How chimpanzees decide in the face of social and nonsocial uncertainty

Lou M. Haux [a], Jan M. Engelmann [b], Esther Herrmann [c] *, Ralph Hertwig [a] *

[a] Center for Adaptive Rationality, Max Planck Institute for Human Development, Berlin, Germany

[b] Department of Psychology, University of California, Berkeley, United States

[c] Centre for Comparative and Evolutionary Psychology, Department of Psychology, University of Portsmouth, Portsmouth, United Kingdom

* These authors share senior authorship

Accepted for publication at *Animal Behaviour* in October 2020

Correspondence:

Lou Marie Haux

Center for Adaptive Rationality

Max Planck Institute for Human Development

Lentzeallee 94, 14195 Berlin, Germany

+49 30 82406-598

haux@mpib-berlin.mpg.de

Abstract

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 studies, each involving a social and a nonsocial condition. In both studies, 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 Study 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 Study 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.

Keywords: chimpanzees, decision making, risk, trust, uncertainty

In their natural habitat, chimpanzees 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), 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" (p. 13). 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" (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 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 chimpanzees' and bonobos' behaviour 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, and orangutans. 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. Despite the fact that this effect diminished with time, the results suggest that great apes were 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 et al., 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, & Tomasello, 2015; Engelmann & Herrmann, 2016) and interdependent, mutualistic scenarios (Melis, Hare, & Tomasello, 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. But whether chimpanzees, like humans, distinguish between social and nonsocial forms of uncertainty and risk 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 more 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 setup and its contingencies (see Calcutt et al., 2019). We therefore conducted two studies 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, & Tomasello, 2015; Engelmann, & Herrmann, 2016), 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 Study 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 Study 2, potential outcomes were visible and probabilities were known (chimpanzees made decisions based on the statistical probabilities experienced in Study 1). The interaction thus involved risk. In Study 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 Study 2, chimpanzees were exposed to the safe and the risky option simultaneously and decided between the two options.

For Study 1, we predicted that chimpanzees 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 takes longer in the social condition, that is, they 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 is greater in uncertain social compared to uncertain nonsocial situations (based on P1). Additionally, we predicted that chimpanzees 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 Study 2, we predicted that chimpanzees are 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 (M = 23 years) participated in the two studies. Each subject was paired with a neutral partner (see the Supplementary Material, SM, 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 studies themselves. For more information on subjects and their partners, see Table A1 of the SM.

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 studies 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 (~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 one, 10 females and 7 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, thirteen chimpanzees participated in the two studies.

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 hectares; group 2: 35.31 hectares). 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 their 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 Figure 1) were used for both studies. 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 ¼ apple) on a 300 cm track. Pulling the rope for the uncertain/risky option resulted in the vehicle moving along the track to a partner (social condition) or a machine (nonsocial condition).

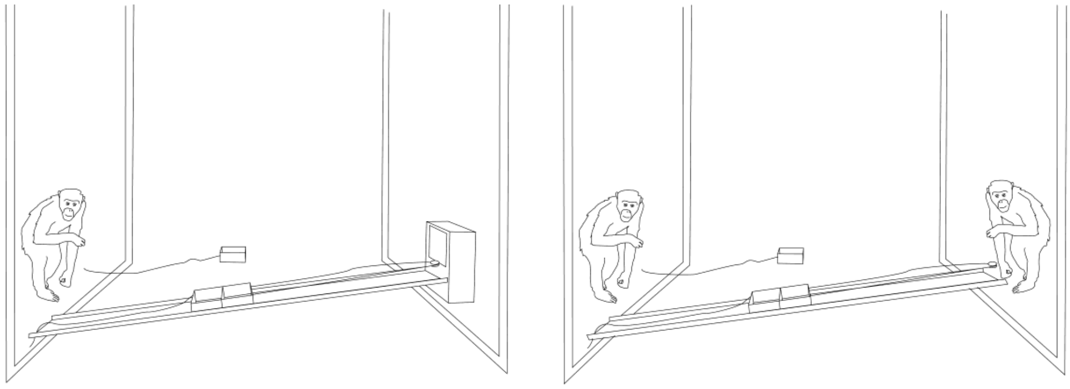

Figure 1. Experimental setup. Nonsocial condition (left) and social condition (right). The subject is depicted on the left and the machine (or partner) on the right side of the apparatus. The safe rope is on the left side of the subject and the uncertain/risky rope on the right side. In Study 1 (decision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

Design

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

Study 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 Study 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). Study 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 Study 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 setup and their understanding of the apparatus was tested. Those subjects who passed the apparatus understanding test participated in the two studies.

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 ¼ 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 toward 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 ¼ apple.

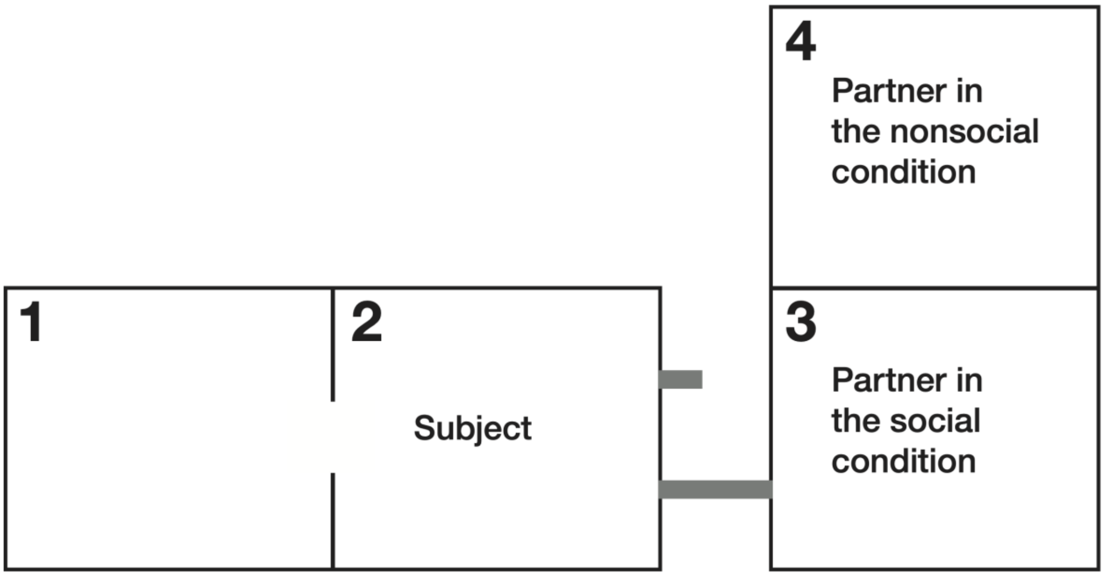

Figure 2. Testing rooms with position of the chimpanzees (subject and partner) in Studies 1 and 2. The grey bars between rooms 2 and 3 represent the safe option (small bar) and the uncertain/risky option (larger bar).

Apparatus understanding. In four consecutive steps, all subjects were then individually introduced to the experimental setup 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 seconds 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 seconds (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 Figure 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 out 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 out 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 setup closely matching that of the actual studies: 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; 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 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 studies.

Study 1: Social and Nonsocial Uncertainty

In Study 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 Figures 1 and 2). Choosing the uncertain option thus could 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 actually 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 pseudorandomised, 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 Figure 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 seconds to pull the rope. If chimpanzee subjects did not pull the rope within 30 seconds, the experimenter pulled the rope after 30 seconds to ensure that all chimpanzees had the same experience of the relative frequencies (in preparation for Study 2). To control for the delay in receiving the reward in the uncertain option in both conditions, the food was sent back 5 seconds 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 seconds 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 seconds, we coded this as aversion to pull. If chimpanzees 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 seconds. Finally, we coded whether chimpanzees showed an affective response. The following behaviours were coded (see Baker & Aureli, 1997; Jensen, Call, & Tomasello, 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 seconds 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. Due 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 κ) for nominal-scaled data and kripp.alpha (Krippendorff's α) 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 $\kappa = 0.69$).

Study 2: Social and Nonsocial Risk

In Study 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 Study 1. Subjects received four reminder trials about each option before each test session (see Design). As in Study 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 setup and procedure was the same as in Study 1, with the only difference that during each test trial both options—the safe rope and the risky rope—were present. Chimpanzees had 60 seconds to make a choice. Once the subject had decided to pull one rope, the experimenter removed the other rope.

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

All trials were videotaped with two cameras. The first author coded all trials live as well as later from videotape. Due 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 κ = 1.00) and latency to pull (Krippendorff's α = 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 Study 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 among 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 Study 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 among random slopes. Barr, Levy, Scheepers, and Tily (2013) have shown that exclusion of these correlations does not substantially affect Type I error rate.

RESULTS

Study 1: Social and Nonsocial Uncertainty

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

According to P1, chimpanzees 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 SM for details). The full model differed significantly from the null model (χ^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 a total of 12% of uncertain trials but only in a total of 4% of the trials in the nonsocial condition (Figure 3). We found no significant effect of session (χ^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 (χ^2_1 = 0.076, P = 0.783, N = 96).

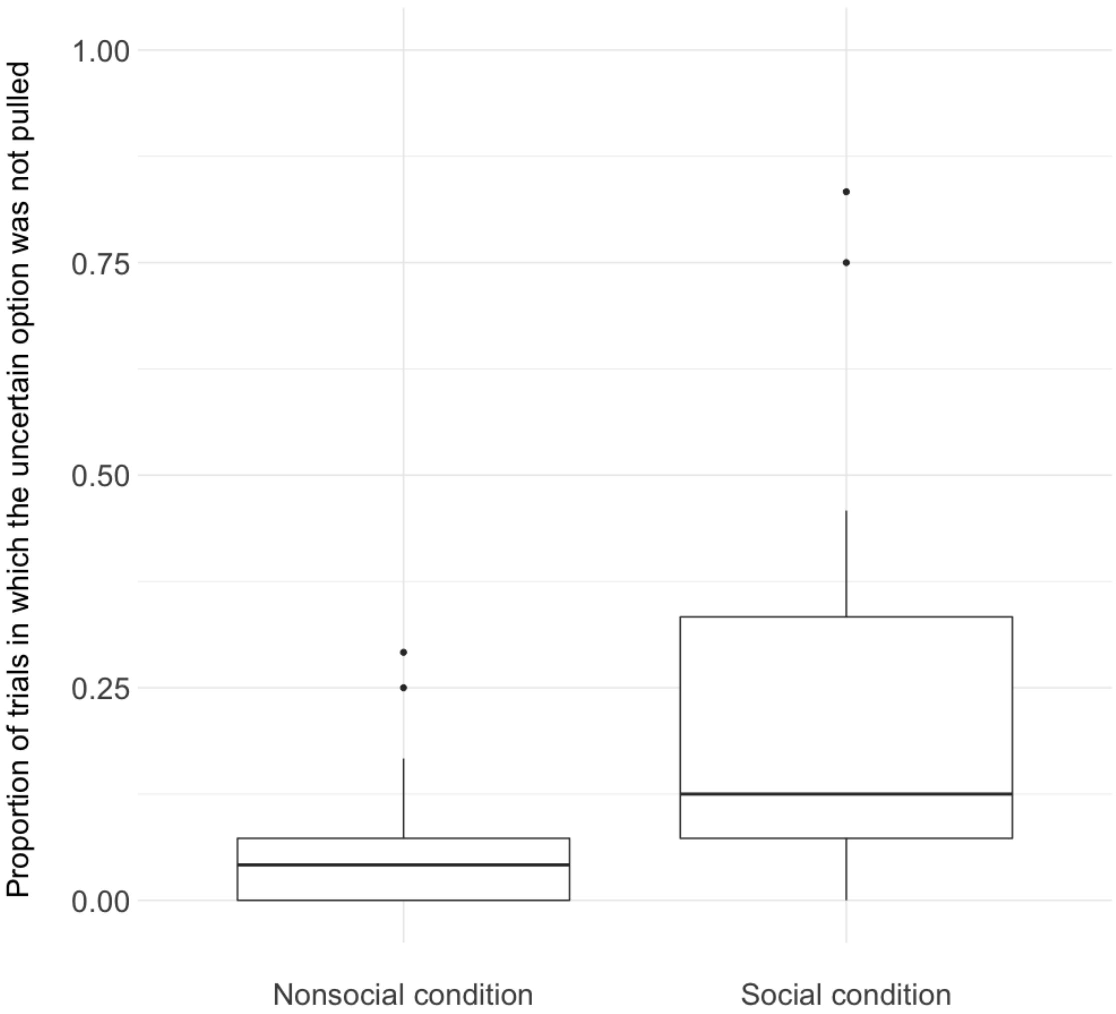

Figure 3. Aversion to pull the uncertain option in the nonsocial and the social condition (Study 1). The boxplots depict the proportion of trials in which the uncertain option was not pulled within 30 seconds. The thick vertical lines represent the median. The lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the largest value no further than 1.5 * IQR (inter-quartile range) from the hinge. The lower whisker extends from the hinge to the smallest value at most 1.5 * IQR of the hinge. Data beyond the end of the whiskers are outliers and plotted as individual points.

According to P2, chimpanzees' decision to pull the uncertain option takes longer in the social condition—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 SM 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 (Figure 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 ($\chi^2_1 = 0.069$, $P = 0.793$, $N = 568$).

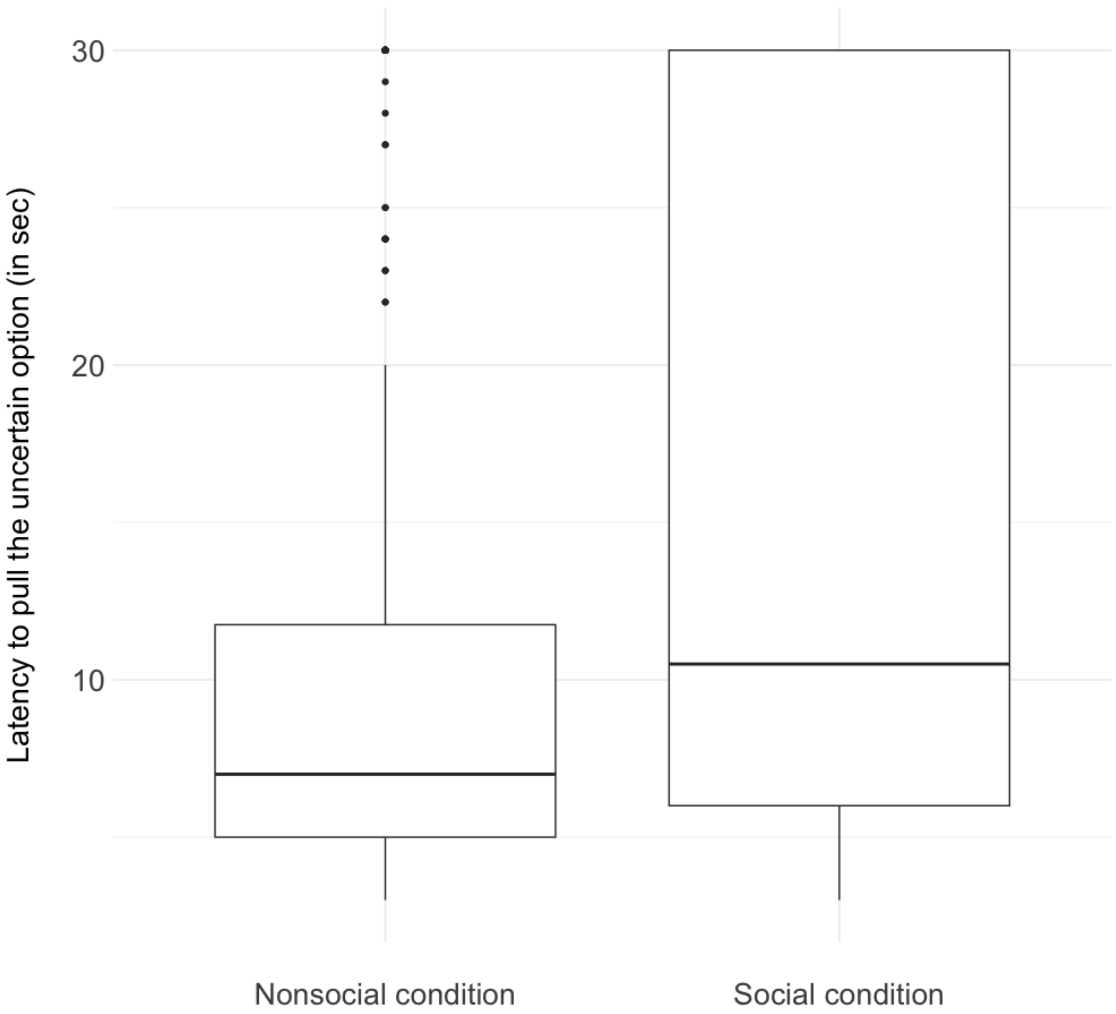

Figure 4. Latency to pull the uncertain option (Study 1). The boxplots depict the latency (in sec) to pull the uncertain option in the nonsocial and the social condition. The thick vertical lines represent the median. The lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the largest value no further than 1.5 * IQR (inter-quartile range) from the hinge. The lower whisker extends from the hinge to the smallest value at most 1.5 * IQR of the hinge. Data beyond the end of the whiskers are outliers and plotted as individual points.

According to P3, chimpanzees 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 SM 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 a total of 15% of the uncertain trials. In the nonsocial condition, 11 subjects showed negative emotional responses in a total of 11% of the trials.

Study 2: Social and Nonsocial Risk

According to P4, chimpanzees are more averse to choosing the risky option in the social condition than in the nonsocial condition. P5 (nondirectional): Additionally, we 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 SM 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 a total of 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 (χ^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 (*Mdn* = 10) than the safe option (*Mdn* = 38, *n* = 12, *z* = −2.36, *p* = 0.018; see Figure 5).

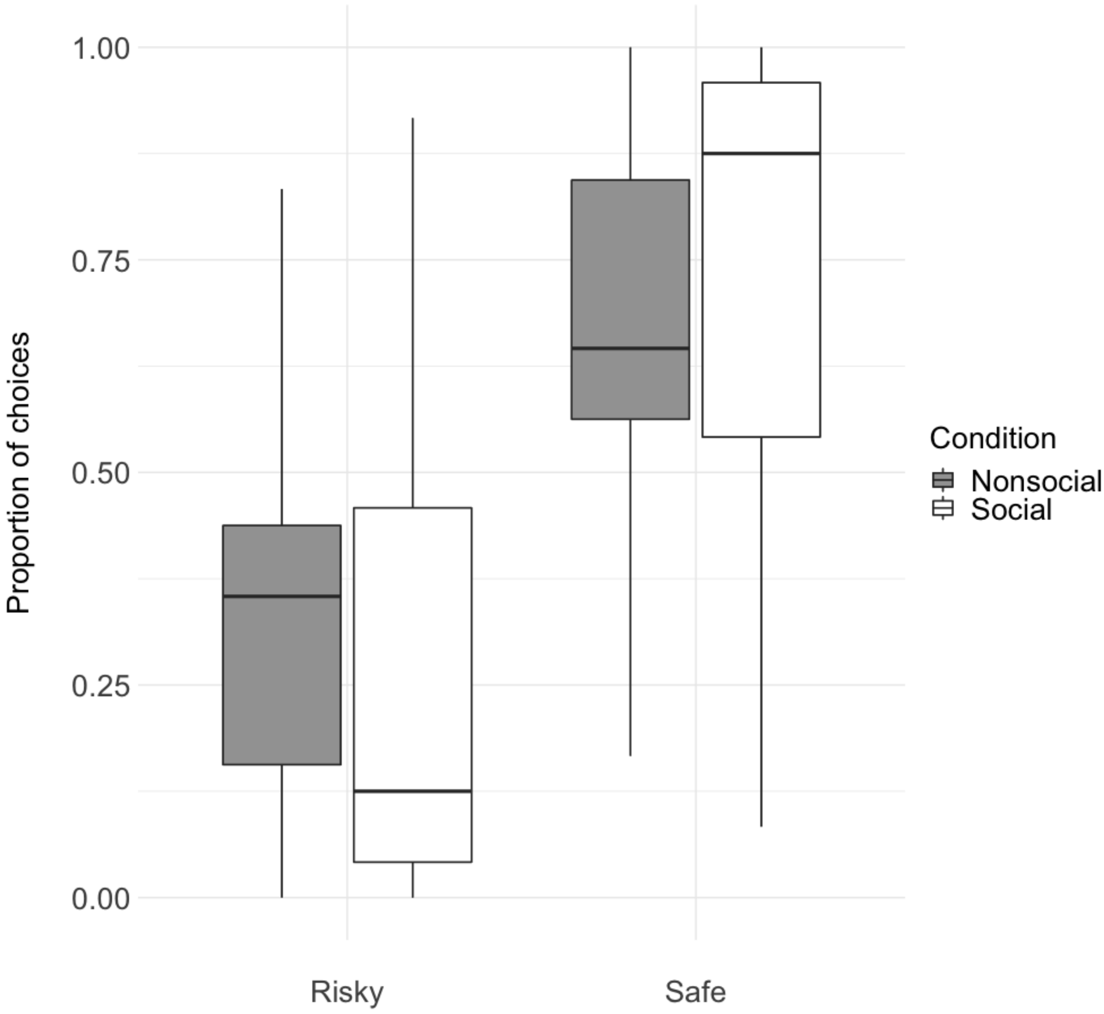

Figure 5. Proportion of risky and safe choices (Study 2). The boxplots depict the proportion of risky and safe choices in the social and nonsocial condition. The thick vertical lines represent the median. The lower and upper hinges correspond to the first and third quartiles. The upper whisker extends from the hinge to the

largest value no further than 1.5 * IQR (inter-quartile range) from the hinge. The lower whisker extends from the hinge to the smallest value at most 1.5 * IQR of the hinge.

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 SM 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 SM 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 (*Mdn* = 5; I*QR* = 4–6) and the nonsocial (*Mdn* = 5; I*QR* = 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 (Mdn = 0.5) and nonsocial condition (Mdn = 0, n = 12, z = −0.99, P = 0.32). In the social condition, six subjects showed negative emotional responses in a total of 5% of the trials. In the nonsocial condition, five subjects showed negative emotional responses in a total of 3% of the trials. Finally, we investigated whether the emotional reactions differed between Study 1 and Study 2. A Wilcoxon signed-rank test revealed that across conditions the emotional reactions were significantly stronger in Study 1 (Mdn = 10) than in Study 2 (Mdn = 1, n = 12, z = −2.95, P = 0.003).

DISCUSSION

In two studies, we investigated whether chimpanzees distinguish between social and nonsocial forms of uncertainty and risk. In Study 1, chimpanzees were exposed to social and nonsocial uncertainty; in Study 2, they were exposed to social and nonsocial risk. In Study 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 Study 2, in contrast, chimpanzees' decision making in situations involving risk did not differ along the social/nonsocial dimension. Prediction 4 was thus not supported.

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 not only be concerned 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 relative to 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 Study 1 compared to Study 2, which might be due to the fact that in Study 1 chimpanzees could not preempt or terminate decisional conflict by choosing the safe reward.

In Study 1, chimpanzees were presented with one option at a time, rendering it possible to examine chimpanzees' 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. Results of

Study 1 suggest that in the absence of another option chimpanzees "skip" the food more often in uncertain social situations than in uncertain nonsocial situations.

Social and nonsocial risk

Study 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 gives us the possibility to compare our result to previous findings. At first sight, our result conflicts with Calcutt et al. (2019), who found that female chimpanzees are less risk-taking in a social than in a nonsocial condition. Yet our results and theirs actually 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 of whether to engage in a social situation is usually a decision 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 (like in Study 1), chimpanzees would differentiate between social and nonsocial situations.

Risk preference

Irrespective of the factor social versus nonsocial, chimpanzees in Study 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 studies 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 et al., 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, Pleskac, & Hertwig, 2010; Heilbronner & Hayden, 2016; Hertwig, 2015; Wulff, Mergenthaler-Canseco, & Hertwig, 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 Study 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 ($P=.5$), three ($P=.33$), or four ($P=.25$) 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 et al., 2020). Chimpanzees' sex, age, and hierarchy position did not affect their risk preference in Study 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 Study 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 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 & 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 et al., 2010 for a discussion of risk-seeking behaviour under loss in humans). This explanation implies that chimpanzees' choices are not simply guided by a process of reinforcement learning (in which the value of each action is updated according to its outcome) but also by some kind of 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, one key question for the future is: 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 in order to reduce uncertainty before making a choice?

Acknowledgments

We thank Richard Vigne, Samuel Mutisya, Stephen Ngulu and the board members and staff of Sweetwaters Chimpanzee Sanctuary in Kenya for their crucial support throughout this research. Special thanks go to Joseph Maiyo, David Mundia, Steven Mukundi, and Charles Mussasia. We thank Ol Pejeta Conservancy, Kenya Wildlife Service (KWS), and the National Council for Science and Technology (NCST) for approving our research. Thanks go to Roger Mundy for statistical advice, Oded Ritov for reliability coding, Sebastian Schütte for building the apparatus, Shona Duguid and Hanna Schleihauf for helpful discussions, and Susannah Goss and Deb Ain for editing the manuscript.

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Appendix

Supplemental Information

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 Study 1 and thus could not learn the payoff structure for the risky option of Study 2. We therefore adopted a new procedure for all following chimpanzees: If subjects did not pull the rope within 30 seconds, the experimenter pulled the rope after 30 seconds to ensure that all chimpanzees had the same experience of the statistical probabilities (in preparation for Study 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, Herrmann, & Tomasello, 2015), social facilitation (Engelmann, Haux, & Herrmann, 2019; Herrmann, Haux, Zeidler, & Engelmann, 2019), and an executive function and physical cognition test battery (unpublished). However, only the setup 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 experimental studies, three research assistants collected observational data (412 hours) 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 minutes. During this time, research assistants conducted a scan every 10 minutes, 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 individual 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):

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

In this equation, f_{ixy} is the frequency of behaviour i for dyad xy, and $\bar{f}_i$ 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

($\bar{f}_i$), 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 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, Levy, Scheepers, & Tily, 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, Study 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. Due 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 homogenous 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 no issue (maximum variance inflation factor: 1.0 for condition and session). The model revealed to be stable (for the model output, see Table A2).

Model 1.2, Study 1: We used a linear mixed model (Baayen, 2008) to analyse the effect of condition on the latency to pull the uncertain rope. Due 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 homogenous 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 no issue (maximum variance inflation factor: 1.0 for condition and session). The model was revealed to be stable (for the model output, see Table A3).

Model 1.3, Study 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. Due 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, Study 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. Due 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, Study 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. Due 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, Study 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. Due 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 Study 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% CI = [–0.53, 0.98]). As our analysis revealed a nonsignificant result, the confidence interval 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 confidence intervals overlap in the range of no or a small effect size, and the confidence interval in our study 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 Studies 1 and 2.

No.	**Subjects**			**Partners**		
	Name	**Sex**	**Age**	**Name**	**Sex**	**Age**
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, Study 1

	Estimate	SE	χ^2	p	95% CI	
(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, Study 1

	Estimate	SE	χ^2	p	95% CI	
(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, Study 1

	Estimate	SE	χ^2	p	95% CI	
(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, Study 2

	Estimate	SE	χ^2	p	95% CI	
(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, Study 2

	Estimate	SE	χ²	p	95% CI	
(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, Study 2

	Estimate	SE	χ²	p	95% CI	
(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