			68
Qz (F, 1)														
Ry (F, 1)														24
Ve (M, 4)								40						
Zd (F, 2)										6		4		

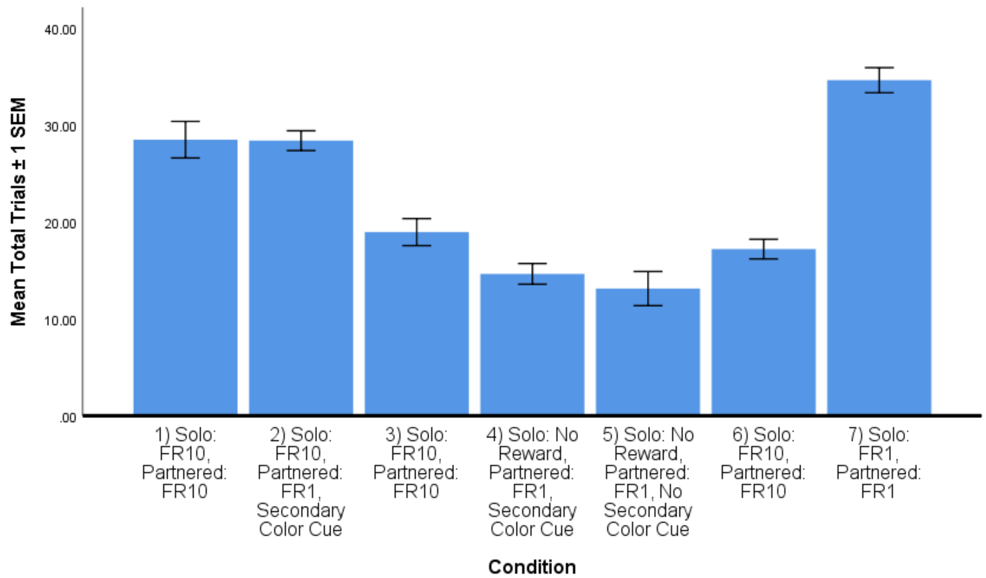
Figure 20. This figure displays the partnered dyads for partnered trials with dual activation observed in Condition 5 (solo: no reward, partnered: FR1, no secondary color cue). Monkeys are listed on the left, and potential partners listed on top, with their sex and family rank in parentheses. The percentage of partnered trials with dual activation completed with a specific partner (top) and the total partnered trials with dual activation completed with a specific partner (bottom) are listed. The color map transitions from green-yellow-red and indicates the strength of the dyad, with red indicating the highest level of partnership with a particular monkey.

Appendix

Total Trials

A main effect of condition on mean total trials was observed $F(2.44, 29.27) = 54.58$, $p < 0.001$, $\eta_p = 0.79$ (Appendix Figure 1). The lowest mean total trials occurred in Condition 4 and Condition 5, where solo trials were not rewarded at all, and total trials were highest in Condition 7, when all trials were rewarded on FR1. Condition 3 (solo: FR10, partnered: FR10), Condition 4 (solo: no reward, partnered: FR1, secondary color cue), Condition 5 (solo: no reward, partnered: FR1, no secondary color cue), and Condition 6 (solo: FR10, partnered: FR10) all had significantly more total trials than Condition 7 (solo: FR1, partnered: FR1): $p < 0.001$, $d = 3.23$, 95% CI [-20.58, -10.74]; $p < 0.001$, $d = 3.76$, 95% CI [-25.29, -14.63]; $p < 0.001$, $d = 3.92$, 95% CI [-26.98, -15.97]; $p < 0.001$, $d = 4.27$, 95% CI [-21.51, -13.31], respectively. Other significant differences were detected, with a pattern of decreased total trials completed after Condition 2 which continued until Condition 6. Condition 1 (solo: FR10, partnered: FR10) had significantly more total trials than Condition 3(solo: FR10, partnered: FR10) $p = 0.024$, $d = 1.11$, 95% CI [0.91, 18.14], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.88$, 95% CI [6.44, 21.22], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.001$, $d = 1.64$, 95% CI [5.92, 24.76], and Condition 6 (solo: FR10, partnered: FR10) $p = 0.003$, $d = 1.41$, 95% CI [3.25, 19.30]. Condition 2 (FR10 solo, FR1 partnered) had significantly more total trials than Condition 3 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.41$, 95% CI [3.84, 15.01], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 3.48$, 95% CI [9.77, 17.69], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 2.65$, 95% CI [9.46, 21.03], and Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 2.39$, 95% CI [6.47, 15.88]. Condition 2 (FR10 solo, FR1 partnered) had significantly fewer total trials than Condition 7 (FR1: $p = 0.004$, $d = 1.37$, 95% CI

[-10.80, -1.67]). Condition 3 (solo: FR10, partnered: FR10) had significantly more total trials completed than Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.22$, $d = 0.81$, 95% CI [0.62, 11.02]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly fewer total trials than Condition 6 (solo: FR10, partnered: FR10) $p = 0.004$, $d = 0.88$, 95% CI [-7.02, -1.12].

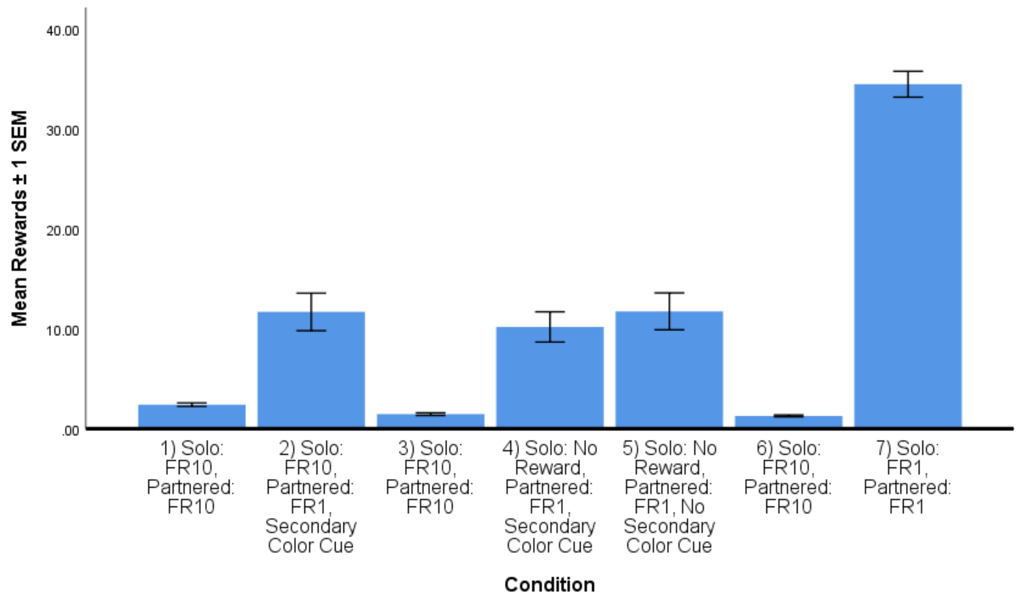


Appendix Figure 1. Mean total trials completed per monkey per day ± 1 SEM by condition.

Rewards

Mean rewards received varied significantly by condition F(2.26, 27.14) = 345.09, $p < 0.001$, $\eta_p = 0.91$ (Appendix Figure 2). The mean rewards differed as would be expected based on the different FR schedules in each condition. In conditions with FR10 only schedules, mean rewards were significantly less than those in conditions where monkeys could receive rewards at FR1. The first FR10 condition had higher mean rewards than the following two conditions with the same schedule, indicating a possible decrease in participation after experiencing rewards at FR1. Condition 1 (solo: FR10, partnered: FR10) had significantly fewer rewards dispensed than Condition 2 (solo: FR10, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.32$, 95% CI [-

12.67, -5.86], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.37$, 95% CI [-9.8, -5.74], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.35$, 95% CI [-11.83, -6.82], and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 6.28$, 95% CI [-37.09, -26.96]. Condition 1 (solo: FR10, partnered: FR10) had significantly more rewards dispensed than Condition 3 (solo: FR10, partnered: FR10) $p = 0.025$, $d = 1.17$, 95% CI [0.09, 1.82] and Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.52$, 95% CI [0.35, 1.91]. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly more rewards dispensed than Condition 3 (solo: FR10, partnered: FR10) $p < 0.001$ $d = 1.47$, 95% CI [7.00, 13.44] and Condition 6 (solo: FR10, partnered: FR10) $p = < 0.001$, $d = 1.52$, 95% CI [7.11, 13.68] and had significantly fewer rewards dispensed than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 3.50$, 95% CI [-28.02, -17.50]. Condition 3 (solo: FR10, partnered: FR10) had significantly fewer rewards dispensed than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.55$, 95% CI [-10.89, -6.56], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.51$, 95% CI [-12.48, -8.08], and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 7.16$, 95% CI [-37.47, -28.49]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more rewards dispensed than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.63$, 95% CI [8.27, 12.63] and significantly fewer rewards dispensed than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 3.83$, 95% CI [-29.99, -18.52]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly more rewards dispensed than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.57$, 95% CI [8.27, 12.63] and significantly fewer rewards dispensed than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 3.70$, 95% CI [-27.02, -18.39]. Condition 6 (solo: FR10, partnered: FR10) had significantly fewer rewards dispensed than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 7.07$, 95% CI [-37.80, -28.51].

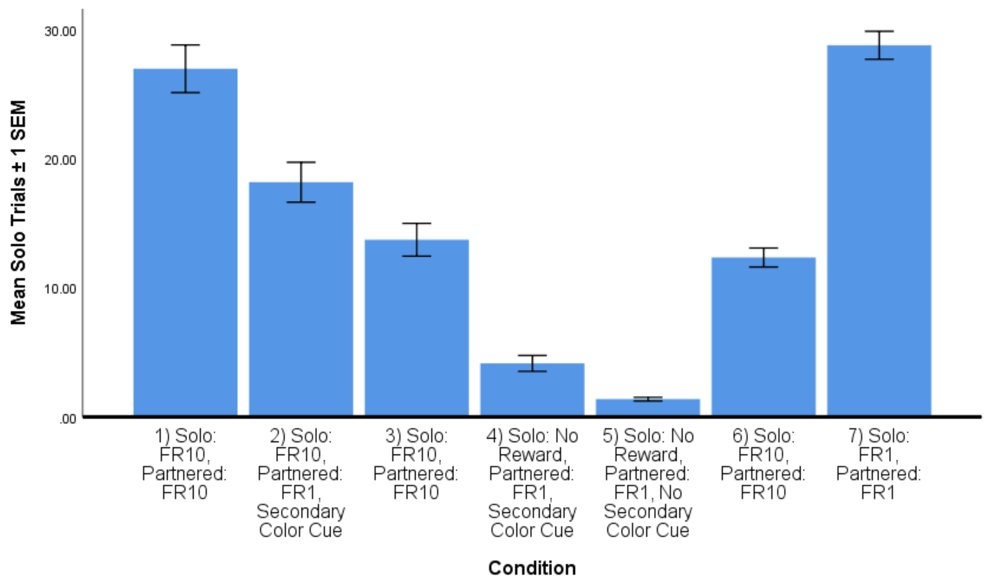


Appendix Figure 2. Mean rewards obtained per monkey per day ± 1 SEM by condition.

Solo Trials

A main effect of condition on mean solo trials was observed $F(2.18, 26.10) = 109.93$, $p < 0.001$, $\eta_p = 0.86$ (Appendix Figure 3). Solo trials were more frequent in conditions where partnered trials and solo trials had the same reward outcomes and decreased during conditions where partnered trials were rewarded better than solo trials. Solo trials were significantly higher in Condition 1 (solo: FR10, partnered: FR10) than Condition 2 (solo: FR10, partnered: FR1, secondary color cue) $p = 0.03$, $d = 0.87$, 95% CI [0.60, 16.95], Condition 3 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.65$, 95% CI [4.67, 21.79], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 3.00$, 95% CI [15.41, 30.18], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 3.69$, 95% CI [18.33, 32.79], and Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 2.50$, 95% CI [6.88, 22.33]. Condition 2 (solo: FR10, partnered: FR1) had significantly more solo trials than

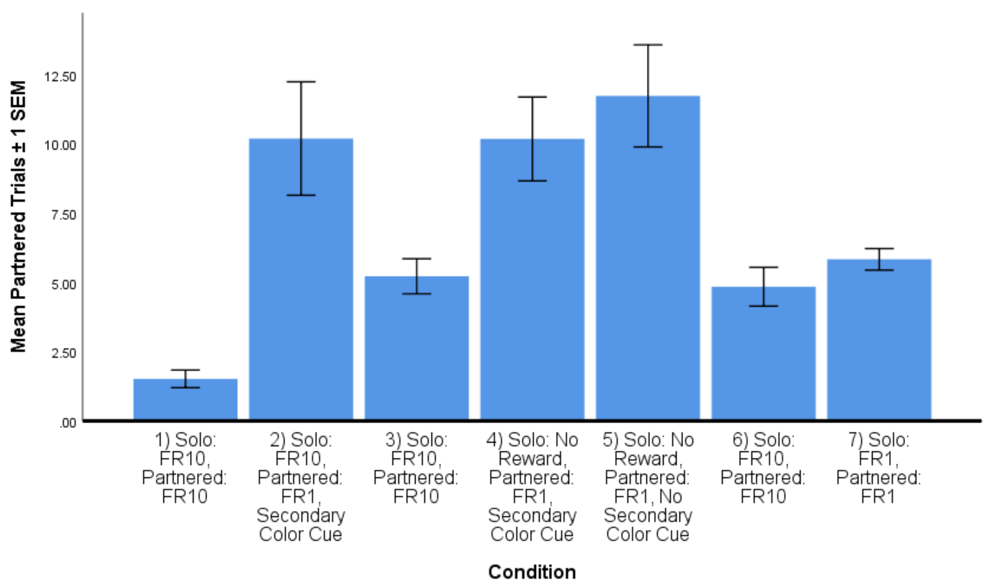
Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 6.08$, 95% CI [12.29, 15.75], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 3.08$, 95% CI [14.86, 18.71], and Condition 6 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 0.86$, 95% CI [2.38, 9.28]. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly fewer solo trials than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 0.52$, 95% CI [-14.17, -7.02]. Condition 3 (solo: FR10, partnered: FR10) had significantly more solo trials than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p = 0.001$, $d = 1.48$, 95% CI [3.92, 15.21] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 2.50$, 95% CI [7.34, 17.32], and significantly fewer solo trials than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 2.80$, 95% CI [-20.67, -9.43]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more solo trials than Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.42$, 95% CI [1.81, 3.72] and significantly fewer solo trials than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.98$, 95% CI [-11.69, -4.70] and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 4.65$, 95% CI [-28.40, -20.83]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly fewer solo trials than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 3.93$, 95% CI [-13.81, -8.10] and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 6.81$, 95% CI [-30.97, -23.78]. Condition 6 (solo: FR10, partnered: FR10) had significantly fewer solo trials than Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 4.10$, 95% CI [-20.42, -12.42].



Appendix Figure 3. Mean solo trials completed per monkey per day ± 1 SEM by condition.

Partnered Trials

There was a significant main effect of condition on mean partnered trials $F(3.82, 45.78) = 61.95$, $p < 0.001$, $\eta_p = 0.52$ (Appendix Figure 4). Partnered trials were more frequent in conditions where they were incentivized, and less frequent in conditions where partnered trials and solo trials were rewarded on the same schedule. There also appear to be more partnered trials during the two later FR10 conditions (Conditions 3 and 6) than in the initial FR10 condition (Condition 1), suggesting that there may be some carry-over effects with partnering. Condition 1 (solo: FR10, partnered: FR10) had significantly fewer partnered trials than Condition 2 (solo: FR10, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.07$, 95% CI [-11.76, -5.59], Condition 3 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.62$, 95% CI [-6.09, -1.32], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 3.06$, 95% CI [-10.93, -6.40], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.37$, 95% CI [-12.99,-7.44]), Condition 6 (solo: FR10, partnered: FR10) $p = 0.002$, $d = 1.04$, 95% CI [-5.50, -1.16], and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 2.22$, 95% CI [-6.26, -2.36]. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly more partnered trials than Condition 3 (solo: FR10, partnered: FR10) $p = 0.003$, $d = 0.64$, 95% CI [1.49, 8.45], Condition 6 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 0.90$, 95% CI [2.10, 8.60], and Condition 7 (solo: FR1, partnered: FR1) $p = 0.001$, $d = 0.60$, 95% CI [1.83, 6.89]. Condition 3 (solo: FR10, partnered: FR10) had significantly fewer partnered trials than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p = 0.001$, $d = 0.82$, 95% CI [-8.16, -1.76] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 0.94$, 95% CI [-9.10,-3.92]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more partnered trials than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.32$, 95% CI [2.78, 7.88] and Condition 7 (solo: FR1, partnered: FR1) $p = 0.001$, $d = 0.77$, 95% CI [1.74, 6.95]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly more partnered trials than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.37$, 95% CI [4.57, 9.21] and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 0.89$, 95% CI [3.86, 7.94].

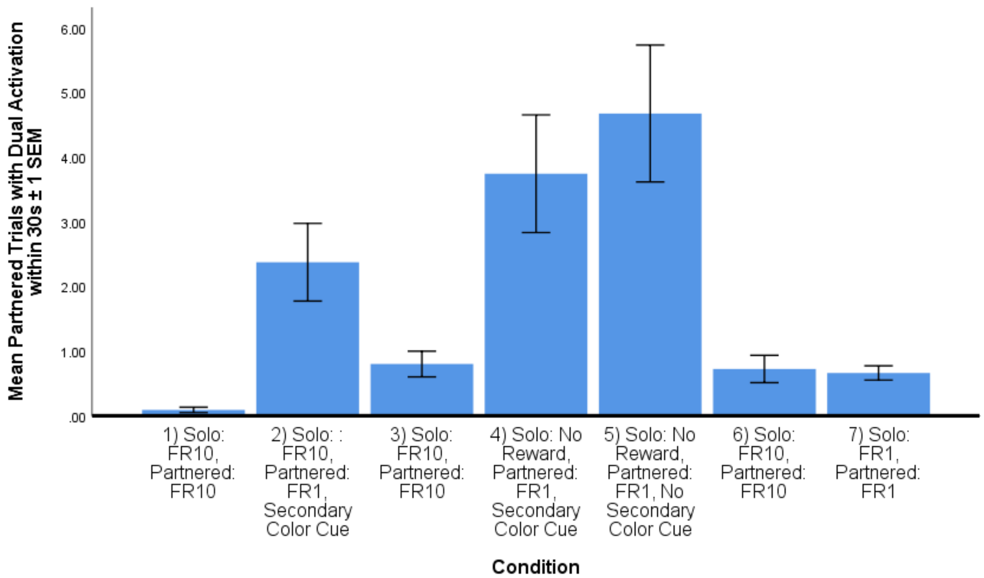


Appendix Figure 4. Mean partnered trials completed per monkey per day ± 1 SEM by condition.

Partnered Trials with Dual Activation

A main effect of condition on mean partnered trials with dual activation was observed $F(2.25, 27.04) = 53.76$, $p < 0.001$, $\eta_p = 0.50$ (Appendix Figure 5). Monkeys completed more partnered trials with dual activation in conditions where partnered trials were incentivized than in conditions where partnered and solo trials did not differ in reward outcome. Condition 1 (solo: FR10, partnered: FR10) had significantly fewer partnered trials with dual activation than Condition 2 (solo: FR10, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.05$, 95% CI [-3.46, -1.11], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.06$, 95% CI [-4.74, -2.57], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.14$, 95% CI [-6.16, -3.00], and Condition 7 (solo: FR1, partnered: FR1) $p = 0.009$, $d = 1.27$, 95% CI [-1.03, -0.12]. Condition 2 (solo: FR10, partnered: FR1, secondary color cue) had significantly more partnered trials with dual activation than Condition 3 (solo: FR10, partnered: FR10) $p = 0.019$, $d = 0.71$, 95% CI [0.19, 2.96], Condition 6 (solo: FR10, partnered: FR10) $p = 0.042$, $d = 0.78$, 95% CI [0.04, 3.26], and Condition 7 (solo: FR1, partnered: FR1) $p = 0.012$, $d = 0.76$, 95% CI [0.30, 3.13]. Condition 3 (solo: FR10, partnered: FR10) had significantly fewer partnered trials with dual activation than Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 0.88$, 95% CI [-4.23, -1.65] and Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.04$, 95% CI [-5.09, -2.65]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly more partnered trials with dual activation than Condition 6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 0.97$, 95% CI [1.66, 4.38] and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 0.92$, 95% CI [1.91, 4.25]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly more partnered trials with dual activation than Condition

6 (solo: FR10, partnered: FR10) $p < 0.001$, $d = 1.14$, 95% CI [2.73, 5.17] and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 1.04$, 95% CI [2.53, 5.49].

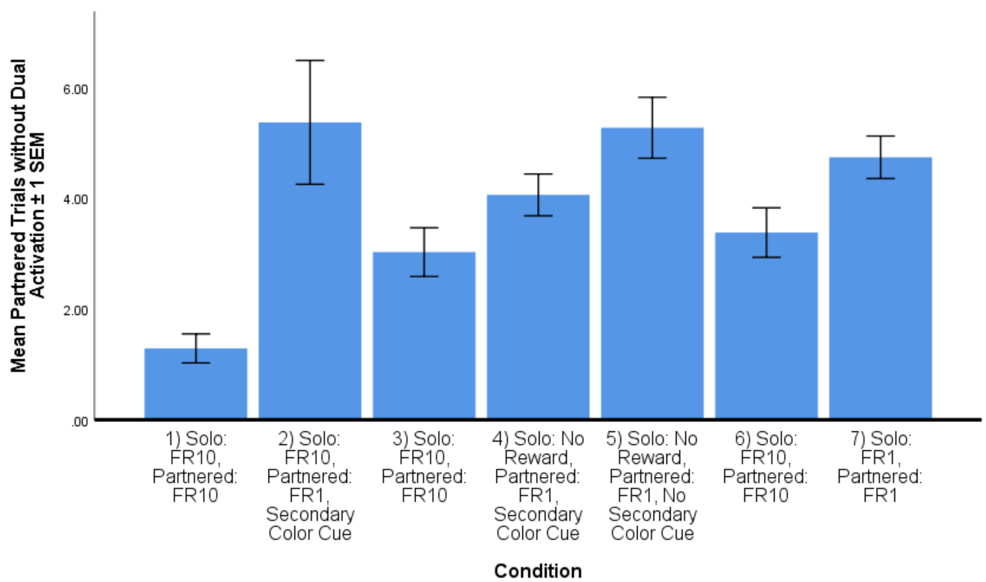


Appendix Figure 5. Mean partnered trials with dual activation completed per monkey per day ± 1 SEM by condition.

Partnered Trials without Dual Activation

A main effect of condition on mean partnered trials without dual activation was detected $F(2.62, 31.48) = 16.48$, $p < 0.001$, $\eta_p = 0.41$ (Appendix Figure 6). There was no clear overall pattern of more or less frequent partnered trials without dual approach in conditions when partnered trials were or were not rewarded differently than solo trials. Condition 1 (solo: FR10, partnered: FR10) had significantly fewer partnered trials without dual activation than Condition 2 (solo: FR10, partnered: FR1, secondary color cue) $p = 0.003$, $d = 0.93$, 95% CI [-6.88, -1.27], Condition 3 (solo: FR10, partnered: FR10 $p = 0.039$, $d = 1.11$, 95% CI [-3.41, -0.06], Condition 4 (solo: no reward, partnered: FR1, secondary color cue) $p < 0.001$, $d = 1.61$, 95% CI [-3.95, -1.59], Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p < 0.001$, $d = 1.61$, 95% CI [-5.20, -2.76], Condition 6 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.04$, 95% CI [-

3.37, -0.81], and Condition 7 (solo: FR1, partnered: FR1) $p < 0.001$, $d = 1.87$, 95% CI [-5.26, -1.63]. Condition 3 (solo: FR10, partnered: FR10) had significantly fewer partnered trials without dual activation than Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) $p = 0.017$, $d = 0.78$, 95% CI [-4.188, -0.31]. Condition 4 (solo: no reward, partnered: FR1, secondary color cue) had significantly fewer partnered trials without dual activation than Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) p 0.034, $d = 0.87$, 95% CI [-2.36, -0.06]. Condition 5 (solo: no reward, partnered: FR1, no secondary color cue) had significantly more partnered trials without dual activation than Condition 6 (solo: FR10, partnered: FR10) $p = 0.001$, $d = 1.52$, 95% CI [0.71, 3.06].



Appendix Figure 6. Mean partnered trials without dual activation completed per monkey per day ± 1 SEM by condition.