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# How chimpanzees decide in the face of social and nonsocial uncertainty

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Uncertainty can arise in interactions with both social partners and nonliving objects. Previous research has shown that humans display higher aversion to uncertainty arising from social interactions than to uncertainty caused by interactions with objects such as gambling machines, and that this difference may be mediated by betrayal aversion. We investigated whether chimpanzees, *Pan troglodytes*, differentiate between social and nonsocial forms of uncertainty. Subjects participated in two experiments, each involving a social and a nonsocial condition. In both experiments, choosing the safe option resulted in immediate access to low-value food. Choosing the uncertain option could result in access to high-value food, but only if the partner (social condition) or a machine (nonsocial condition) proved trustworthy. In experiment 1, where chimpanzees had no prior information on reciprocation rates (i.e. decided under uncertainty), chimpanzees were less likely to choose the uncertain option when they interacted with a partner than with a machine. When they did choose the uncertain option, chimpanzees also hesitated longer in the social condition. In experiment 2, where chimpanzees had learned the statistical probabilities on reciprocation rates (i.e. decided under risk), they did not distinguish between social and nonsocial situations and were generally risk averse. These results suggest that chimpanzees are more averse to engaging in uncertain choices when the source of uncertainty is a conspecific than when it is a machine; when confronted with risky choices, chimpanzees show no such tendency.

In their natural habitat, chimpanzees, *Pan troglodytes*, face myriad situations that present substantial risks and require choices. Should they enter situations of conflict and engage in intergroup aggression (Wittig & Boesch, 2003)? Should they cross a potentially dangerous road (Hockings, Anderson, & Matsuzawa, 2006)? How should the risks and benefits of hunting and mating be traded off (Gilby, Eberly, Pintea, & Pusey, 2006)? With which conspecific should one tackle a problem that requires collaboration (Melis, Hare, & Tomasello, 2006)? Chimpanzees' behavioural decision making in such contexts exhibits important similarities to human decision making (Rosati, 2017; Santos & Rosati, 2015). For instance, it has been argued that chimpanzees, like humans, show systematic deviations from rational choice theory, such as framing effects (Krupenye, Rosati, & Hare, 2015; but see Kanngiesser & Woike, 2016) and endowment effects (Brosnan et al., 2007; but see Kanngiesser, Santos, Hood, & Call, 2011).

One especially important condition for adaptive decision making is uncertainty (see Kozyreva & Hertwig, 2019). Frequently, decision makers have no or very incomplete knowledge with respect to the outcome and probability space of the consequences of their decisions and actions. Knight (1921/1964; see also Keynes, 1936/1973, 1937) distinguished the world of unmeasurable uncertainty from the world of measurable risk. Using the classic terminology of Luce and Raiffa (1957/1989, p. 13), in decision making under risk, ‘each action leads to one of a set of possible specific outcomes, each outcome occurring with a known probability. The probabilities are assumed to be known to the decision maker’. In contrast, the realm of decision making under uncertainty encompasses situations in which ‘either action or both has as its consequence a set of possible specific outcomes, but where the probabilities of these outcomes are completely unknown or are not even meaningful’ (Luce & Raiffa, 1957/1989, p. 13). It is worth emphasizing that in Knight's and Keynes's original notion of uncertainty, the state of the world or mind is characterized by incomplete or lack of knowledge of

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possible outcomes. In humans, choices under risk and uncertainty are commonly studied by giving participants a series of choices between monetary lotteries. In line with Luce and Raiffa's definition, probability information is (sometimes partly) removed under uncertainty (in economics this situation is also referred to as ambiguity; Ellsberg, 1961), whereas outcomes and probabilities are fully stated (either visually or numerically) under risk. In the latter context, participants make decisions from description: in choosing one option, they can rely on a priori communicated probabilities (Hertwig, Barron, Weber, & Erev, 2004). As other animals do not base their communication on symbols, all their decisions (e.g. about where to forage) are necessarily decisions from experience (but see Heilbronner & Hayden, 2016). When making decisions, animals may rely on subjective estimates or intuitive statistics based on past experiences (for a discussion on the description–experience gap in humans see Hau, Pleskac, & Hertwig, 2010; Hertwig, 2015; Wulff, Mergenthaler-Canseco, & Hertwig, 2018).

In recent years, comparative researchers have begun to investigate the evolutionary pathway of decision mechanisms under uncertainty and risk by adapting economic risk paradigms for use with great apes (Rosati, 2017; Santos & Rosati, 2015). For instance, Heilbronner, Rosati, Stevens, Hare, and Hauser (2008) studied the behaviour of chimpanzees and bonobos, *Pan paniscus*, in an economic risk-taking task. Subjects made a series of choices between a safe option that granted four pieces of food and a risky option that granted either one piece or seven pieces with equal probability. Although both options had the same expected value, chimpanzees preferred the risky option (with risk defined as outcome variance, as is common in economic choice theory). Moreover, chimpanzees were more risk taking than bonobos. Haun, Nawroth, and Call (2011) investigated risky choices in all four great ape species: chimpanzees, bonobos, gorillas, *Gorilla gorilla*, and orang-utans, *Pongo abelii*. Apes chose between a safe and a risky reward with varying expected values. The size of the safe reward and the number of cups under which the risky reward was potentially hidden were systematically manipulated. Findings indicated a high overall rate of choosing the risky option in all four great apes. Rosati and Hare (2010) investigated how uncertainty affects chimpanzees' and bonobos' decision strategies. In one condition, subjects chose between a safe and a risky option with known outcomes and probabilities; in another condition, subjects selected between a safe and an uncertain option with unknown probabilities and outcomes of obtaining food. Although the options' expected values in both conditions were identical, chimpanzees and bonobos chose the risky option, relative to the safe option, more often than they chose the uncertain option relative to the same option. Although this effect diminished with time, the results suggest that great apes are sensitive to different degrees of lack of knowledge when making decisions. These findings converge in suggesting that chimpanzees are generally risk seeking and thus appear to differ in their risk attitude from humans' frequently observed risk aversion.

The studies reviewed above share a common feature: They investigated chimpanzees' decision making under uncertainty and risk as a game against nature, that is, in the context of an interaction with the physical environment. In these studies, the human experimenter can be considered part of the physical environment, given that the experimenter draws rewards randomly, without looking, and acts like a 'nonsocial' chance generator (see Eckert, Rakoczy, Call, Herrmann, & Hanus, 2018, showing that chimpanzees appear to assume random sampling by human experimenters, an assumption that can be altered under specific circumstances). However, individuals also make decisions under uncertainty and risk when interacting with the social environment (see also Hertwig, Hoffrage, & the ABC Research Group, 2013). Several lines of evidence suggest that humans process and view risk and uncertainty in social and nonsocial settings differently (Blount, 1995; Bohnet & Zeckhauser, 2004; Fehr, 2009; FeldmanHall & Shenhav, 2019; Li, Turmunkh, & Wakker, 2019; Rilling, King-Casas, & Sanfey, 2008). For instance, in a series of experiments, Bohnet, Greig, Herrmann, and Zeckhauser (2008) compared individuals' willingness to engage in two odds-and-payoffs situations that differed only in terms of the possible outcome: in one, the possible outcome was a function of a chance device in a dictator game and, in the other, the possible outcome was a function of the trustworthiness of another player in a trust game. Results from six different cultures suggest that participants' stated minimum acceptable odds were higher for the trust game than for the risky dictator game. Humans are thus more averse to risks brought about by social partners than to risks brought about by random chance. One factor that may explain this difference is betrayal aversion (Bohnet et al., 2008; Fehr, 2009): being duped by a social partner prompts stronger negative emotions than does being let down by a nonsocial agent (e.g. nature or a machine).

Several primate species have been shown to be sensitive to the degree of uncertainty in situations where payoffs vary as a function of a partner's choice (for a review, see Rosati, 2017). Specifically, chimpanzees display sensitivity to social uncertainty in competitive interactions: they use their knowledge about what conspecifics can and cannot see to devise effective social-cognitive strategies in food competition situations (Hare, Call, Agnetta, & Tomasello, 2000). Similarly, many cooperative social interactions that have been studied in chimpanzees are also characterized by a degree of uncertainty to the extent that their outcome depends on the behaviour of another individual, as in the stag hunt game (Bullinger, Wyman, Melis, & Tomasello, 2011; Duguid, Wyman, Bullinger, Herfurth-Majstorovic, & Tomasello, 2014), the ultimatum game and other negotiation games (Jensen, Call, & Tomasello, 2007a; Melis, Hare, & Tomasello, 2009), the trust game (Engelmann & Herrmann, 2016; Engelmann, Herrmann, & Tomasello, 2015) and interdependent, mutualistic scenarios (Melis et al., 2006).

Previous research thus suggests that chimpanzees take uncertainty about their partner's behaviour into account when making decisions in competitive and cooperative social situations. Whether chimpanzees, like humans, distinguish between social and nonsocial forms of uncertainty and risk, however, is unclear. This question is of considerable interest as chimpanzees are highly social animals and regularly make decisions in both social and nonsocial contexts. Studying how chimpanzees respond to uncertainty and risk in social and nonsocial situations will shed light on how, and how differently, one of humans' closest living relatives navigates these contexts. Most relevant to the current investigation is the recent study by Calcutt, Proctor, Berman, and de Waal (2019), which found that female chimpanzees are more averse to social than to nonsocial risk. However, the authors did not differentiate between chimpanzees' behaviour in uncertain situations and their behaviour in risky situations. In addition, their results are hard to interpret because it is unclear whether chimpanzees fully understood the set-up and its contingencies (see Calcutt et al., 2019). We therefore conducted two experiments to investigate whether chimpanzees distinguish between social and nonsocial forms of uncertainty as well as risk. To this end, we adapted a method that has previously been used with chimpanzees, the trust game (Engelmann & Herrmann, 2016; Engelmann et al., 2015), and we took the necessary steps to confirm chimpanzees' understanding of the task. Chimpanzees were presented with a safe option, in which low-value food was reliably provided, and an uncertain (or risky) option, in which high-value food was provided only half of the time. In the social condition, the outcome of the uncertain (or risky) option ostensibly depended on a conspecific's decision to send the food back to the subject; in the nonsocial condition, it depended on a machine. In experiment 1, the potential outcomes were visible to the subject, but the reciprocation rates of the partner/machine were unknown; the interaction thus involved uncertainty and provided us with a measure of chimpanzees' behaviour in uncertain contexts. In experiment 2, potential outcomes were visible, and probabilities were known (chimpanzees made decisions based on the statistical probabilities experienced in experiment 1). The interaction thus involved risk. In experiment 1, chimpanzees were exposed to the safe option and the uncertain option in separate trials; they decided to pull or not pull (go/no-go) the rope leading to that option. This allowed us to study their preferences towards both options separately and to familiarize them with the payoff probabilities associated with each option. In experiment 2, chimpanzees were exposed to the safe and the risky option simultaneously and decided between the two options.

For experiment 1, we predicted that chimpanzees would pull the uncertain option less often in the social than in the nonsocial condition (P1). This is based on findings demonstrating that in decisions under uncertainty, humans are more averse to social than to nonsocial settings (Bohnet et al., 2008; Fehr, 2009). Furthermore, we predicted that chimpanzees' decision to pull the uncertain option would take longer in the social condition, that is, they would hesitate longer than in the nonsocial condition (P2). This prediction is based on findings showing that under uncertainty an increase in response latency is a proxy of cognitive conflict in nonhuman animals (Call, 2012). We predicted that the cognitive conflict would be greater in uncertain social compared to uncertain nonsocial situations (based on P1). Additionally, we predicted that chimpanzees would show more negative emotional reactions to the uncertain option in the social condition than in the nonsocial condition (P3). This prediction is based on findings suggesting that humans exhibit betrayal aversion in uncertain social situations (Bohnet et al., 2008; Fehr, 2009). In nonhuman animals, affective responses are often accompanied by changes in arousal level, as indicated by behavioural responses (see Baker & Aureli, 1997; Call, 2012; Jensen, Call, & Tomasello, 2007b; Rosati & Hare, 2013).

For experiment 2, we predicted that chimpanzees would be more averse to choosing the risky option in the social condition than in the nonsocial condition (P4). This prediction is based on the finding that humans (Bohnet et al., 2008) and female chimpanzees are more averse to social than to nonsocial risk (Calcutt et al., 2019). We also investigated whether subjects' sex, age and hierarchy position are possible predictors for chimpanzees' risk-taking behaviour (P5). We refrained from stating a prediction as it is an open question whether these properties of individuals, like in humans, influence risk-taking behaviour in chimpanzees. Finally, we were interested in whether subjects' choice of the risky option depended on whether the risky choice in the previous trial led to a reward (P6). Existing results on this possible contingency have been mixed (see Calcutt et al., 2019; Melis et al., 2006; Rosati & Hare, 2013).

## METHODS

### *Participants*

Thirteen chimpanzees (eight females) ranging in age from 11 to 30 years (mean = 23 years) participated in the two experiments. Each subject was paired with a neutral partner (see the Appendix for details on how we determined neutral partners). One additional male chimpanzee did not pass the apparatus understanding test and therefore acted solely as a partner. Four of the subjects (two females) acted as partners after participating in the experiments themselves. For more information on subjects and their partners, see Appendix Table A1.

### *Ethical Note*

Chimpanzees had access to a large outdoor enclosure during the day and received regular daily feedings, daily enrichment sessions, and water ad libitum. Subjects participated in the experiments voluntarily and were never deprived of food or water. The research was noninvasive and carried out in accordance with the guidelines of the Pan African Sanctuary Alliance and the regulations of Sweetwaters Chimpanzee Sanctuary.

Most of the apes at Sweetwaters Chimpanzee Sanctuary were born in the wild and came to the sanctuary after being confiscated at an early age (ca. 2–3 years old) as a result of the trade in apes for pets and bushmeat. Once the apes arrived at the sanctuary, they were raised by humans together with peers until they were old enough to join a mixed-age social group. Sweetwaters Chimpanzee Sanctuary hosts two groups of chimpanzees (17 individuals in group 1, 10 females and seven males, all between 4 and 31 years of age, and 22 individuals in the second group, 10 females and 12 males, all between 1 and 39 years of age). From group 1, 13 chimpanzees participated in the two experiments.

All chimpanzees live in social groups. During the day chimpanzees have access to large tracts of outdoor enclosures, including trees, bushes and climbing structures (group 1: 29.09 ha; group 2: 35.31 ha). In the evening, all individuals return from the outdoor enclosures and stay in indoor enclosures overnight. Subjects are tested in familiar rooms in their indoor enclosures and are never deprived of food or water for any reason; they are fed a combination of fruits, vegetables and other species-appropriate foods three times daily.

The full procedure of the study was approved by the local ethics committee at the Sanctuary (board members and veterinarian), the Kenya Wildlife Service and the National Council for Science and Technology, Kenya. A research permit was issued by the National Council for Science and Technology, Kenya (NACOSTI/P/19/7557/27803; NACOSTI/P/18/24055/20857).

All testing was strictly voluntary. During testing a subject could indicate its wish to stop participating at any time (e.g. by leaving the test area and/or sitting by the door). All chimpanzees were highly motivated to participate.

### *Materials*

The same apparatuses (see Fig. 1) were used for both experiments. The safe option consisted of a small vehicle loaded with low-value food (one piece of banana) on an 80 cm long track. Pulling the rope for the safe option resulted in direct access to the food reward. The uncertain/risky option consisted of a small vehicle loaded with high-value food (two pieces of banana and a quarter of an apple) on a 300 cm track. Pulling the rope for this option resulted in the vehicle moving along the track to a partner (social condition) or a machine (nonsocial condition).

### *Design*

In a within-subjects design, subjects participated in two experiments: decision making under uncertainty (experiment 1) and decision making under risk (experiment 2). Both experiments comprised both a social condition and a nonsocial condition. Half of the subjects were first presented with both social conditions (experiment 1 followed by experiment 2), followed by both nonsocial conditions (experiment 1 followed by experiment 2); the other half were first presented with both nonsocial conditions, followed by both social conditions. Each chimpanzee had the same partner in both experiments and conditions. Subjects participated in one test session per day.

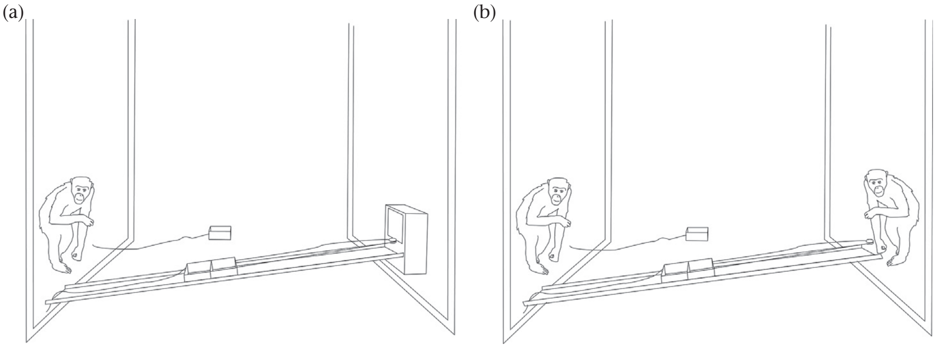

**Figure 1.** Experimental set-up. (a) Nonsocial condition and (b) social condition. The subject is depicted on the left and the machine (or partner) on the right side of the apparatus. The safe rope is on the left side of the subject and the uncertain/risky rope on the right side. In experiment 1 (decision making under uncertainty), only one of the two ropes was present at a time. In experiment 2 (decision making under risk), both ropes were present and subjects could choose between the two options.

Experiment 1, decision making under uncertainty, consisted of 48 decision-making trials per condition (24 safe trials; 24 uncertain trials), presented across four sessions. Each session consisted of six safe trials (i.e. only the safe option was present) and six uncertain trials (i.e. only the uncertain option was present). The safe option guaranteed immediate access to low-value food (100% rewarded); the uncertain option gave access to high-value food, but only 50% of the time. Throughout experiment 1, chimpanzees experienced the relative frequencies (probabilities) and outcomes of the respective options. Our use of 24 trials per option was based on reported learning effects of relative frequencies in apes (see Rosati & Hare, 2010). Experiment 2, decision making under risk, consisted of 24 decision-making trials per condition, presented across four sessions. In all trials, both the safe and the risky option were available. Prior to each test session in experiment 2, chimpanzees received four reminder trials to remind them of the outcomes and probabilities of each option: two safe trials resulting in immediate access to low-value food and two uncertain trials with a 50% chance of obtaining high-value food.

### Familiarization Phase

All subjects first completed a food preference test. They were then introduced to the experimental set-up and their understanding of the apparatus was tested. Those subjects who passed the apparatus understanding test participated in the two experiments.

#### Food preference

Each subject completed a food preference test comprising two consecutive sessions of 10 trials each. Subjects chose between two food options: one the same as the safe option (one piece of banana) and the other the same as the uncertain/risky option (two pieces of banana and a quarter of an apple). For each trial, food pieces were placed on two dishes on a sliding platform behind an occluder. The occluder was then removed and the sliding platform was pushed towards the subject. The subject selected one of the two food options and received the selected food. The nonselected option was removed and placed in a food bucket. After each trial, the occluder was placed back on the platform, and preparation for the next trial began. The location of the two food options (left or right side) was randomized and evenly distributed over the 10 trials. The option selected in at least 80% of trials in the two consecutive sessions was categorized as high-value food. For all subjects, this was two pieces of banana and a quarter of an apple.

#### Apparatus understanding

In four consecutive steps, all subjects were then individually introduced to the experimental set-up and their understanding of the apparatus was tested. Partners were not present. Individuals participated in one session per day.

In the first step, subjects were exposed to the safe rope and the uncertain/risky rope separately. The criterion for apparatus understanding was that they successfully pulled the respective rope within 60 s eight out of 10 times in one session. In the case of the uncertain/risky rope, moreover, they had to pull the rope within 60 s (room 2), move to the opposite room (room 3) via the overhead runway, eat the high-value food from the second compartment, send the vehicle back, move back to room 2, and eat the high-value food from the first compartment (see Fig. 2). This procedure was implemented to ensure that subjects learned to pull the vehicle all the way up to the other side, as the food in the second compartment was accessible only once the vehicle was pulled to the top of the track. In the test trials, only the compartment close to the subject was baited with food.

In the second step, both ropes were present but only one option was baited. The criterion for apparatus understanding was that subjects chose the correct rope (the one giving access to food) in at least eight of 10 trials in two subsequent sessions. Once subjects started pulling one rope, an experimenter removed the other rope. Chimpanzees thus experienced that they could only pull one rope during each trial.

The third step was identical to the second, except that there was no food in the second food compartment in the uncertain/risky option. The criterion for apparatus understanding was that subjects chose the correct rope (the one giving access to food) in at least eight of 10 trials. Again, once subjects started pulling a rope, an experimenter removed the other. Chimpanzees thus experienced that they could only pull one rope during each trial and that their partner would not be able to access food on the other side (room 3) if only the first food compartment was baited.

The fourth step exposed subjects to a set-up closely matching that of the actual experiments: both ropes were present and both options were baited (there was no food in the second food compartment in the uncertain/risky option). The overhead runway between the two rooms was open and chimpanzees could move between the rooms. Subjects participated in two sessions of 10 trials each. Chimpanzees chose to pull the uncertain/risky rope in 72% of the trials.

Importantly, chimpanzees were not in any way trained to pull the uncertain/risky or safe rope. In steps 1, 2 and 3 they pulled each

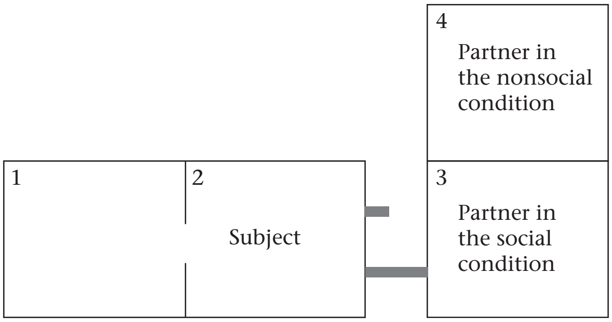

**Figure 2.** Testing rooms with position of the chimpanzees (subject and partner) in experiments 1 and 2. The grey bars between rooms 2 and 3 represent the safe option (small bar) and the uncertain/risky option (larger bar).

rope an equal proportion of times. In step 4, they were rewarded for pulling either the uncertain/risky rope or the safe rope. Following the familiarization phase, chimpanzees engaged in the two experiments.

## *Experiment 1: Social and Nonsocial Uncertainty*

### *Procedure*

In experiment 1, chimpanzees were separately exposed to the safe option and the uncertain option and decided to pull or not pull (go/no-go) the rope leading to that option in both a social and a nonsocial condition. More specifically, chimpanzees entered room 2 at the beginning of each trial and only one option (i.e. the safe rope or the uncertain rope) was present. Pulling the safe rope resulted in immediate access to low-value food for the subject. Pulling the uncertain rope resulted in the vehicle moving along the track to the partner (social condition) or machine (nonsocial condition). The partner or machine could not access the high-value food but ostensibly sent, or did not send, the baited vehicle back to the subject (see Figs. 1 and 2). Choosing the uncertain option could thus result in access to high-value food for the subject, but only if the partner or machine proved trustworthy. To the subject, it looked as if the partner or machine had made the choice, but it was the experimenter who covertly pulled a transparent fishing line to send the vehicle back. In both conditions, the experimenter systematically manipulated the reciprocation rate for the uncertain option, ensuring that subjects were rewarded 50% of the times that they pulled the uncertain rope. The reciprocation rate was pseudorandomized, with a maximum of two consecutively rewarded (or not rewarded) trials in a row. To ensure that the partner in the social condition was close to the rope for the uncertain option when the decision to send the food back was made, the experimenter placed peanuts in the partner's food tray (located directly under the compartment where the vehicle arrived in room 3) before the actual trial started. In the nonsocial condition, partners were present in room 4 (to control for the mere presence of another individual) and the experimenter placed peanuts in room 4 to keep this feeding aspect constant across conditions (see Fig. 2). The social and nonsocial test trials were thus identical, except that the nonsocial condition involved a machine rather than a conspecific partner. Chimpanzees had 30 s to pull the rope. If they did not pull the rope within 30 s, the experimenter pulled the rope after 30 s to ensure that all chimpanzees had the same experience of the relative frequencies (in preparation for experiment 2). To control for the delay in receiving the reward in the uncertain option in both conditions, the food was sent back 5 s after the vehicle reached the other side in rewarded trials. All rewarded trials ended once subjects finished eating the food. If the uncertain trial was not rewarded, it ended 30 s after the vehicle reached the other side. This was to ensure that the duration of trials was identical, regardless of whether the subject's choice was rewarded or not.

### *Coding and reliability*

We were interested in whether and, if so, when chimpanzees pulled the uncertain rope. If chimpanzees did not pull the uncertain rope within 30 s, we coded this as aversion to pull. If they did pull the rope, we measured the latency from chimpanzees entering the room to starting to pull the rope. The latency for trials in which chimpanzees did not pull the rope was set to 30 s. Finally, we coded whether chimpanzees showed an affective response. The following behaviours were coded (see Baker & Aureli, 1997; Jensen et al., 2007b; Rosati & Hare, 2013): (1) negative emotional vocalizations, particularly screams; (2) scratching, particularly body or head scratches with nails; (3) banging, particularly banging against the apparatus or the mesh with hands or feet; (4) agitated movements, that is, restless behaviour such as walking in circles or swinging. Coding of affective responses began as soon as chimpanzees entered room 2 and ended when they received food (or 5 s after the food vehicle reached the partner's side in trials where chimpanzees received no food).

All trials were videotaped with two cameras. The first author coded all trials live as well as later from videotape. Owing to camera failure, eight trials could not be coded. A research assistant who was unaware of the study design and our predictions independently coded 20% of all trials. Interrater agreement was calculated in R (R Core Team, 2019) using the function kappa2 (Cohen's $\kappa$) for nominal-scaled data and kripp. alpha (Krippendorff's $\alpha$) for ratio-scaled data of the irr package (Gamer, Lemon, & Singh, 2019). Interrater agreement was good to excellent for aversion to pull (Cohen's $\kappa = 1.00$), latency to pull (Krippendorff's $\alpha = 0.95$) and negative affective responses (Cohen's $\kappa = 0.69$).

## *Experiment 2: Social and Nonsocial Risk*

### *Procedure*

In experiment 2, chimpanzees were simultaneously confronted with a safe option and a risky option in both a social and a nonsocial condition. They could decide to pull either rope, and made their decisions based on the statistical probabilities and outcomes experienced in experiment 1. Subjects received four reminder trials about each option before each test session (see Design). As in experiment 1, only one option was present at a time in these reminder trials. After completing the reminder trials, chimpanzees engaged in the actual test trials. The set-up and procedure were the same as in experiment 1, with the only difference that during each test trial both options, the safe rope and the risky rope, were present. Chimpanzees had 60 s to make a choice. Once the subject had decided to pull one rope, the experimenter removed the other rope.

Owing to experimenter error, one chimpanzee (Kisa) participated in his last nonsocial session of experiment 2 after completing both social conditions (experiment 1, followed by experiment 2).

### *Coding and reliability*

We were interested in whether chimpanzees pulled the risky rope. Moreover, to analyse whether the choice of the risky option was predicted by a rewarded or not rewarded risky choice in the previous trial, we analysed all trials (from the second trial onwards) that followed the choice of the risky rope. (By design, the first trial could not be influenced by a previous reward.) Additionally, in an exploratory analysis, we investigated whether chimpanzees waited longer before making a decision in the social condition than in the nonsocial condition. Specifically, we coded the time between chimpanzees entering the room and starting to pull either rope.

Finally, we coded chimpanzees' affective responses (for coding details see experiment 1).

All trials were videotaped with two cameras. The first author coded all trials live as well as later from videotape. Owing to camera failure, 19 trials could not be coded. A research assistant who was unaware of the study design and hypothesis independently coded 20% of all trials. Interrater agreement was excellent for choice of the risky option (Cohen's $\kappa = 1.00$) and latency to pull (Krippendorff's $\alpha = 0.90$).

### Analysis

The predictions (P1–P6) and the analysis plan of this project were preregistered at the Open Science Foundation (see Stevens, 2017, for a discussion of replicability and reproducibility in comparative psychology). All models were fitted in R (R Core Team, 2019) using the function lmer (for linear mixed models) or glmer (for generalized linear mixed models) of the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) with the optimizer bobyqa. The general procedure for all analyses was as follows. We first established the significance of the full model by running a full–null model comparison using a likelihood ratio test (Dobson, 2002). We compared the full model with the respective reduced model that lacked the effect to be tested but had the same random effect structure (Forstmeier & Schielzeth, 2011). For the preregistered models in experiment 1, we included condition as a fixed effect. To control for the sequence of testing days, session was included as a further fixed effect. The random effect structure comprised subject, partner and session ID (nested in subject) as random intercepts. We included session ID to account for the possibility that the effect of session varied between individual chimpanzees. As random slopes, we included session number in subject and partner, as well as condition in subject and partner. For the preregistered models in experiment 2, we included condition as well as subject's sex, age and hierarchy position as fixed effects. Session was included as a further fixed effect. The random effect structure comprised subject, partner and session ID (nested in subject) as random intercepts. As random slopes, we included session number and condition in subject, as well as session number, condition and subject's sex, age and hierarchy position in partner. Session number, age and hierarchy position were *z* transformed. Factors entered as random slopes (sex and condition) were dummy coded and centred. To avoid creating an excessively complex model, we did not include correlations between random intercepts and random slopes or correlations between random slopes. Barr, Levy, Scheepers, and Tily (2013) have shown that exclusion of these correlations does not substantially affect Type I error rate.

## RESULTS

### Experiment 1: Social and Nonsocial Uncertainty

For the analysis of experiment 1 we investigated all trials in which only the uncertain option was present.

According to P1, chimpanzees should pull the uncertain option less often in the social than in the nonsocial condition. To test this prediction, we used a generalized linear mixed model with binomial error distribution and logit link function to analyse whether aversion to pull the uncertain rope was influenced by condition (Model 1.1; see Appendix for details). The full model differed significantly from the null model ($\chi^2_1 = 41.486$, $P < 0.001$, $N = 96$). More specifically and consistent with P1, in the social condition, chimpanzees refused to pull the uncertain rope in 12% of uncertain trials but only in 4% of the trials in the nonsocial condition (Fig. 3). We found no significant effect of session ($\chi^2_1 = 0.056$, $P = 0.812$). Furthermore, we investigated whether order of presentation (social or nonsocial condition first) affected the aversion to pull by including the first condition as a fixed effect in the model. Order of presentation had no significant effect on the aversion to pull ($\chi^2_1 = 0.076$, $P = 0.783$, $N = 96$).

According to P2, chimpanzees' decision to pull the uncertain option should take longer in the social condition, i.e. more hesitation, than in the nonsocial condition. To test this prediction, a linear mixed model (Baayen, 2008) analysed the effect of condition on the latency to pull the uncertain rope (Model 1.2; see Appendix for details). The full model differed significantly from the null model ($\chi^2_1 = 4.601$, $P = 0.032$, $N = 568$). More specifically and consistent with P2, chimpanzees took more time before pulling the uncertain rope in the social condition than in the nonsocial condition (Fig. 4). We found no significant effect of session ($\chi^2_1 = 0.565$, $P = 0.452$). Furthermore, we investigated whether order of presentation (social or nonsocial condition first) affected the latency to pull by including the first condition as a fixed effect in the model. Order of presentation had no significant effect on the latency to pull ($\chi^2_1 = 0.069$, $P = 0.793$, $N = 568$).

According to P3, chimpanzees should show more negative emotional reactions to the uncertain option in the social condition than in the nonsocial condition. To test this prediction, we used a generalized linear mixed model with binomial error distribution and logit link function to analyse whether negative emotional reactions in uncertain trials were influenced by condition (Model 1.3; see Appendix for details). Inconsistent with P3, the full model did not differ significantly from the null model ($\chi^2_1 = 1.443$, $P = 0.23$, $N = 95$). The results suggest that chimpanzees' behaviour did not differ between conditions: in the social condition, 10 subjects showed negative emotional responses in 15% of the uncertain trials. In the nonsocial condition, 11 subjects showed negative emotional responses in 11% of the trials.

### Experiment 2: Social and Nonsocial Risk

According to P4, chimpanzees should be more averse to choosing the risky option in the social condition than in the

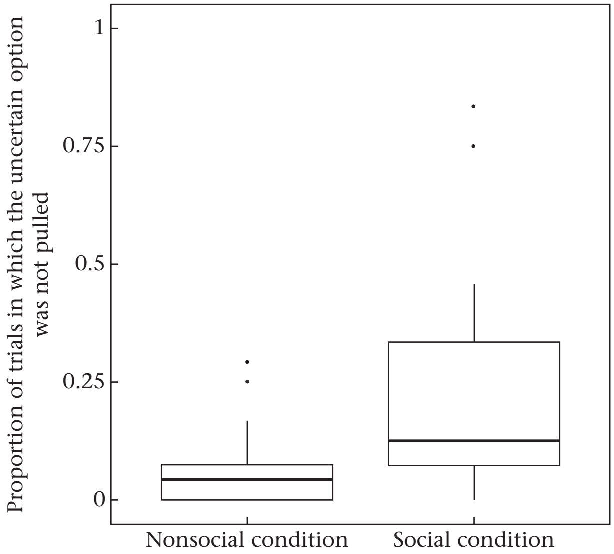

**Figure 3.** Aversion to pull the uncertain option in the nonsocial and the social condition (experiment 1). The box plots depict the proportion of trials in which the uncertain option was not pulled within 30 s. The boxes show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

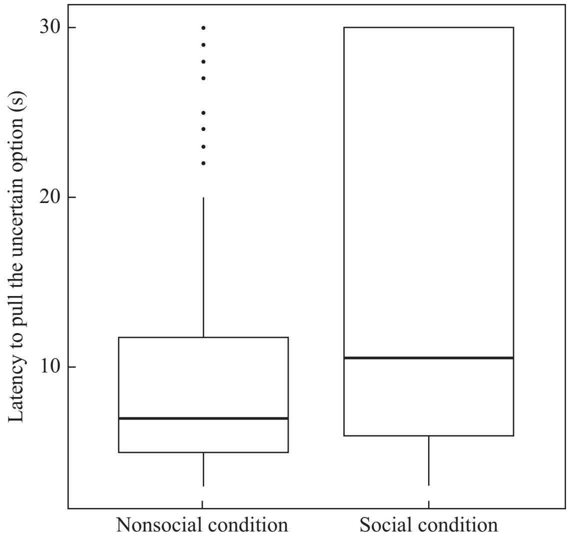

**Figure 4.** Latency to pull the uncertain option (experiment 1). The box plots depict the latency (s) to pull the uncertain option in the nonsocial and the social condition. The boxes show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

nonsocial condition. To test P5 (nondirectional), we additionally investigated whether subjects' sex, age and hierarchy position are possible predictors for their risk-taking behaviour. Using a generalized linear mixed model with binomial error distribution and logit link function, we investigated whether the choice of the risky option was influenced by condition, subject's sex, age and hierarchy position (Model 2.1; see Appendix for details). Inconsistent with P4, the full model did not differ significantly from the null model ($\chi^2_4 = 2.785$, $P = 0.594$, $N = 576$). In the social condition, chimpanzees chose the risky option in 27% of trials; in the nonsocial condition, they chose the risky option in 33% of trials. Furthermore, we investigated whether order of presentation (social or nonsocial condition first) affected the choice of the risky option by including the first condition as a fixed effect in the model. The order of presentation had no significant effect on the risky choice; the full model did not differ significantly from the null model ($\chi^2_5 = 4.520$, $P = 0.477$, $N = 576$). Across both conditions, a Wilcoxon signed-rank test revealed that chimpanzees were significantly less likely to choose the risky option (median = 10) than the safe option (median = 38, $N = 12$, $z = -2.36$, $P = 0.018$; see Fig. 5).

We next used a generalized linear mixed model with binomial error distribution and logit link function to investigate whether chimpanzees were more likely to choose the risky option after rewarded risky trials (Model 2.2, see Appendix for details). We included the outcome of the risky choice (rewarded or not rewarded) in the previous trial as a fixed effect. The full model did not differ significantly from the null model ($\chi^2_1 = 3.255$, $P = 0.071$, $N = 141$). The results, however, suggest a weak preference of chimpanzees to choose the risky option more often after not being rewarded in risky trials. Chimpanzees chose the risky option in 76% of trials when they previously received nothing, relative to 64% of trials after the previous risky choice was rewarded. Regardless of the previous outcome, in the trial following a risky decision, chimpanzees stuck with the risky option in 70% of the trials.

In an exploratory analysis, we investigated whether chimpanzees waited longer before making a decision (i.e. pulling either rope) in the social condition than in the nonsocial condition. We used a linear mixed model (Baayen, 2008) to analyse the effect of condition on the latency to choose one option (Model 2.3; see Appendix for details) by including condition as a fixed effect. Session was included as a further fixed effect. The full model did not differ significantly from the null model ($\chi^2_1 = 0.612$, $P = 0.434$, $N = 557$), suggesting that chimpanzees did not wait longer before making a decision in the social condition than in the nonsocial condition. Moreover, we investigated whether the latency to pull the risky option differed between conditions. This was not the case; chimpanzees pulled the risky rope equally fast in the social (median = 5; interquartile range, IQR = 4–6) and the nonsocial (median = 5; IQR = 4–7) condition. Furthermore, using a Wilcoxon signed-rank test we also found that in their emotional reactions, chimpanzees did not differentiate between the social (median = 0.5) and nonsocial condition (median = 0, $N = 12$, $z = -0.99$, $P = 0.32$). In the social condition, six subjects showed negative emotional responses in 5% of the trials. In the nonsocial condition, five subjects showed negative emotional responses in 3% of the trials. Finally, we investigated whether the emotional reactions differed between experiment 1 and experiment 2. A Wilcoxon signed-rank test revealed that across conditions the emotional reactions were significantly stronger in experiment 1 (median = 10) than in experiment 2 (median = 1, $N = 12$, $z = -2.95$, $P = 0.003$).

## DISCUSSION

In two experiments, we investigated whether chimpanzees distinguish between social and nonsocial forms of uncertainty and risk. In experiment 1, chimpanzees were exposed to social and nonsocial uncertainty; in experiment 2, they were exposed to social and nonsocial risk. In experiment 1, we found that our key variable of interest, uncertainty in social versus nonsocial contexts, is relevant in chimpanzees' decision making. They were less likely to pull the uncertain rope under social than under nonsocial uncertainty. Additionally, they hesitated longer before trusting a conspecific compared to a machine. Predictions 1 and 2 were thus supported. In experiment 2, in contrast, chimpanzees' decision making in situations involving risk did not differ along the social/nonsocial dimension. Prediction 4 was thus not supported.

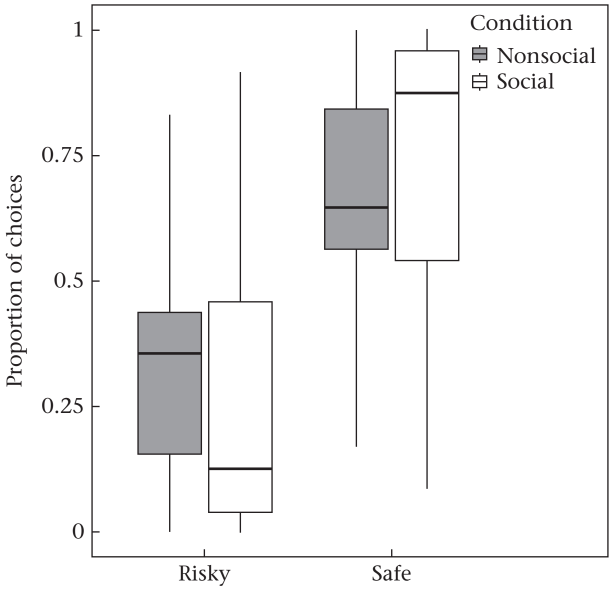

**Figure 5.** Proportion of risky and safe choices (experiment 2). The box plots depict the proportion of risky and safe choices in the social and nonsocial condition. The boxes show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range.

### *Social and Nonsocial Uncertainty*

Our findings suggest that chimpanzees experience more cognitive conflict in uncertain social contexts, which require them to trust a conspecific to return the food, than in uncertain nonsocial contexts, where they must trust a machine to return the food. Thus, chimpanzees appear to be concerned not only with outcomes per se but also with how they come to be. They are less willing to engage when the agent of uncertainty is a conspecific than a machine. In humans, similar preferences are explained in terms of the notion of betrayal aversion (Bohnet et al., 2008). To examine whether this may be the driving force for chimpanzees' discrimination between agents of uncertainty, we coded their emotional responses before, during and after decision making. In nonhuman animals, a cognitive conflict is often accompanied by changes in arousal level, which, in turn, are indicated by behavioural responses such as scratching (Call, 2012). However, we found no evidence for a differential emotional response as a function of social versus nonsocial context (Prediction 3). It is, however, possible that our behavioural coding did not detect subtle shifts in the chimpanzees' affective response; therefore, future research should take physiological indicators such as body posture or pupil dilation into account. Across conditions, however, we found that emotional reactions were generally stronger in experiment 1 compared to experiment 2, which might be because in experiment 1 chimpanzees could not pre-empt or terminate decisional conflict by choosing the safe reward.

In experiment 1, chimpanzees were presented with one option at a time, rendering it possible to examine their response to social and nonsocial uncertainty, without giving them the choice to dodge the decision (by simply choosing the safe option). This design decision was meant to mimic choices in the animals' natural habitat, in which they rarely encounter foraging options simultaneously (an observation raised by Kacelnik, Vasconcelos, Monteiro, & Aw, 2011; Simon, 1955). Kacelnik et al. further argued that the latency to act mirrors a tendency to skip the encountered food in order to continue foraging. The results of experiment 1 suggest that in the absence of another option chimpanzees ‘skip’ the food more often in uncertain social situations than in uncertain nonsocial ones.

### *Social and Nonsocial Risk*

Experiment 2 focused on risk rather than uncertainty. We found that animals' choices, latency and emotional responses did not differ between the social and nonsocial condition. As in most previous risky choice tasks, chimpanzees were simultaneously presented with both options, which allowed us to compare our result to previous findings. At first sight, our result conflicts with Calcutt et al. (2019), who found that female chimpanzees take fewer risks in a social than in a nonsocial condition. Yet our result and theirs do converge. Calcutt et al. did not distinguish between uncertain and risky trials and, instead, described both interactions as risky interactions: the initial ones when chimpanzees were without knowledge of reciprocation probabilities, thus making a decision under uncertainty, and the latter ones when chimpanzees had experienced the respective relative frequencies, thus making decisions under risk. Importantly, however, chimpanzees in the Calcutt et al. (2019) study weighted early interactions within the experiment more heavily than later ones. The partner's reciprocation rate in the first testing block of the social condition significantly influenced the subject's choice. This observation is in line with our findings, suggesting that chimpanzees distinguish between the social and nonsocial domain during early interactions when reciprocation rates are uncertain, but not once reciprocation rates have been experienced, and uncertainty has morphed into risk. It is important to point out that in everyday life, the decision whether to engage in a social situation is usually a decision made under uncertainty, as humans and nonhuman animals rarely know precisely with what probability others will cooperate. Future studies should examine whether after having experienced the respective relative frequencies (i.e. when making decisions under risk) and when only presented with one option at a time (as in experiment 1), chimpanzees would differentiate between social and nonsocial situations.

### *Risk Preference*

Irrespective of the factor social versus nonsocial, chimpanzees in experiment 2 proved to be risk averse. They preferred the safe option over the risky option, even though the expected value of the latter was higher. This finding is in line with findings of risk aversion across diverse nonhuman animals (e.g. Kacelnik & Bateson, 1996) and humans (see references in Hintze, Olson, Adami, & Hertwig, 2015). However, it is not in line with past experiments that reported chimpanzees to be risk prone in nonsocial contexts (see Calcutt et al., 2019; Haun et al., 2011; Heilbronner et al., 2008; but see ; Proctor, Williamson, Latzman, de Waal, & Brosnan, 2014). What could explain this difference between the present and past results?

Possible explanations may pertain to the presentation and experience of probabilities (see Hau et al., 2010; Heilbronner & Hayden, 2016; Hertwig, 2015; Wulff et al., 2018), as well as to specific elements of task design (see Frey, Pedroni, Mata, Rieskamp, & Hertwig, 2017; Heilbronner & Hayden, 2013; Rosati & Hare, 2016). Specifically, in experiment 2, chimpanzees made decisions based on experienced relative frequencies (probabilities), whereas in other studies (e.g. Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2010; Rosati & Hare, 2012) chimpanzees inferred probabilities from the task design. For instance, in the study by Haun et al. (2011), the number of cups represented the probability of success. The safe option consisted of one cup, whereas the risky option comprised (depending on the condition) two ($P = 0.5$), three ($P = 0.33$) or four ($P = 0.25$) cups. Learning the probabilistic structure of the choice context through experience, rather than inferring it from the task design, seems a more naturalistic way to study decisions under risk in chimpanzees (and humans). Probabilities are rarely explicitly stated or presented to the decision maker, but are rather learned through experience, resulting in what Knight (1921/1964) called statistical probabilities rather than a priori probabilities.

A further difference between the current and previous studies (e.g. Heilbronner et al., 2008; Rosati & Hare, 2010; Rosati & Hare, 2012) is that in the present study the uncertain/risky decision was an all-or-none decision insofar as one possible outcome of the nonsafe option was the animal coming away empty handed. In past studies, in contrast, the risky option always provided food; even bad luck still resulted in low-value food. This meant that the choice was indeed less risky per se (in terms of outcome variance). It is not implausible to argue that risk in the real world implies the threat of receiving nothing. It will be important to see in future studies whether this crucial aspect of outcome variance and the presence of the threat of coming away empty handed make chimpanzees more risk averse and thus more akin to humans and other nonhuman animals in their appetite for risk.

### *Potential Correlates of Risk Preference*

Research on risk preference in humans has identified a number of robust correlates. Sex, age (e.g. Josef et al., 2016) and income have been found to be consistently associated with risk preference (see

Frey, Richter, Schupp, Hertwig, & Mata, 2020). Chimpanzees' sex, age and hierarchy position did not affect their risk preference in experiment 2. This could be due to two factors: small sample size and behavioural risk measures. Frey et al. (2020) found that behavioural measures of risk, relative to self-reports, largely fail to pick up associations between correlates and risk preference. Future studies may take on the challenging task of increasing sample sizes and exploiting different risk measures (e.g. behavioural and observational) to investigate correlates and heterogeneity of risk preference.

### The Influence of Previous Outcomes on Risky Choice

We noted earlier that our implementation of the risky option in experiment 2 entailed the possibility of coming away empty handed. Both the experience of such a 'loss' as well as the experience of gain may systematically influence the choice of whether to gamble again in the next trial. When testing for this, we found that the outcome of the previous risky choice had a weak influence on the decision in the following trial: chimpanzees tended to gamble more when they previously received nothing. Rosati and Hare (2013) found that bonobos, but not chimpanzees, modulated their choices based on previous outcomes. In our study, regardless of the outcome and in the trial following a risky decision, chimpanzees chose the risky option more often than they chose the safe one. Our results suggest that chimpanzees are generally risk averse, preferring the safe option over the risky one. However, once chimpanzees chose the risky option, they tended to gamble again, especially if they had not been rewarded in the previous risky trial. One possible explanation for this behaviour is that chimpanzees interpreted unsuccessful trials as a loss and thus aimed at restoring the previous state of affairs by gambling again (see Scholer, Zou, Fujita, Stroessner, & Higgins, 2010 for a discussion of risk-seeking behaviour under loss in humans). This explanation implies that chimpanzees' choices are guided not simply by a process of reinforcement learning (in which the value of each action is updated according to its outcome) but also by a belief-updating process in which the present outcome informs expectations about what is going to happen in the next round.

### Conclusion

Our findings indicate that chimpanzees, like humans, distinguish between social and nonsocial contexts when making decisions under uncertainty. Chimpanzees are more reluctant to engage in a situation when the source of uncertainty is a conspecific than when it is a machine. This aversion manifests both in choice behaviour and in response latency. Having observed this dynamic, key questions for the future are why do chimpanzees experience interactions with social partners as less predictable and why are they less trusting and more hesitant to make daring decisions in uncertain social contexts? Unlike in the world of uncertainty, chimpanzees did not discriminate between social and nonsocial contexts in the world of risk. Furthermore, we found them to be, like humans and various nonhuman animals, risk averse, with a tendency to seek risk after the experience of coming away empty handed. Another key task for the future is to reveal the cognitive, possibly heuristic mechanisms behind chimpanzees' choices: how do they search for information to reduce uncertainty before making a choice?

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## Appendix

### *Participants*

All partners (except Romeo, who did not pass the apparatus understanding test) completed all test sessions as subjects before taking on the role of partner. One chimpanzee (Bahati) from the original sample did not follow the procedure on the first day of testing. She did not pull the uncertain rope in experiment 1 and thus could not learn the payoff structure for the risky option of experiment 2. We therefore adopted a new procedure for all following chimpanzees. If subjects did not pull the rope within 30 s, the experimenter pulled the rope after 30 s to ensure that all chimpanzees had the same experience of the statistical probabilities (in preparation for experiment 2). Bahati was excluded from all analyses.

### *Prior Experimental Experience*

Chimpanzees had some exposure to cognitive testing, having participated in cooperation tasks (Engelmann & Herrmann, 2016; Engelmann et al., 2015), social facilitation (Engelmann, Haux, & Herrmann, 2019; Herrmann, Haux, Zeidler, & Engelmann, 2019) and an executive function and physical cognition test battery (Völter et al., n. d.). However, only the set-up in the study investigating trust in cooperation was similar to the current project.

### *Observational Phase*

To control for the social relationships between subjects and partners, we determined a neutral partner for each subject.

### *Collection of observational data*

Prior to the experiments, three research assistants collected observational data (412 h) between March 2017 and March 2018 using a Samsung tablet equipped with CyberTracker software (Version 3.389). Observations were recorded as follows. Scan samples were collected for 60 min. During this time, research assistants conducted a scan every 10 min, noting the activities of each group member in the same predefined order. These activities included grooming (assistant noted who the focal animal groomed and/or was groomed by), contact (defined as any affiliative body contact between two individuals), arm's reach (two individuals sitting at a distance that would allow them to have contact if both extended their arms) and co-feeding (two individuals eating simultaneously while within arm's reach). In addition, it was noted whether a given individual was present or not.

### *Analysis of observational data*

We first calculated the frequency with which each individual was grooming, in contact, at arm's reach or co-feeding with all other individuals (by e.g. dividing the number of grooming events between individuals A and B by the number of times A and B were simultaneously present). The frequencies of the four activities were positively correlated within dyads and consequently cannot be considered independent sources of information about relationship quality. Using the obtained frequencies, we then calculated the composite index of sociality (CSI) for each dyad using the following formula (based on Silk, Cheney, & Seyfarth, 2013):

$$\mathrm{CSI}_{xy}=\frac{\sum_{\mathrm{i}=1}^{4}\frac{f_{ixy}}{\overline{f}_i}}{4}$$

In this equation, $f_{ixy}$ is the frequency of behaviour $i$ for dyad $xy$, and $\overline{f}_i$ is the mean frequency of behaviour $i$ across all dyads. Since the CSI involves dividing the frequency of a given behaviour within a dyad ($f_{ixy}$) by the average of that behaviour across all dyads ($\overline{f}_i$), its outcome describes the extent to which a particular dyad deviates from the average of all dyads. Dyads with a high score are more closely bonded than the average dyad; conversely, dyads with a low score are less closely bonded than the average dyad.

### *Determination of a neutral partner*

A neutral partner was defined as being neither one of the three individuals with the highest CSI for the subject nor one of the three individuals with the lowest CSI for the subject. We strictly adhered to the results of the CSI computations, and did not, for example, selectively focus on same-sex dyads. Because we were interested in social bonds among unrelated partners, the one exception to this general rule was kinship. While both male–male (Muller & Mitani, 2005; Watts, 2000) and female–female (Langergraber, Mitani, & Vigilant, 2009) bonds are common in chimpanzees, Langergraber, Mitani, Watts, and Vigilant (2013) suggest that bonds between the sexes also exist.

### *Models*

We assessed $P$ values for the individual effects based on likelihood ratio tests comparing the full with respective reduced models (Barr et al., 2013) using R function drop1 with argument ‘test’ set to ‘Chisq’. Confidence intervals for the estimates were assessed by using the function confint. merMod. Variance inflation factors (VIF; Field, 2005) were derived using the vif function of the ‘car’ package (Fox & Weisberg, 2011), applied to a standard linear model excluding the random effects. We assessed model stability by comparing the estimates obtained from the model based on all data with those obtained from models with the levels of the random effects excluded one at a time.

### *Model 1.1, experiment 1*

We first used a generalized linear mixed model with binomial error distribution and logit link function to analyse whether aversion to pull the uncertain rope was influenced by condition. Owing to singular fit warnings, we simplified the random slope structure. The random slopes of session in subject and condition in partner were estimated to be essentially 0. Because of further singular fit warnings, we continued to simplify the random effect structure. The final model comprised condition and session as fixed effects and subject as a random effect. We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations from these assumptions. Collinearity was not an issue (maximum VIF: 1.0 for condition and session). The model was revealed to be stable (for the model output, see Table A2).

### *Model 1.2, experiment 1*

We used a linear mixed model (Baayen, 2008) to analyse the effect of condition on the latency to pull the uncertain rope. Owing to singular fit warnings, we simplified the random slope structure. The random slopes of session and condition in partner were estimated to be essentially 0; we therefore did not include them in the final model. We log transformed the variable latency to pull the uncertain rope because the distribution of the response was right skewed. We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations from these assumptions. Collinearity was not an issue (maximum VIF: 1.0 for condition and session). The model was revealed to be stable (for the model output, see Table A3).

*Model 1.3, experiment 1*

We used a generalized linear mixed model with binomial error distribution and logit link function to analyse whether negative emotional reactions in uncertain trials were influenced by condition. Owing to singular fit warnings, we simplified the random effect structure. The random effect of partner and the random slope of session in subject were estimated to be essentially 0; we therefore did not include them in the final model (for the model output, see Table A4).

*Model 2.1, experiment 2*

We used a generalized linear mixed model with binomial error distribution and logit link function to investigate whether the choice of the risky option was influenced by condition and subject's sex, age and hierarchy position. Owing to singular fit warnings, we simplified the random effect structure. The random effect of partner was estimated to be essentially 0; we therefore did not include it in the final model (for the model output, see Table A5).

*Model 2.2, experiment 2*

To investigate whether chimpanzees chose the risky option more often after being rewarded in risky trials, we used a generalized linear mixed model with binomial error distribution and logit link function. As we did not find an effect of subject's sex, age or hierarchy position in the previous model, we did not include them as fixed effects. Owing to singular fit warnings, we simplified the random effect structure. The random effect of partner and the random slope of session and condition in subject were estimated to be essentially 0; we therefore did not include them in the final model (for the model output, see Table A6).

*Model 2.3, experiment 2*

We used a linear mixed model (Baayen, 2008) to analyse the effect of condition on the latency to choose one option. The random effect structure comprised subject, partner and session ID (nested in subject) as random intercepts and session number and condition in subject and partner as random slopes. We log transformed the variable latency to pull either rope because the distribution of the response was right skewed. Owing to singular fit warnings, we simplified the random effect structure. The random effect of partner was estimated to be essentially 0; we therefore did not include it in the final model (for the model output, see Table A7).

### *Effect Size*

We calculated the effect size and confidence intervals for the choice of the risky option in the social and nonsocial condition of experiment 2. The effect size was calculated in R (R Core Team, 2019) using the function cohen. d (Cohen's $d$) of the effsize package (Torchiano, 2020). This revealed a small effect size ($d = 0.22$, 95% confidence interval, CI = [−0.53, 0.98]). As our analysis revealed a nonsignificant result, the CI of the effect size spans the null value of zero. Calcutt et al. (2019) reported a medium effect size ($d = 0.69$, 95% CI = [−0.08, 2.01]). The two CIs overlap in the range of no or a small effect size, and the CI in our experiment is narrower. This suggests that the null hypothesis of no (or a small) effect is true (see Colegrave & Ruxton, 2003; Kelly, 2006).

**Table A1**
Sex and age of all subjects and partners participating in experiments 1 and 2

| No. | Subjects | | | Partners | | |
|---|---|---|---|---|---|---|
| | Name | Sex | Age (years) | Name | Sex | Age (years) |
| 1 | Roy | Male | 11 | Romeo | Male | 14 |
| 2 | William | Male | 18 | Romeo | Male | 14 |
| 3 | Niyonkuru | Male | 28 | Roy | Male | 11 |
| 4 | Tess | Female | 26 | Roy | Male | 11 |
| 5 | Uruhara | Male | 29 | Roy | Male | 11 |
| 6 | Chipie | Female | 27 | William | Male | 18 |
| 7 | Kisa | Male | 25 | Chipie | Female | 27 |
| 8 | Akela | Female | 30 | Chipie | Female | 27 |
| 9 | Amizero | Female | 29 | Chipie | Female | 27 |
| 10 | Joy | Female | 13 | Bahati | Female | 25 |
| 11 | Dufatanya | Female | 27 | Bahati | Female | 25 |
| 12 | Jane | Female | 14 | Bahati | Female | 25 |

**Table A2**
Output of Model 1.1, experiment 1

| | Estimate | SE | $\chi^2$ | $P$ | 95% confidence interval | |
|---|---|---|---|---|---|---|
| (Intercept) | -3.385 | 0.541 | | | | |
| Condition | 1.763 | 0.295 | 41.486 | <.001 | 1.196 | 2.376 |
| Session | 0.032 | 0.131 | 0.056 | 0.812 | -0.230 | 0.294 |

**Table A3**
Output of Model 1.2, experiment 1

| | Estimate | SE | $\chi^2$ | $P$ | 95% confidence interval | |
|---|---|---|---|---|---|---|
| (Intercept) | 2.069 | 0.144 | | | | |
| Condition | 0.336 | 0.142 | 4.601 | 0.032 | 0.034 | 0.638 |
| Session | 0.025 | 0.033 | 0.565 | 0.452 | -0.046 | 0.096 |

**Table A4**
Output of Model 1.3, experiment 1

| | Estimate | SE | $\chi^2$ | $P$ | 95% confidence interval | |
|---|---|---|---|---|---|---|
| (Intercept) | -1.617 | 0.453 | | | | |
| Condition | 0.434 | 0.334 | 1.443 | 0.230 | -0.328 | 1.136 |
| Session | -0.036 | 0.132 | 0.070 | 0.791 | -0.313 | 0.237 |

**Table A5**
Output of Model 2.1, experiment 2

| | Estimate | SE | $\chi^2$ | $P$ | 95% confidence interval | |
|---|---|---|---|---|---|---|
| (Intercept) | -0.408 | 0.805 | | | | |
| Condition | -0.604 | 0.805 | 0.542 | 0.462 | -2.416 | 1.156 |
| Session | -0.040 | 0.269 | 0.021 | 0.886 | -0.626 | 0.574 |
| Sex | -1.924 | 1.412 | 1.676 | 0.195 | -5.013 | 1.160 |
| Age | -0.165 | 0.422 | 0.146 | 0.702 | -1.084 | 0.767 |
| Hierarchy position | -1.094 | 0.711 | 2.107 | 0.147 | -2.673 | 0.446 |

**Table A6**
Output of Model 2.2, experiment 2

| | Estimate | SE | $\chi^2$ | *P* | 95% confidence interval | |
|---|---|---|---|---|---|---|
| (Intercept) | 0.752 | 0.457 | | | | |
| Rewarded risky decision in the previous trial | -0.763 | 0.428 | 3.255 | 0.071 | -1.656 | 0.065 |
| Condition | 0.771 | 0.479 | 2.573 | 0.109 | -0.173 | 1.766 |
| Session | -0.110 | 0.237 | 0.211 | 0.646 | -0.608 | 0.379 |

**Table A7**
Output of Model 2.3, experiment 2

| | Estimate | SE | $\chi^2$ | *P* | 95% confidence interval | |
|---|---|---|---|---|---|---|
| (Intercept) | 1.665 | 0.057 | | | | |
| Condition | -0.062 | 0.078 | 0.612 | 0.434 | -0.229 | 0.105 |
| Session | 0.006 | 0.020 | 0.089 | 0.766 | -0.036 | 0.047 |