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The Origins of Behavior Under Risk and Uncertainty

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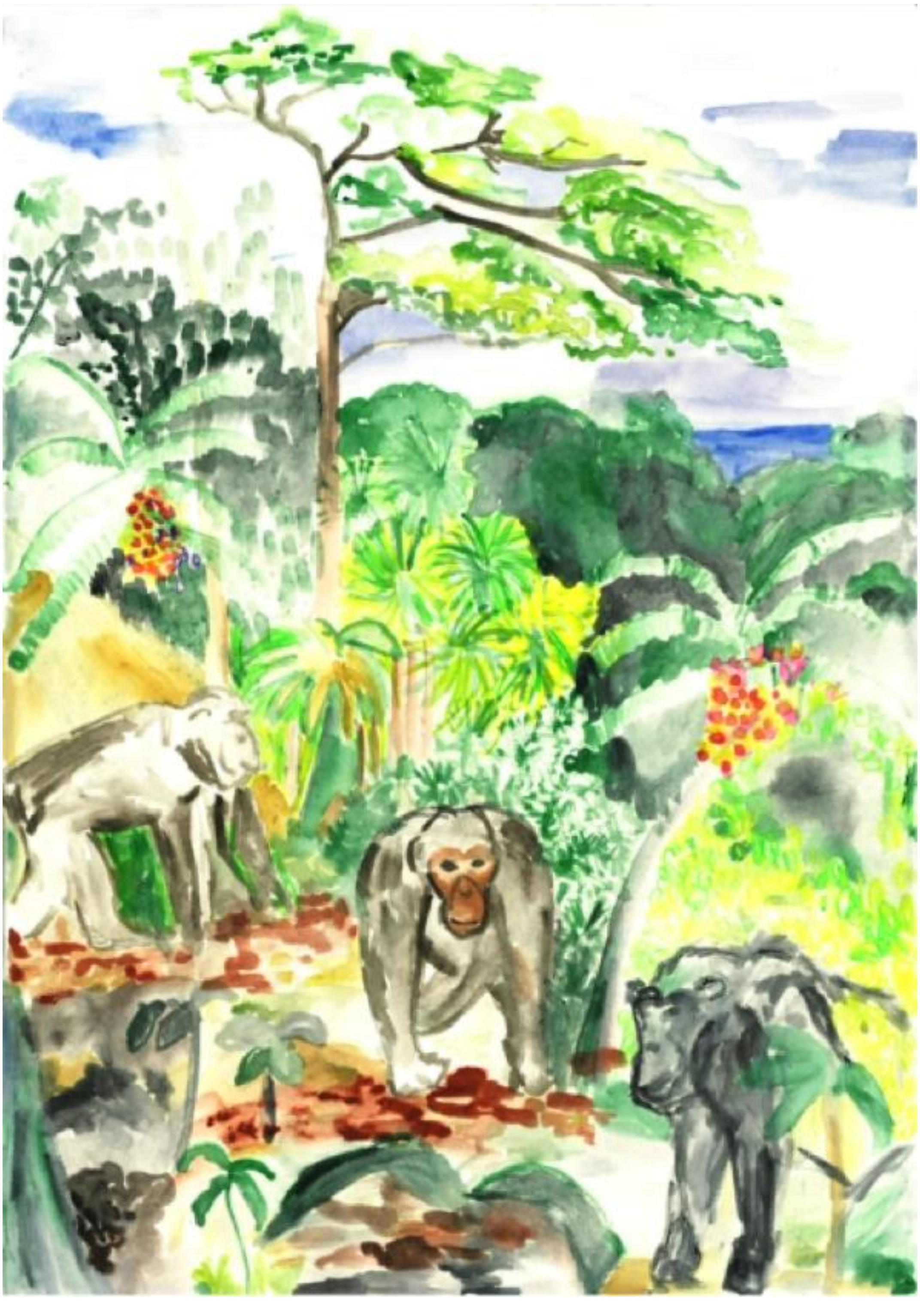

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Summary

Risk and uncertainty are central to all adaptive decisions human and nonhuman animals make — including when deciding where to forage, with whom to mate and how to deal with dangerous situations. Yet the evolutionary roots of human and nonhuman primate risk–taking behavior remain poorly understood. In my dissertation, I investigate the behaviour under risk and uncertainty of chimpanzees (*Pan troglodytes*), as they are an ideal reference for such an endeavour (The Chimpanzee Sequencing and Analysis Consortium, 2005): they are one of humans' two closest living relatives; live in large, mixed–sex social groups; and have similar developmental stages, with extended infant dependency, a period of adolescence, young adulthood, and have a long life expectancy of up to 50 years. Chimpanzees occupy a variety of habitats—from savannas to evergreen forests—and face myriad risks in their socioecological environments (De Waal, 1973; Goodall, 1968).

Across three empirical studies I show that chimpanzee and human behavior under risk and uncertainty converge in crucial ways. Specifically, in Study 1, I determine whether the willingness to take risks is similar to that in humans (see Chapter 2). This is achieved using an exceptionally large sample size and a novel multimethod approach to study chimpanzees from infancy to adulthood in a cross–sectional design. The results show that chimpanzee and human risk preferences share key structural similarities: chimpanzee willingness to take risks manifests as a trait–like preference that is consistent across domains and measurements; chimpanzees are ambiguity averse; males are more willing to take risks than are females; and appetite for risk peaks during young adulthood.

In Study 2, I show that chimpanzees, like humans, display higher aversion to uncertainty arising from social interactions than to uncertainty caused by interactions with an unanimated reward mechanism (see Chapter 3). In Experiment 1 of the study, where chimpanzees have no prior information on reciprocation rates (i.e. decide under uncertainty), chimpanzees are less likely to choose the uncertain option when they interact with a partner than with a machine. When they do choose the uncertain option, chimpanzees also hesitate longer in the social condition. In Experiment 2, where chimpanzees have learned the statistical probabilities of reciprocation rates (i.e. decide under risk), they do not distinguish between social and nonsocial situations and are generally risk averse.

In Study 3, I investigate how chimpanzees explore their uncertain environment prior to a risky decision (see Chapter 4). Across two experiments I show that chimpanzee exploration is shaped both by ecological properties and individual characteristics and is similar to humans in important aspects. The results suggest that experiencing variance prompts more exploration, for instance, over the course of the experiment, chimpanzees explore changing environments more than stable ones. I further investigate distinct exploration patterns and demonstrate that chimpanzees adapt their exploration to the environment: in changing environments, they have a

clear preference for exploring only one option, whereas in stable environments, exploration of one option and sequential exploration of both options are equally prevalent. The data shows substantial interindividual differences in exploration, with risk–seeking individuals tending to explore less.

Taken together these findings suggest that key dimensions of behavior under risk and uncertainty — like more exploration in changing compared to stable environments, a greater aversion towards social uncertainty, and a heightened willingness to take risks by young adult males — emerge independently of the influence of human cultural evolution and thus may have deeper phylogenetic roots than previously suspected. Understanding the biological underpinnings of risk preference is of wide interest to a number of disciplines — e.g. Psychology, Economics, Behavioral Biology, Cognitive Sciences, Anthropology — because it is fundamental to how organisms behave and make decisions and constitutes a central issue for perspectives on life–history strategies.

Zusammenfassung

Menschen und andere Tiere treffen zahlreiche adaptive Entscheidungen bei denen Risiko und Ungewissheit eine zentrale Rolle spielen. Dies gilt beispielsweise für die Entscheidung, wo sie nach Nahrung suchen, mit wem sie sich paaren und wie sie mit gefährlichen Situationen umgehen. Die evolutionären Wurzeln des Risikoverhaltens von Menschen und nichtmenschlichen Primaten sind jedoch nur unzureichend erforscht. Um diese Forschungslücke zu schließen, untersuche ich in meiner Dissertation, inwieweit das Verhalten von Schimpansen (*Pan troglodytes*) unter Risiko und Unsicherheit dem des Menschen ähnelt. Schimpansen sind hierbei eine ideale Vergleichsgruppe (The Chimpanzee Sequencing and Analysis Consortium, 2005): Sie sind einer der beiden nächsten lebenden Verwandten des Menschen und leben in großen, gemischtgeschlechtlichen sozialen Gruppen. Darüber hinaus haben sie ähnliche Entwicklungsstadien wie Menschen, mit einer verlängerten Säuglingszeit, einer Phase der Adoleszenz, einem jungen Erwachsenenalter und einer hohen Lebenserwartung von bis zu 50 Jahren. Schimpansen leben in einer Vielzahl von Lebensräumen — von Savannen bis hin zu immergrünen Wäldern — und sind in ihrem sozio-ökologischen Umfeld unzähligen Risiken ausgesetzt (De Waal, 1973; Goodall, 1968).

In drei empirischen Studien zeige ich, dass das Verhalten von Schimpansen und Menschen unter Risiko und Unsicherheit sich in entscheidender Weise ähnelt. In Studie 1 untersuche ich, ob wesentliche Aspekte des Risikoverhaltens von Schimpansen, ähnlich zu derjenigen des Menschen ist (siehe Kapitel 2). Hierfür habe ich eine außerordentlich große Stichprobe untersucht und einen Multimethodenansatz angewendet, um Schimpansen vom Kindes- bis zum Erwachsenenalter in einem Querschnittsdesign zu untersuchen. Die Ergebnisse zeigen, dass die Risikopräferenzen von Schimpansen und Menschen wichtige strukturelle Ähnlichkeiten aufweisen: Die Risikobereitschaft von Schimpansen manifestiert sich als eine eigenschaftsähnliche Präferenz, die über verschiedene Bereiche und Messungen hinweg konsistent ist; Schimpansen sind ambiguitätsscheu; Männchen sind risikobereiter als Weibchen; und die Risikobereitschaft erreicht im jungen Erwachsenenalter ihren Höhepunkt.

In Studie 2 zeige ich, dass Schimpansen, genauso wie Menschen, eine höhere Abneigung gegenüber Ungewissheit durch soziale Interaktionen aufweisen, als gegenüber Ungewissheit bei Interaktionen mit einer Maschine (siehe Kapitel 3). In Experiment 1 der Studie, hatten die Schimpansen keine Erfahrung mit den Reziprozitätsraten (d. h. sie entschieden unter Unsicherheit). Hier wählen sie weniger häufig die unsichere Option, wenn sie mit einem Partner interagieren, als bei der Interaktion mit einer Maschine. Außerdem zögern Schimpansen, wenn sie sich für die unsichere Option entscheiden, in der sozialen Situation länger als in der nicht-sozialen Situation. In Experiment 2, hatten die Schimpansen die statistischen Wahrscheinlichkeiten der Reziprozitätsraten gelernt (d. h. entschieden unter Risiko) und

unterscheiden nun nicht mehr zwischen sozialen und nicht–sozialen Situationen. Überdies sind sie generell risikoscheu.

In Studie 3 untersuche ich, wie Schimpansen ihre unsichere Umgebung explorieren, bevor sie eine riskante Entscheidung treffen (siehe Kapitel 4). In zwei Experimenten zeige ich, dass die Exploration bei Schimpansen sowohl von Umwelt-, als auch von individuellen Merkmalen geprägt ist, und in wichtigen Aspekten der des Menschen ähnelt. Die Ergebnisse deuten darauf hin, dass das Erleben von Varianz zu mehr Exploration führt. So explorieren Schimpansen im Verlauf des Experiments wechselnde Umgebungen stärker als stabile. Die Untersuchung von Explorationsmustern zeigt zudem, dass Schimpansen ihre Exploration an die Umgebung anpassen. In sich verändernden Umgebungen ziehen sie es vor, nur eine Option zu explorieren, während sie in stabilen Umgebungen zwei bevorzugte Explorationsmuster zeigen: Sie explorieren entweder nur eine Option oder beide Optionen nacheinander. Die Daten zeigen zudem erhebliche interindividuelle Unterschiede in der Exploration, wobei risikofreudige Schimpansen tendenziell weniger explorationsfreudig sind.

Die Ergebnisse meiner Dissertation deuten darauf hin, dass zentrale Dimensionen des Verhaltens unter Risiko und Ungewissheit, wie z.B. die stärkere Exploration in wechselnden im Vergleich zu stabilen Umgebungen, die größere Abneigung gegenüber sozialer Ungewissheit und eine erhöhte Risikobereitschaft junger Erwachsener Männchen, unabhängig vom Einfluss der kulturellen Evolution des Menschen entstanden sind. Daher möglicherweise tiefere phylogenetische Wurzeln haben als bisher angenommen. Das Verständnis der biologischen Grundlagen der Risikopräferenz ist von großem Interesse für eine Reihe von Disziplinen, z. B. für die Psychologie, die Ökonomie, die Verhaltensbiologie, die kognitiven Wissenschaften und die Anthropologie, da es von zentraler Bedeutung für das Verständnis vom Verhalten und Entscheiden ist und Zentral für die Untersuchung von Life–History–Strategien.

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1

General Introduction

In 1519, the Spanish conquistador Hernando Córtes landed with about 600 men and eleven ships on the shores of a mysterious new land in faraway America. Soon they learned that it was an outpost of a powerful, warlike empire. According to the legend, Córtes responded by burning all his ships to deprive himself and his men of any safe means of retreat. He thus hoped to prevent the risk of a mutiny and the takeover of his ships. Hernando Córtes and his troops were now left with no other option but to venture into the uncertain new land (Huber, 2019).

Although this might be an extreme case, human decision making often represents a leap into the unknown, e.g. when experimenting with recreational drugs, investing one's life savings in a business idea, or undergoing elective surgery, to name but a few. One important factor that influences how humans decide in the face of uncertainties, risks, dangers or undesirable events is their risk preference (Frey et al., 2017). As a primary decision–making factor in determining health, wealth, and wellbeing, risk preference has the potential to influence the course of entire lives, and as such entails wide–ranging consequences for society (Barseghyan et al., 2013; Brailovskaia et al., 2018; Clark & Lisowski, 2017; Dohmen et al., 2011; Mata et al., 2018; Schonberg et al., 2011; Slovic, 1987). But what determines our risk preferences? It has been proposed that "modern attitudes to risk are, at least in part, the product of biological evolution" (Robson, 1996, p. 397). One way to tackle this question is to compare extant species and their phylogenetic relationships to make inferences about the evolutionary history of traits (Martins, 1995). However, few nonhuman animal species live in socio–ecological conditions that are comparable to the human niche, and even fewer animals show comparable life–history strategies. Chimpanzees (*Pan troglodytes*), are an ideal reference (The Chimpanzee Sequencing and Analysis Consortium, 2005): they are one of humans' two closest living relatives; live in large, mixed–sex social groups; and have similar developmental stages, with extended infant dependency, a period of adolescence, young adulthood, and long life expectancy of up to 50 years. Chimpanzees occupy a variety of habitats—from savannas to evergreen forests—and face myriad uncertainties in their socio–ecological environments (De Waal, 1973; Goodall, 1968).

In the following, I will first discuss how risk preferences are measured in humans and chimpanzees, present a series of key properties of human risk preference and summarize how some of these structural aspects have been investigated in great apes. I will then move from pure risk preference and choice data to exploration behavior to discuss the processes underlying risky decision making. In this context, I will introduce the decisions–from–experience paradigm (Hertwig et al., 2004) which captures the explorative tendencies of humans under uncertainty and discuss how comparative research could profit from this method to investigate how chimpanzees explore their environment prior to a risky decision. Finally, I will briefly discuss sample size in primate cognition research before presenting an overview of the three empirical studies which I conducted for my dissertation during nine months of field work in Kenya at Sweetwaters Chimpanzee Sanctuary and three months in Uganda at Ngamba Island Chimpanzee Sanctuary.

The Study of Human and Chimpanzee Risk Preferences

Risk preferences in humans. Debates about how to define and measure risk preferences have a long tradition in the behavioral sciences (Bernoulli, 1738/1954; Edwards, 1954; Friedman et al., 2014; Schonberg et al., 2011; Slovic, 1964). In Psychology, risk preference pertains to the tendency to exhibit behaviors or (criminal) activities that are rewarding but involve some potential harms or losses (Mata et al., 2018). In Economics, risk preference refers to the willingness to engage in choices that involve higher variance in outcomes with known probabilities (Hertwig et al., 2019). In the early 20th century, economist Frank H. Knight (1921/1964; see also Keynes, 1936/1973; Keynes, 1937) drew a conceptual map which influenced the way psychologists and economists think about risk: he distinguished the world of measurable risk from the world of unmeasurable uncertainty. 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” (Luce & Raiffa, 1957/1989, p.13). In contrast, decision making under *uncertainty* (also sometimes referred to as *ambiguity* in Economics; Ellsberg, 1961), involves 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 deserves highlighting that in Knight's and Keynes' original concept of uncertainty, the state of the world or mind is characterized by incomplete or absent knowledge of possible outcomes such that making decisions under uncertainty, rather than risk, is the default.

Theorists have not only discussed how to conceptualize risk, but also how to measure it (see Frey et al., 2017). In the revealed–preference measurement tradition, choices under risk are studied using behavioral measures. These range from abstract experiments, such as monetary lotteries, to more naturalistic, game-like tasks (such as the Balloon Analogue Risk Task; e.g. Lejuez et al., 2002). The experimental paradigms are designed to capture specific cognitive processes such as the integration of gains and losses or the role of learning and experience (Frey et al., 2017). In the most commonly used setup, subjects make monetary decisions between a safe (reliable outcome; e.g. 5€) and a risky option (variable option; e.g. 50% chance of getting 10€ or nothing). In line with Luce and Raiffa's (1957/1989) definition, outcomes and probabilities are fully stated (either visually or numerically) under risk, whereas probability information is (sometimes partly) removed under uncertainty. Another major measurement tradition assesses human’s willingness to take risks by relying on stated preferences obtained in response either to relatively abstract questions (“Are you generally a risk-taking person or do you try to avoid risks?”) or to more specific scenarios (e.g., “How is your willingness to take risks in business and professional matters?”) (Blais & Weber, 2006; Dohmen et al., 2011; Josef et al., 2016). These propensity measures are widely used in practice, for example by financial firms, to assess the risk preference of their customers in compliance with regulatory requirements for the sale of financial products (Marinelli & Mazzoli, 2011).

Risk preferences in chimpanzees. In order to measure chimpanzees’ risk–taking behavior, comparative researchers have adapted paradigms from Behavioral Economics and typically define risk in terms of food variance (Haun et al., 2011; Heilbronner et al., 2008; Rosati, 2017; Rosati & Hare, 2011; Santos & Rosati, 2015). Analogous to many human experimental set–ups, nonhuman subjects make foraging decisions between safe (reliable outcome; e.g. one piece of food) and risky options (variable option; e.g. 50% chance of getting two pieces of food or nothing). Alternative measurement traditions for assessing primate risk–taking behavior are limited (but see field studies on e.g. responses to novelty: Kalan et al., 2019). However, behavioral assessment by long–time caregivers have been used to reliably measure other psychological domains such as well–being (e.g., Weiss et al., 2012) or personality (e.g., King & Figueredo, 1997; King et al., 2005; Uher & Asendorpf, 2008; Weiss et al., 2007). For example, Weiss and colleagues (2012) investigated whether great apes, like humans, show a midlife crisis. Their results suggest a pattern which is comparable to the U–shaped pattern observed in human well–being. Observer reports thus seem like a promising avenue to assess risk preferences in chimpanzees (Gosling & Vazire, 2002; McCrae, 1994). Furthermore, in their chapter on measuring personality in nonhuman animals, Vazire and colleagues (2007) showed that personality ratings of chimpanzees predict relevant real world behaviors. The authors concluded that trait rating methods yield more reliable and valid results than behavioral ratings— a point that has also been made in research on human risk preference (see Frey et al., 2017). Furthermore, using propensity measures in addition to behavioral assessments has the enormous advantage of permitting the comparison of results with well–established findings on human risk preferences (e.g. with the widely used Socio–Economic Panel (SOEP) risk preference measure; see Dohmen et al., 2011). In the next section I will highlight key theoretical and empirical findings on the study of human and great ape risk–taking behavior.

Key Properties of Risk Preferences

Psychological theories and studies have put forth a series of key properties of human risk preference and comparative researchers have begun to investigate some of these structural aspects in great apes. In this dissertation, I will focus on six well–studied properties of human risk preference and study them in chimpanzees, namely: risk aversion, ambiguity aversion, behavior under social risk, sex differences, age differences, as well as trait characteristics.

Risk Aversion. Many species, including humans, are sensitive to variance in the probability distribution of rewards and risk aversion is a common behavior (e.g., Hintze et al., 2015; Kacelnik & Bateson, 1996). However, previous research in primates, particularly chimpanzees, finds highly inconsistent results on risk aversion. Depending on the methodology and the rewards involved, some studies report that chimpanzees are––like humans––risk averse, preferring safe over the risky options (Keupp et al., 2021); others suggest, however, that chimpanzees are risk–seeking (Haun et al., 2011; Heilbronner et al., 2008; Rosati & Hare, 2011, 2012, 2013). Various factors might account for these inconsistent results. De Petrillo and Rosati (2021) propose that feeding ecology might explain chimpanzees' relatively high willingness to take risks, as they exploit seasonally variable and widely distributed fruit locations and engage in more risky hunting than other primates such as bonobos. Keupp and colleagues (2021), on the other hand, focus more on specific task characteristics and argue that the possibility of getting nothing (rather than a smaller reward) when choosing the risky option, influences choice behavior significantly and leads to less risk–seeking behavior in chimpanzees. In order to understand these inconsistencies, in Study 1 and 2 of my dissertation I investigated chimpanzees' attitudes towards risk using multiple methodological approaches.

Ambiguity Aversion. In many situations, the decision maker has only vague information about the probabilities of potential outcomes of her actions. Such situations with unknown or uncertain probabilities are often called ambiguous in Economics (Ellsberg, 1961), to distinguish them from situations with objectively known probabilities, which are typically called risky (see previous section). A broad body of literature suggests that humans prefer risky over ambiguous options that are equivalent under subjective expected utility (see Trautmann & Van De Kuilen, 2015). A study by Rosati and Hare (2011) indicates that chimpanzees and bonobos are sensitive to ambiguity in the first trials of their experiment, suggesting that subjects dislike choosing ambiguous options. Yet it remains unclear whether risky and ambiguous choices are positively or negatively correlated and whether they are supported by the same or a different cognitive system (Trautmann & Van De Kuilen, 2015). In Study 1 of my dissertation, I investigated ambiguity aversion and examined whether risky and ambiguous choices are correlated in chimpanzees and thus likely supported by the same cognitive mechanisms.

Social Risk. The studies reviewed above share a common feature: They investigated decision making under uncertainty and risk as a game against nature, that is, in the context of an interaction with the physical environment. However, individuals also make decisions under uncertainty and risk when interacting with the social environment (see also Hertwig et al., 2013). Several lines of evidence suggest that humans process and view risk and uncertainty in social and nonsocial settings differently (Blount, 1995; Bohnet et al., 2008; Bohnet & Zeckhauser, 2004; Fehr, 2009; FeldmanHall & Shenhav, 2019; Li et al., 2019; Rilling et al., 2008). In a series of experiments, Bohnet and colleagues (2008) showed that humans are 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): we experience stronger negative emotions if a social partner dupes us, compared to when we are let down by a nonsocial agent (e.g. nature or a machine). In a recent study, Calcutt, Proctor, Berman and DeWaal (2019) found that female chimpanzees are more averse to social than to nonsocial risk. However, the authors did not differentiate between chimpanzees' behavior in uncertain compared to risky situations. In addition, their results are difficult to interpret because it is unclear whether chimpanzees fully understood the set–up and its contingencies (see Calcutt et al., 2019). Therefore, in Study 2 of my dissertation I studied how chimpanzees deal with social and nonsocial uncertainty, using an established experimental paradigm.

Sex Differences. In his seminal review on the theory of decision making, Ward Edwards proposed that it would be essential to investigate to what extent people differ in their risk preference, and whether these differences could be explained with environmental, historical, or personality differences (Edwards, 1954). In humans, a person's sex is probably the most frequently theorized candidate correlate of risk preference. Empirical evidence suggests that men are generally more risk–taking than women (see Frey et al., 2021). Some theories have proposed that culturally acquired gender roles (Croson & Gneezy, 2009) contribute to sex differences in risk preference. Others have put forward sex related differences in neural correlates of risky decision making (Bolla et al., 2004; Cazzell et al., 2012) and proposed testosterone as a modulator of risky behaviors (Apicella et al., 2015). As other primates show strong parallels in terms of sexual differentiation in brain and body (Franklin et al., 2000), but do not share a human–like gender socialization (but see De Waal, 2022), they may help to differentiate between these mechanistic explanations (De Petrillo & Rosati, 2021). In chimpanzees, studies that compared risk preferences across males and females (Heilbronner et al., 2008; Rosati & Hare, 2013) did not find any appreciable effect. It remains unclear whether this may be due to relatively small sample sizes or whether the differences in risk–taking observed in humans may be primarily attributed to socialization experiences and not to biological differences that are shared with other primates. Using an exceptionally large sample, in Study 1 of my dissertation, I thus investigated how sex influences risk–taking behavior in chimpanzees.

Age Differences. Sexual selection theory proposes that the willingness to take risks is most pronounced in age–sex classes that have experienced the most intense reproductive competition (fitness variance) during the species' evolutionary history (see Wilson & Daly, 1985). In humans, the taste for risks peaks in adolescence and early adulthood (especially for men) and is lower in older age (Frey et al., 2021; Josef et al., 2016; Mata et al., 2016). However, most studies investigating chimpanzee risk preferences have not found major age–related changes (Heilbronner et al., 2008; Rosati & Hare, 2013). As with sex differences, it should be noted that past research has generally involved relatively small sample sizes with limited age ranges, so a key step is to examine populations with larger age variation. In Study 1 of my dissertation, I will make use of a large sample size to investigate the effect of age on chimpanzee risk preferences.

A Trait–Like Preference. Finally, recent evidence in humans suggests that risk preference can be seen as a trait–like preference which is stable across domains (e.g. financial, health, recreational risk) and measurement approaches (see Frey et al., 2017). In chimpanzees, it is an open question whether the willingness to take risks correlates across different domains (e.g., interactions with venomous animals, intergroup encounters, hierarchy fights) and measures of risk and whether this willingness can be regarded as a trait–like preference. I addressed this question in Study 1 of my dissertation.

In the next section I will shift focus from considering preference and choice data to discussing how chimpanzees explore their environment prior to a risky decision. This will help to better understand the processes underlying risky decision making.

Exploration Under Uncertainty

When humans and chimpanzees enter situations of conflict, forage in uncertain environments, get involved in hierarchy fights or encounter a venomous snake—their knowledge of the possible consequences and their respective probabilities is likely to be vague. However, they often have the opportunity to search for information before deciding whether to engage in risky behavior. For example, while foraging, animals may have the choice between two different fig trees differing in their degree of ripeness. Before deciding which tree to climb, they can inspect the environment, thus minimizing the chance that they end up sitting in a tree with unripe fruit. Through exploration individuals can thus get a better understanding of outcomes and probabilities and, in doing so, uncertainty morphs into calculable risk.

Most classic behavioral risky decision making tasks do not assess individuals' exploration tendencies and the most commonly used paradigm are behavioral measures in which participants are given a series of choices between monetary lotteries whose probabilities and outcomes are clearly stated. In choosing one option, participants can rely on a priori communicated probabilities and thus make decisions–from–description (Hertwig et al., 2004). Although there are, no doubt, real–world analogs of such summary description (e.g. of weather forecast, see Gigerenzer et al., 2005), human and nonhuman animals alike must often rely on exploration when deciding where to forage and shelter, or who to mate with (Hertwig et al., 2004; Weber et al., 2004).

In an innovative experimental paradigm involving experience rather than description, Hertwig and colleagues (2004) use a simple tool to capture decisions–from–experience. In this paradigm, subjects face two options, both representing an initially uncertain payoff distribution. They are not told anything about the properties of the options, but are allowed to explore them. They are encouraged to sample until they feel confident enough to decide which option is "better" and this is the option they would prefer to draw in a final trial with real payoffs. When choosing between options, participants rely on statistical probabilities based on their explorative experience (see Hau et al., 2010). In order to shed light on the evolution of adaptive behavior, the decisions–from–experience paradigm seems especially relevant to study how chimpanzees explore, choose, and adapt to their environment and offers a great opportunity to compare chimpanzee and human processes underlying risky decision making.

To date, the most commonly applied exploration set–up in nonhuman primates is Call and Carpenter's (2001) information–seeking paradigm (see Beran & Smith, 2011; Bohn et al., 2017; Call, 2010; Krachun & Call, 2009; Marsh & MacDonald, 2012; Paukner et al., 2006; Rosati & Santos, 2016). In this paradigm, the experimenter hides a reward in one of two horizontal opaque tubes, with the ends of the tubes in front of the participant. Subjects can then choose one of the tubes. Critically, subjects are allowed to watch the hiding of the reward on some of the trials; on other trials the hiding event is blocked from participants' view. On all trials, subjects have the option to peek into the tubes before making a decision. The hypothesis is that if subjects are aware of their knowledge states they should only search for information in trials where they had not seen the hiding process. Search on the other trials would be redundant. The apes and children in the original study behaved as predicted, exploring significantly more often on trials in which they were lacking information than on those in which they were informed.

Call and Carpenter's (2001) information–seeking paradigm allows subjects to eliminate all uncertainty before making a decision, but this will often not be possible in real–world situations. In the decisions–from–experience paradigm, even after extensive exploration, irreducible randomness remains because here uncertainty is due to stochastic factors in the environment (aleatory uncertainty), relative to the information–seeking paradigm in which uncertainty is due to lack of knowledge (epistemic uncertainty; see Hacking, 1975). Implementing the decisions–from–experience paradigm for use in great apes would extend our understanding of primates' coping with uncertainty and broaden the questions from "whether" primates seek for information to "what" types, "where" it is acquired and "how" adaptively the information source is used (Marsh, 2019).

In order to understand how chimpanzees explore their environment prior to a risky decision, I focused on two properties that have been investigated in humans to map the psychology of search in decisions–from–experience (Lejarraga et al., 2012). Specifically, I studied how environmental characteristics, in particular variance, and individual characteristics, such as the decision maker's risk and ambiguity preferences (assessed in a different context), influence exploration and decision making.

Environmental Characteristics. The ability to adapt to available resources, ecological characteristics and environmental features is an essential part of animal functioning. A greater degree of exploration is optimal when individuals possess little knowledge about the environment and when the environment is uncertain, variable or dynamic. A series of studies provide support for the proposition that human children (Bonawitz et al., 2012; Cook et al., 2011; Legare et al., 2016; Ruggeri et al., 2019; Schulz & Bonawitz, 2007; Stahl & Feigenson, 2015), adults (Gold & Shadlen, 2007; Kaelbling et al., 1996; Speekenbrink & Shanks, 2010) and other animals (Kramer & Weary, 1991; Nonacs, 2010; The Modelling Animal Decisions Group, 2014) engage in more exploration in response to unpredictable, as well as complex environments (Frey et al., 2015; Hills et al., 2013; Noguchi & Hills, 2016). Similarly, humans are inclined to adapt to the outcome variance of an environment and explore more in options where they experience outcome variance—a psychological proxy for perceived risk—compared to options they experience as invariant and safe (Lejarraga et al., 2012). Environmental characteristics can also influence the use of specific exploration patterns and impact how subjects switch between options during exploration (Hills & Hertwig, 2010). As frequent switching is associated with energy and memory costs, the question arises: what drives animals to switch between options? For example, a number of species apply basic exploration strategies that respond to the outcome of the previous choice, either by returning to previously rewarding locations ("win–stay", e.g. Rosati & Hare, 2013; Stopper & Floresco, 2011; Worthy et al., 2013) or by avoiding them ("win–shift", e.g. Reed, 2018). In Study 3 of my dissertation, I investigated the influence of environmental characteristics on chimpanzees' exploration and risky decision making.

Individual Characteristics. In addition to environmental features, a number of individual factors also influence exploratory behavior (Mehlhorn et al., 2015). In humans, exploration generally increases with cognitive capacity, physical strength and reduced dopamine levels and decreases with age, prior knowledge about the environment and high current resource levels. Some of these characteristics are dynamic and can change between different decision making events, e.g., experience with the current task and the current energy level. Other characteristics are less flexible, e.g. one's morphology and working memory capacity (Frey et al., 2015; Mehlhorn et al., 2015). Yet, there is only limited research on whether risk–taking and ambiguity–tolerant individuals tend to explore more or less than their risk– and ambiguity–averse peers. In one study, van den Bos & Hertwig (2017) showed that adolescents were more accepting of ambiguity yet also tended to explore less. The association between risk, ambiguity preferences and exploration effort is particularly relevant because in many real–world situations individuals only have limited knowledge of the consequences of their decisions and all of their associated likelihoods. However, they may still be in a position to search for information and thus reduce some of the uncertainty before acting on their knowledge. In Study 3 of my dissertation, I investigated the relationship between risk, ambiguity preferences and exploration effort.

Sample Size in Primate Cognition Research

Psychologists have adopted the comparative method to shed light on the evolutionary origins of behavior and cognition (Martins, 1995). Yet, data collection with primates is costly (Childers & Phillips, 2019; Conlee et al., 2004), as nonhuman primate subjects often belong to rare and endangered species and can only be studied in a few facilities around the world. This leads to inherently smaller sample sizes compared to other research fields. The results of a recent systematic review of studies in primate cognition (ManyPrimates, 2019) shows that the median sample size across all species and studies was 7 subjects. Investigations tackling individual differences in cognitive abilities are thus often hampered (for reviews, see Shaw & Schmelz, 2017; Völter et al., 2018), as such sample sizes are likely to have relatively low statistical power to detect small to medium effects of for example age and sex differences. In my dissertation I aimed to rely on an exceptionally large sample to determine whether the willingness to take risks in one of human's closest living relatives is isomorphic to that in humans. Therefore, I assessed risk preferences of all chimpanzees living in Kenya at Sweetwaters Chimpanzee Sanctuary and in Uganda at Ngamba Island Chimpanzee Sanctuary

Overview of the Dissertation

In this publication–based dissertation I shed light on the origins of behavior under risk and uncertainty. Using a comparative psychological approach, I conducted three empirical studies with chimpanzees, one of human's closest living relatives. Chapters 2–4 of this dissertation have been prepared for publication or are already published, and can thus also be read as self–contained.

In chapter 2, I demonstrate that chimpanzee and human risk preferences show key structural similarities (Study 1). Specifically, I investigate chimpanzees from infancy to adulthood in a cross–sectional design, considering domains that represent major classes of risks in the chimpanzee ecology. With an exceptionally large sample size and a multimethod approach, I combine observer ratings with behavioral choice experiments which build on stated willingness ratings and experimental studies on risk and ambiguity preferences in humans. I show that chimpanzees' willingness to take risks shares structural similarities with that of humans (see section on key properties). First, chimpanzee risk preference manifests as a trait–like preference that is consistent across domains and measurements. Second, chimpanzees are ambiguity averse. Third, males are more risk prone than females. Fourth, the appetite for risk shows an inverted U–shape relation to age and peaks in young adulthood.

In chapter 3, I show that chimpanzees, like humans, display higher aversion to uncertainty arising from social interactions than to uncertainty caused by interactions with a random mechanism (Study 2). 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 of 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.

In chapter 4, I investigate how chimpanzees explore their environment prior to a risky decision and across two experiments I show that exploration is shaped both by ecological properties and individual characteristics and is isomorphic to humans in important aspects (Study 3). In Experiment 1, I used a modified version of the information–seeking–paradigm (Call & Carpenter, 2001) and show that chimpanzees explore risky (outcome variance) more than safe conditions (no outcome variance). In Experiment 2, I adapted the decisions–from–experience (Hertwig et al., 2004) paradigm for use in great apes. Chimpanzees were simultaneously confronted with a risky (outcome variance) and a safe (no outcome variance) option and tested in two different environments, one stable and one changing. The results suggest that experiencing variance prompts more exploration. Over the course of the experiment, chimpanzees explore changing environments more than stable ones and they are more likely to explore within the risky than within the safe option when they experience outcome variance relative to when they do not. I further demonstrate that chimpanzees adapt their exploration patterns to the environment: in changing environments, chimpanzees have a clear preference for exploring only one option, whereas in stable environments, exploration of one option and sequential exploration of both options (i.e. one switch between options) are equally prevalent. The data reveals large interindividual differences in exploration and suggest that risk–taking individuals tended to explore less.

2

Chimpanzee and Human Risk Preferences Show Key Similarities

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3

How Chimpanzees Decide in the Face of Social and Nonsocial Uncertainty

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4

Adaptive exploration in chimpanzees

This chapter is in preparation

Abstract

Exploration is an important strategy for reducing the uncertainty that pervades daily life. Yet the evolutionary roots of adaptive exploration are poorly understood. In chimpanzees, humans' closest relatives, experimental studies on individual and environmental properties that shape their explorative behavior are rare. We investigated exploration under uncertainty in chimpanzees harnessing and adapting the human decisions-from-experience paradigm. Chimpanzees ($N = 15$) were simultaneously confronted with an uncertain (outcome variance) and a safe option (no outcome variance) and tested in both stable and changing environments. Similar to human exploration, how and how much chimpanzees explore are functions of environment and organism. One key environmental property is change: Chimpanzees explored more across trials in changing conditions than in stable conditions. Chimpanzees also explored more when they experienced variance in options' possible outcomes, consistent with the assumption in classic economic models that variance indicates risk. Furthermore, in changing environments chimpanzees' exploration focused on only one option, whereas in stable environments, a one-option focus and a sequential exploration of both options were equally frequent. Chimpanzee risk and uncertainty preferences also had effects on exploratory efforts, with risk-seeking individuals tending to explore less, thus accepting more uncertainty. These findings suggest that humans and chimpanzees share key similarities in the way they respond to uncertainty.

Keywords: chimpanzees, exploration, uncertainty, adaptive rationality, risk, decision making

The inescapable need to deal with an uncertain world has been proposed as the key adaptive pressure leading to complex cognition and behavior (1). One key and potentially sophisticated tool to cope with an uncertain world is the ability to adaptively explore it. The investigation of exploratory strategies preceding and informing choices with tangible consequences offers a window onto agents' ability to reckon with uncertainty (2, 3). Explorative behavior depends on both properties of the environment and the agent (4). Humans and other animals engage in more exploration in unpredictable and complex environments (5-7) and adapt their exploration strategies to the environment (8). Furthermore, specific dispositions that vary across individuals, such as openness and risk preference, have also been associated with explorative behavior (9, 10). Yet the biological evolutionary roots of humans' adaptive exploration remain poorly understood. Focusing on the exploration strategies of chimpanzees (*Pan troglodytes*) promises to shed light on how adaptively humans' closest living relatives inform themselves about the options they face. Previous studies investigating strategic information search in nonhuman primates have mainly focused on whether or not subjects searched for a desired object rather than on how properties of the environment and the agent influence search (11-15). Here we turn to how chimpanzees explore uncertain environments by adapting the decisions-from-experience paradigm used in humans (2) (see proof of concept in SI). We investigate how explorative behavior under uncertainty is shaped by environmental properties and risk and uncertainty preferences of the individual.

Chimpanzees chose between a safe option (without outcome variance) and an uncertain option (with outcome variance; Fig.1A), each comprising four covered trays. In the safe option, each tray was baited with a quarter of an apple. In the uncertain option, two trays were baited with half an apple each and two trays were empty. The chimpanzees began with no knowledge of the payoff distributions and could explore before choosing an option (Fig. 1B–F; Video S01). In a within-subjects design, chimpanzees participated in a stable and a changing environment condition. In the stable environment (Fig. 1G), the safe and uncertain options each stayed on the same side over trials and the same trays in the uncertain option were baited with food. In the changing environment (Fig. 1H), the safe and uncertain options changed sides over trials, as did the baited trays in the uncertain option.

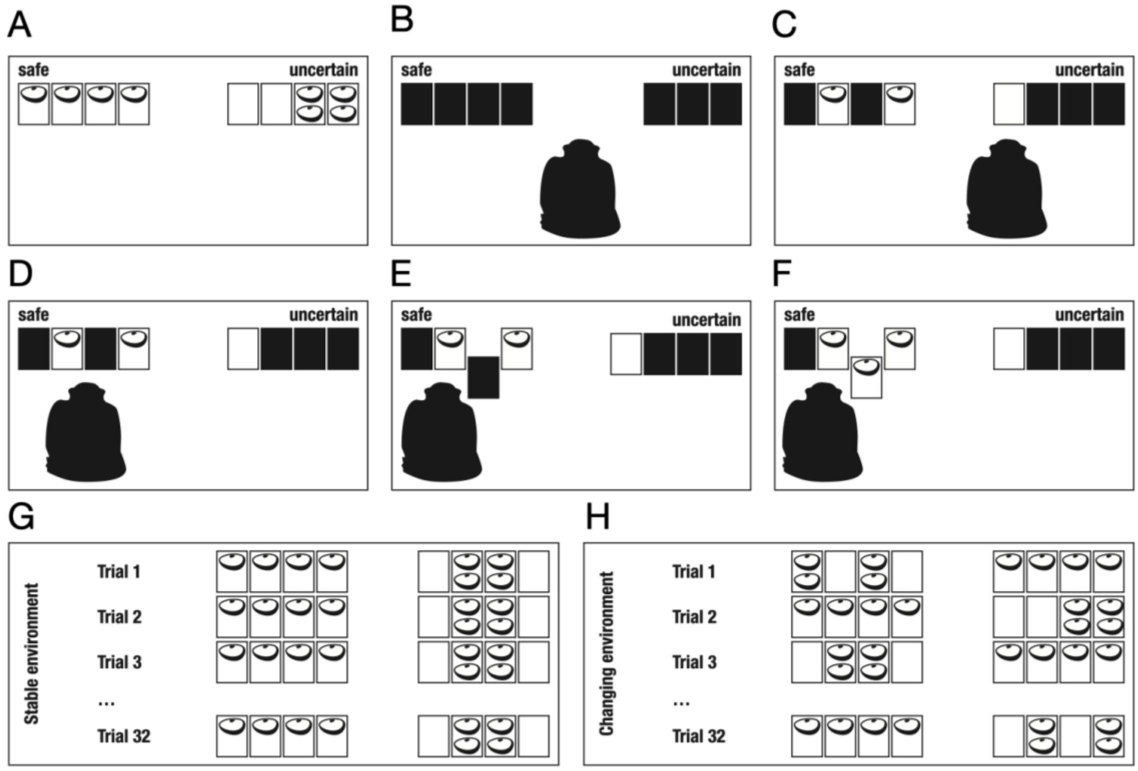

Figure 1. Schematic overview of the experimental set-up. (A) Underlying payoff structure. (B) Presentation of two options. (C) Exploration. (D) Choice of one option. (E) Random draw. (F) Reward (or no reward). (G) Stable environment. (H) Changing environment.

Results

Effect of environmental change. We investigated the effect of environmental change on exploratory behavior, by placing chimpanzee in stable and changing environments. Comparisons between binomial regression models (see SI) showed that those including the test predictors condition and trial made better predictions, with the model including the interaction between condition and trials performing best. The model estimate for the interaction term was negative (b = –0.19 [–0.31, –0.08]), suggesting that over trials chimpanzees explored changing environments more than stable environments. (Fig. 2A; SI). The uncertainty around the estimates is likely due to marked interindividual differences in exploration (Fig. 2B).

Effect of outcome variance. We studied whether chimpanzees were more likely to open trays in the uncertain than in the safe option, conditioned on them experiencing outcome variance in the former. In both stable and changing environments, chimpanzees were significantly more likely to open trays in the uncertain than in the safe option after they had experienced outcome variance relative to the absence of such experience (Wilcoxon signed-rank test, z = –3.84, p < 0.01; Fig. 3C; SI).

Exploration strategies and switching behaviors. Given two options, at least three distinct strategies can be used to explore them: Exploring only one option; extensively sampling from one then switching to the other; or exploring both options piecewise, switching back and forth between them (16). Across subjects and conditions, chimpanzees explored only one option in half of the trials (*Mdn* = 0.48). When exploring both options, chimpanzees preferred to explore sequentially (*Mdn* = 0.35), switching between options only once (Fig. 2D; SI). In the changing environment, chimpanzees clearly preferred to explore only one option (one option: *Mdn* = 0.57; sequential: *Mdn* = 0.35). In the stable environment, in contrast, chimpanzees explored one option (*Mdn* = 0.42) and sequentially explored options (*Mdn* = 0.44) equally often (Fig. 2E; SI).

Exploration effort. Subjects on average explored only half of the trays, albeit with high interindividual variation. This mirrors findings in humans which suggest that humans typically explore little, instead relying on surprisingly small samples (17). Given that exploration is commonly associated with opportunity and processing costs, limiting exploration effort can be rational (18) and may even be advantageous.

Risk and uncertainty preferences. We investigated the relationship between mean exploration effort (number of opened trays) in the current study and risk and uncertainty preferences measured previously in the same chimpanzees (19). Risk preferences were determined using behavioral choice experiments (potential outcomes and probabilities were known) as well as observer reports; uncertainty preferences were elicited using behavioral choice experiments (potential outcomes and probabilities were uncertain). Mean exploration effort and all risk measures were negatively correlated (behavioral risk measure: –.10 [–.62, .48]; observational risk measure, e.g., general risk: –.44 [–.79, .12]; see SI), meaning that risk-seeking chimpanzees explored less. Furthermore, we found positive correlations between mean exploration effort and the behavioral uncertainty measure (.32 [–.28, .74]), suggesting that uncertainty-tolerant chimpanzees explored more.

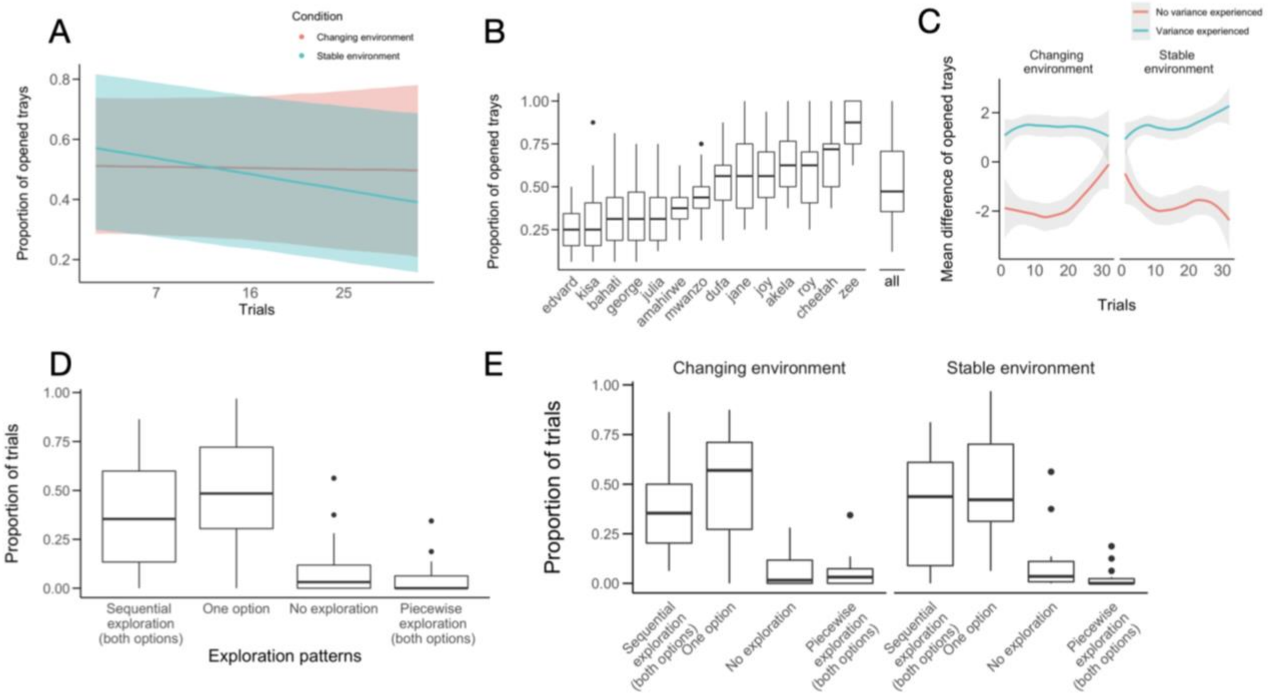

Figure 2. Adaptive exploration. (A) Effect of condition on exploration effort. Lines show regression splines with shaded 95% credible intervals. (B) Interindividual differences in exploration effort across conditions. (C) Mean difference in the number of opened trays between the uncertain and the safe option across 32 trials. Red lines indicate trials in which no outcome variance was experienced; blue lines, trials in which outcome variance was experienced. A positive difference indicates more exploration in the uncertain than in the safe option. Regression lines with 95% confidence intervals were plotted with the function geom_smooth. (D) Exploration strategies and their proportional use across trials. (E) Condition-specific exploration strategies and their proportional use across trials. (B, D, E) Box plots show the median and 25th and 75th percentiles; whiskers indicate the values within 1.5 times the interquartile range; circles are outliers.

Discussion

Taken together, our results suggest that chimpanzees, like humans, engage in adaptive exploration to reduce uncertainty. Both species flexibly adapt their exploration to properties of the environment. Furthermore, their risk and uncertainty preferences influence their exploration behavior. First, change in environments attracted attention and affected explorative behavior: Chimpanzees explored more across trials in changing environments than in stable ones. Second, the experience of outcome variance boosted exploration: Chimpanzees were more likely to open trays in the uncertain option than in the safe option once the experience of varying outcomes signaled the presence of variance and risk (as defined in the economic definition of risk). These results are in line with earlier findings suggesting that humans explore riskier options more than safer options when they experience outcome variance—a reasonable response to the signal of risk (8). Third, chimpanzees adapted their exploration strategies to the environment. In changing environments, they preferred to explore only one option, whereas in stable environments, they relied equally often on exploring one option and exploring sequentially. In changing environments, focusing on one option leads to surprises, but also reduces important energy and memory costs (16). This is also in line with previous findings suggesting that if expectations about an option are violated, explorative behavior will then be directed to this option (6). Finally, we found that chimpanzees' explorative behavior is also shaped by personality differences. We observed marked interindividual differences in exploration, with risk-seeking chimpanzees tending to explore less. Notably, uncertainty-tolerating chimpanzees tended to search more rather than less. This finding diverges from observations in humans: van den Bos and Hertwig (10) found that adolescents are more uncertainty-tolerant than children and adults and tend to explore less. With the exception of this possible divergence from stable patterns in human explorative search, our results suggest that human and nonhuman primates in terms of their exploratory efforts respond similarly to uncertainty in the environment.

Materials and Methods

Participants. We tested 15 semi-free-ranging chimpanzees from Sweetwaters Chimpanzee Sanctuary in Kenya (eight females; age: *M* = 22.83 years, range = 13–33 years; for individual characteristics, see Dataset S01). 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, Ol Pejeta Conservancy, in Kenya (see SI). Due to the COVID-19 pandemic, 5% of the planned trials could not be run (see Dataset S01 for details on missing trials). We excluded the data of one chimpanzee, Niyonkuru, as he was tested in only one condition.

Supporting Information. is available for this paper.

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5

General Discussion

Across three empirical studies, I investigated the origins of behavior under risk and uncertainty. In the following, I will highlight and discuss the main findings and relate them to the broader literature.

The Main Aspects of Risk Preferences in Chimpanzees and Humans are Isomorphic

Risk preference is of key importance for human and nonhuman behavior. The results of the current dissertation show that chimpanzee and human risk preferences share major structural similarities. In the following, I will focus on six well–studied properties of human risk preference (that I introduced in the general introduction) and discuss my findings in chimpanzees in light of these characteristics.

Risk Aversion. The results of Study 1 suggest that, when confronted with two urns with the same expected values, chimpanzees were risk neutral to (minimally) risk prone. In Study 2, irrespective of whether the context was social or nonsocial, chimpanzees proved to be risk averse. They preferred the safe option over the risky option, even though the expected value of the latter was higher. These contradictory findings are in line with the inconsistent findings of past research in this regard. In Study 1 chimpanzees had to infer probabilities from the task design, whereas in Study 2, chimpanzees learned the frequencies (probabilities) through experience. In both studies the risky option included the possibility of receiving nothing. The variation in chimpanzee risk sensitivity may thus be explainable in terms of the presentation and experience of probabilities (see Hau et al., 2010; Heilbronner & Hayden, 2016; Hertwig, 2015; Wulff et al., 2018), i.e. whether subjects had to infer probabilities from the task design (Haun et al., 2011; Rosati & Hare, 2011, 2012, 2013, 2016) or whether decisions were based on experienced relative frequencies (probabilities) (see Calcutt et al., 2019; Haux et al., 2021; Heilbronner et al., 2008; Keupp et al., 2021). In humans it has been shown that these different representation formats trigger different choices (Hau et al., 2010). Future research should systematically tackle the question of how specific elements of the task design and the presentation or experience of frequencies (probabilities) causes variation in chimpanzee risk preference.

Ambiguity Aversion. The results of Study 1 suggest that chimpanzees were clearly ambiguity averse, i.e. they disliked choosing options with missing probability information. This finding is in line with results by Rosati and Hare (2011) who found that chimpanzees and bonobos were sensitive to ambiguity in the first trials of their experiment. Furthermore, the results of Study 1 indicate that risky and ambiguous choices are negatively correlated for chimpanzees (r = –.50 [–.70, –.23]). Taken together, these results indicate that, in chimpanzees, risky and ambiguous choices might not be manifestations of the same psychological phenomenon. This suggests that the cognitive mechanisms supporting risk and ambiguity preferences may be distinct (Santos & Rosati, 2015). In humans the relationship between risk and ambiguity preference has received much attention. Although the overall evidence is suggestive of a positive correlation, several studies also report negative correlations or the absence of a correlation (see Trautmann & Van De Kuilen, 2015). Further research is needed to explore potential moderators, study the underlying psychological mechanisms, and investigate the relationship of ambiguity attitudes to real–world behavior in human and nonhuman primates (see Trautmann & Van De Kuilen, 2015).

Social Risk. In Experiment 1 of Study 2, I found that uncertainty in social versus nonsocial contexts, is relevant to chimpanzee decision making. Subjects were less likely to engage with the uncertain option under social than under nonsocial uncertainty. Additionally, they hesitated longer before they trusted a partner compared to a machine. The results suggest that chimpanzees experienced more cognitive conflict in uncertain social contexts that require them to place trust in a peer compared to uncertain nonsocial contexts in which they must trust a machine. In humans, similar preferences are explained in terms of betrayal aversion (Bohnet et al., 2008). Chimpanzees thus do not seem to be only concerned with outcomes per se, but also about how they come about. Experiment 2 focused on risk rather than uncertainty. Animals' choices and latency did not differ between the social and nonsocial condition. Overall, these findings suggest 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 turned into risk (see also Calcutt et al., 2019). It is important to point out that in everyday life, the decision of whether or not to engage in a social situation is usually a decision made under uncertainty, as humans and nonhuman animals rarely know precisely how likely others will cooperate.

Sex Differences. Using a multimethod approach and examining major ecological domains of risk, in Study 1, I investigated sex differences in chimpanzees. The results show that, across domains (foraging, interacting with snakes, escaping from their territory, competing for higher rank in the dominance hierarchy, and interacting with (human) strangers) and measurements, males were more risk–seeking than females, mirroring stable differences in human risk preference (Frey et al., 2021). To further compare the size of the sex difference in chimpanzee and human risk preference, I calculated POMP (percentage of the maximum possible score, see Cohen et al., 1999) for the general risk item of the observer ratings. Chimpanzee males had 8 percentage points of the maximum possible more than females. This corresponds closely to the effect size reported for sex differences in humans (e.g., 6 POMPs, see Dohmen et al., 2011). Consistent with life–history theory, the sex difference was most pronounced in the hierarchy domain, i.e. the willingness to take risks in order to get a better position in the hierarchy (e.g. Stearns, 1992). The findings indicate that sex differences in risk preferences may not only be shaped by socialization experiences but that they have deeper biological roots (Dohmen et al., 2012; Plank, 2019; Roberts et al., 2005; Slovic, 1987).

Age Differences. According to life–history theory, risk–taking should be elevated during periods when the goal of reproduction and related proximate goals (e.g., attaining social status) are predominant (Stearns, 1992). In Study 1, for the first time, I investigated whether chimpanzee risk–taking mirrored that of humans, where risk–taking peaks in adolescence and early adulthood and is lower in older age (Frey et al., 2021; Josef et al., 2016; Mata et al., 2016). An inverted U–shaped relationship emerged consistently across domains and was least pronounced for interactions with strangers. This finding reflects data in humans demonstrating that the willingness to take risks in the strangers domain peaks in early adulthood, decreases in older age, but remains relatively stable across the lifespan (Josef et al., 2016). This echoes theoretical and empirical findings which suggest that in humans and chimpanzees the social domain remains important across adulthood (Carstensen et al., 1999; Rosati et al., 2020). Furthermore, the finding of a general increase in risk–taking during young adulthood complements a recent overview of risk behavior across age groups (Willoughby et al., 2021) which suggests that emerging adulthood (rather than adolescence) is a period of heightened risk–taking also in humans.

A Trait–Like preference. In line with recent findings in humans (Frey et al., 2017), in Study 1, I found that chimpanzee willingness to take risks manifests as a trait–like preference, with high rank–order stability across major domains in both behavior and observers' assessments. This is consistent with previous investigations suggesting that animal personalities exist across a range of species and that risk related traits are common characteristics (Wolf et al., 2007). Furthermore, I found that the strangers risk domain is only weakly correlated with the other risk domains. This is in line with Study 2 and earlier investigations which indicate that trusting others is not just a special case of risk–taking but is based on important forms of social preferences such as betrayal aversion (Calcutt et al., 2019; Fehr, 2009).

The Assessment of Risk Preferences in Chimpanzees

As a crucial determinant of life outcomes such as health, wealth, and wellbeing, risk preference is a mainstay construct in the behavioral sciences and a key building block in theories of choice (Barseghyan et al., 2013; Brailovskaia et al., 2018; Clark & Lisowski, 2017; Dohmen et al., 2011; Mata et al., 2018; Schonberg et al., 2011; Slovic, 1987). In the past few years, measurement and stability have been at the center of the debate about the nature of risk preferences (Frey et al., 2017; 2021; Josef et al., 2016; Schildberg-Hörisch, 2018; Weber et al., 2002). Study 1’s novel multimethod approach provides a sound empirical basis to enrich this discussion and allows us to compare the current results with recent findings on human risk preferences (Frey et al., 2017). To assess chimpanzee risk–taking across major domains, I combined, for the first time, observer ratings of stated willingness (Gosling & Vazire, 2002; McCrae, 1994) with behavioral choice experiments. Importantly, the interrater reliabilities of the observers were excellent and I find positive correlations between the different risk domains: they were strongest between general and foraging risk (r = .85 [.77, .90]) and weakest (even though still relatively high) between escape and hierarchy risk (r = .48 [.30, .63]). The only exception was strangers risk, which was only weakly correlated with the other risk domains (general risk: r = .10 [–.11, .31]). These divergent findings mirror past results indicating that social risk–taking involves an element of trust, and thus is rooted or is co–determined by social preferences (Engelmann et al., 2015; Fehr, 2009). Furthermore, the risky choices in the experiment were positively correlated with the observer ratings (e.g. risky choices*general risk: r = .36 [.06, .60]; risky choices*risk rank order: r = .38 [.08, .62]). In humans, behavioral and stated risk measures correlate only weakly (M = 0.06, HDI = 0.05 to 0.06) (see Frey et al., 2017). Taken together, the findings reveal that across various aspects of chimpanzee risk preference, both observer ratings and behavioral choices converge in crucial ways. The next step towards a general mapping of the construct of risk preference will be the understanding of temporal stability and systematic individual change. In humans, individual risk preferences appear to be persistent and moderately stable over time (Schildberg-Hörisch, 2018).

Environmental and Individual Characteristics Influence Exploration Under Uncertainty

In Study 3 I investigated how explorative behavior under uncertainty is shaped by ecological properties and individual characteristics and I analyzed the exploration processes underlying risky decision making. I therefore adapted the experience–based sampling paradigm (see Wulff et al., 2018) for use in great apes. Chimpanzees were initially ignorant about the properties of the options (payoff distributions). However, they had the opportunity to explore the distributions to develop an understanding of the underlying structure. Individuals were presented with two options representing unknown payoff distributions. To learn about the possible outcomes and frequencies, participants could draw random samples from each of the payoff distributions. This exploration process was under the participants' own control: They could decide whether to explore, which option to explore, and when to switch between options. After the exploration they could choose one of the options.

Exploration. On average, chimpanzees explored half of the available options in both experiments, although with large differences between subjects. Given that exploration tends to involve opportunity costs and, at a very minimum, processing costs, relying on low exploration may be rational and even beneficial in some situations (Hertwig & Pleskac, 2010; Ostwald et al., 2015; Vul et al., 2014). Over trials, chimpanzees' exploration rate dropped notably. One interpretation of this effect is that subjects learned the structure of the choice problem during the experiment, an effect that has also been observed in humans (see Lejarraga et al., 2012).

Environmental Characteristics. The results of Study 3 indicate that chimpanzees adapted their search to the specificity of the environment. First, I show that the variance of the environment impacts chimpanzees' explorative behavior. In Experiment 1, I found that chimpanzees were more likely to explore risky (outcome variance) compared to safe (no outcome variance) conditions. In Experiment 2, when deciding between a safe (no outcome variance) and a risky (outcome variance) option, chimpanzees explored changing more than stable environments over trials. Chimpanzees were also more likely to open trays within the risky than within the safe option when they experienced outcome variance relative to when they did not. This is in line with empirical findings in humans, which indicate that when humans experience outcome variance—a psychologically suitable proxy for perceived risk—they explore riskier more than safer options (see Lejarraga et al., 2012). More exploration seems recommendable when there is greater uncertainty, i.e. when one knows little about the environment, or when the environment is variable. The necessity to deal with uncertain and changing environments has been described as the key adaptive pressure leading to complex cognition and behavior (Godfrey-Smith, 1998; Sterelny, 2003).

Furthermore, I investigated exploration patterns and switching behavior in Experiment 2. Chimpanzees explored only one option in half of the trials. When exploring both options, subjects overall switched only once between options, which is compatible with the idea that switching behavior involves high energy and memory costs (see Hills & Hertwig, 2010). I then looked at both conditions separately and found that chimpanzees adapt their exploration to the specificity of the environment: in changing environments, they had a clear preference for exploring only one option, whereas in stable environments, exploration of one option and sequential exploration of both options (i.e. one switch between options) were equally prevalent. This is in line with previous findings, suggesting that if expectations about options are violated, explorative behaviour about that specific option is promoted (e.g. Stahl & Feigenson, 2015). In changing environments, exploring only one option will continuously lead to surprises. Focusing on one, rather than multiple options, can thus enhance learning while reducing switching costs. Delving deeper into which other environmental cues drove chimpanzees' switching, I found that chimpanzees were more likely to switch to the safe option if they previously had found food. Implying that subjects leave the vicinity of the first find and explore elsewhere. Such a "win–shift" strategy is adaptive in environments where food sources are dispersed or require time to regrow: obtaining food in one location decreases the likelihood of finding additional food there (see Reed, 2018).

Individual Characteristics. Next, I investigated whether chimpanzees' explorative effort in Study 3 is related to their risk and ambiguity preferences assessed in Study 1 (same chimpanzees). I found consistent negative correlations between the mean exploration effort and the two types of risk measure: behavioral and observational. I also found positive correlations between exploration effort and behavioral ambiguous choices. This suggests that risk–taking (but not ambiguity tolerant) individuals tend to explore less. To my knowledge, there is no study with nonhuman primates and only one with humans that has analyzed this relationship systematically. Van den Bos & Hertwig (2017) examined participants' risk and ambiguity preferences (aged 8 to 22 years) and their exploration effort. Contrary to the current findings, their results point to the fact that adolescents are more accepting of ambiguity but also tend to explore less.

Risky Choices. Finally, Study 3 shows that in chimpanzees, not only exploration, but general decision making is influenced by environmental characteristics. Regardless of how much they explored, in changing environments, chimpanzees were risk neutral, choosing the safe and risky option equally often, whereas in stable environments chimpanzees were risk–seeking and preferentially chose the risky over the safe option. These results indicate that in both humans and chimpanzees the environment should be taken into account when investigating exploration and choices under risk and uncertainty.

Overall, in Study 3, by adapting a modified version of the information–seeking paradigm (Experiment 1, see Call & Carpenter, 2001) and implementing the decisions–from–experience paradigm (Experiment 2, see Hertwig et al., 2004) for use in great apes, I could show that both environmental and individual characteristics influence chimpanzee exploration in important ways. Past studies investigating behavior under uncertainty in nonhuman primates mainly focused on *whether* subjects searched for desired but hidden objects (Beran & Smith, 2011; Bohn et al., 2017; Call, 2010; Call & Carpenter, 2001;

Krachun & Call, 2009; Marsh & MacDonald, 2012; Paukner et al., 2006). The decisions–from–experience paradigm seems like an especially exciting avenue to further understand how chimpanzees explore, choose, and adapt to their environment and offers a great opportunity to compare chimpanzee and human processes underlying risky decision making.

Advances in Primate Cognition Research

Previous studies investigating chimpanzee risk preference had sample sizes ranging from 4 to 24 subjects, as well as relatively narrow age ranges (De Petrillo & Rosati, 2021). At such sample sizes, power to detect small to medium age and sex effects is low. In my dissertation I relied on an exceptionally large sample ($N = 86$) to determine interindividual differences in chimpanzee willingness to take risks. Studies involving chimpanzees from different groups and environments will further enrich the discussion about the generalizability of behavioral variations, as sanctuary chimpanzees might display divergent risk preferences from those living in zoos and those in the wild (for a discussion on the generalizability across groups see: King et al., 2005; Weiss et al., 2007; Wobber & Hare, 2011). Last but not least, since it has been proposed that bonobos (*Pan paniscus*) and chimpanzees (humans' two closest living relatives) show divergent risk preferences (see Rosati, 2017), for a complete reconstruction of human's last common ape ancestor, it is essential to also study bonobos' willingness to take risks in more depth in the future.

Conclusion

Risk and uncertainty are central to all adaptive decisions human and nonhuman animals make — including deciding where to forage, with whom to mate, and how to deal with dangerous situations. In my dissertation I studied the evolutionary roots of behavior under risk and uncertainty and investigated to what extent chimpanzee behaviour is isomorphic to that of humans. Understanding the biological underpinnings of this key building block of decision processes is of wide interest to a number of disciplines — e.g. Psychology, Economics, Behavioral Biology, Cognitive Sciences, Anthropology because it is fundamental to how organisms behave and make choices and constitutes a central issue for perspectives on life–history strategies. In sum, the results of the three empirical studies show that chimpanzee and human behavior under risk and uncertainty converge in crucial ways. Such structural similarities likely reflect adaptations to similar dynamics in human and primate life–histories, suggesting that human preferences are not only shaped by human specific cultural development and socialization, but also have evolutionary roots.

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Appendices

A. Supplemental Materials for Chapter 2

Chimpanzee and Human Risk Preferences Show Key Similarities

This chapter is published as

Haux, L. M., Engelmann, J. M., Arslan, R. C., Hertwig, R., & Herrmann, E. (2023). Chimpanzee and Human Risk Preferences Show Key Similarities. *Psychological Science, 34*(3), 358–369.

SM can be accessed at:
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The Supplementary Material includes:

Methods
Figure S1
Tables S1 to S9

Other Supplementary Materials: can be requested from Lou M. Haux (haux@mpib-berlin.mpg.de)

Dataset S1 (Separate File). Background information on the chimpanzees assessed by means of observer ratings and included in the behavioral experiments.

Dataset S2 (Separate File). Data of the observer ratings.

Dataset S3 (Separate File). Data of the behavioral experiments.

B. Supplemental Materials for Chapter 3

How Chimpanzees Decide in the Face of Social and Nonsocial Uncertainty

This chapter is published as

Haux, L.M., Engelmann, J.M., Herrmann, E, Hertwig, R (2021). How chimpanzees decide in the face of social and nonsocial uncertainty. *Animal Behaviour, 173,* 177-189.

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https://doi.org/10.1016/j.anbehav.2021.01.015

The Supplementary Material includes:

Methods
Tables A1 to A7

C. Supplemental Materials for Chapter 4

Adaptive Exploration in Chimpanzees

The Supplementary Material includes:

Methods

Other Supplementary Materials: can be requested from Lou M. Haux (haux@mpib-berlin.mpg.de)

Dataset S01 (separate file). Background information on the chimpanzees.

Dataset S02 (separate file). Data of the experiment.

Video S01 (separate file). Experimental set-up.

Proof of concept

Prior to the actual study, we investigated whether chimpanzees are sensitive to environmental variance (Lejarraga et al. 2012) using a modified version of the information-seeking paradigm (Call & Carpenter, 2001; see also Beran & Smith, 2011; Bohn et al., 2017; Call, 2010; Call & Carpenter, 2001; Krachun & Call, 2009; Marsh & MacDonald, 2012; Rosati & Santos, 2016). In this paradigm, the experimenter hides a reward in one of two horizontal opaque tubes. Subjects then choose one of the tubes. Critically, subjects can watch the reward being hidden in some trials but not in others. In all trials, they can peek into the tubes before making a decision. The hypothesis is that if they are aware of their knowledge states (i.e., having or not having seen the reward being placed into the tube), they should only search for information in trials where they did not see the reward being hidden. The apes and children in the original study behaved as predicted, exploring significantly more often when they had not seen the reward being hidden. Broadening the questions addressed from if and when primates seek information to what kind of information they seek, where it is acquired, and how adaptively the information source is used, offers an opportunity to expand the paradigm in terms of the complexity of tasks and the cognitive capacities involved (Marsh, 2019). Here we studied whether chimpanzees explore uncertain conditions (with outcome variance) more than safe conditions (without outcome variance). Chimpanzees were tested in an uncertain and safe condition. In a within-subject design, we exposed the chimpanzees to both environmental conditions by presenting them sequentially.

Methods

Participants. We tested eight semi-free-ranging chimpanzees from Sweetwaters Chimpanzee Sanctuary in Kenya (three females; age: *M* = 22.38 years, range = 16–35 years; for individual characteristics, see Dataset S01). Chimpanzees were socially housed, had access to a large outdoor enclosure during the day and received regular daily feedings, daily enrichment sessions, and water ad libitum. They participated in the study voluntarily and were not 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.

Materials. The set-up consisted of two opaque buckets (height: 25.5 cm, diameter of the opening: 30 cm), each with a lid, standing 200 cm apart from each other. A rope was attached to each lid and bucket.

Design. In a within-subjects design, chimpanzees participated in a safe and an uncertain condition. Each condition comprised 24 trials (blocked) presented across four sessions. The order of conditions was counterbalanced across subjects. The safe and uncertain option were not presented simultaneously and therefore no choice between them was required. In both conditions, chimpanzees were presented with two buckets (options). In the safe condition, both buckets were baited with half an apple (i.e., both options were safe and none included outcome variance). In the uncertain condition, one bucket was baited with half an apple and one bucket was empty (outcome variance). The location of the food was counterbalanced across trials. Note that uncertainty here does not arise from choosing between a safe and an uncertain option (e.g., a choice between $3 for certain and $32 with a probability of 10% and $0 otherwise) but from not knowing which of the two options holds the reward. Outcome variance thus does not refer to an option (a bucket) but rather to the whole trial (i.e., choosing one of the two buckets). In both the safe and the uncertain conditions, the possible reward was the same: half an apple.

Test Phase. At the beginning of each trial, the experimenter showed the chimpanzee the contents of both buckets. In the safe condition, both buckets contained half an apple. In the uncertain condition, one bucket contained half an apple, whereas the other bucket was empty. The experimenter then turned around so that the chimpanzees could no longer monitor which buckets were baited (both in the safe condition, one in the uncertain condition), shuffled the buckets, and closed them with a lid. They then turned back around to face the chimpanzee, placed both buckets in front of the chimpanzee, and made the lid ropes available. The experimenter moved away and the chimpanzee had 20 seconds to explore the content of the buckets by pulling away the lids and standing up to peek into the buckets (eye line had to reach 1 m). After this exploration phase, the experimenter pulled the lids back onto the buckets and made the choice ropes available to the chimpanzee. They chose a bucket by pulling the respective choice rope. They received the reward if they chose the baited bucket and were shown the contents of the bucket they had not chosen. If no choice was made within 30 seconds, the trial was repeated. If a chimpanzee refused to make a choice twice in a row, the session was ended and the remaining trials were run the next day.

Coding and Reliability. To analyse whether chimpanzees explored more in the uncertain condition than in the safe condition, we coded whether chimpanzees pulled away the lids and stood up to peek into each bucket. All trials were recorded with one camera and coded live as well as later from video. A research assistant who was unaware of the study design and research question independently coded 20% of all trials. Interrater agreement was excellent for exploration (Cohen's $k = 0.94$) and choice (Cohen's $k = 1$).

Analysis

For both experiments, we relied on Bayesian estimation techniques, applying Bayesian generalized linear models using Stan in R (R Core Team, 2020) for regression analyses with the brms package using the function brm (Bürkner, 2017). We specified weakly informative normal priors with mean 0 and standard deviation 2 on all population-level effects (Gelman, 2006). We assessed the convergence of posteriors through visual inspection and the Gelman–Rubin diagnostic, Rhat (Gelman & Rubin, 1992). In general, we report the mean of the posterior distribution of the parameter and two-sided 95% equal tail credible intervals (CI) around each value. For all data figures, we used the function conditional_effects to display the conditional effects of the predictors of the fitted models (Bürkner, 2017). We computed leave-one-out cross-validation (LOO) values for every model (Vehtari et al., 2017). The LOO value indicates a model's pointwise out-of-sample prediction accuracy; models with lower LOO values are preferred. For the model comparison, we also added LOO weights (weights add up to 1). Following McElreath (2016), we used these metrics to rank models.

Results

Effect of variance. We used binomial regression models to investigate chimpanzees' exploration of the buckets (no, yes). We included the predictors condition (safe, uncertain), sex (female, male), age (in years), trial number within condition, and order of condition (coded as factor: control first, test first) as fixed effects and subject ID as a random intercept. As random slopes, we included condition and trial number within subject ID (but not the correlation among random slopes and intercept). The covariates age and trial number were *z*-transformed and condition was dummy-coded and centered for the random slope part.

Chimpanzees explored at least one bucket in 45% of the trials overall: 32% in the safe condition and 57% in the uncertain condition. Model comparisons showed that models including the predictors condition and trial made better predictions, with the model including the interaction between condition and trials showing the best performance (interaction: weight = 0.57; main effects: weight = 0.33; without trial and condition: weight = 0.09). The model estimate for the interaction term was large and positive (b = 0.47 [–0.06, 1.01]), suggesting that over trials chimpanzees increasingly explored more in the uncertain than in the safe condition. In the main effects model excluding the interaction, the estimate for condition was reliably positive (b = 1.35 [0.33, 2.24]), suggesting that chimpanzees were more likely to explore the buckets in the uncertain condition than in the safe condition. The estimate for trial was associated with some uncertainty because the corresponding 95% CI included 0 (b = –0.47 [–1.04, 0.03]).

Experiment

We investigated how environmental change (RQ1; see Ruggeri et al., 2019) and outcome variance (RQ2; see Lejarraga et al., 2012) prompt chimpanzees' exploration; with which strategies they implement their explorative behavior (RQ3; see Hills & Hertwig, 2010); and how individual characteristics, specifically risk and uncertainty preferences, shape chimpanzees' explorative behavior (RQ4; Mehlhorn et al., 2015; van den Bos & Hertwig, 2017). Finally, we also investigated whether chimpanzees' decision making differs between environments.

Materials. The set-up consisted of eight small black trays (14 cm × 22 cm), each with a lid. A rope was attached to each lid. A safe and an uncertain option, each comprising four trays, were presented 115 cm apart from each other. In the safe option, each tray was baited with a quarter of an apple (without outcome variance). In the uncertain option, two trays were baited with half an apple each and two trays were empty (with outcome variance). After the exploration phase, the experimenter removed the lid ropes and made two choice ropes (one for each option) available to the chimpanzee, who chose one of the options by pulling the respective rope. The chimpanzee received access to one tray randomly drawn from that option (see Figure 1 and Video S01).

Design. In a within-subjects design, chimpanzees participated in a stable and a changing environment condition (Figure 1). In the stable environment condition, the safe and uncertain options stayed on the same sides across all trials and the same trays in the uncertain option were baited with food. In the changing environment condition, the safe and uncertain options changed sides over trials and the baiting of the trays in the uncertain option changed (six possible baiting patterns were implemented). Each condition comprised 32 trials (blocked), presented across eight sessions. The order of conditions was counterbalanced across subjects. The side of the safe option and the baiting pattern of the uncertain option was counterbalanced between subjects and within subjects.

Methods. In the decisions-from-experience paradigm, established in research on risky choice in humans, participants are confronted with two boxes, each containing a set of outcomes that occur with some probability. In the simplest version, participants face an uncertain (with outcome variance) and a safe (without outcome variance) option. They are not signalled anything about the properties of the options, but are encouraged to explore them until they feel confident enough to decide which is "better." When deciding between options, participants rely on subjective estimates of the (expected) values based on their explorative experience; final choices remain probabilistic (risky) choices. In the decisions-from-experience paradigm, irreducible uncertainty remains (e.g., have all possible states of the world been encountered?) even if decision makers engage in extensive exploration—because uncertainty is here due to stochastic factors in the environment (aleatory uncertainty), whereas in the information-seeking paradigm uncertainty is due to lack of knowledge (epistemic uncertainty; see Hacking, 1975).

Familiarization Phase. Prior to the test sessions, each chimpanzee was individually familiarized with the set-up. Familiarization consisted of a food quantity test using the same rewards as in the actual test (i.e., apples) followed by three consecutive pretest steps with bananas as rewards. During all familiarization steps but the last, the trays were presented without lids. Chimpanzees who passed the familiarization phase participated in the test trials.

Food quantity test. Each chimpanzee completed a food quantity test involving two consecutive sessions of four trials each, where they chose between a quarter of an apple and half an apple (two quarter pieces). The criterion was that they chose the tray baited with half an apple in seven of eight trials. For each trial, the rewards were placed on two separate trays, each furnished with a rope. Chimpanzees selected a tray by pulling its rope, then received the selected food. The nonselected food was removed and placed in a food bucket. The location of the half apple (left or right of the chimpanzee) was randomized and evenly distributed over trials.

Pretest. All chimpanzees were individually introduced to the experimental set-up in three consecutive pretest steps.

In the first pretest (four consecutive sessions of eight trials each), chimpanzees were familiarized with the random mechanism. They experienced that they would only receive one of the four trays after each choice. The criterion was that they pulled the rope. For each trial, only one option was present. Its location (left or right of the chimpanzee), as well as which of the four trays was drawn, was randomized and evenly distributed over the trials. In the first two sessions, chimpanzees were familiarized with the safe option, in which each of the four trays were baited with a quarter of a banana. Chimpanzees were thus rewarded for pulling the rope on every trial. In the third and fourth sessions, chimpanzees were familiarized with the uncertain option, in which two trays were baited with half a banana each and two trays were empty. Chimpanzees were thus rewarded for pulling the rope in half of the trials. The reward pattern was pseudorandomized, with a maximum of two rewarded/nonrewarded trials in a row. In the third session, chimpanzees were exposed to a stable uncertain option (i.e., the same food pattern was presented across all trials); in the fourth session, they were exposed to a changing uncertain option (i.e., different food patterns were presented across trials).

In the second pretest (two consecutive sessions of eight trials each), chimpanzees were familiarized with the choice mechanism. They experienced that they could pull only one choice rope per trial. As in the first pretest, they experienced that they would receive only one of the four trays after each choice. In this pretest, however, both options were present in each trial. The criterion was that the chimpanzee pulled one of the choice ropes. Once they started pulling one rope, an experimenter removed the other. As in the first pretest, which of the four trays was drawn was randomized and evenly distributed over the trials. In a counterbalanced order across subjects, chimpanzees first chose between either two safe options (all eight trays baited with a quarter of a banana each; every trial rewarded) or two uncertain options (two trays baited with half a banana each, two trays empty; half the trials rewarded). The reward pattern was pseudorandomized, with a maximum of two rewarded/nonrewarded trials in a row.

In the third pretest (one session of four trials), chimpanzees were familiarized with the exploration mechanism. This was the first time they experienced closed trays. For one minute, they had the opportunity to explore the trays by opening their lids. There was no criterion. Unlike in the real test, chimpanzees did not receive any of the food rewards they saw. In a counterbalanced order across subjects, chimpanzees were either first confronted with one safe option and one uncertain stable option (i.e., two trials with the same food pattern) or with one safe option and one uncertain changing option (i.e., two trials with different food patterns). The location of the options (left or right of the chimpanzee) was randomized and evenly distributed over the trials.

Test Phase. The experimental procedure is an adaptation of the experience-based sampling paradigm used with humans (see Wulff et al., 2018). Chimpanzees began with no knowledge of the payoff distributions and could learn about the possible outcomes and their frequencies by drawing random samples from each option. This exploration process was under the chimpanzees' own control: They could decide whether to explore, which option to explore, and when to switch between options.

During the exploration phase only the lid ropes were available. Chimpanzees had one minute to explore the content of all trays by pulling away the corresponding lids. After the exploration phase, the experimenter removed the lid ropes and made the choice ropes available. Chimpanzees chose one of the options by pulling the corresponding rope. One tray was then randomly drawn from the option chosen, and the chimpanzee obtained the corresponding reward (or no reward if the selected tray was empty). If no choice was made within 30 seconds, the trial was repeated. If a chimpanzee refused to make a choice twice in a row, the session was ended and the remaining trials were run the next day. We counterbalanced the side of the safe option (left or right), the reward pattern of the uncertain option (each side was rewarded equally often), which tray was pseudorandomly drawn from the option chosen, and the food pattern within the uncertain option (six different ways to bait four trays).

Coding and Reliability. To assess how chimpanzees explore their environment, we coded whether and which trays were opened and which option was chosen. All trials were recorded with one camera and coded live as well as later from video. A research assistant who was unaware of the study design and hypotheses independently coded 20% of all trials. Interrater agreement was excellent for exploration (Cohen's $k = 0.98$) and choice (Cohen's $k = 0.99$).

Analysis

RQ1. Environmental change . To investigate whether chimpanzees explored more in changing than in stable environments, we used binomial regression models to examine their exploration of the trays (no, yes). We specified weakly informative normal priors with mean zero 0 and standard deviation 2 on all population-level effects (Gelman, 2006). We included the interaction of the predictors condition (changing, stable) and trial number within condition; as control predictors we included sex (female, male), age (in years), and order of condition (coded as factor: control first, test first) as fixed effects and subject ID as a random intercept. As random slopes, we included condition and trial number within subject ID (but not the correlation among random slopes and intercept). The covariates age and trial number were *z*-transformed and condition was dummy-coded and centered for the random slope part. Model comparisons showed that models including the test predictors condition and trial made better predictions, with the model including the interaction between condition and trials showing the best performance (interaction: weight = 0.99; main effects: weight = 0.01; without trial and condition: weight = 0). The model estimate for the interaction term was negative ($b = –0.19$ [–0.31, –0.08]), suggesting that over trials chimpanzees, on average, explored fewer trays in the stable than in the changing condition (Figure 2A). In the main effects model excluding the interaction, there was no effect of stable condition ($b = –0.04$ [–0.77, 0.69]) or trial ($b = –0.11$ [–0.37, 0.15]). There were marked interindividual differences in exploration effort (Figure 2B). The results suggest that over trials, when deciding between a safe and an uncertain option, chimpanzees explored changing environments more than stable environments.

RQ2. Outcome variance. Next, we analyzed whether chimpanzees during exploration were more likely to open trays in the uncertain option than in the safe option, conditioned on them experiencing outcome variance in the former. Overall, chimpanzees explored (i.e., opened at least one tray) in 91% of trials. Within these trials, they experienced variance in the uncertain option in 62% of trials. Following Lejarraga et al. (2012), we first examined, for each trial, whether a chimpanzee experienced more than one kind of outcome within the uncertain option. In this case, we classified them as having experienced variance during this trial. Thus separating trials with and without the experience of outcome variance, we then calculated the difference between the number of opened trays in the uncertain versus the safe option in each of the 32 trials for both conditions and separately for each subject. A positive difference indicates more exploration in the uncertain than in the safe option. As Figure 2C shows, averaged across all chimpanzees, those who experienced outcome variance (blue lines) opened more trays in the uncertain option than in the safe option. In contrast, those who did not experience the variance of the uncertain option (red lines) allocated more exploration effort to the safe option than to the uncertain option. In both conditions, chimpanzees were significantly more likely to open trays in the uncertain option than in the safe option when they experienced outcome variance compared to when they did not (Wilcoxon signed-rank test, $z = –3.84$, $p < 0.01$). Our results are in line with earlier findings suggesting that humans explore riskier options more than safer options when they experience outcome variance—a reasonable response to experienced risk (outcome variance; see Lejarraga et al., 2012).

In the decisions-from-experience paradigm, participants are initially unaware of the possible outcomes and outcome variances in the safe and uncertain option and learn about them through exploration. The relationship between sample size and experienced variance is thus bidirectional: Outcome variance within the uncertain option may lead to more exploration, but more exploration also leads to a greater likelihood of experiencing outcome variance. The direction of the causal relationship between experienced outcome variance and exploration could thus be confounded. To overcome this confound, we applied the analysis proposed by Lejarraga et al. (2012).

RQ3. Exploration strategies and switching behavior. We further investigated chimpanzee exploration and switching behaviors. Across subjects, chimpanzees explored only one option in half of the trials (*Mdn* = 0.48). When exploring both options, chimpanzees preferentially explored sequentially (*Mdn* = 0.35)—that is, they only switched once, rather than employing a piecewise sampling strategy with multiple switches (*Mdn* = 0). In 9% of all trials, chimpanzees did not explore at all (see Figure 2D). Looking at both conditions separately, we found that the preferred strategies in both environments were exploring only one option and sequential exploration. Yet, whereas in the stable environment, both strategies were used equally often (exploration of one option: *Mdn* = 0.42; sequential exploration: *Mdn* = 0.44), in the changing environment, there was a clear preference for exploring only one option (*Mdn* = 0.57) rather than exploring sequentially (*Mdn* = 0.35; see Figure 2E).When exploring both options, chimpanzees generally switched only once between options, consistent with the idea that switching behavior incurs energy and memory costs (see Hills & Hertwig, 2010). We then looked at both environments separately and found that in the changing environment, there was a clear preference for exploring only one option, whereas in the stable environment, exploration of one option and sequential exploration were used equally often. This is in line with previous findings, suggesting that if expectations about an option are violated, explorative behavior towards that option is promoted (e.g., Stahl & Feigenson, 2015). In the changing environment, exploring only one option will continuously lead to surprises. Focusing on one rather than multiple options can thus enhance learning without making it overly taxing to track change in different payoff distributions.

Delving deeper into which other environmental cues drove chimpanzees' switching, we investigated whether subjects were more likely to switch to the safe option after finding food. We again used binomial regression models to model the data and specified weakly informative normal priors with mean 0 and standard deviation 2 on all population-level effects (Gelman, 2006). We included the predictors previous sample (found no food, found food) and, as control predictors, condition (changing, stable), trial number within condition, sex (female, male), and age (in years) as fixed effects and subject ID as a random intercept. As random slopes, we included condition and trial number within subject ID (but not the correlation of random slopes and intercept). The covariates age and trial number were z-transformed and condition was dummy-coded and centered for the random slope part. Overall, chimpanzees switched to the safe option in 16% of trials after finding food (they continued to search in the risky option in 84% of trials) and in 12% of trials after not finding food (they continued to search in the risky option in 88% of trials). Model comparisons showed that models including the predictor previous sample (found food) showed the best performance, outperforming the model including the interaction of condition and previous sample (found food) (main effect: weight = 0.50; without previous sample (found food): weight = 0.12, interaction: weight = 0.38). The main effect model estimate for previous sample (found food) was positive (b = 0.37 [0.05, 0.68]), suggesting that chimpanzees were more likely to switch to the safe option after finding food. This "win–shift" strategy is adaptive in environments where food sources are dispersed (rather than clustered) or require time to be replenished: Obtaining food in one location decreases the likelihood of finding more food there (Kamil, 1978; Olton & Schlosberg, 1978).

RQ4. Correlations with risk and uncertainty preferences. We further investigated the relationship between mean exploration effort (number of opened trays) in the current study and chimpanzee risk and uncertainty preferences reported by Haux et al. (2023), as the same chimpanzees participated in both studies. We found consistent negative correlations between mean exploration effort and all risk measures (behavioral risk measure: –.10 [–.62, .48]; observational risk measures: general risk: –.44 [–.79, .12]; foraging risk: –.18 [–.65, .38]; snake risk: –.14 [–.63, .42]; escape risk: –.53 [–.83, –.01]; hierarchy risk: –.10 [–.62, .48]; stranger risk: –.18 [–.65, .38]; risk ranking: –.43 [–.78, .13]). These results converge to indicate that risk-seeking chimpanzees tended to explore less. Furthermore, we found positive correlations with the behavioral uncertainty measure (.32 [–.28, .74]), suggesting that uncertainty-tolerant chimpanzees tended to explore more.

Choice behavior. Finally, we examined how chimpanzees decided between the safe and uncertain options across both conditions. In the changing environment, their choices were split fairly equally between the two options, but in the stable condition there was a clear preference for the uncertain option, which was chosen in 75% of trials. We further investigated whether chimpanzees chose the uncertain option if they had *only* encountered an empty tray when exploring this option. Overall, this occurred in only 5% of trials, upon which chimpanzees chose the uncertain option in 59% and the safe option in 41% of trials. This is also consistent with a clear preference for the uncertain option, assuming that sampling an empty tray was taken as a cue signalling the presence of the uncertain option.

D. List of Manuscripts

The chapters 2–4 of this dissertation have been prepared with co–authors as manuscripts for peer reviewed journals.

* These authors share senior authorship

Chapter 2 (Study 1):

Haux, L. M., Engelmann, J. M., Arslan, R. C., Hertwig, R.*, & Herrmann, E.* (2023). Chimpanzee and Human Risk Preferences Show Key Similarities. *Psychological Science, 34*(3), 358–369.

Chapter 3 (Study 2):

Haux, L.M., Engelmann, J.M., Herrmann, E.*, Hertwig, R.* (2021). How chimpanzees decide in the face of social and nonsocial uncertainty. *Animal Behaviour, 173*, 177-189.

Chapter 4 (Study 3):

Haux, L. M., Engelmann, J. M., Herrmann, E.*, & Hertwig, R.* (in prep.). Adaptive exploration in chimpanzees.

E. Figures

All figures, photos and images by Lou Marie Haux.

F. Declaration of Contributions

Declaration regarding my own share of the submitted scientific or scholarly work that has been published or is intended for publication within the scope of my publication–based work.

I. General information

1. Last name, first name: Haux, Lou Marie
2. Institutes: Fachbereich Erziehungswissenschaft und Psychologie & Max Planck Institute for Human Development
3. Doctoral study subjects: Psychology
4. Title: Master of Science (M.Sc.)

II. Numbered listings of scientific or scholarly work that has been published or is intended for publication

1. Haux, L. M., Engelmann, J. M., Arslan, R. C., Hertwig, R.*, & Herrmann, E.* (2023). Chimpanzee and Human Risk Preferences Show Key Similarities. *Psychological Science, 34*(3), 358–369.
2. Haux, L.M., Engelmann, J.M., Herrmann, E.*, Hertwig, R.* (2021). How chimpanzees decide in the face of social and nonsocial uncertainty. *Animal Behaviour, 173*, 177-189.
3. Haux, L. M., Engelmann, J. M., Herrmann, E.*, & Hertwig, R.* (in prep.). Adaptive exploration in chimpanzees.

* These authors share senior authorship

III. Explanation of own share of the manuscripts

The chapters 2-4 have been prepared with co-authors. In the following I clarify the authors' contributions to each chapter. The amount of my own contribution is declared on the following scale: "all – in vast majority – in majority – in large parts – in parts – equally with *co-author(s)*"

Chapter 2: *Chimpanzee and human risk preferences share key similarities.*

Haux, L. M.: Conceptualization (in large parts), Data curation (all), Formal analysis (in large parts), Funding acquisition (in large parts), Investigation (all), Methodology (in large parts), Project administration (in large parts), Visualization, Writing – original draft (all), Writing – review & editing (in large parts)
Engelmann, J. M.: Conceptualization, Methodology, Supervision, Writing – review & editing
Arslan, R.: Conceptualization, Formal analysis, Methodology, Writing – review & editing
Hertwig, R.: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing
Herrmann, E.: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing

Chapter 3: *How chimpanzees decide in the face of social and nonsocial uncertainty.*

Haux, L. M.: Conceptualization (in large parts), Data curation (all), Formal analysis (in large parts), Funding acquisition (in large parts), Investigation (all), Methodology (in large parts), Project administration (in large parts), Visualization, Writing – original draft (all), Writing – review & editing (in large parts)
Engelmann, J. M.: Conceptualization, Methodology, Supervision, Writing – review & editing
Herrmann, E.: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing
Hertwig, R.: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing

Chapter 4: *Adaptive exploration in chimpanzees*.

Haux, L. M.: Conceptualization (in large parts), Data curation (all), Formal analysis (in large parts), Funding acquisition (in large parts), Investigation (all), Methodology (in large parts), Project administration (in large parts), Visualization, Writing – original draft (all), Writing – review & editing (in large parts)
Engelmann, J. M.: Conceptualization, Methodology, Supervision, Writing – review & editing

Herrmann, E.: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing
Hertwig, R.: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing – review & editing

IV. Names, addresses, and e-mail addresses for the relevant co-authors

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Hertwig, Ralph.: Center for Adaptive Rationality, Max Planck Institute for Human Development, 14195 Berlin, Germany, sekhertwig@mpib-berlin.mpg.de

V. Written confirmation of III. by co-authors (signatures):

- All co-authors have confirmed *III.* in written form (signatures).
- For reasons of data protection, the signatures of the co-authors are separately submitted to the Doctoral Examination Office (promotion@ewi-psy.fu-berlin.de), and are not directly included in this dissertation.

Berlin, June 30th 2022

G. Selection of Other Projects

Engelmann, J. M., **Haux, L. M.**, Völter, C., Schleihauf, H., Call, J., Rakoczy, H., & Herrmann, E. (2022). Do chimpanzees reason logically? *Child Development*, 00, 1– 15. [Registered Report]

ManyPrimates et al. (2019) Establishing an infrastructure for collaboration in primate cognition research. *PloS One 14*(10), e0223675. [large scale collaboration project]

Engelmann, J. M., **Haux, L. M.**, & Herrmann, E. (2019). Helping in young children and chimpanzees shows partiality towards friends. *Evolution and Human Behavior*, *40*(3), 292-300.

Herrmann, E., **Haux, L.M.**, Zeidler, H., & Engelmann, J.M. (2019). Human children but not chimpanzees make irrational decisions driven by social comparison. *Proceedings of the Royal Society B*, *286*(1894), 20182228.

Haux, L., Engelmann, J. M., Herrmann, E., & Tomasello, M. (2017). Do young children preferentially trust gossip or firsthand observation in choosing a collaborative partner? *Social Development*, *26*(3), 466-474.

H. Curriculum Vitae

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Professional Experience

2018–2022	PhD at the Max Planck Institute for Human Development, Center for Adaptive Rationality, Supervisors: Ralph Hertwig (Max Planck Institute for Human Development), Esther Herrmann (University of Portsmouth), Jan M. Engelmann (University of California, Berkeley)
2012–2018	Research assistant at the Max Planck Institute for Evolutionary Anthropology, Department of Developmental and Comparative Psychology, Michael Tomasello

Funding

2018–2022	German National Academic Foundation (Studienstiftung)
2014–2016	German National Academic Foundation (Studienstiftung)

Teaching

2022	University of Leipzig, Comparative Development (Seminar): Session on risk preferences in chimpanzees

Media Coverage and public outreach

2023	Similarities in Human and Chimpanzee Behavior Support Evolutionary Basis for Risk Taking, APS, Association for Psychological Science
2021	Why we place too much trust in machines, BBC Future
2021	Wie Schimpansen Risikoentscheidungen treffen, Campus Talks, Television program, ARDalpha
2020	Kaputtnik, Artist Catalog by Paule Hammer, Lubok Verlag
2020	Affenmensch, Movie by Paule Hammer at Museum der Bildenen Künste Leipzig
2019	Living side by side with chimpanzees, MaxPlanckResearch Science Magazine

I. Declaration of Independent Work

I hereby declare that:

I completed this doctoral thesis independently. Except where otherwise stated, I confirm that the work presented in this thesis is my own.

Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

I have not applied for a doctoral degree elsewhere and do not have a corresponding doctoral degree.

I have acknowledged the Doctoral Degree Regulations which underlie the procedure of the Department of Education and Psychology of Freie Universität Berlin, as amended on August 8th 2016.

The principles of Freie Universität Berlin for ensuring good academic practice have been complied with.

Berlin, June 30th 2022