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**Can dogs generalize what they learned in a cooperative
task to new human and conspecific partners?**

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Plagiarism disclaimer

I hereby declare that this thesis is my own and autonomous work. All sources and aids used have been indicated as such. All texts either quoted directly or paraphrased have been indicated by in-text citations. Full bibliographic details are given in the reference list, which also contains internet sources containing URL and access date. This work has not been submitted to any other examination authority.

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Abstract

Cooperation is defined as two or more individuals acting together towards a common goal (Noë 2006). Cooperative behaviors can occur without the actual understanding of the cooperative action. While humans have outstanding skills to understand their partner's role and adjust their actions accordingly, cooperative behaviors can occur in other species without actual understanding of the causal role of their partner in the task (Duguid and Melis 2020). To better understand the evolutionary origins of cooperation, research must explore whether individuals from different species understand the role with whom they cooperate or whether they act simultaneously yet independently towards the same goal (Boesch and Boesch 1989, Tomasello and Call 1997). A recent study carried out by Martínez et al. (2023) showed that pet dogs consider the actions of their human partners in a coordination task and adjust their own actions accordingly. However, because dogs participated in this task with their owners as partners, it is possible that their success was due to obedience and leader-follower dynamics, rather than an understanding of the cooperative situation. In the present study we address this question by testing whether those same subjects would be able to keep their success rate when they are not paired with their owner but with a new partner, both human and conspecific. We showed that dogs generalize what they learned with their owner in the previous study also on other partners; either another dog or a human partner they have never met before, and no statistical differences were found when comparing both human and dog partners. This suggests that in Martínez et al. (2023) dogs' performance was not solely based on following their owner's actions, but rather that they have learned the cooperative nature of the task.

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1 INTRODUCTION

1.1 Understanding the partner's role: theoretical background

Many species (from insects to humans) live in social groups, within which individuals continuously interact with each other and often appear to work together (Dugatkin 1997). There are numerous examples of cooperation in the animal kingdom, namely in raising the offspring produced by the dominant pair of the group (Clutton-Brock 2002), in coalitions of males controlling and monopolizing females (Connor and Krutzen 2015), in joint defense of the territory and against predators (Wilson 1975), and when capturing prey (Dugatkin 1997). Thus, cooperation, defined as two or more individuals acting together to achieve a common goal (Noë 2006), it is a widespread phenomenon in the animal kingdom. Among all species, humans have exceptional cooperative abilities compared to other animals (Tomasello 2016), potentially due to our species' ability to understand the role and intentions of cooperative partners.

In contrast, cooperation can emerge by co-production, when two individuals act simultaneously yet independently towards the same goal (Tomasello and Call 1997, Boesch and Boesch 1989), without actively understanding the cooperative situation. Consequently, a key question to understand the evolutionary roots of human cooperation is to which extent other species understand the role of those with whom they cooperate (Albiach-Serrano 2015). Addressing this issue, Boesch and Boesch (1989) proposed a categorization of cooperation, depending on to which extent the participants in the cooperative interaction understand the role of their partner. This categorization was based on the group hunting behavior of wild Chimpanzees and consisted of four levels: similarity, synchrony, coordination, and collaboration. The first category, similarity, does not require any understanding of the role of their partner. Cooperation here emerges as a by-product of individuals acting simultaneously towards the same prey. Synchrony and coordination require the subjects to pay some attention to the actions of their partners, to coordinate with them in time of the start and speed (synchrony) of working together and/or in space based on their conspecifics' position (coordination). Finally, collaboration is defined by the flexibility with which subjects take distinct and complementary roles. While the latter has been difficult to study in non-human

animals (Albiach-Serrano 2015, Duguid and Melis 2020), researchers have studied a wide range of animal species investigating whether they take the presence of their partners into account and whether they coordinate with them in time and space.

1.2 Experimental studies: the cooperative pulling paradigm

A paradigm specially designed to study whether animals pay attention to the presence of their partner is the “cooperative pulling task”, in which two individuals need to pull two handles/ropes at the same time to bring into reach a platform baited with food (Crawford 1937). In a further version of the cooperative pulling task, the “loose-string cooperative pulling task” (Hirata and Fuvva 2007) that has been widely used in the last decades, the string is attached using loops, in a way that it comes loose if only one individual pulls it. Thus, if one individual pulls the rope while the other individual is not present and pulling too, this results in an unsuccessful trial where the food can no longer be retrieved. For the reward to be successfully obtained, the animals should coordinate their actions and pull on both ends of the string simultaneously, thereby moving the tray towards them and reaching the food. However, either version of the cooperative pulling task can be solved without any active coordination when the animals repeatedly pull the handles/rope (Chalmeau et al. 1997). To address this issue, researchers often include an additional condition, the “delay condition”, in which one of the subjects gains its access to the string a few seconds after the other (Melis et al. 2006). If the first subject that arrives waits before pulling their end of the string until the partner has reached the apparatus, it is thought to demonstrate that they understood the need of a partner to solve the task (Schwing et al. 2018). To this day a wide range of species have been shown to wait for their partner in the delay condition: keas (Heaney et al. 2017, Schwing et al. 2018), elephants (Plotnik et al. 2011), macaques (Molesti and Majolo 2016), chimpanzees (Melis et al. 2006, Hirata and Fuwa 2007), wolves (Pescini et al. 2017) and many others (for a review, see Massen et al. 2019).

However, success in the delay condition does not always imply that the subjects understand the role of their partner. An alternative explanation is that subjects succeed thanks to low level cues if they learn to pull the rope in response to small movements or tension of the rope caused by the other subject pulling it (Albiach-Serrano 2015). To prevent the animals from

coordinating their behavior with the movement of the rope, Jaakkola et. al (2018) implemented the delay condition in a setup using buttons instead of a rope. In their task, pairs of bottlenose dolphins were presented with their own underwater button that they had to press simultaneously, within a 1second time window, to obtain a food reward. In this study, dolphins waited up to 20 seconds for a delayed partner. While the design of this study prevented the animals from following external cues coming from the apparatus (i.e., the movement of the rope in the string-pulling task), explanations other than understanding the partners role can account for these results. For example, the act of pressing the button only when the partner is present might be due to social facilitation (i.e. a subject is more likely to perform an action if there are other individuals present (Zajonc 1965), that is, if the animal learns to press the button in the presence of another subject independently of the actions of that partner (Seed and Jensen 2011). Further control conditions could have been used to demonstrate that the dolphins understand that they need a partner to solve the task. For example, in a study of Mendres and De Waal (2000) pairs of capuchin monkeys were tested in a task in which they had to pull a bar at the same time to be rewarded. They implemented a “Non-visibility condition” in which the subject’s visual access of their partner was eliminated. Because subjects could still know that their partners were present (movements, noise, smell, etc.), changes in their pulling behavior could not be attributed merely to the partner’s presence. The authors found that the monkeys were able to coordinate their actions when they could see their partner, but in the Non-visibility condition the number of successful pulls dropped drastically. The change in the level of success when they could not see their partner’s actions suggests that pairs of subjects were coordinating the actions, and that their behavior was not merely driven by social facilitation.

1.3 The case of pet dogs

Recently Martínez et al. (2023) published a study in which they tested pet dogs in a setup similar to Jaakkola’s et al. (2018) button task, with the addition of a Non-visibility condition. In their study, dogs participated with their owners in a task in which they were required to press a button at the same time as their owners. In the training phase, the partner’s button was shown 3 seconds after the dog’s button. Thus, dogs had to refrain themselves from pushing the button until both buttons were presented, and then press the button at the same time as

their partner. After the training, they tested the dogs in a series of conditions to investigate what they understood about the role of their partner in the task. In these conditions, they introduced different delays that the subjects had never experienced during the training (from 3 to 9 seconds, while in the training the delay was always 3 seconds) in which either the button of their partners was unavailable (Delayed-button condition), their partner was far away from the button (Delayed-partner), or the partner and the button were present, but the partner waited a few seconds before pressing the button (Delayed-action condition). Finally, they set a “Non-visibility” control condition, where the dogs were prevented from seeing or hearing their owner, to assess the chance levels of dogs coordinating with their partners when they could not see or hear their partner’s actions.

Dogs in this study waited before pressing their button in all the conditions except the Non-visibility condition, in which most of them rarely interacted with the button. That showed not only that dogs are sensitive to the presence of their partner as shown in previous studies (Range et al. 2019, Range et al. 2019) but also that they coordinate by paying attention to the actions of their partner. However, dogs in Martínez et al. (2023) were all trained and tested with their owner, which might have biased the results. First, because dogs were trained with the same partner that they were tested with, it is possible that they only learned to react to certain gestures of that particular partners. Second, because that partner was human, it is possible that dogs coordinate with them without understanding the cooperativeness of the task, but because they interpret their actions as a command (Horowitz and Hecht 2016). This would be in line with previous research suggesting that dog-human coordination is based in leader-follower dynamics, with humans initiating the movement and dogs following. Finally, because the partner was their owner, this special relationship might have affected the dogs’ performance. In fact, dogs have been shown to pay special attention to the actions of their owners (Horn et al. 2013) and tend to synchronize their movements with them (Duranton et al. 2017, Duranton et al. 2018). In the current study, we aimed to address whether dogs in Martínez et al. (2023) really understood cooperative nature of the task or, on the contrary, other factors such as affiliation, obedience, or leader-follower dynamics could account for the results. Specifically, we tested the same dogs with different partners, both human and

conspecific, in the same task to address whether they would be able to generalize what they have learnt and also coordinate with them.

If dogs are able to coordinate with a new unfamiliar human partner other than their owner, we can rule out that they learned to respond only to specific cues from their owner. If dogs are able to coordinate with conspecifics, we could rule out that their performance in Martínez et al. (2023) was merely due to obedience towards human gestures. Furthermore, testing dogs with dog partners would give us insight about dogs' cooperative skills with conspecific. Some authors have claimed that dogs have acquired exceptional cooperative skills through the process of domestication (Hare and Tomasello 2005) but it is still a matter of debate whether those cooperative skills are limited to their interactions with humans. While most dog-human interactions are cooperative (Range and Virányi 2015), dogs interactions with other dogs usually occur in a context of competition over resources, which might obstruct the emergence of cooperation. Therefore, it can be difficult for dogs to perceive conspecifics as cooperative partners.

To date, evidence of dog cooperation with conspecifics in lab context is scarce and mixed. One study showed that dogs succeed in a cooperative task (Bräuer et al. 2013, 2020), but the solution of the task involved the partners moving in opposite directions, and authors failed to provide any evidence of coordination between the partners. A further study using the loose string-pulling paradigm claimed that dyads of dogs were able to coordinate in the task and wait for their partner before pulling the rope (Ostojić and Clayton 2014). However, the average time that dogs waited was only 2.2 seconds, which is arguably even a delay. Additionally, dogs tested in this study were pet dogs that participated with their owners present in the testing arena, which might have mediated tolerance issues among partners. Conversely, other studies showed that dyads of pack-living dogs are not able to succeed in the task without nor with prior training (Marshall-Pescini et al. 2017, 2018). The authors argued that their failure was not due to cognitive limitations or lack of understanding of the task, but rather due to tolerance problems that prevented the dogs from operating the apparatus in close proximity with a conspecific partner.

1.4 Aims and hypothesis of the current study

In the present study the same dogs as in the previous study were tested in two separate experiments. In Experiment 1 dogs were paired with other (familiar or unfamiliar) dogs and tested in 3 conditions. In the Partner delayed condition, the partner approached the button with a delay of a few seconds; in the Button delayed condition, the partner's button appeared with a delay. Finally, we ran the Non-visibility condition in which the dogs were unable to see or hear their partner dog during the task. This condition was set to assess the rate of success that dogs could achieve by chance, when they could not see their partners' actions. In Experiment 2, which included the Button delayed and Partner delayed condition, the dogs were paired and tested with new human partners, unfamiliar to the dogs. We did not run the Non-visibility condition in the second experiment, since it was not our main question whether dogs perform above chance levels with humans (it was already tested in the previous study).

The aim of the present study was twofold:

First, we wanted to test if dogs that already succeeded in a coordination task with their owners as partners would be able to generalize this knowledge and coordinate with a different partner than whom they've been trained with. For that, we compared the dogs' performance in the Button delayed and Partner delayed condition when paired with a conspecific (Experiment 1) and an unfamiliar human (Experiment 2). If the dogs' performance in Martínez et al. (2023) study was motivated by low-level cues and they learned to respond only to the actions of their owners, we predict that dogs will not be able to coordinate with neither of their new partners (conspecific or human). If the dogs are able to coordinate with both new partners that would suggest that the coordination skills that dogs showed in Martínez et al. (2023) was driven by an understanding of the cooperative situation. In case if dogs struggle to perceive conspecifics as cooperative partners, we predict that they would perform better in the task when they are paired with a new human partner than if they participate together with a conspecific.

Secondly, we wanted to test whether dogs' cooperative abilities are specific to humans, or they are also able to coordinate with a conspecific. To explore whether dogs coordinate with other dogs, we used the data from Experiment 1 and we compared the results of the Non-visibility condition with the other conditions (Partner delayed and Button delayed). If dogs

coordinate with other dogs, we predicted that they would be able to coordinate in the conditions in which they could see and hear the actions of their dog partner (Button delayed and Partner delayed) but not in Non-visibility condition.

Finally, with the combination of Button delayed and Partner delayed condition we explored the strategies that the dogs are using to solve the task. If they only pay attention to the presence of the button, they could not succeed in the Partner delayed condition in which the two buttons are presented from the start of the trial. If dogs pay attention only to the presence of their partner, they could not solve the Button delayed condition because their partner is present during the whole length of the trial.

2 METHODS

2.1 Ethical statement

The study and its procedures commensurate with the institutional guidelines of good scientific practice and national legislation (ethical approval: University of Veterinary Medicine Vienna ETK-028/02/2020). A written consent was signed by the dog owners before the onset of the experiment. All the procedures of the experiment were non-invasive and only positive reinforcement techniques were used. All the dogs were pet dogs living with their families and water was always available ad libitum during the tests.

2.2 Subjects

We tested 14 dogs (9 females and 5 males, range 1.4-12.9 years, on average 5.08 years; see Appendix 2 for details) that already participated in the previous study with a similar setup (Martínez et al. 2023). All our subjects were already trained in the task and showed the ability to coordinate with their owners in pressing a button at the same time. Additionally, 8 dogs (3 females, 5 males) naive to the setup, participated in the study as partners for Experiment 1. Six of them participated twice (i.e., they participated as the partners to two different subjects) and 2 of them participated only once (i.e., were partners to only one subject) (see Appendix 2 for the formed dyads). There were differences in familiarity within the dog-dog dyads, which comprised 6 familiar dyads (3 pairs living in the same household, 2 out of which were also related, and 3 pairs of dogs that often interacted due to close acquaintance of their owners) and 8 unfamiliar dyads where the dogs didn't know each other before the start of the study (see Appendix 2). In Experiment 2, 14 humans played the role of partners. All the human partners were unfamiliar to the dogs and never met them before the study. All the dogs participated with unfamiliar human partners of the same sex as their owners, that is, if a dog performed the task with a female owner in the previous study, the human partner in the current study was also female. Human partners (13 women, one man) were paired only with one dog during the study (i.e., none of them participated more than once).

2.3 Design of the study

Some of the subjects finished the first study (Martínez et al. 2023) in December 2019, while others did so in June 2020. Therefore, to ensure that all dogs remembered the task, all the subjects went through a *refresher* in which they were briefly trained again with their owners as partners. All the partner dogs also went through a training phase in which we ensured that they would reliably press the button when presented to them. All dog-human and dog-dog dyads went through a *habituation phase* before the start of the test, in which we assessed that dogs did not show discomfort receiving food in close proximity to their partners. After those pre-test procedures, dogs participated together with conspecifics (*Experiment 1*) or unfamiliar humans (*Experiment 2*) in a coordination task in which they needed to press a button at the same time as their partner to obtain food. Both Experiment 1 and Experiment 2 consisted of the *Simultaneous pressing test*, in which we tested whether dogs would press the button with their partners when they both had immediate access to it, followed by a series of conditions to explore if the dogs understood the need of a partner to complete the task, in which the partners did not have immediate access to the button (see Table 1 for clarification on the schedule).

In *Experiment 1*, the dogs were tested in three conditions with a conspecific partner:

Button delayed condition: both dogs were free to approach the setup at any time, but the partner's button appeared a few seconds after the subject's button.

Partner delay condition: both buttons were shown to the subject and its partner at the same time, but the partner was held by the owner at the back of the room and could only approach the button after a number of seconds.

Non-visibility condition: which was similar to the Button delayed condition but with an opaque barrier between the dogs, preventing them from seeing each other. We included this condition to assess how much success was possible in our task only by chance, when dogs could not see the actions of their partners.

In *Experiment 2* we repeated two of the previous conditions:

the *Button delayed* and *Partner delayed* condition, but this time dogs were paired with an unfamiliar person as their partner. We did not run the NV condition in the second experiment,

since it was not our main question whether dogs perform above chance levels with humans (this was already showed in Martínez et al. (2023) but rather to find out if they perform better with the unfamiliar human or a conspecific. Dogs participated in the experiments in a counterbalanced order (half of the sample started with Experiment 1 and half of the sample started with Experiment 2). The order of the conditions within the experiment was also randomized and counterbalanced.

2.4 Setup

All the training and tests were conducted from early June to the end of September 2020 at the Clever Dog Lab Vienna (CDL) in a large-sized (7m x 6m) testing room. The setup was the same as in Martínez et al. (2023). A see-through wired fence divided the room in two equal parts (one for the subject and one for the partner). On one end of the fence there was a wired cage-like enclosure (1.5m x 1.5m), covered with black curtains, where the experimenter was hiding (see Figure 1). The apparatus itself consisted of two red buttons (20cm of diameter) each one attached to a wooden plank (20cm x 70cm), which were embedded in a pedestal enabling the planks with buttons to be slid in and out of the experimenter's enclosure. The pedestal was positioned under the junction of the fence and the enclosure; therefore, each button was presented on one side of the separated room. On the outer side of each button a tube was placed where the experimenter was able to deliver food to the participants. During all the test conditions, we played a recording with the sound of the button being slid out of the fence and pressed. We did this to prevent the subjects from getting cues by the sound of the partner pressing the button, instead of paying attention to their actual actions and movements. Two web cams were placed on the fence of the enclosure, right above the point where the buttons were presented, connected with a computer placed inside the enclosure, from which the experimenter was able to monitor the subject and its partner's behavior around the button. There were three additional cameras connected to the CDL camera system, located on the ceiling and in the corners of the room, which were functioning as backup recordings where the whole room is visible. On the opposite side of the experimenter's enclosure two chairs were placed on each half of the room where the owners were sitting (subject's owner in case of the dog-human dyads, and subject's and partner's owner in case of dog-dog dyads), instructed to remain silent and not to interact with the dog in any way to avoid giving any

cues. In addition to the original setup, we made some small adjustments of the setup to adapt to dog-dog dyads in Experiment 1. We included an additional tube on the partner's side of the enclosure accompanied with a water bowl, which was always present also on the subject's side, although without the additional tube (see the left part of Figure 1).

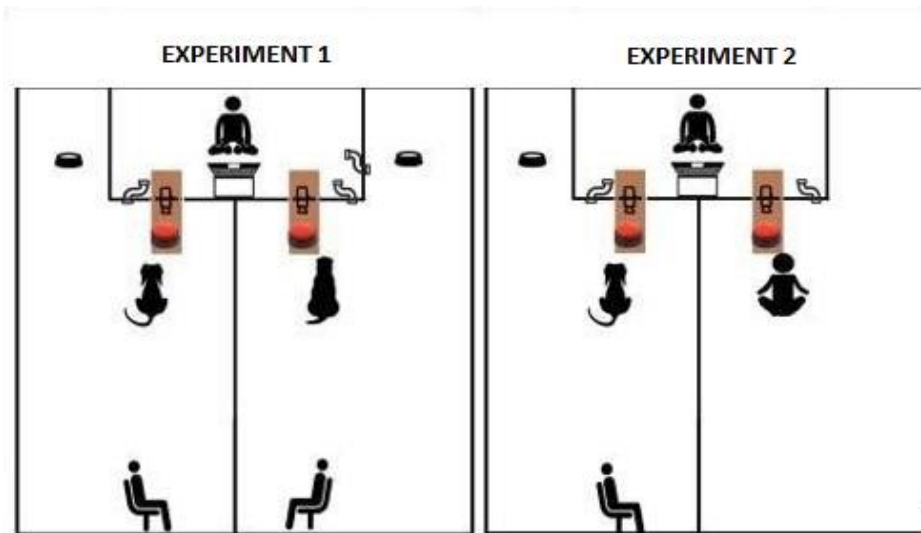


Figure 1. Experimental setup of the room; Experiment 1 (dog-dog dyad) on the left, with an additional food tube on the partner's side, and Experiment 2 (dog-unfamiliar human dyad) on the right. Experimenter is sitting inside the enclosure, hidden from the participants who are sitting in front of the buttons. Owners are seated at the back of the testing room (both, subject's, and partner's owner on the left representation; only subject's owner on the right).

2.5 Pre-test procedures

2.5.1 Refresher

We started the study with a refresher where the subjects had to perform the coordination task paired with their original partners, their owners. We ran 2 rounds of 21 trials where the subject's button appeared, but the partner's button had a delay of 3 seconds. Independently of the success of the subject's performance, all dogs participated in 42 refresher trials in one single session (around 10 minutes).

2.5.2 Habituations

During the tests the subjects were required to work and receive food rewards in close proximity to their partners (dogs and unfamiliar humans). In order to make sure they are

comfortable with that and above all that the dogs don't show any signs of stress or aggression, we ran one habituation session before each experiment (once with dog-dog dyads and once with dog-unfamiliar human dyads). In case of dog-dog dyads the owners were instructed to bring the dogs to the testing room on the leash and sit on 2 chairs separated by the wired fence. The experimenter sat down in front of both dogs, gave them the command "paw" in sequential order and rewarded them with high value food (e.g., sausage or cheese) (for the setup see Figure 2). This was repeated ten times.

In case of dog-unfamiliar human dyads the owner was instructed to bring the dog to the testing room and unleash it, while the unfamiliar human was already sitting in front of the standard setup (see Figure 3). The dog was free to approach the partner and the human could pet the dog when approached. This lasted for 5 minutes. From this familiarization step on, unfamiliar humans were instructed not to look or interact with the dogs during the trials. If the dogs would show any signs of stress or aggression in the habituation phases, either with the human or the dog partner, we would have stopped their participation, but that never happened.



Figure 2. Habituation session with the experimenter on the left side of the fence and both dogs on the right, also separated with a fence and accompanied with their owners. In the picture above, the experimenter put the hand towards the partner dog and asked it to give paw, while in the picture below, she gave the paw command to the subject dog. They were both rewarded with sausages.



Figure 3. Habituation session between dog-unfamiliar human dyad. The partner/unfamiliar human sitting in front of the setup on the left side of the fence with the dog approaching and the dog's owner present in the room.

2.5.3 Partner dog training

We had to train partner dogs to reliably press the button whenever it was presented to them. First, we trained the dog to press the button using sausage as a reward (see the details in part 1 of the Appendix). After the dog-partners learned to certainly press the button, we introduced them to the setup. In this phase of the training, the dog was placed on their side of the room (but without the subject present in the room). Then, the experimenter slid the button out of the experimenter's enclosure and waited for the dog to press it. Every time the dog pressed the button within 1 second after it was shown, it was rewarded with food. As later in the testing phase partner dogs sometimes received the food from the side tube, also during the training we delivered the food through the front or the side tube (in random order) to familiarize the partner dog with the rewards coming from both tubes. When the partner dog reliably pressed the button at least 20 consecutive times, it was ready to participate in the following phase.

Table 1. Schedule of the study for the pre-test and test phases in Experiment 1 and Experiment 2 according to the number of appointments.

		EXPERIMENT 1	EXPERIMENT 2	Additional requirements
#Appointment		Dog-dog dyad	Dog-unfamiliar human dyad	Partner dog
1.	Pre-test	Refresher		Training for pressing the button
2.		Habituation	Habituation	
	Testing	Simultaneous pressing	Simultaneous pressing	
3.		Condition 1	Condition 1	
4.		Condition 2	Condition 2	
5.		Condition 3		

2.6 Testing

Dogs were required to each press a button at the same time as their partner (within a 2 second time window) to receive a food reward. Dog-partner dyads were together in the room but were separated by a wire fence that allowed them to see each other (the subjects' positions were counterbalanced to the right or left between subjects). While the subject-dogs were always free to move and to decide when to interact with the apparatus, the behavior of the partner depended on the condition (i.e., in the Partner delayed condition, partners started the trial at the back of the room, held by their owner in the case of dog partners, see General procedure below). Therefore, the owners of partner-dogs were sometimes instructed to hold the partner away from the setup and only release it with a delay indicated by the experimenter. If both, the subject and his/her partner (dog/unfamiliar human), pressed the button within a time frame of 2 seconds, the trial was counted as successful, therefore both were rewarded with food at the same time and the experimenter used a positive sound ("super"). Conversely, when the dogs failed, a negative sound was produced ("ah-ah") and the buttons were withdrawn for another trial to start. The trial was counted as unsuccessful if the subject pressed the button too early, too late, or did not press at all. Additionally, when the trial was unsuccessful due to the subject's failure (i.e., the partner pressed the button, but the subject did not), the partner dog was still rewarded with food (without the positive sound

“super”) through the additional tube on the side which was not visible to the subject. In cases when the partner (dog) pressed the button too soon or didn’t press the button within 2 seconds after its button was reachable, the trial was counted as invalid and was repeated. We used dry food for rewarding the subjects (following the lines of Martínez et al. (2023)), peanuts for human partners and sausages or cheese for partner dogs. We chose to use a different food for the partner dogs because of two reasons. First, we used a high-quality food to ensure motivation to consistently press the button whenever it was presented. Secondly, when partners were rewarded using the side-tube (i.e. when the subject failed to press their button on time), we used sausages or cheese as rewards because it makes no noise when falling out of the tube, therefore preventing the subject to hear that their partner was being rewarded.

2.6.1 Simultaneous pressing

Simultaneous pressing condition was introduced to test whether the dogs were equally willing to manipulate the apparatus when paired with a dog or a human partner. For this reason, each subject participated in two simultaneous pressing tests, once before Experiment 1 paired with their dog partner, and once with the unfamiliar human-partner before starting the Experiment 2. Here the participants were presented with the standard setup. The buttons were shown to them simultaneously (i.e., the subject’s and partner’s button were shown at the same time) and they were both required to press them at the same time (within the time frame of 2 seconds between the two individuals pressing). We conducted sessions of 20 trials until they did 2 consecutive rounds of 14/20 correct trials.

2.6.2 General procedure: Experiment 1 and Experiment 2

After each dyad successfully completed the pre-testing procedures and simultaneous pressing test we continued with the testing, where the partner’s access to the button was delayed. We ran only one test condition per day, with a maximum of 2 conditions per week. Every test condition started with 10 warmup trials followed by 84 test trials (with a few minutes of break after every 21st trial) with delays of 3, 6 or 9 seconds. The warmup trials were identical to the test trials, with the only exception being the length of the delay. While in the warmup trials we used shorter delays (3 seconds), in the test trials we used a variety of delays (3, 6 or 9 seconds). The warmup trials worked as an introduction for the test procedure and to

familiarize the subjects to the changes in their partner's behavior. Specifically, partners no longer pressed the button immediately after it was shown. The delays were always said out loud by the experimenter at the beginning of every trial and were pseudorandomized (no delay was ever presented more than three times in a row).

During **Experiment 1**, the dog owner sat at the back of the room and was instructed to remain neutral. Partner-dogs' owners, who also sat behind his/her dogs, were instructed to remain neutral or participate according to the experimenter's instructions for each condition:

In the *Button delayed condition* (BD) the experimenter slid the subject's button out of the enclosure, but the partner's button had a delay (3, 6, or 9 seconds). The purpose of this condition was to test whether dogs understand that not only a partner's presence is important to coordinate, but also the presence of the button (see Figure 4a).

In the *Partner delayed condition* (PD) the partner dog was held by its owner at the back of the room. Here both buttons appeared simultaneously, only the owners released the partner dog after the number of seconds that the experimenter indicated at the beginning of the trial. After every trial, the owner called or retrieved the partner-dog back to the starting position for a new trial to begin. With the Partner delay condition, we tested if the dogs understand the need of a partner and not only that they obtain rewards when both buttons are reachable (see Figure 4b).

In the *Non-visibility condition* (NV) the fence between the subject was covered with black curtains, disabling the dogs to see each other, and there was a foam rug placed in the partner's area with the intention of silencing the sound of steps (note that also the sounds played by the speaker were intended especially for this condition, to cover all the partner's noises). As in the PD condition both buttons appeared simultaneously and the partner's owner was holding the dog, only this time they were not located at the back of the room but were seated only 1m away from the setup. The goal of the Non-visibility condition was to control for the subject's chance levels of performance since it is unable to see (or hear) the partner and should therefore be unable to coordinate (see Figure 4c).

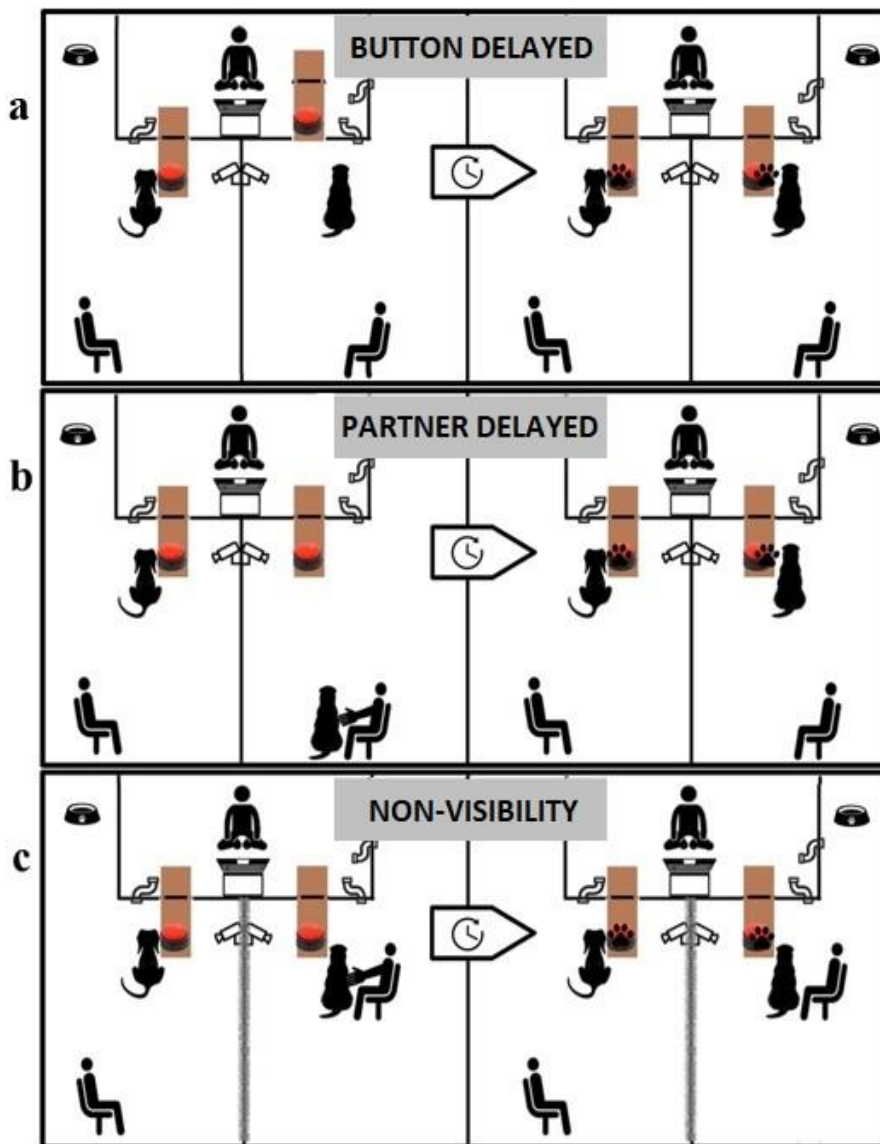


Figure 4. Conditions of Experiment 1: a) Button delayed, b) Partner delayed and c) Non-visibility. In the Figure, subjects (and their owner at the back of the room) are shown on the left side of the setup and the partner dog on the right accompanied with its owner (whose position is dependent on the condition). In all three conditions (the left part (from the arrow with a clock) shows the positions at the beginning of the trial and the right one represents the positions after the delay).

In **Experiment 2** dogs participated in two conditions with an unfamiliar human partner:

In the *Button delayed condition* (BD) the partner was seated in front of the setup and was instructed to wait for its button to appear and then to press it. Here the experimenter slid the subject's button out of the enclosure, while the partner's button had a delay (of 3, 6, or 9 seconds) (see Figure 5a).

In the *Partner delayed condition* (PD) every trial started with the partner standing at the back of the room. Both buttons were shown simultaneously but the partner was instructed to wait before approaching the apparatus according to the delay indicated by the experimenter in the beginning of the trial. The partner could count those seconds using a digital clock attached to the wall. After that time, if the dog was still waiting without pressing the button, the partner walked towards the apparatus and pressed the button (see Figure 5b).

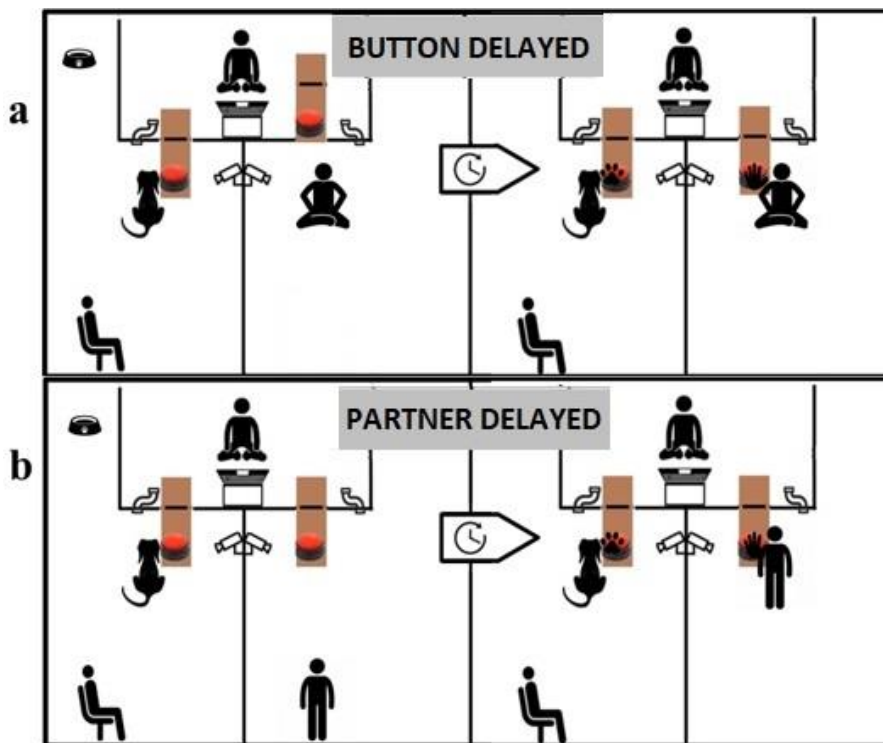


Figure 5. Conditions of Experiment 2: a) Button delayed and b) Partner delayed. In the Figure, subjects (and their owners at the back of the room) are shown on the left side of the setup and the human partner on the right. The vignette of both conditions (a and b) is divided so that the left part (from the arrow with a clock) shows the positions at the beginning of the trial and the right one represents the positions after the delay

2.7 Variables and data coding

The tests were video recorded and then coded using the Loopy system. For each test trial (both for Experiment 1 and Experiment 2) we coded whether the dog and the partner pressed the button and their latency to press the button from the beginning of the trial (when the first button was presented). The trial was coded as successful if the difference between the partner's and subject's latency was less than 2 seconds, otherwise, we coded it as a failure. For interobserver purposes, a second person, blind to the aim of the study, coded 20 % of the videos. We analyzed interobserver reliability using intraclass correlation coefficients (ICC) with the R package "irr". This revealed excellent consistency between coders (for partner's latency ICC=0.992; for subject's latency ICC=0.998).

2.8 Data analysis

All statistical analyses were conducted in R (version 4.0.3; R Core Team 2000). We fitted all the models using the function glmer of the R package "lme4" (1.1-21; Bates et al. 2018) with the optimizer "bobyqa".

2.8.1 Simultaneous pressing: are the dogs equally willing to manipulate the apparatus when paired with a dog or a human partner?

We first assessed whether dogs that were paired with familiar conspecifics performed similarly than dogs that were paired with unfamiliar conspecifics. To do that, we compared the number of sessions to pass the Simultaneous pressing test (i.e. two consecutive sessions with 14/20 successful trials) between the two types of dogs (paired with familiar vs unfamiliar dog partner) using Mann-Whitney U tests, a non-parametric test for independent samples. In addition, we compared whether dogs were faster to reach this criterion with human partners as opposed to with dog partners. To do that, we compared the number of sessions that took for each subject to pass the Simultaneous pressing test with a human partner and with a conspecific partner, using Wilcoxon Signed rank test, a non-parametric test for paired samples. All the test were two-tailed.

2.8.2 Experiment 1: Do dogs coordinate with conspecifics?

To assess if dogs coordinated with their conspecific partners above chance level, our initial plan was to compare the probability of success in the Button delayed (BD) and Partner delayed (PD) condition with the probability of success in the Non-Visibility (NV) condition. To do that we first selected only data from the tests in which dogs participated with a conspecific and then we fitted a Generalized Linear Mixed Model (GLMM; Baayen 2008) with binomial error structure and logit link function (McCullagh and Nelder 1989). We included the condition (BD, PD and NV as predictors). As there were differences in familiarity between the dog dyads and that might have had an effect on the performance of the subjects, we also included the familiarity of the partner (familiar or unfamiliar) as a predictor. We further included in the model the length of the delay (3, 6 or 9 seconds), the interaction between condition, familiarity and delay, the trial number and the test order as fixed effects. To avoid pseudo replication, both the subject identity and the partner identity were included as random factors, together with all the theoretically identifiable random slopes (interaction between condition and delay, and trial number and test order). We fitted four different versions of the model: including all the correlation parameters among the random intercepts and random slopes (Barr et al. 2013), including only those correlations for the subject random intercept, only for the partner random intercept, and finally lacking the correlation parameters. We decided to keep the simplest model without any correlation to reduce model complexity, resulting in a minor decrease in the model fit (model with correlations: $\text{LogLik}=-1817.933$, $\text{df}=86$; model with correlations for subject: $\text{LogLik}=-1822.831$, $\text{df}=58$; model with correlations for partner: $\text{LogLik}=-1838.437$, $\text{df}=58$; and model without correlations: $\text{LogLik}=-1840.99$, $\text{df}=30$). Test order, trial number and delay were z-transformed (to a mean zero and standard deviation of one) to facilitate the convergence of the model. Condition was dummy coded (the categories in the factor were replaced by several variables consisting of 0 and 1) and then centered to a mean zero before including them in the random slopes. To avoid increasing type I error due to multiple testing (Fostmeier and Schielzeth 2011), we tested the significance of the model with all the variables (full model) as compared to a null model lacking the predictors (condition and familiarity), but otherwise identical to their respective full model. We compared the full and the null model using likelihood ratio test (Dobson 2002). The hypothesis behind this model was that dogs would not be able to coordinate with

their partners when they cannot see them or hear them (NV condition). However, as during the study we failed to prevent the dogs to hear the noise of their partners pressing the button, the results of this model are not a reliable measure of how dogs' success depends on the possibility of seeing and hearing the partner's actions. For this reason, we looked for an alternative way to assess if dogs coordinated with their conspecific partners.

2.8.3 Do dogs coordinate with conspecifics? Post-hoc analysis of the latencies

Due to the unsuccessful implementation of the NV condition, we alternatively analyzed whether subject's latency to press the button (seconds from the start of the trial, when the subject's button is shown, until the subject presses) were longer in the trials with longer delays. We did not use the partner's latency as a predictor because, in the trials in which the subject pressed the button too early, the experimenter hid the button(s) and stopped the trial, so the partners never had the opportunity to press their button. Therefore, including partner's latency as a predictor would reduce our sample size to only successful trials and trials in which the subject pressed the button too late, which would have biased our model as a result of including mostly successful trials. Our approach is more conservative since we include the moment in which the partners should have pressed their button (the length of the delay) even in the failed trials.

If dogs were coordinating with their partners, they would wait for them to press the button and, therefore, they should show higher latencies in trials with longer delays. In contrast, if dogs' latencies are roughly the same independently of the length of the delay, that would show that dogs are not affected by their partner's behavior. To test this hypothesis, we selected all the trials in which the subject pressed the button (2665 trials), removing 862 trials in which subjects never pressed the button before or after the partner pressed his/her button. With this data, we fitted a model with subject's latency as variable response and length of the delay (as a factor with three levels: 3 seconds, 6 seconds, and 9 seconds delay) as predictor. We further included the interaction between condition and delay, and the trial number and test order as fixed effects. We included subject and partner's identity as random factors, together with all the theoretically identifiable random slopes (condition, delay, trial number and test order). Since our variable response (subject's latency) was not normally distributed, we fitted

the model twice: one of them with gamma distribution and the other with gaussian distribution after log transformation of the response variable. Visual inspection of the plotted residuals against the fitted values showed a most homogeneous pattern in the gaussian model, so we decided to keep that one. We fitted four different versions of the model: including all the correlation parameters among the random intercepts and random slopes, only for the subject, only for the partner, and none of them. We decided to keep the simplest model without any correlation to reduce model complexity, resulting in a minor decrease in the model fit (model with correlations: LogLik=-2060.885, df=68; model with correlations for subject: LogLik=-2080.483, df=47; model with correlations for partner: LogLik=-2064.789, df=47; and model without correlations: LogLik=-2083.288, df=26). We then compared by means of the likelihood ratio test the full model with all the variables to a null model lacking the predictor (length of delay), but otherwise identical to the full model.

2.8.4 Experiment 2: Do dogs coordinate better with unfamiliar humans than with conspecifics?

To assess if the partner had an influence on the success, we compared the dog's performance when paired with a conspecific and their performance when they participated with an unfamiliar partner. We fitted a GLMM with binomial error structure and logit link function. We included partner (human or dog) as predictor, and condition (BD and PD), length of the delay, trial and test order (if they do first with dog or with human) as fixed effects, and the interaction between condition, delay and test partner. We did not include the level of familiarity with the dog partner since it was not significant in the previous model (see results). Subject identity and partner identity were included as random factors, together with all the theoretically identifiable random slopes (interaction between condition, test partner and delay, and trial and order for subject, and interaction between condition and delay, and trial and test for partner). We fitted four different versions of the model: including all the correlation parameters among the random intercepts and random slopes (Barr et al. 2013), including those correlations only for the subject random intercept, only for the partner random intercept, and finally lacking the correlation parameters. We decided to keep the simplest model without any correlation to reduce model complexity, resulting in a minor decrease in the model fit (model with correlations: LogLik=-1817.933, df=86; model with correlations for subject:

LogLik=-1822.831, df=58; model with correlations for partner: -1838.437 LogLik=58, df=58; and model without correlations: LogLik=1840.99, df=30). Test order, trial number and delay were z-transformed (to a mean zero and standard deviation of one) to facilitate the convergence of the model. Condition and partner were dummy coded (the categories in the factor were replaced by several variables consisting of 0 and 1) and then centered to a mean zero before including them in the random slopes. We then compared by means of the likelihood ratio test the full model with all the variables to a null model lacking the predictor (partner), but otherwise identical to the full model.

2.8.5 Experiment 1 and 2: Do dogs follow different strategies between conditions?

To assess if dogs followed a different strategy (i.e., pressing when they see the partner coming vs. pressing when the partner already pressed) between conditions and between partners we compared the probability of the dog pressing the button before the partner in the successful trials in the different conditions with different partners. Here we combined the data from Experiment 1 and Experiment 2. We fitted this model excluding two of the dogs (Flora and Sixtus), that hardly have any successful trials with dog partners. We first selected all the successful trials and then we fitted a generalized linear mixed model with binomial error structure and logit link function. We included the condition and the partner (dog or human) as predictors as well as their interaction. We also included as fixed effects the length of the delay (3, 6 or 9 seconds) the trial number as the test order. To avoid pseudo replication, both the subject identity and the partner identity were included as random factors, together with all the theoretically identifiable random slopes (condition, test partner, delay, and trial number and test order for the subject; condition, delay, trial number and test order for the partner). We fitted four different versions of the model: including all the correlation parameters among the random intercepts and random slopes), including those correlations only for the subject random intercept, only for the partner random intercept, and finally lacking the correlation parameters. We decided to keep the simplest model without any correlation to reduce model complexity, resulting in a minor decrease in the model fit (model with correlations: LogLik=-1748.867, df=44; model with correlations for subject: LogLik=-1757.121, df=31; model with correlations for partner: LogLik=-1758.226, df=29; and model without correlations: LogLik=-1768.965, df=19). Test order, trial number and delay were z-transformed (to a mean zero and

standard deviation of one) to facilitate the convergence of the model. Condition was dummy coded (the categories in the factor were replaced by several variables consisting of 0 and 1) and then centered to a mean zero before including them in the random slopes. We then compared by means of the likelihood ratio test the full model with all the variables to a null model lacking the predictors (condition and partner), but otherwise identical to the full model.

For all the models, we assessed the model stability by comparing the estimates obtained from the model with estimates obtained from models with the levels of the random effects excluded one at a time (Nieuwenhuis et al. 2012). All the models were fairly stable with the exception of the model on the success in the dog-dog dyads, which was unstable for the familiarity of the partner. This was probably due to one subject that did not succeed in any trial in any of the three conditions. Visual inspection of the BLUPs (best linear unbiased predictors, Harrison, 2018) showed a deviation from normal distribution for the subject random factor. Specifically, the histogram showed that two subjects had intercepts very different from the rest which might have contributed to the instability of the model. For the test of models, BLUPs were small and/or normally distributed.

To rule out collinearity, we determined Variance Inflation Factors (VIF, Field 2005) for a standard linear model similar to the main models but lacking interactions and random effects. The maximum VIF was 1.2, which means there are no problems with collinearity. Confidence intervals were obtained using the function `bootMer`, using 1000 parametric bootstraps. To obtain more reliable p values, we obtained the p values of the fixed effects using likelihood ratio tests (Barr et al. 2013), using the function `mixed` of the package `afex` (Singman et al. 2016). Finally, in the cases in which a factor with more than two levels or its interaction was significant, we used the package “`emmeans`” (Lenth 2017) to compare the estimated marginal means of each condition with Tukey correction.

3 RESULTS

3.1 Simultaneous pressing: are the dogs equally willing to manipulate the apparatus when paired with a dog or a human partner?

To complete the Simultaneous pressing tests, dogs had to complete two consecutive rounds of 20 trials, in which they had at least 14/20 correct trials. On average, dog-human dyads needed 2.143 rounds ($sd=0.636$) to finish the simultaneous pressing training, and this phase took 2.643 rounds ($sd=0.36$) for dog-dog dyads. From those, dogs that were paired with a familiar conspecific succeeded after an average of 2.667 rounds ($sd=1.633$), and dogs paired with an unfamiliar conspecific needed an average of 2.625 rounds ($sd=1.188$). That is, dogs that were paired with unfamiliar conspecifics were equally fast to pass this test than dogs that were paired with familiar conspecifics (*Mann-Whitney* $U=25$, $p=0.929$). Additionally, it took a similar number of rounds for the dogs to succeed in the Simultaneous pressing test when paired with an unfamiliar human than with a conspecific (*Wilcoxon signed rank test* $z=12$, $p=0.279$). However, it is important to notice that dog performance shows a strong floor effect, with most of our sample being able to meet the criteria within the first two sessions (12 out of 14 dogs when paired with a human partner, 6 out of 8 dogs paired with an unfamiliar conspecific partner, and 5 out of 6 dogs paired with a familiar conspecific partner).

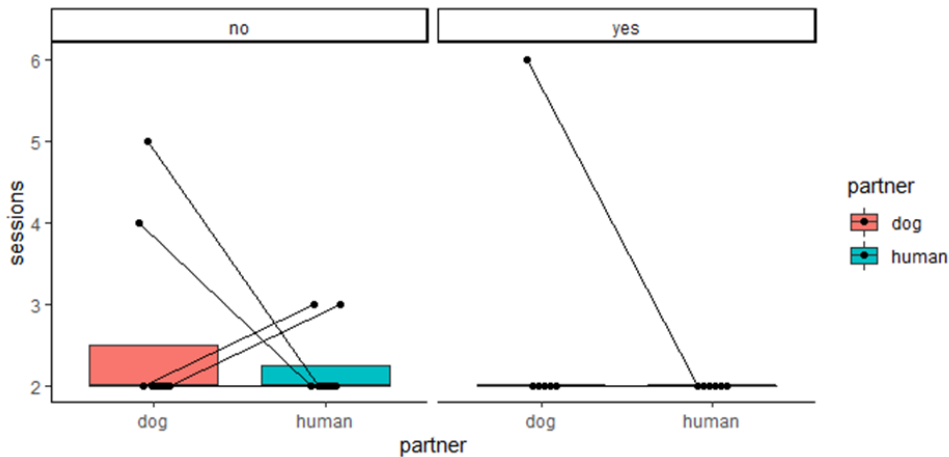


Figure 6. Boxplot showing the number of sessions the subjects needed to succeed on the x axis and different partners on the y axis. The “no” part of the y axis shows the results of subjects that participated with unfamiliar dog partners, while the “yes” represents the data of subjects paired with familiar dog partners. The lines connecting the dots represent the same subjects.

3.2 Experiment 1: Do dogs coordinate with conspecifics?

The comparison between the full and null model revealed that, overall, neither condition nor familiarity with the partner influenced the proportion of successful trials (likelihood ratio test: $\chi^2=14.645$, $df=10$, $p=0.145$). The average proportion of successful trials with familiar partners was: BD=0.619; PD=0.653; NV=0.502, while with unfamiliar ones it was: BD=0.533; PD=0.558; NV=0.449. Visual inspection of the results (see Figure 7) revealed a huge variability within the subjects. In the BD condition this happened with 13-Sixtus and 5-Flora who barely approached the apparatus also in the PD condition. Finally, in the NV condition, where we expected lower levels of success and manipulation of the setup with all dogs, this occurred only with 3 subjects. For more detailed results see also Appendix 4.

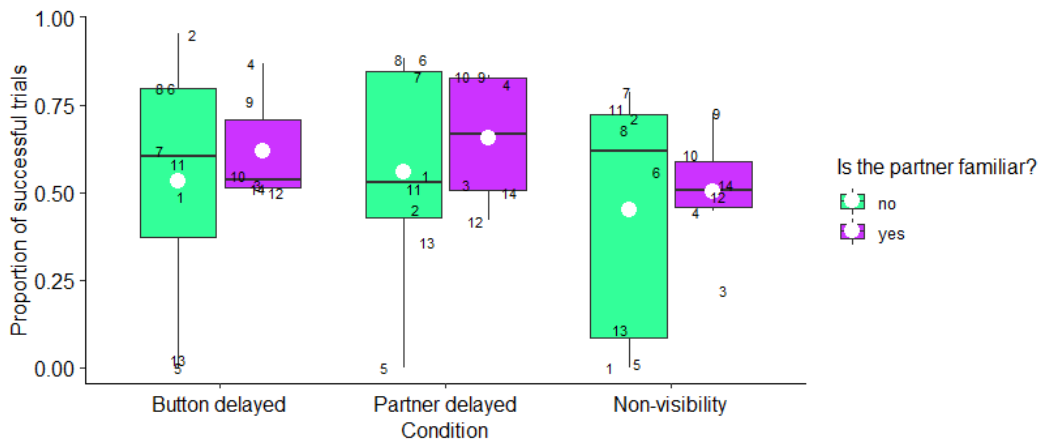


Figure 7. Boxplot showing the proportion of successful trials on the y-axis and different conditions on the x-axis. Two different colours represent familiarity among dog-dog dyads. Boxes display the interquartile range and numbers show individual data points. The black line represents the median while the white circle represents the average.

3.3 Experiment 1: Do dogs coordinate with conspecifics? Post-hoc analysis of latencies

Due to the unsuccessful implementation of the NV condition, we alternatively explored whether the subjects waited for their partners to press the button as a measure of coordination. To do that, we tested whether subject's latencies to press the button were different depending on the length of the delay in each trial (3, 6, or 9 seconds). The comparison between the full and null model revealed that the length of the delay had an influence on the subject's latency (likelihood ratio test: $\chi^2=60.120$, $df=6$, $p<0.001$). The model showed that the interaction between condition and delay was significant ($\chi^2=17.00$, $df=4$, $p<0.002$). That means that, independently of success, the length of the delay influenced the latency of the subjects, but this effect was modulated by the condition. Specifically, Post-hoc comparison revealed that, according to our prediction, subject pressed the button faster in the 3s delay than in the 6s delay, and faster in the 6s delay than in the 9s delay, both in the BD and PD condition. This means that subjects were indeed waiting when their partner/partner's button was delayed. In the NV condition, latencies were shorter in the 3s delay than the 6s second delay (estimate \pm SE=-0.365 \pm 0.066, $p<0.001$), but subject latency was not significantly different in the 6s delay than in the 9s delay (estimate \pm SE=-0.178 \pm 0.083, $p=0.114$). This suggests that dogs relied on acoustic cues to solve the task when the delays were shorter but in longer delays, they tended to press the button at random. Regarding differences between conditions, dogs were slower in the NV condition compared to the PD if the delay was 3

(estimate±SE=0.287±0.072, p=0.004) or 6 seconds (estimate±SE=0.267±0.071, p=0.007), but not in the 9 second delay (estimate±SE=0.070±0.071, p=0.597). To sum up, we see the same trend in all the conditions: subjects adjust the moment in which they press to the delay, with longer latencies the longer the delay is, and subjects are generally slower in the NV condition than in the PD condition. The only exception is the 9s delay in the NV condition, that is identical in terms to subject latency to the 6s delay.

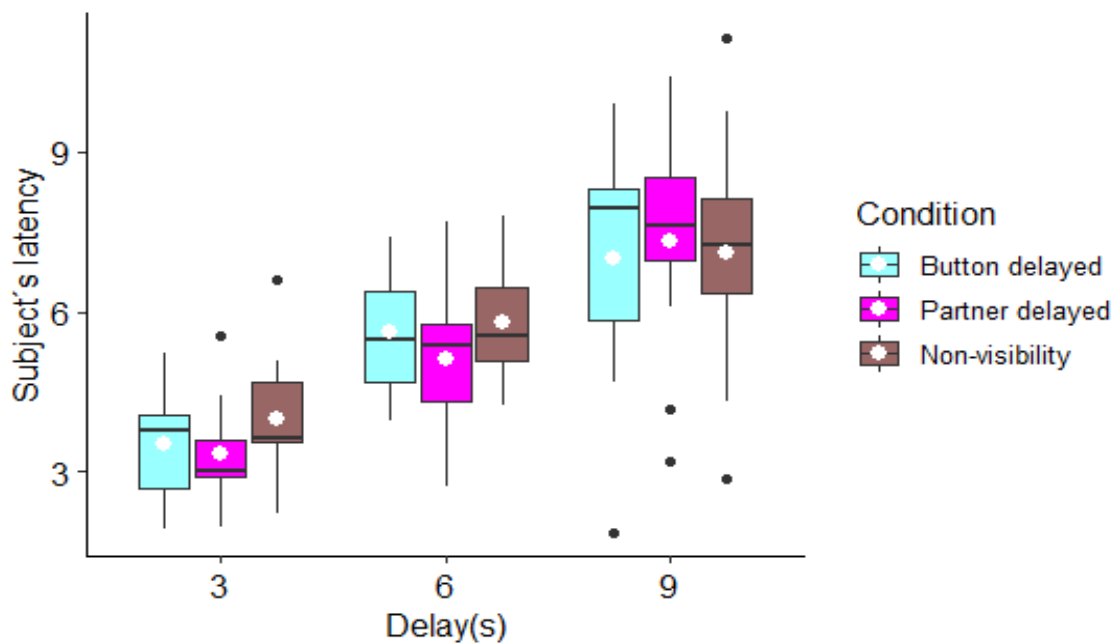


Figure 8. Boxplot representing subjects' latencies on the y-axis and the delays on the x-axis. The conditions are distinguished by three colors. Boxes display the interquartile range, whiskers represent the range of the data points within 1.5x times the interquartile range. Black horizontal line represents the median and white circles represent the average. Black circles are outliers.

3.4 Experiment 2: Do dogs coordinate better with unfamiliar humans than with conspecifics?

The comparison between the full and null model revealed that, overall, the partner (unfamiliar human or conspecific) did not have an effect on the proportion of successful trials (likelihood ratio test: $\chi^2=4.520$, $df=4$, $p=0.340$). Plotting the results, it seems that dogs performed better with human partners than with dogs. This is in line with a trend in the estimate of the effect of the partner (human or conspecific) dogs better with humans than with dogs (*estimate*=1.107, *standard error* = 0.514, $p=0.065$).

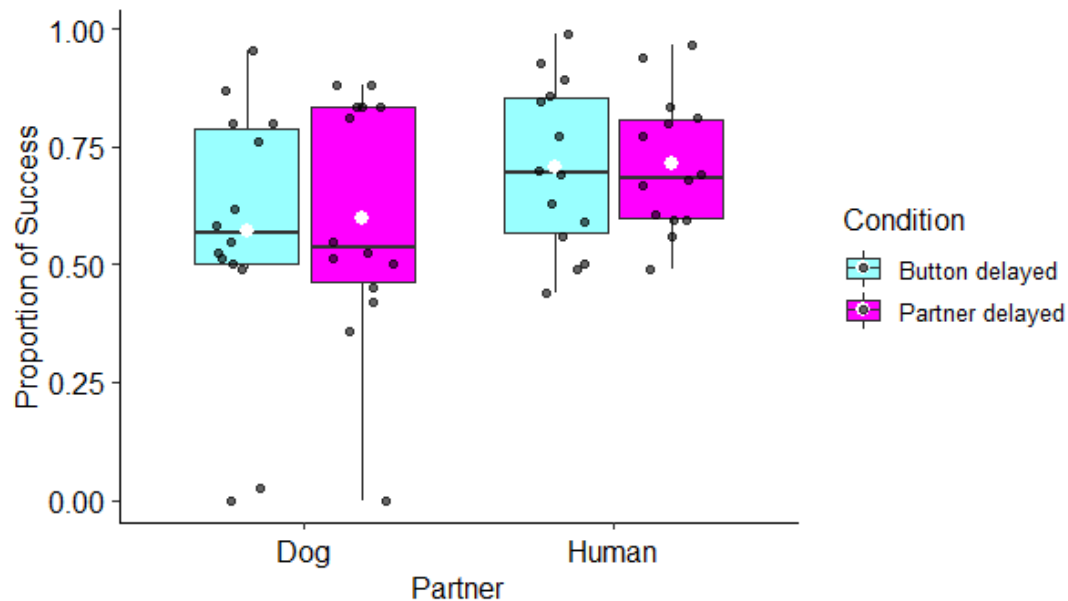


Figure 9. Boxplot representing the proportion of success (y axis) by partner (x axis) and condition (color) Boxes show the interquartile range and whiskers display the range of data points within 1.5 times the interquartile range. Black horizontal lines show the median and white circles show the mean. Black circles represent individual data points.

3.5 Experiment 1 and 2: Do dogs follow different strategies between conditions?

The comparison between the full and null model revealed that, overall, the predictors (partner and condition) have an effect on the proportion of trials in which the dog pressed the button before their partner did (likelihood ratio test: $\chi^2=16.091$, $df=4$, $p=0.003$). Specifically, we found that the interaction between condition and test partner was significant (*estimate* -1.097, *standard error* = 0.352, $p=0.003$). In dog-dog dyads, in the NV condition subjects were less likely to press first than in the BD condition (*estimate*= 1.106, *standard error*= 0.407, $p=0.018$) and PD (*estimate*= 1.647, *standard error*= 0.551, $p=0.007$), but there was no difference between the BD and the PD condition (*estimate*= 0.541, *standard error*= 0.329, $p=0.351$). With a human partner, dogs did not significantly differ in the proportion of trials in which they pressed the button first in the two different conditions (*estimate*= 0.556, *standard error*= 0.361, $p=0.272$). When comparing dog-dog dyads with dog-human dyads, dogs were more likely to be the first ones to press in the BD condition if the partner was human (*estimate*= -1.029, *standard error*= 0.616, $p=0.045$), but there was no difference in the PD condition (*estimate*=0.0678, *standard error* = 0.115, $p=0.908$).

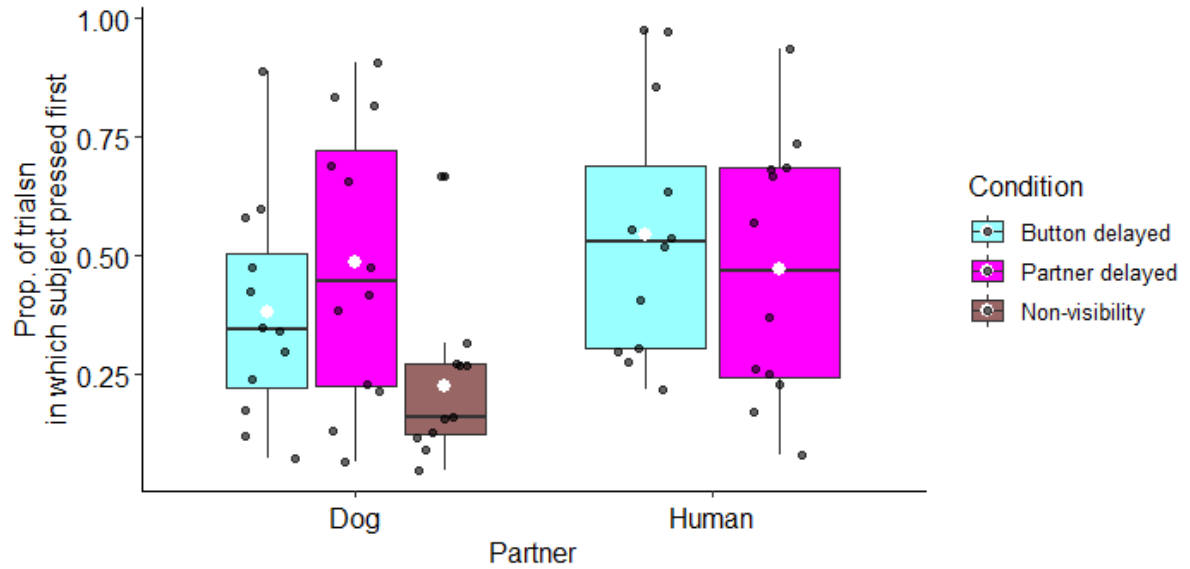


Figure 10. Boxplot representing the proportion of trials in which the subject pressed the button before the partner did. The x-axis shows different partners: Dog and Human. The conditions are distinguished with mint for BD, pink for PD and brown for NV. Boxes show the interquartile range and whiskers display the range of data points within 1.5 times the interquartile range. Black horizontal lines show the mean and white circles show the mean. Black circles represent individual data points.

4 DISCUSSION

Martinez et al. (2023) showed that dogs take into account the actions of their owners when they coordinate with them. Here we extended those findings and show that dogs in that study can generalize what they learned to new conspecifics, dogs and partners. This demonstrates that dogs' performance in Martinez et al. (2023) was not only due to the dogs responding to some specific cue from their owners or interpreting the human movement as a command that they had to obey. We also showed that, under certain circumstances, dogs can coordinate actions with conspecifics. We will discuss those findings in detail below.

Dogs in our study succeeded in the BD and PD, as an average, in approximately half of the trials. These rates are quite similar to the ones found in Martinez et al. (2023), when dogs were paired with their owner as a partner. Initially, we followed that study in using a NV condition, in which dogs could not see their partners, to use as a baseline measure of success by chance. However, in Martínez et al. (2023) human partners were instructed to remain silent and press the button softly, avoiding any noises that the dogs could use as a cue. In our study, we were unable to completely control the behavior of partner-dogs and, even if we made every possible effort to prevent the subjects from hearing the sound of their partner's actions (i.e. using a rubber mat to dampen the noise of the dogs' steps, playing different noises in the background), we noticed during the study that we failed to mask these sounds and the subjects could still use the sound as a clue. However, we decided to proceed with this condition in all our samples, so all the dogs had the same experience and test conditions. Contrary to our hypothesis, elimination of visual contact between partners did not significantly decrease the success in the NV condition. However, since we failed in the implementation of the NV condition, we cannot make any conclusions based on these results. While this was a difficulty in our planned analysis, we think it is an interesting finding for several reasons. One of them is that it allows us to compare dogs' performance with other studies that have implemented a NV condition when testing subjects with conspecific partners. Those studies have obtained different results depending on the species. In capuchin monkeys (Mendres and de Waal, 2001), coordination broke down when an opaque barrier was introduced between the members of the dyad. On the contrary, blue-throated macaws (Montaigu et al. 2020) could

still succeed in a cooperative pulling task when they could not see their partners. The reason for this difference might be due to different ecologies of each species. Capuchin monkeys live in cohesive groups in which they can usually rely on visual access to each other (Janson 1990), while for blue-throated macaws that fly in groups through dense vegetation (Yamashita and Machado de Barros 1997), auditory cues might be more relevant to detect and identify other members of the flock. Pet dogs are accustomed to urban environments, therefore auditory cues are key to their survival, allowing them to detect, for example, approaching vehicles (Singletary, 2021) or to respond to their owners calling them. Of course, this argument is highly speculative, and a wider range of animals have to be tested in the NV condition to provide a stronger conclusion.

Montaigu et al. (2020) offer a different interpretation of the macaw's performance. They argued that the task was solved using acoustic cues without considering their partner's actions. Nevertheless, we consider that explanation highly unlikely to be true in the dogs' case. When we analyzed the proportion of correct trials in which subjects pressed the button before their partner, we found that dogs' behavior was different in the NV condition compared with the BD and PD conditions. Specifically, in most successful trials in the NV condition, dogs pressed the button only after their partner already pressed theirs. In contrast, the proportion of trials in which that happened was lower for the BD and PD condition, potentially because they could anticipate their partner's movements when having visual access to them, but not in the NV condition, where the only cue available was the sound of the button. Thus, it is possible that dogs used visual information from their partners to anticipate when they would press the button but, when that information was lacking, they used a different strategy and then waited until they could hear their partners pressing the button to successfully coordinate with their action and press at the same time.

Because we could not use the NV condition as a baseline to address whether dogs were actively coordinating with their conspecific partners when they could see their actions, we analyzed whether dogs were adjusting the moment in which they pressed the button to the length of the delay for each trial. Even considering both successful and unsuccessful trials, results showed that the length of the delay had an influence on the subject's latency, meaning

that dogs were not pressing the button randomly, but they were waiting (potentially until they could see and hear their partner pressing the button) before pressing their own button depending on those delays. Therefore, we concluded that dogs in our study were coordinating with their conspecific partners, adjusting their own actions to them in order to successfully press the button at the same time.

Not only we found that dogs coordinated with their partners when they were delayed, but we found that in the first test, the Simultaneous pressing, they were equally likely to approach and manipulate the apparatus. Dogs took similar number of sessions to succeed, when tested with a conspecific compared to when tested with an unfamiliar human partner. These results might be surprising considering previous literature showing that pairs of dogs were not willing to work in proximity with a conspecific partner due to following an avoidance strategy (proximity of a food source limits their ability to cooperate) (Marshall-Pescini et al. 2017, 2018). However, the contradictory findings between our results and the previous ones can be easily explained by a few crucial differences of our study. Notably, we actively tried to minimize the tolerance problems that were affecting the previous studies. For this purpose, we used pet dogs instead of pack-living dogs (Marshall-Pescini et al. 2017, 2018, Range et al. 2019a, 2019b). While dogs in Marshall-Pescini et al. studies were tested without human mediation, in our study dogs were accompanied by their owners, which might mediate tolerance problems and facilitate playful behavior between the dogs (Mehrkam and Wynne 2021). Additionally, our setup included a fence separating the two dogs, which might have reduced potential conflicts between the dogs. It is also important to keep in mind that we carefully selected the dog partners for each subject. When it was possible, we paired them with dogs living in the same household or with subjects they were familiar to. In cases where this was not possible, we recruited dog partners for which we knew beforehand that they do not have aggression problems with other dogs. We also took owners' advice into consideration telling us which kind of dog (sex, size, breed, etc.) would be most suitable for their dog. Even then, we dismissed a variety of dog-dog combinations because they showed avoidance or aggression towards each other in the pre-testing phases. Moreover, several subjects from Martinez et al. (2023) were not included in this study because they could behave aggressively towards other dogs. On the contrary, we did not have any problems finding human partners for the dogs and, even if those were unknown humans, all the subjects

were friendly and eager to interact with them. In retrospect it seems that we pre-selected a sample of dogs that showed high tolerance with conspecifics, which might account for our results. This may also be the reason why we found that dogs paired with familiar dogs were not more successful in performance than dogs paired with unfamiliar dogs, which is contrary to previous studies that highlighted the role of affiliation in cooperative interactions in several animal species, including dogs (Molesti and Majolo 2015, Schwing et al. 2016, Asakaway-Haas et al. 2016, Quervel-Chaumette et al. 2015, Dale et al. 2020). However, while not statistically significant, we would mention the case of two subjects in our study, Flora and Sixtus. Both small breed dogs and paired with unfamiliar conspecific, successfully completed all the habituations and some of the testing phases (i.e. simultaneous testing), but then they stopped approaching the apparatus and pressing the button in the presence of their partner. This anecdotal case can be used to exemplify that when conflicts arise, even tolerant dogs that show no aggression towards conspecifics adopt an avoidance strategy, which results in cooperation breaking down (Range, Ritter and Viranyi 2015).

In summary, our results support the conclusion of previous studies pointing to tolerance problems as the explanatory factor behind the failure of dogs to cooperate with conspecifics. By demonstrating that dog-dog cooperation is possible when controlling for tolerance problems, we argue that dogs have the cognitive abilities to coordinate with conspecifics and motivational and tolerance problems can account for previous results. This can also account for the findings of Ostojic and Clayton (2014), who found that highly trained pet dogs can solve the cooperative pulling table task with conspecifics.

To further explore whether dogs were using different strategies to coordinate with conspecifics or with humans we tested the dogs in the PD and BD conditions, paired with unfamiliar human partners. Even if the performance was similar in terms of success, our results suggest that dogs followed a different strategy depending on the partner. When comparing dog-dog dyads with dog-human dyads, dogs were more likely to be the first ones to press the button in the BD condition if the partner was human. This seems to be contrary to the results of Range et al. (2019) where the dogs adapted a following role and were likely to follow their human partner's actions and wait for them to initiate the coordination. However,

a closer look suggests a different interpretation. Because we are considering only the successful trials in the current study, the dog and owner actions are in close temporal proximity to each other (maximum 2 seconds). It is possible that dogs did not wait for the human to press the button, but that they reacted when the human started to move the arm. In fact, pet dogs have been shown to be especially skilled paying attention to human actions and reading human gestures (Kaminski 2021; Udell, Dorey and Wynne 2009), which may have been helpful in our task. Alternatively, it is possible that dogs used the human button being shown as a cue to start pressing their own button. As human partners were always reliable, dogs could anticipate their partner's movements, or react to the button being shown, and immediately press their own button without waiting for their partner actually pressing. In the case of dog-dog dyads, subjects might be more likely to wait until their partners' press, as those other strategies would not be efficient in this case. Specifically, dog partners in the BD condition were not restricted, and sometimes would scratch the apparatus or move their paws even if the button was not shown there. Then, dog subjects needed to pay attention until their partners pressed to be sure they were pressing the actual button and not only scratching the wooden platform. On this note, in the PD condition there was approximately the same proportion of trials in which the subject pressed first, independently of the partner, potentially because both partners were equally reliable. Both stayed away from the apparatus and then approached and pressed.

Our study has some limitations. For example, using dogs as partners brought some difficulties to control for their performance in the study. For one, the partners were trained to press their button when it was reachable, but they did not receive any further training to ensure that they understood the task as a cooperative task. We did this because we wanted the partner dogs to reliably press the button independently of the actions of the subjects. However, partner dogs were sometimes eager to press the button and, when they had to wait, they sometimes scratched the fence or the wooden platform. Those behaviors might have caused confusion in the subjects that ended up pressing their button too early. Those errors were not observed in dog-human dyads, because the humans were strictly following instructions. Also, regarding the fact that both dog and human partners were requested to

perform the task individually and not cooperatively (they should behave in a predetermined way independently of the actions of the subject) might not be ecologically relevant.

Despite those limitations, we demonstrated that dogs in Martinez et al. (2023) did not only react to human cues or perform due to obedience, but they acquire some understanding of the mechanisms of the task, and actually coordinate with their partners actions. We also showed that dogs were flexible in their strategy, and they used different cues to solve the task depending on the partner and the condition. To provide evidence of subjects' understanding of their partner role in cooperative tasks, studies typically observe the frequency of glancing at the partner (Chalmeau and Gallo 1996, Chalmeau et al. 1997, Mendres and De Waal 2000, Hirata and Fuvva 2007), and whether subjects would wait for a delayed partner before operating the apparatus (Melis et al. 2006, Seed et al. 2008, Péron et al. 2011, Plotnik et al. 2011, Ostojić and Clayton 2014, Marshall-Pescini et al. 2017, Heaney et al. 2017, Schmelz et al. 2017, Massen et al. 2017, Jakkaola et al. 2018). In Martinez et al. (2023) they show evidence of both behaviors, with dogs waiting for their owner and looking at them before pressing the button. Here, the quality of our recordings did not allow us to analyze gazing behavior, but we replicated those findings regarding the PD condition, and we extended them to new partners, human and conspecifics. While our results show that, once tolerance problems are controlled, dogs can coordinate with both humans and conspecifics, it is still an open question whether they would be able to learn the task with another dog as a partner. This is an exciting question for future studies.

5 CONCLUSION

In conclusion, the present study shows that dogs successfully generalize what they have learned about the cooperative button task with their owner also to conspecifics and new human partners. They can wait for their partner independently if the delay is 3, 6 or 9 seconds. Contrary to our predictions, dogs were equally successful if their partner was a conspecific or a human they have never met before, showing that pet dogs' cooperative skills are not only specific to work with human partners. However, more research is needed to assess if they could not only generalize what they learned with a human partner, but also learn to coordinate with a dog partner from the beginning. Their understanding of the cooperative nature of the task is also reflected in the different strategies they use depending on the condition, behavior of their partner and the cues they are able to use to successfully participate in the task. It remains to be examined whether future studies addressing the disadvantages of our setup of the study (small sample size, controlling for aggressiveness, naïve partners and the simplicity of the task) would shed light on the factors affecting cooperative abilities of pet dogs with conspecifics.

6 ZUSAMMENFASSUNG

Zusammenfassend zeigt die vorliegende Studie, dass Hunde das, was sie über die kooperative Knopfaufgabe mit ihrem Besitzer gelernt haben, erfolgreich auch auf Artgenossen und neue menschliche Partner übertragen können. Sie können selbständig auf ihren Partner warten, wenn die Verzögerung 3, 6 oder 9 Sekunden beträgt. Entgegen unseren Vorhersagen waren die Hunde gleichermaßen erfolgreich, wenn ihr Partner ein Artgenosse oder ein Mensch war, dem sie noch nie zuvor begegnet waren, was zeigt, dass die kooperativen Fähigkeiten von Haushunden nicht nur für die Arbeit mit menschlichen Partnern spezifisch sind. Dies zeigt, dass die kooperativen Fähigkeiten von Heimtierhunden nicht nur für die Arbeit mit menschlichen Partnern spezifisch sind. Es sind jedoch weitere Untersuchungen erforderlich, um festzustellen, ob sie nicht nur verallgemeinern können, was sie mit einem menschlichen Partner gelernt haben, sondern auch lernen, sich von Anfang an mit einem Hundepartner zu koordinieren. Ihr Verständnis des kooperativen Charakters der Aufgabe spiegelt sich auch in den unterschiedlichen Strategien wider, die sie je nach Bedingung, Verhalten ihres Partners und den Hinweisen, die sie zur erfolgreichen Teilnahme an der Aufgabe nutzen können, einsetzen. Es bleibt zu prüfen, ob künftige Studien, die sich mit den Nachteilen unseres Studienaufbaus befassen (kleine Stichprobengröße, Kontrolle der Aggressivität, naive Partner und die Einfachheit der Aufgabe), Licht auf die Faktoren werfen würden, die die kooperativen Fähigkeiten von Haushunden mit Artgenossen beeinflussen.

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Table 1. Schedule of the study divided in Experiment 1, Experiment 2 and Additional requirements concerning partner dogs, all according to the number of appointments and divided on pre-test procedures and testing. 14

9 APPENDIX

9.1 Training of partner dogs to press the button

The training started independently from the setup with the experimenter giving the dog command “paw” and rewarding it constantly with high valued food. In the next step the experimenter placed the hand on top of the button and again asked the dog to give the paw. After a few successful trials the experimenter removed her hand and presented only a bare button to the dog and again gave the same command. When the dog learned to press the button whenever it was presented to it, also without the command, the training moved to the setup.

Appendix 2. Names of all 14 subjects, their sex, state of neutering, age and breed name according to AKC and their partners with their characteristics.

SUBJECT	SEX	NEUTERED	AGE (years)	BREED (AKC)	DOG PARTNER		
					familiarity ¹	sex	breed
AMY	f	no	10.20	Border Collie	Jean	f	Mixed breed
ASTA	f	no	1.75	Border Collie	Gismo	m	Mixed breed
CANDY	f	yes	12.90	Mixed breed	<u>Damon</u>	m	Whippet
FINLEY	m	no	2.85	Shetland Sheepdog	<u>Damon</u>	m	Whippet
FLORA	f	yes	1.8	Russian Toy	Miley	f	Border Collie
GRYFFINDOR	m	yes	1.85	Border Collie	Jasper	m	Labradoodle

HETTI	f	no	1.35	Mixed breed	Miley	f	Border Collie
LOKI	m	yes	3.15	Australian Shepherd	Vega	f	Border Collie
RUBY	f	yes	4.45	Mixed breed	<u>Schnee</u>	m	Mixed breed
SAHIBU	m	no	6.35	Mixed breed	<u>Jasper</u>	m	Labradoodle
SAMIRA	f	yes	6.20	Yorkshire Terrier	Jean	f	Mixed breed
SHEILA	f	yes	7.4	Mixed breed	<u>Gismo</u>	m	Mixed breed
SIXTUS	m	no	3.8	Petit Brabancon	Ben	m	Springer Spaniel
TIARA	f	no	7.10	Border Collie	<u>Vega</u>	f	Border Collie

¹Conspecifics partners that were familiar with the respective subjects are underlined.

Appendix 3. Success model detailed results.

variable	ESTIMATE	SE	DF	x ²	p	Model stability		CI	
						Min	Max	Lower	Upper
intercept	-0.830	0.655				-1.321	-0.222	-2.080	0.416
Condition (BD)	0.575	0.492	2	6.62	0.036	-0.023	1.252	-0.478	1.620
Condition (PD)	0.855	0.469				0.263	1.338	-0.039	1.820
Delay ²	-0.380	0.140	1	13.32	<0.001	-0.403	-0.317	-0.660	-0.132
Familiarity	0.829	0.990	1	0.80	0.372	0.231	1.472	-1.265	2.840
Trial ¹	0.155	0.080	1	3.17	0.075	0.109	0.217	-0.015	0.308

Test order ¹	0.127	0.228	1	0.30	0.584	-0.098	0.254	-0.364	0.615
Condition (BD)*delay	0.170	0.210	2	2.02	0.364	0.005	0.234	-0.227	0.577
Condition (PD)*delay	0.278	0.146				0.192	0.338	0.001	0.573
Condition (BD)*familiarity	0.078	0.731	2	0.02	0.991	-1.315	0.668	-1.357	1.595
Condition (PD)*familiarity	-0.054	0.694				-0.489	0.575	-1.569	1.405
Delay*familiarity	-0.036	0.192	1	2.63	0.105	-0.109	0.040	-0.4122	0.380
Condition (BD)*delay*familiarity	-0.356	0.253	2	2.74	0.254	-0.441	-0.182	-0.928	0.180
Condition (PD)*delay*familiarity	-0.277	0.207				-0.383	-0.156	-0.732	0.161

Statistically significant p-values are shown in bold.

The reference levels for the conditions was the Non-visibility condition and for familiarity the unknown partner.

¹ Predictors that were z-transformed to a mean zero and a standard deviation of one; original means (SD) were delay: 5.97(2.45), trial: 42.48(24.24), and test order: 3.00(1.29).

Appendix 4. Latencies model detailed results.

variables	ESTIMATE	SE	DF	x ²	p	Model stability		CI	
						min	max	Lower	Upper
Intercept	1.265	0.090				1.212	1.300	1.096	1.441
Condition (BD)	-0.130	0.075	2			-0.162	-0.089	-0.280	0.012
Condition (PD)	-0.287	0.065		-0.319	-0.208	-0.412	-0.152		

Delay6	0.365	0.064	2			0.326	0.423	0.247	0.486
Delay9	0.542	0.068				0.485	0.601	0.420	0.668
Trial ¹	0.114	0.019	1	15.42	<0.001	0.104	0.123	0.078	0.153
Condition order ¹	0.034	0.054	1	0.27	0.602	-0.005	0.078	-0.078	0.141
Condition (BD)*delay6	0.046	0.61	4	17.00	0.002	0.012	0.072	-0.063	0.166
Condition (PD)*delay6	0.020	0.61				-0.025	0.069	-0.096	0.135
Condition (BD)*delay9	0.0090	0.61				0.027	0.142	-0.023	0.192
Condition (PD)*delay9	0.217	0.61				0.143	0.280	0.098	0.330

Statistically significant p-values are shown in bold.

The reference levels are condition non visibility and delay 3 seconds.

¹ Predictors that were z-transformed to a mean zero and a standard deviation of one; original means(SD) were condition order: 2.89(1.30) and trial: 41.84(24.25).

Appendix 5. Partner comparison model detailed results.

variables	ESTIMATE	SE	DF	x ²	p	Model stability		CI	
						min	max	Lower	Upper
Intercept	0.129	0.406				-0.148	0.544	-0.655	0.950
Condition (PD)	0.262	0.338	1	0.11	0.745	0.056	0.707	-0.336	0.921
Delay	-0.387	0.133	1	9.65	0.002	-0.447	-0.317	-0.656	-0.143
Test partner stranger	1.107	0.514	1	3.41	0.065	0.697	1.410	0.083	2.135
Trial	0.102	0.103	1	0.92	0.337	0.054	0.158	-0.091	0.300
Test order	-0.207	0.240	1	0.73	0.393	-0.321	0.002	-0.668	0.206
Condition (PD)*delay	0.161	0.161	1	1.16	0.282	0.003	0.295	-0.149	0.495
Condition (PD)*test partner stranger	-0.337	0.353	1	0.85	0.357	-0.767	-0.148	-1.038	0.356
Delay*test partner stranger	0.012	0.162	1	0.08	0.782	-	0.102	-0.317	0.327

						0.074			
Condition (PD)*delay*test partner stranger	-0.091	0.213	1	0.18	0.672	-0.230	0.065	-0.502	0.321

Predictors that were z-transformed to a mean zero and a standard deviation of one; original means (SD) were test order: 1.5(0.5), delay 5.97(2.45): and trial: 42.5(24.25)

Appendix 6. Strategies model detailed results.

variables	ESTIMATE	SE	DF	x ²	p	Model stability		CI	
						min	max	Lower	Upper
Intercept	-0.620	0.460				-0.877	-0.316	-1.563	0.352
Condition (NV)	-1.106	0.407	2			-1.491	-0.768	-1.947	-0.316
Condition (PD)	0.541	0.392				0.314	0.807	-0.248	1.385
Test partner (unfamiliar human)	1.029	0.515	1			0.741	1.287	0.032	2.060
Condition order	0.219	0.163	1	2.05	0.153	-0.081	0.378	-0.086	0.518
Delay	0.280	0.087	1	7.43	0.006	0.238	0.320	0.111	0.449
Trial	-0.032	0.111	1	0.08	0.777	-0.083	0.033	-0.248	0.193
Condition (PD)*test partner (unfamiliar human)	-1.097	0.352	1	7.87	0.005	-1.337	-0.873	-1.781	-0.385

The reference level for the test partner (unfamiliar human) was the dog partner.

Predictors that were z-transformed to a mean zero and a standard deviation of one; original means (SD) were test order: 3.07(1.46), delay 5.73(2.43): and trial: 43.5(24.21).