



Beyond lottery-evoked ambiguity aversion: The neural signature of the types and the sources of uncertainty

Kim Fairley^{a,d,*}, Jana Vyrastekova^b, Utz Weitzel^{b,c}, Alan G. Sanfey^{d,e}

^a Institute of Tax Law and Economics, Department of Economics, Leiden University, Leiden, the Netherlands

^b Institute for Management Research, Radboud University, Nijmegen, the Netherlands

^c School of Economics and Business, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands

^d Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, the Netherlands

^e Behavioral Science Institute, Radboud University, Nijmegen, the Netherlands

ARTICLE INFO

Keywords:

risk
ambiguity
beliefs
neuroeconomics

ABSTRACT

Studies on decision-making under uncertainty have mainly focused on understanding preferences for either risk or ambiguity using standard lottery designs. However, people often face uncertainty that directly stems from interacting with other people, which may be processed differently from lottery-based uncertainty. Here, we substantially extend the investigation of uncertainty by examining a fourfold pattern of the sources and the types of uncertainty, assessing behavioral and neural responses to both risk and ambiguity across both social and non-social contexts. A key element in our research design was to control for participants' naturally occurring social beliefs, and taking these a priori beliefs into account allow us to elicit individual preferences in accordance with economic approaches that stress the dynamics of ambiguity preference as a function of underlying likelihoods. Using this design, we find a behavioral main effect of ambiguity aversion, with increasing ambiguity aversion as a function of higher beliefs regarding the likelihood of reciprocity, and related neural activity in the right IPS. This brain region was primarily involved when participants experienced lottery-based uncertainty as opposed to social uncertainty. However, we found that the right IFG was more involved when participants made decisions under social, as compared to non-social, uncertainty. Overall, therefore, the IPS may activate an analytic mindset, which might resonate more with a lottery than a social context, whereas the IFG is engaged when the context requires players to resolve uncertainty, such as unraveling the intentions behind the choice of another person.

1. Introduction

Decision-making under uncertainty is an unavoidable feature of daily life. For instance, imagine a friend has just lost his job and asks to borrow money. Presumably you know your friend well, and have confidence in your estimation of his likelihood of repayment. But, what if a casual acquaintance, or even a stranger, approaches you and also asks for a loan after a similar job loss? In the latter situation, without knowing anything about this stranger, it is very difficult to make an accurate prediction of repayment. The differences between these two estimates, for a friend and for a stranger, illustrate the distinction between the economic concepts of risk and ambiguity respectively (Wakker, 2010). In this study, we focus on these two distinct *types of uncertainty*.

Within the context of this study – and within the discipline of economic decision-making under uncertainty in general – a *type* of uncertainty refers to the characterization of probabilities. Namely,

ambiguity¹ is a type of uncertainty characterized by outcomes with vague or unknown probabilities whereas risk is a type of uncertainty characterized by the availability of explicit probabilities (Trautmann and van de Kuilen, 2015). In addition to this distinction, the example above also highlights an additional feature of decision-making under uncertainty (DMUU), namely its *source*. The uncertainty described here can be said to have a *social source*, as the uncertainty stems from the question whether your friend or casual acquaintance will repay your loan. As social beings we are constantly interacting with others, and indeed many of the uncertainties we face on a daily basis are related to the behavior of other people (Trautmann and Vieider, 2012). Though clearly important, social sources of uncertainty have nonetheless been relatively understudied compared to standard, non-social sources of uncertainty, usually operationalized as lotteries in experiments. Our study aims to close this gap by examining the behavioral and neural differences, and overlap, between social and non-social un-

* Corresponding author at: Department of Economics, Leiden University, Steenschuur 25, 2311 ES Leiden, The Netherlands.

E-mail address: k.fairley@law.leidenuniv.nl (K. Fairley).

¹ Formally, an individual's ambiguity attitude represents their distinct preference between risk and uncertainty, but ambiguity has become synonymous for uncertainty, and therefore we speak of risk and ambiguity as two types of uncertainty (Wakker, 2010).

certainly, in conjunction with exploring risk and ambiguity as types of uncertainty.

There are several good reasons as to why decisions may differ between lottery selections and social interactive choices. An important consideration in this regard is that losing money due to the acts of another person instead of via a random mechanistic device can induce strong feelings of betrayal aversion (Bohnet and Zeckhauser, 2004; Aimone and Houser, 2012). Furthermore, a decision-maker can perceive either violated trust or a norm violation as stemming from incorrect judgment regarding the behavior of another individual, whereas they are more likely to perceive the same negative outcome as mere bad luck in a lottery domain with a computerized ‘partner’ (Trautmann et al., 2008). For this reason, decision-makers are more inclined to invest money in a lottery than an otherwise comparable human partner (Bohnet and Zeckhauser, 2004).

Several fMRI studies have focused on types of uncertainty, though not yet in conjunction with social sources (Hsu et al., 2005; Huettel et al., 2006; Bach et al., 2009, 2011; Levy et al., 2010; Rustichini et al., 2005). These studies consistently show evidence of ambiguity aversion in lottery contexts, that is, a preference for the risky option over the ambiguous option, but offer different interpretations as to the neural correlates underlying these observed behavioral patterns. One group has highlighted the role of the amygdala and the orbitofrontal cortex (OFC), explaining ambiguity aversion in terms of neural alertness to unknown, and potentially dangerous, consequences of missing information (Hsu et al., 2005, p.1683). However, an alternate view implicates brain regions such as the inferior frontal gyrus (IFG), the posterior parietal cortex, precuneus and middle temporal gyrus (Huettel et al., 2006; Bach et al., 2011), and instead explains ambiguity aversion as a complex expected value calculation where one is integrating multiple potential subjective probability distributions in an effort to resolve ambiguity.

On the other hand, social uncertainty stemming from potential negative social interactions in games such as the Trust Game, Prisoner’s Dilemma Game and Ultimatum Game have been related to activation in the anterior insula (Bellucci et al., 2017; Lauharatanahirum et al., 2012; Aimone et al., 2014; Chen et al., 2016; Feng et al., 2015; Rilling et al., 2008; Sanfey et al., 2003). This activation is understood to stem from an aversive feeling of uncertainty related to potential betrayal by, and a norm violation of, a game partner. Moreover, the activation in this region is generally much stronger when the interaction stems from a human than a computer counter partner, indicating that the aversive response to negative social interactions is influenced by the type of partner, and not just the process of violation itself (Bellucci et al., 2017). Finally, a related domain of social behavior focuses on altruistic behavior (Hu et al., 2017; Xiong et al., 2020) Xiong et al. (2020). specifically looked at the influence of the type of uncertainty within this class of social decision-making and found that additional social uncertainty in the generation of gratitude – in response to being a potential target of an altruistic act by somebody else – recruited areas such as the dorsal medial prefrontal cortex and anterior cingulate cortex, which the authors attributed to mentalizing- and conflict monitoring-related processes.

In this study, we will specifically focus on the Trust Game as the social source of uncertainty. We believe this question to be relevant as there are instances when a reciprocal interaction is sometimes more of the risky type (e.g. lending money to a relative/family member/friend) and other times more ambiguous in nature (business transaction with an unknown person/new business partner). A second point as to why our research question is relevant concerns its methodological foundation. Namely, it is not uncommon that the distinction between risk and ambiguity is itself uncertain when dealing with lottery and social contexts. For example, in Kosfeld et al. (2005) the Trust Game is ambiguous as investors do not receive information regarding the likelihood of reciprocation, while they do receive probabilistic information regarding reciprocation in the non-social computerized treatment. Are behavioral differences then due to the source or type of uncertainty?

A key element in our design, inspired by work in experimental economics which stresses the importance of internal belief states on ambiguity preferences (Abdellaoui et al., 2011; Trautmann and van de Kuilen, 2015), is that we take individual subjective estimates of social uncertainty into account, as participants of course have naturally occurring priors regarding the likelihood of reciprocation in general. This is important, as it allows us to tailor and equate the underlying risk and ambiguity across social and non-social contexts individually to each participant, and not make (likely incorrect) general assumptions about ‘typical’ beliefs as to how our participants view the trustworthiness of others.

This multi-faceted approach allows us to investigate if the source of uncertainty affects the neural underpinnings of ambiguity preferences. Furthermore, we can explore the brain processes underlying individual differences in ambiguity preferences as a function of individual beliefs about others’ reciprocal behavior (in the Trust Game) and likelihoods (lottery context). Taken together, this approach allows us to critically evaluate the proposed explanations suggested thus far as to the underlying mechanism of ambiguity aversion as a function of the source of uncertainty.

Based on the prior work in this area thus far, we predict that participants will exhibit ambiguity aversion in general, but we expect this aversion to be greatest in the social interactive context (as compared to lottery context) due to additional social factors such as, for example, betrayal aversion. Furthermore, we expect that frontal brain regions, such as the OFC and IFG, as well as parietal brain regions, such as the posterior parietal cortex, will be involved in general risk and ambiguity processing, while we expect the anterior insula to be responsive for social ambiguity specifically.

2. Materials and methods

2.1. Participants

Twenty-six participants (age range = 19–28 years, $M_{age} = 22.33$ years, 50% female) were recruited via SONA, the online system used by the Donders Institute for Brain, Cognition and Behaviour to manage the research participant pool. All participants were pre-screened for any behavioral and health related abnormalities via an online questionnaire, and the study was approved by the local ethical committee.

We excluded five participants from our sample prior to neuroimaging analysis. Two participants were excluded because of technical issues with the neuroimaging session (e.g. head coil was not applied accordingly), one because they did not believe that there was real human interaction in the social condition (which led to extreme choices such as investing all tokens in the lottery condition and hardly any tokens in the Trust Game), and finally two participants because they selected the exact same investment for all experimental trials. The analyses reported here are therefore based on twenty-one participants ($M_{age} = 22.27$ years, 57% female).

We performed a power analysis based on the expected effect size of ambiguity aversion in order to determine an appropriate sample size. We used the package *simr* (Green and MacLeod, 2016) to calculate the observed power in our experimental study with an expected effect size of 0.3, as determined by the literature (Trautmann and van de Kuilen, 2015), and importantly not based on our findings themselves. Based on 1000 simulations, a sample size of 21 participants resulted in 90.20% power for the estimated behavioral effect of ambiguity aversion, suggesting adequate power for this expected effect. We could not perform a power analysis on the neural level as we did not have pilot data nor could we locate a suitable related dataset on NeuroVault.

2.2. Experimental design and statistical analysis

2.2.1. Sources of uncertainty

The Trust Game (Berg et al., 1995) explores the social source of uncertainty in our experiment. In our version of this game there were two

players: the sender (known as Trustor in the original paper) and receiver (known as Trustee in the original paper). The sender was endowed with 10 tokens and could choose between six investment amounts (termed ‘transfers’ in our instructions), namely, 0, 2, 4, 6, 8 or all 10 tokens to be sent to the receiver. As per common practice, we then tripled sender’s chosen transfer before sending this multiplied amount to the receiver. In a pre-scanning behavioral session, receivers’ return choices were collected. Receivers could either choose to reciprocate half of the received tokens or not reciprocate at all, thus keeping all the received tokens. Importantly, receivers had to make their return choice unconditionally, that is, not knowing if, and how many, tokens they would receive (see Part A.2 in the Appendix for detailed instructions given to participants in their role as receiver).² This element in our design was crucial, as senders should then make investment decisions solely based on their beliefs about the receivers’ reciprocity. In this way we ensured that the decision to invest was not confounded by other motives, for example signaling trust (McCabe et al., 2003) or the elicitation of positive reciprocity (Houser et al., 2010). Therefore, in making the transfer decision, the sender had to consider the likelihood of receiving an increase in their original endowment with the risk of losing it all.

We used a standard Ellsberg urn setup (Ellsberg, 1961; Trautmann and van de Kuilen, 2015) for our lottery, i.e. non-social, context. In this setup an imaginary urn is filled with colored marbles and participants can bet on drawing a particular colored marble. As in the Trust Game, participants could choose any investment amount between 0 and 10 tokens before it was tripled. The return choice in the lottery however in this case stems from a random mechanistic device instead of a conscious choice made by a human being. To control for the fact that there is of course a second player in the Trust Game, we introduced a dummy player to the lottery context. This dummy player did not make any choice, but acted as a recipient who received the exact same outcome as the receiver would have earned in the Trust Game, but now based on the lottery outcome. Therefore, if a winning (losing) marble was drawn in the lottery, half (all) of the tripled investment went to the dummy recipient. By implementing this feature, we can control for social preferences – for example, warm glow from investing – as a potential confounding factor (Houser et al., 2010), and thereby made sure that any difference in transfer choices was solely due to the source of uncertainty.

2.2.2. Type of uncertainty

Participants made transfer choices in four different treatments: a risky Trust Game (RTG), an ambiguous Trust Game (ATG), a risky lottery (RLOT) and an ambiguous lottery (ALOT). Senders therefore invested in either a Trust Game or lottery which consisted of either nine human receivers or nine marbles.

In the RTG the sender received information about the prior history of nine receivers, that is, how many of the nine receivers chose to reciprocate and how many did not, ensuring that decisions made about how much to transfer were essentially risk-based. However, in the ATG they did not receive any such probabilistic information, thereby also adding ambiguity to the transfer decisions.³

In the RLOT each of nine marbles had a different, known, color, whereas in the ALOT the lottery was made up of an unknown composition

of the nine available colors. Essentially any set of combination of nine colors is possible in the ALOT (thus 9^9 combinations). In both the RLOT and ALOT participants received information as to which of the nine colors were ‘winning’ colors. As the ALOT is an urn filled with nine marbles of unknown color composition, receiving information regarding the number of winning colors represents the underlying likelihood of drawing a winning color, but is not the same as the objective probability provided in the RLOT, whereby players knew the exact likelihood of winning. Therefore, deciding on a transfer in the ALOT does not provide an objective probability as in a standard risky setting, yet the uncertainty in the form of an underlying likelihood corresponds to a prior a participant likely forms when trusting in another receiver in the ATG, albeit its source stems from a random mechanistic device instead of an actual human being.

To reiterate the similarity between the ATG and the ALOT – except for its source – it is important to notice that we aim to create a similar underlying subjective probability in both games. In the ALOT, participants are not certain about the probability with which a winning colored marble is drawn, as it is unknown how many winning and losing colors are present in the ambiguous urn. Likewise, when we form a group of 9 receivers in the ATG (which come from the bigger population of 27 receivers), the participant does not know the composition of (un)trustworthy receivers. Both in the ALOT and the ATG the participant is unaware of the exact number of winning colors present in the ALOT and unaware of the exact number of trustworthy receivers present in the ATG. Below, we explain carefully how we pick the underlying subjective probability in the ATG and ALOT on an individual basis.

2.2.3. Tailor-made design structure based on participants’ beliefs

In our design, it was important that we controlled for individual beliefs. Namely, in the social context, participants likely had underlying prior beliefs about receivers’ general reciprocal behavior based on prior experiences. Although we made sure that fMRI participants received the same basic information regarding the pool of receivers they would interact with, e.g., age, gender, study, hobbies – which were answered by receivers after they had placed their return decision (please see Part A.2 in the Appendix for the questionnaire filled in by receivers, and importantly this social information was not linked to the silhouette pictures we took from the receivers) – it is nonetheless likely that participants’ beliefs regarding reciprocal behavior generally varied. In our aim to study the effect of sources and types of uncertainty, it is crucial therefore that we controlled for individuals’ beliefs in order to rule out a mismatch between underlying likelihoods and objective probabilities across our four experimental settings. For instance, imagine a sender who in general believes that two out of any randomly selected nine receivers will likely reciprocate in a Trust Game (thus being the ‘prior’ in the ATG). If this participant is placed in a RTG where in actual fact eight of nine receivers decided to transfer back half of the investment, we cannot assess whether differences in investment behaviors across scenarios are caused by the type of uncertainty itself, or rather by a mismatch between a subjective probability of 2/9 in the ATG and an objective probability of 8/9 in the RTG.

In order to control for these differences, we elicited individual beliefs in the ATG before participants made their investment decisions. Using an incentive-compatible belief elicitation technique (quadratic scoring rule, e.g., see Schlag et al., 2015), we first asked how many receivers they thought (from a pool of nine) would reciprocate their investment. This belief was then used to present participants with *belief-corresponding* scenarios in the other experimental settings. Our previous imaginary sender who believed that two out of nine receivers would reciprocate in a Trust Game, will then receive information that two out of nine colors are winning colors in the ALOT, but is otherwise unaware of the composition of the ambiguous urn (hence we create a subjective underlying probability of 2/9). Furthermore, he will be presented with an objective probability that two out of nine receivers (colored marbles) will reciprocate in the RTG (RLOT). Essentially, based on participants’ underlying

² A total of 27 receivers made an unconditional return choice and 9 decided to return sender’s investment amount, while the remaining 18 receivers decided to keep the amount transferred by the sender. Based on this composition, in each Trust Game trial, we could randomly draw a new set of 9 receivers the fMRI participants in their role as senders would interact with, with the obvious restriction that this draw of 9 receivers would correspond to the objective probability of reciprocation in the respective RTG and the true underlying likelihood of reciprocation of 3/9 receivers in the ATG.

³ The operationalization of social risk and ambiguity in a RTG and ATG respectively was developed by us and previously tested in the behavioral laboratory (Fairley et al., 2016).

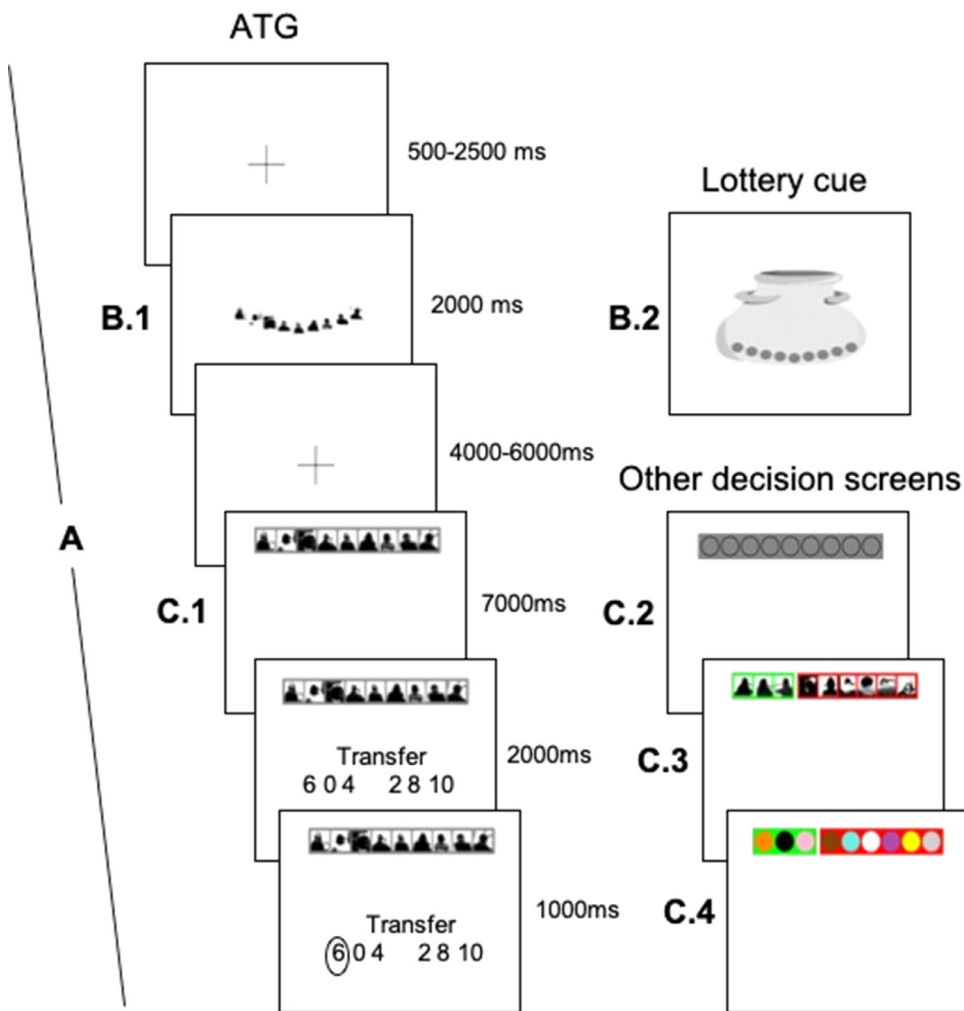


Fig. 1. Experimental design

Each trial consists of six screens. Panel A is an example of a trial from the ATG. The second screen indicates the source of uncertainty. Panel B.1 indicates the social cue and Panel B.2 indicates the lottery cue. Panel B.1 displays nine silhouettes (taken from the actual receivers after consent) in the social context. Nine marbles are displayed when participants face a lottery context (Panel B.2). The fourth screen is the decision screen (Panel C.1). They have 7 s to reflect on how many tokens they wish to transfer. As the six possible transfer options appear in a random order on the next screen, they are unable to prepare for a specific button press. They have 2 s to simply search for their preferred number of tokens transferred and indicate this choice by an MRI-compatible button box. The last screen confirms their chosen amount of transfer by circling the chosen option. In the ATG (Panel C.1) nine human silhouettes on a gray background indicate that no information is given about the distribution of receivers that decided to send back half or keep the investment.

To illustrate the tailor-made structure of our design, we assume a participant who believes three out of nine receivers will reciprocate. In the ALOT (Panel C.2), the participant receives instruction that three out of nine colors that can be used in any combination in this lottery are winning colors. In this way we align underlying subjective probabilities between the ATG and ALOT. In the risky trials we align individual's beliefs to objective probabilities. A participant who believes three out of nine receivers will reciprocate, will most often face a RTG, which is composed of three receivers (green background) that decided to send back half of any received investment versus six receivers (red background) that decided to keep their investment (Panel C.3). Finally, in the RLOT the urn is composed of all nine colors out of which three are winning colors and six are losing colors (Panel C.4).

naturally-occurring beliefs we designed a tailor-made trial structure for each participant (see Fig. 1 for an overview and another example of our experimental setup).

Participants also decided on a level of transfer in trials of the game types RTG and RLOT in which probabilities did not match participants' beliefs. Otherwise, our previous imaginary sender would only make choices in the RTG and RLOT when the likelihood of reciprocation would be 2/9 and this would be problematic in a few ways. Namely, the participant might think that his belief captures the true distribution of receivers who returned and not returned sender's transferred tokens, which is not the case. Moreover, the variation in trials would be very low, which could lead to disinterest and affect our imaging results. By offering participants a wide range of probabilities in the RTG and RLOT (which could occur based on receivers' return choices, see footnote 2), we could solve these potential issues. Moreover, we ensured participants would not easily detect the tailor-made structure of our design, and indeed this was not mentioned by any of our participants during debriefing after the experiment.

2.2.4. Procedures

All behavioral sessions in this study took place at the Nijmegen School of Management decision laboratory. Here we collected the receivers' decisions for the Trust Games and recruited dummy players to

act as lottery recipients. The fMRI experiment took place at the center for Cognitive Neuroimaging at the Donders Institute for Brain, Cognition and Behavior.

The fMRI task was presented using Matlab's Psychtoolbox (Kleiner et al., 2007). After detailed instructions and ample practice trials,⁴ participants took part in two experimental runs while lying in the magnet, with a short break in between. The first run, during which they made their decisions, is the focus of this paper. There were 96 decision trials in total (15 trials per experimental condition and 36 risky trials which did not match participants' beliefs⁵), equally divided across 16

⁴ Participants took on average one hour to complete the instructions, but we had reserved 1.5 hours if participants were slower to understand our task. In this way we could accommodate participants who needed more time to understand the decision-making part of our experiment. This latter situation did occur a few times. If participants answered any questions incorrectly as part of the comprehension test (see Part A.1 of the Appendix), we reviewed with them the relevant part of the task. In this way we aimed to ensure that all participants understood what was asked from them in the experiment. Finally, we excluded participants studying Economics or Psychology as they might be aware of the optimal behavior of receivers in the Trust Game respectively would not believe our non-deceptive social interaction.

⁵ The 36 risky trials which not matched participants' beliefs were equally divided across the remaining probabilities. Thus a participant who believes 4/9

blocks of Trust Game and lottery trials. Within each block, both risky and ambiguous trials were presented in a random order. Our main analysis will thus focus on a total of 15 trials per experimental condition, which adhered to the feature of belief-corresponding scenarios as discussed above.

Participants had 7 s to decide on their level of investment (Panel C.1 in Fig. 1) before they could indicate their preferred investment amount on the next screen. In each trial the investment options were randomly positioned on the screen and participants had to search for their preferred number of tokens. Participants selected their preferred number of tokens invested by pressing one of six buttons arrayed on two MRI compatible button boxes, which were placed on the participant's lap. The three transfer options on the left of the screen were linked to the left button box and the options of the right were linked to the right box (Fifth screen in Panel A in Fig. 1). No participants reported any problems in indicating their choices via this procedure. With this procedure our experimental design is able to separate the actual decision-making from the motion preparation and actual motion of picking the preferred level of transfer with the button box.

Participants did not learn the outcome of their transfer decisions during this experimental phase. In this way we aimed to reduce the effect of learning the underlying likelihoods in the ambiguous setups. After all decisions were completed, the outcomes were shown in the second run of our experiment. This second part of the experiment focused on a different research question, namely whether individuals' own beliefs, when they were reminded of their transfer choice, acted as a cue for reward anticipation. Results from this phase were separately analyzed and are discussed in Fairley et al., 2019.

Finally, and notably, no deception was used in this experiment. Participants were financially compensated based on their actual choices and the accuracy of their stated beliefs as described above. The instructions for all the aforementioned sessions and the payment details can be found in Part A1-A3 in the Appendix. All data and codes will be made available in the Donders repository.

2.2.5. Imaging parameters

Scanning was carried out on a 3-Tesla Siemens MRI system (Magnetom Skyra). Functional MRI (fMRI) images were acquired using a 32-channel head coil, with a standard multi-echo imaging pulse T2*-weighted sequence (field of view = 224 mm, matrix = 64 × 64, repetition time (TR) = 2390 ms; echo times (TE) = 9.4 ms, 20.6 ms, 32.0 ms, 43.0 ms, 54.0 ms, flip angle = 90°, slice gap = 0.5 mm; Poser et al., 2006). We combined the five read-outs acquired for each TR via the multi-echo by using an echo-weighting estimated from the first 31 vol acquired at the beginning of the experiment. This was done according to one of the three main methods of computing echo weights used within the Donders Center for Cognitive Neuroimaging (for more details, please find all the details of the method 'PAID' at: <https://github.com/Donders-Institute/multiecho>).

Using a multi-echo sequence provides a better signal-to-noise ratio for brain areas susceptible to dropout – mostly brain areas in the frontal lobe and cortex regions, which are relevant for risk and ambiguity processing (Huettel et al., 2005; Hsu et al., 2005) – while allowing for scanning of the whole brain (Poser et al., 2006; Huijsmans et al., 2019; Ikink et al., 2019; Vermeer et al., 2014). One whole-brain volume consisted of thirty-one ascending slices (slice thickness = 3.0 mm, voxel size = 3.5 × 3.5 × 3.0 mm). For each participant we acquired a high-resolution anatomical T1-weighted image (MPRAGE; 192 slices; TR = 2300 ms, voxel size = 1 × 1 × 1 mm). We loosely taped participants' head to the coil within the scanner in order to limit movement during image acquisition.

receivers will reciprocate their investment, will see the risky trials with the following risk property of 0/9, 1/9, 2/9, 3/9, 5/9, 6/9, 7/9, 8/9 and 9/9 twice in the RTG and RLOT, resulting in 36 risky trials in total. All trials are presented in a random order.

2.3. Statistical analysis

2.3.1. Behavioral analysis

We tested whether participants' transferred amount differed across sources and types of uncertainty with a linear mixed effects model in R (R Core Team, 2013). We used the R-packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) to perform this analysis and estimate p-values via Satterthwaite's degrees of freedom method. We included a random intercept per participant to account for repeated trials at the participant level.⁶ Continuous variables were centered and categorical variables were dummy coded before including these to the model.

We defined participants' ambiguity preferences by a normalized parameter according to standard approaches (Sutter et al., 2013): $(Investment_{Risk} - Investment_{Ambiguity}) / (Investment_{Risk} + Investment_{Ambiguity})$. The difference in participants' invested amounts between the risky and ambiguous contexts was divided by the sum of these amounts in order to control for the fact that similar differences in investment amounts will weigh more heavily for a participant who transfers less as compared to another participant who invests a higher amount (Sutter et al., 2013). This parameter ranges from -1 (extreme ambiguity seeking) to 1 (extreme ambiguity aversion). A score of 0 indicates ambiguity neutral preferences.

2.3.2. fMRI preprocessing

fMRI data analysis was performed using SPM12 (Statistical Parametric Mapping; Frackowiak et al., 1997). Prior to preprocessing we combined and realigned the five read-outs acquired via the multi-echo sequence by using standard procedures described by Poser et al. (2006). The first 31 vol, acquired prior to task initiation, were used to estimate the weighted echo time per voxel for optimal echo combination including allowing T1 equilibration effects. These 31 vol were then discarded from the analysis (Poser et al., 2006). After echoes were combined and realigned per Poser et al. (2016), preprocessing continued with slice timing to the middle slice with the aim of correcting images for differences in slice acquisition time. The anatomical image was then co-registered with the mean functional image for each participant, followed by separating all anatomical images into gray matter, white matter and cerebral spinal fluid based on the tissue probability maps available in SPM12 as part of the segmentation process. Functional and structural were then normalized to the standard Montreal Neurological Institute (MNI) T1 template. Functional images were resampled into voxel sizes of 3.5 mm isotropic voxels. Finally, the functional images were smoothed with a Gaussian kernel of 8 mm full-width at half maximum.

2.3.3. fMRI statistical analyses

To study the neural correlates of sources and types of uncertainty on participants' transfer choices, the primary explanatory variables (EV) of our general linear model (GLM) consisted of the time window (the full duration of 7 s) during which participants decided on their transfer level (fourth screen in Panel A in Fig. 1). To be precise, four EV's indicated the onset of the decision screen belonging to the RTG (only belief-corresponding risky trials), ATG, RLOT (only belief-corresponding risky trials) and ALOT. Transfer amount was added as parametric modulator to these four EV's. Other EV's in this model included the remaining decision screens belonging to the RTG and RLOT filler trials, the trust

⁶ Our main model did not include random slopes for the following reason. Our main analysis is only conducted with the belief-corresponding scenarios, not with other subjective and objective probabilities not matching participants' beliefs. Individual differences across our conditions are highly dependent on their beliefs, which is theoretically plausible (Kocher et al., 2018) and quite obvious as we constructed the belief-corresponding scenario's. Our model therefore included beliefs as covariate and interactions of the covariate beliefs with the experimental conditions. Adding random slopes on top of this in the model would over specify our model.

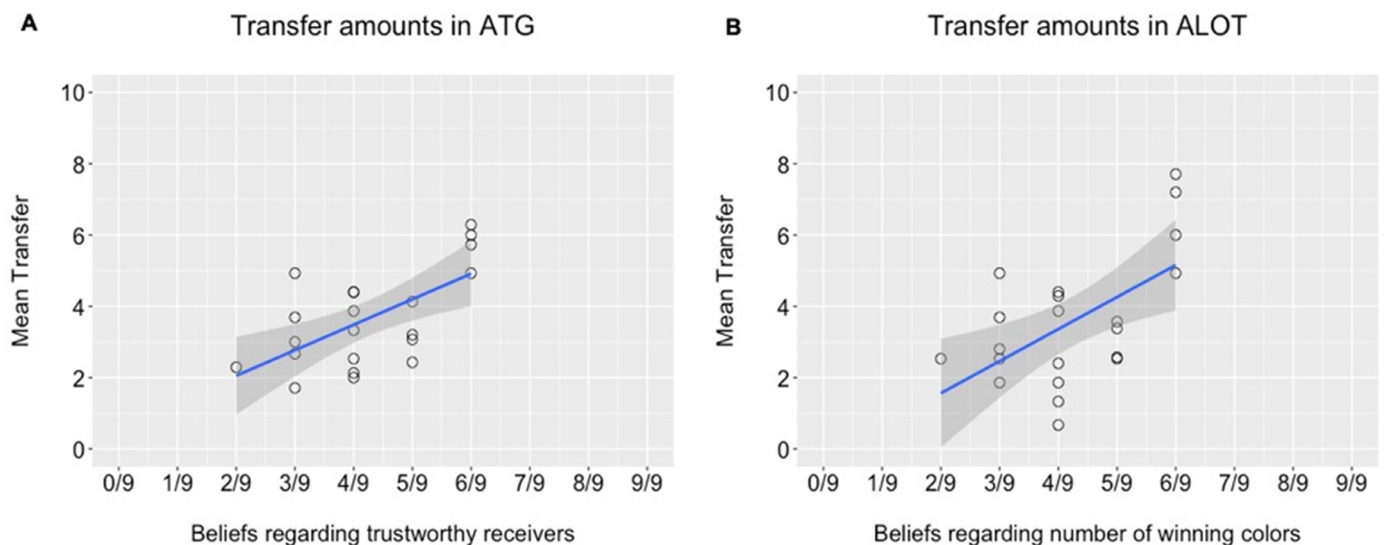


Fig. 2. Participants' beliefs and mean transfer in the ALOT and ATG

Participants' beliefs regarding receivers' reciprocity (elicited prior to decision-making) influenced transferred amounts in the ATG (Panel A and Figure B1 in the Appendix for a reflection the underlying distribution). Based on individual beliefs regarding the number of reciprocating receivers in the ATG, participants received a matching amount of winning colors in the ambiguous lottery. Participants used this information, given during instructions prior to the experiment in the MRI scanner, as transferred amounts positively increased as a function of the amount of winning colors (Panel B and Figure B2 in the Appendix for a reflection the underlying distribution).

or lottery cue (second screen in Panel A in Fig. 1), all trials collapsed across conditions in which participants indicated their choice by a button press and received a confirmation of their choice (fifth and sixth screen in Panel A in Fig. 1) and finally trials in which participants had not made a choice within the required 2 s (modeled at the onset of the decision screen for the full duration of the remainder of the trial). The remaining events are the screens which display the jittered fixation cross, and are therefore considered the implicit baseline.

These EV's were modeled with a canonical hemodynamic response function. The motion parameters from realignment, including its quadratic effect and first derivative (in total 18 motion parameters per individual), were included in the GLM. A standard high-pass filter (cut-off 128 s) and autoregressive (AR) 1 model were used during the GLM analysis to account for possible slow-frequency drifts and temporal autocorrelation, respectively.

The specific contrasts outlined in the results section were generated per participant before simple one-sample t-tests were performed to analyze group effects. Participants' beliefs were standardly included as a covariate. Statistical maps with an initial primary voxel-wise threshold of $p < 0.001$ uncorrected were established and significant clusters of activation were reported if these survived family-wise error (FWE) cluster-correction of $p < 0.05$.

We also performed a conjunction analysis as a random effects analysis at the second level. We computed this test by running an ANOVA at the second group level, which consisted of two groups. Each group was made up of one specific contrast (for all participants). Once this model ran, the two groups of contrasts could be selected simultaneously to perform the conjunction analysis. Statistical maps with an initial primary voxel-wise threshold of $p < 0.001$ uncorrected were established and significant clusters of activation were reported if these survived family-wise error (FWE) cluster-correction of $p < 0.05$.

The voxel-wise threshold of $p < 0.001$ uncorrected is potentially vulnerable to an inflated false discovery rate (Eklund et al., 2016). Therefore, we also report regions which directly survived a FWE threshold of $p < 0.05$ for both our group effects following the one-sample t-tests and the conjunction analysis (denoted with asterisks in the Result tables). Results not meeting this stricter FWE threshold should be interpreted with caution.

Finally, we also compare our fMRI results with the NeuroSynth meta-analysis terms "risk taking", "uncertainty", and "social interactions" and use the Neurosynth decoder to produce overlay images between our neuroimaging findings and the previously mentioned terms (Yarkoni et al., 2011).

3. Results

Our behavioral and neuroimaging analyses focused on participants' investment levels as a function of type and source of uncertainty, controlling for participants' naturally occurring social beliefs regarding receivers' trustworthiness.

3.1. Behavioral results

We start by showing that participants' beliefs regarding receivers' trustworthiness varied substantially. Some participants only expected two out of nine receivers to reciprocate an investment, whereas others were more optimistic and expressed a belief of six of the nine receivers to reciprocate their investment. These beliefs, which were elicited prior to decision-making, were predictive of participants' transfer choices in the ATG. That is, the more that players expected receivers to reciprocate their transfer, the more tokens they invested (Pearson's $r = 0.62$, $p = 0.003$, Panel A in Fig. 2). Per individual, these social beliefs translated to a similar amount of winning colors in the ALOT. In this context we also found a significant positive correlation between the number of winning colors and participants' transferred amount (Pearson's $r = 0.58$, $p = 0.006$, Panel B in Fig. 2).

These results illustrate that participants took beliefs regarding others' trustworthiness into account – and we accurately elicited these – when guiding their decision-making in the ATG. Additionally, they understood how to incorporate the information regarding the number of winning colors in the ALOT. With regard to the risky versions of both the lottery and Trust Game, as expected, participants invested more when the probability of reciprocation increased, either via a purposeful receiver decision (RTG, see Figure B3 in the Appendix) or by a mechanistic device (RLot, see Figure B4 in the Appendix).

Next, we investigated how participants' transfer choices were influenced by both the type and source of uncertainty. The mean transfer

Table 1
Results from the linear mixed-effects model.

Variables	Dependent variable: Transfer amounts			
	Model 1	Model 2	Model 3	Model 4
Intercept	3.579*** (0.363)	3.584*** (0.227)	3.583*** (0.227)	3.529*** (0.301)
Risk	0.365** (0.131)	0.365** (0.131)	0.371** (0.127)	0.353** (0.127)
Trust Game	0.074 (0.131)	0.074 (0.131)	0.082 (0.127)	0.105 (0.128)
Risk * Trust Game	0.094 (0.181)	0.095 (0.185)	0.082 (0.180)	0.090 (0.180)
Beliefs		1.117*** (0.185)	1.117*** (0.185)	0.903*** (0.204)
Risk * Beliefs			0.532*** (0.110)	0.539*** (0.110)
Trust Game * Beliefs			−0.186 (0.111)	−0.181 (0.111)
Risk * Trust Game * Beliefs			0.1730.156	0.1690.156
Male				0.112 (0.448)
Trial number				−0.006* (0.003)
Random effects				
Subjects (Intercept)	Var: 2.589SD: 1.609	Var: 0.902SD: 0.950	Var: 0.907SD: 0.953	Var: 0.958SD: 0.979
AIC	4751.39	4733.48	4684.09	4693.13
Observations	1224	1224	1224	1224

Note: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$; standard errors in parentheses.

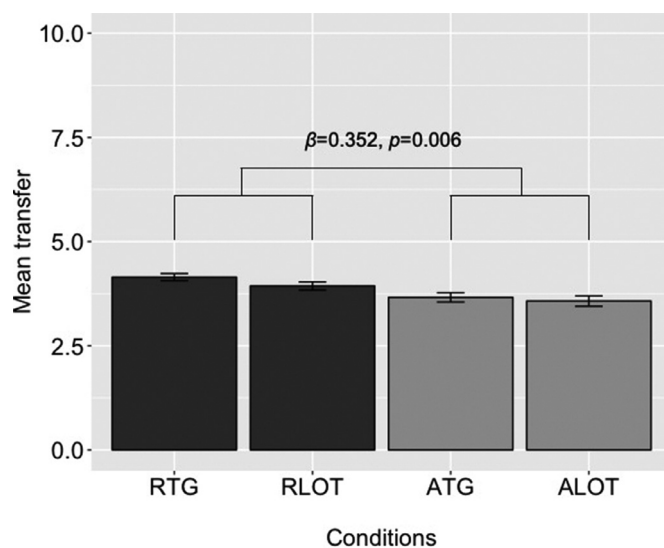


Fig. 3. Mean transfer across experimental conditions

Participants invest less in the ambiguous conditions (overall transferred amount tokens in ATG and ALOT as compared to RTG and RLOT) than the risky conditions, illustrating ambiguity aversion. There was no effect of sources of uncertainty: participants do not alter their transferred amounts between the Trust Games and the lotteries. As participants make repeated choices within each of the four conditions, the standard error bars in this Figure represent within-subject error bars and are calculated based on [Morey \(2008\)](#).

amount, across conditions and participants, was 3.83 tokens (which is very similar to the average transfer of 4.13 tokens in the RTG and ATG in [Fairley et al., 2016](#)). Assessing the mean transfer amounts in our four experimental settings indicated that participants invested less in the ambiguous contexts versus the risky contexts, thus illustrating ambiguity aversion (see [Fig. 3](#) and see Appendix Figure B5 for visualization with a condensed range of 0–5 mean transfer).

These descriptive results were confirmed by a linear mixed-effects model consisting of participants' transfer amounts as the dependent variable and the following independent variables: the type of uncertainty (risk versus ambiguous contexts), the source of uncertainty (Trust Game versus lottery), participants' beliefs, trial number, gender, the two-way and three-way interactions between types and sources of uncertainty with participants' beliefs and a random intercept accounting for clustering of repeated trials at the participant level (see [Table 1](#) for a complete overview of the results from the linear mixed-effects model). Participants were on average ambiguity averse, transfer-

ring more tokens in risky as compared to ambiguous trials ($\beta=0.353$, $p = 0.006$ via Satterthwaite's method), transferring more when they held higher beliefs regarding reciprocation ($\beta=0.903$, $p<0.001$ via Satterthwaite's method) and transferring less tokens as the experiment progressed over time as indicated by a significant, albeit very small, effect of trial number ($\beta=-0.006$, $p = 0.031$ via Satterthwaite's method).

We also found a significant interaction between beliefs and the type of uncertainty. This effect is shown in [Fig. 4](#), which illustrates that ambiguity aversion increased as individuals had greater beliefs in the likelihood of reciprocity. This effect was present in both the Trust Game context (in response to higher beliefs regarding the reciprocity of receivers, see Appendix Figure B6) and the lottery context (in response to a higher likelihood of the number of winning colors, see Appendix Figure B7). Notably, this effect was only evident with regard to type of uncertainty, as there was no significant interaction between participants' beliefs and investment behavior across sources of uncertainty.

Finally, as a robustness check, we investigated whether participants expressed higher variability in transfer amounts as a function of beliefs and experimental conditions. While participants' mean standard deviation across RLOT and ALOT significantly varied across participants' beliefs regarding the likelihood of reciprocity in the lottery (MANOVA: Pillai's trace = 0.374, $F = 2.842$, $p = 0.019$, see Panel A in Appendix Figure B8), there were no systematic differences (MANOVA: Pillai's trace = 0.240, $F = 5.087$, $p = 0.085$) in participants' mean standard deviation in RTG and ATG (see Panel B in Appendix Figure B8). We further reflect on these outcomes in the Discussion.

3.2. Neuroimaging results

Our neuroimaging analyses focused on the decision-time window when participants decided how much to invest under different types and sources of uncertainty. Our neuroimaging results will demonstrate both common regions of brain activity, as well as distinct brain regions of (non-)social sources of risk and ambiguity. Furthermore, we will add additional neuroimaging results accompanying the behavioral relevance of participants' beliefs in relation to their ambiguity preferences. Below, we start off with detailing the neural correlates of our four conditions of uncertainty compared to the implicit baseline in our model (which are the screens showing a fixation cross).

We performed a formal conjunction analysis under the conjunction null hypothesis ([Nichols et al., 2005](#)), requiring that all contrasts are individually significant, which is illustrated in Appendix Table A1. Our results demonstrated a shared increased activation in the right lateral OFC for both risky sources of uncertainty and bilateral lateral OFC for both ambiguous sources of uncertainty ([Table 2](#) and Panels A and B in [Fig. 5](#)). This outcome is consistent with [Hsu et al. \(2005\)](#) and the general

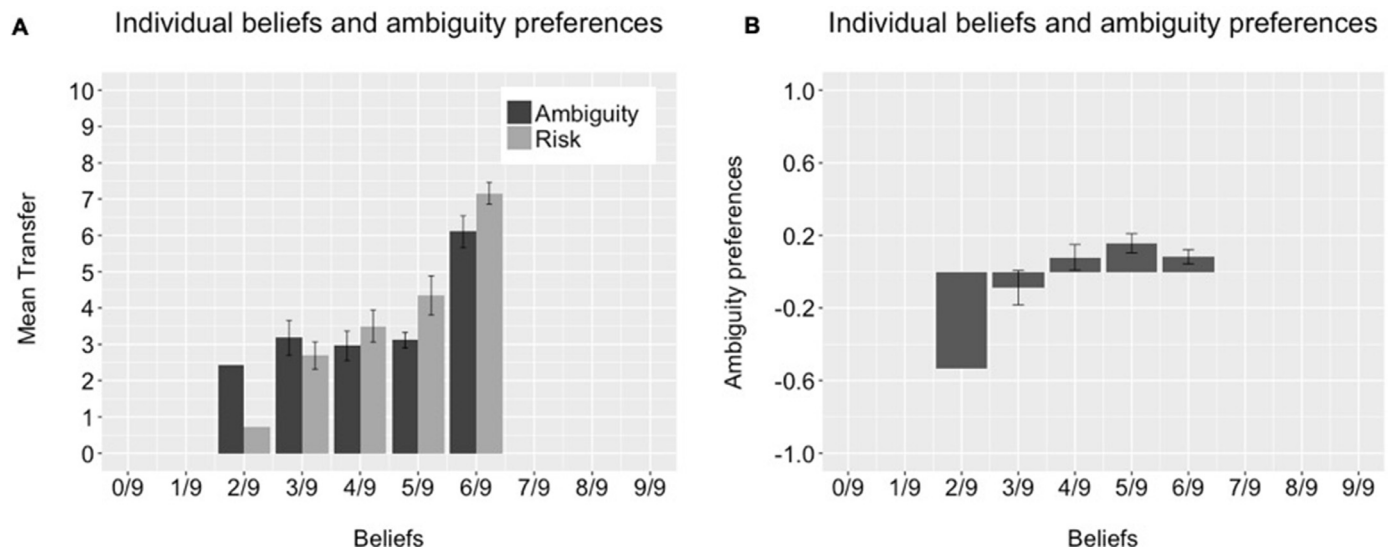


Fig. 4. The effect of individuals' beliefs on ambiguity aversion

Ambiguity preferences change along the probability distribution, represented here by participants' beliefs. The more optimistic the beliefs, the greater the ambiguity aversion. This effect is illustrated as differences in mean transfer between risk and ambiguity (Panel A) and per participants' normalized score on ambiguity preferences (Panel B). This effect was present in both the social domain (ATG vs RTG, see Appendix Figure B6) and the lottery domain (ALOT vs RLOT, see Appendix Figure B7). Error bars indicate between-subjects' standard error of the mean (one participant held a belief of 2/9 and therefore no error bar is present).

Table 2

Overview of conjunction analysis.

Contrast Brain region	P _{FWE-cor} cluster	Cluster size	MNI coordinates (local maxima)			Peak Z-value
			x	y	z	
RLOT ∩ RTG > fix						
R Lingual gyrus*	< 0.001	914	16	-84	-14	6.55
			24	-74	-18	6.48
			16	-80	0	6.21
R OFC*	0.015	70	16	38	-14	4.77
			34	46	-7	4.11
ALOT ∩ ATG > fix						
R Declive*	<0.001	425	16	-77	-18	5.89
L Cuneus*			-4	-88	7	5.10
R Cuneus*			2	-91	18	5.02
L OFC	0.024	60	-4	38	-24	4.09
			-15	42	-21	3.94
RLOT ∩ RTG < fix						
L middle temporal gyrus*	<0.001	341	-54	-60	7	5.03
L supramarginal gyrus			-50	-49	21	4.03
L postcentral gyrus			-60	-21	18	4.02
R supramarginal gyrus	0.004	97	62	-21	28	4.44
			55	-18	21	4.03
L Cingulate gyrus			0.003	105	-8	-32
	-15	-38			35	3.93
R Cingulate gyrus	10	-28			42	3.67
L Anterior Cingulate	0.019	66	-4	38	-4	3.91
R Anterior Cingulate			2	42	0	3.86
ALOT ∩ ATG < fix						
L middle temporal gyrus*	<0.001	562	-54	-63	4	6.22
L inf. parietal lobule*			-57	-28	32	5.14
L sup. temporal gyrus*			-57	-52	10	5.06
R supramarginal gyrus*	<0.001	342	62	-21	28	5.72
			55	-18	21	4.96
			52	-56	4	4.61
R middle temporal gyrus*	0.046	49	-8	-32	42	4.21
L cingulate gyrus			-15	-35	38	4.11
			-1	32	0	4.04
L ant. cingulate gyrus	0.004	93	-4	42	-4	3.79
			-8	49	4	3.71
L medial frontal gyrus						

Abbreviations: L: left, R: right OFC: orbitofrontal cortex, inf: inferior, sup: superior, ant: anterior.

Regions surviving FWE correction $p < 0.05$ for cluster-level inference are marked with an asterisk (*).

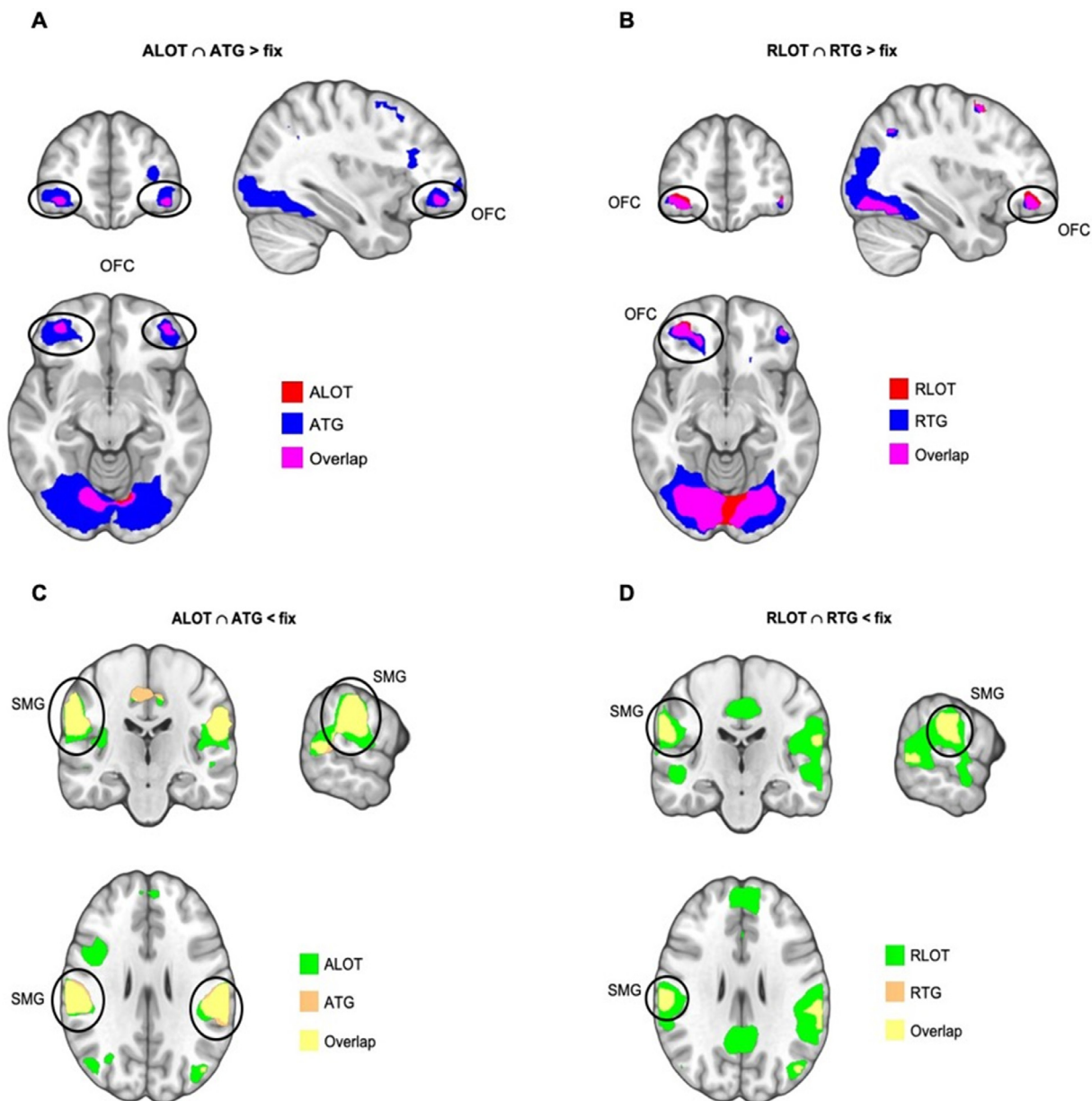


Fig. 5. Shared positive and negative neural correlates between risky and ambiguous sources of uncertainty

The conjunction analysis illustrates how the orbitofrontal cortex (OFC) plays a role in both ambiguous (Panel A) and risky (Panel B) lottery and Trust Game contexts. Furthermore, posterior social regions like the supramarginal gyrus (SMG) were negatively correlated with both ambiguous (Panel C) and risky (Panel D) lottery and Trust Game contexts.

Abbreviations: fix: fixation cross, OFC: orbitofrontal cortex, SMG: supramarginal gyrus.

involvement of the OFC in (social) decision-making under uncertainty. As confirmation of this relationship between OFC and risk, a term-based meta-analysis (Yarkoni et al., 2011) of the terms ‘risk taking’, ‘uncertainty’ and ‘social interactions’ in Neurosynth shows the consistent contribution of the OFC (see Panel A in Appendix Figure B9). However, we have to note that most of the activation for these meta-analysis terms is in medial OFC, whereas our findings are more lateral OFC. Upon further inspection we found that the term ‘risk taking’ from Neurosynth showed activation in both medial and lateral OFC and overlaps with the image saved from the conjunction analysis $R LOT \cap RTG > fix$ (see Panel B in Appendix Fig B9). Furthermore, we let the Neurosynth decoder produce overlay images based on the terms ‘risk taking’ for the baseline activation in RLOT and RTG (from Appendix Table A1) and the meta-analysis term ‘uncertainty’ for ALOT and ATG (from Appendix Table A1) and

Appendix Figure B10 illustrates the large overlap between our findings and the meta-analysis terms.

Lastly, these findings relating medial OFC to risk and ambiguity should not be interpreted as a claim that medial OFC is the sole contributor to risk and ambiguity processing. One can clearly see from Appendix Figure B10 that many brain regions relate to risk and ambiguity processing, most prominently the striatum and medial PFC, which are notably also highlighted on our unthresholded contrast images required for the Neurosynth decoder.

We proceed with our conjunction analysis by showing that the posterior brain regions commonly associated with social cognition, such as the superior temporal gyrus and supramarginal gyrus (Saxe, 2006), were negatively correlated with both (non-)social risk (RLOT and RTG) and (non-)social ambiguity (ALOT and ATG), see Panels C and D in

Table 3

Significant results of the contrasts related to types of uncertainty, sources of uncertainty and its interaction.

Contrast	P _{FWE-cor}	cluster	Cluster size	MNI coordinates (local maxima)			Peak Z-value
Brain region				x	y	z	
Risk>Ambiguity							
R IPS*	< 0.001		665	31	-67	35	5.67
R fusiform gyrus*				31	-70	-14	5.56
R inf temporal gyrus*				52	-56	-11	4.85
L fusiform gyrus*	<0.001		494	-29	-74	-14	4.97
L cuneus*				-15	-98	0	4.83
L lingual gyrus*				-8	-91	-7	4.78
Interaction of types and sources of uncertainty Defined as participant-level contrast: RLOT ALOT RTG ATG: 1 -1 -1 1)							
R parietal lobe	0.002		131	30	-70	32	4.31
R IPS				30	-49	42	4.27
L fusiform gyrus	0.006		106	-32	-60	-14	4.29
L lingual gyrus				-29	-77	-14	4.08
R inf occipital gyrus	0.003		122	38	-74	-10	4.12
R lingual gyrus				30	-80	-7	3.92
R fusiform gyrus				34	-52	-14	3.81
Social>Lottery							
R middle occipital gyrus*	<0.001		1032	41	-74	4	5.46
R lingual gyrus*				20	-91	-4	5.42
R fusiform gyrus*				41	-42	-14	5.26
L inf occipital gyrus*	<0.001		790	-33	-84	-7	5.40
L fusiform gyrus*				-40	-46	-18	5.00
L middle temporal gyrus*				-43	-74	7	4.97
R IFG (opercular)	<0.001		179	55	14	28	4.07
R IFG (triangular)				41	18	25	3.97
R IFG (triangular)				45	28	21	3.73

Abbreviations: L: left, R: right, inf: inferior, ING: inferior frontal gyrus.

Regions surviving FWE correction $p < 0.05$ for cluster-level inference are marked with an asterisk (*).

Fig. 5 and Appendix Table A1 and Table 2 below. As both these regions are sensitive to social reasoning and interpreting others' mental states (Saxe, 2006), it seems that our experimental design was successful in stripping away the process of reasoning regarding the consequential behavior of the receiver in response to sender's transferred amount. This enabled participants in their role as sender to exclusively focus on the source of uncertainty in terms of participants' beliefs regarding the likelihood of reciprocation of a receiver in the Trust Game and a mechanistic device in the lottery.

Lastly, the conjunction analysis underlined the consistent positive neural correlates in the occipital lobe across both risky and ambiguous (non-) social sources of uncertainty (see Table 2). In our view, this is likely due to the fact that the manner in which we communicated the type and source of uncertainty in our design is based on distinct (and distinguishable) visual input across the various conditions, such as colors, marbles, and silhouettes of persons.

We proceeded with our whole-brain neuroimaging analysis by directly comparing the experimental conditions related to types of uncertainty (a directional test of both ambiguity vs. risk and risk vs. ambiguity from the same contrast) and sources of uncertainty (a directional test of both social vs. non-social and non-social vs. social from the same contrast). These results indicated a significant activation in the right intraparietal sulcus (IPS) when participants decided how many tokens to transfer in the main condition of risk versus the ambiguous main condition (see Table 3). This activation pattern was also present in the lottery context (RLOT vs ALOT), but not in the social context (RTG vs ATG). To formally test if the right IPS differentially activated risk, as compared to ambiguity, in the lottery context versus the social context, we performed a whole-brain analysis with this interaction as contrast.

Fig. 6 illustrates our outcome and indeed demonstrates that the right IPS, albeit in this contrast as a sub-peak coordinate of the significant cluster (Table 3), was more active when participants decided on their transfer in the risky lottery versus the ambiguous lottery as compared to the difference between social risk versus social ambiguity.

Notably, no significant neural responses were detected when participants decided under ambiguity versus risk. We further reflect on this null-finding in our Discussion.

Although behaviorally, participants did not appear sensitive to sources of uncertainty, we did find a main effect of social uncertainty (social risk and social ambiguity versus lottery risk and lottery ambiguity) represented in the right inferior frontal gyrus (IFG, see Fig. 7 and Table 3 for details) – which activation pattern slightly overlapped the right dorsolateral prefrontal cortex – a region often linked to uncertainty (Huettel et al., 2006; Bach et al., 2011).

In order to examine the neural underpinnings of ambiguity aversion (defined as a normalized score based on participants' decision-making, as described in the methods section), we first added participants' ambiguity preferences as a covariate to the main contrast ambiguity (ATG and ALOT) versus risk (RTG and RLOT) at the second level, and vice versa. No brain areas surpassed the threshold level, and no brain areas covaried with participants' individual beliefs across these contrasts.

Based on the whole-brain analysis findings (Table 3) and prior evidence of the role of the IPS in ambiguity preferences (Platt and Huettel, 2006; Huettel et al., 2006; Iking et al., 2019), we performed a ROI-analysis exclusively focusing on the potential relationship between the right IPS and participants' ambiguity preferences. We first extracted participants' beta coefficients from the right IPS from the previously discussed comparison – the time window during which participants decided on their investment in the risky context versus the ambiguous context – and, importantly, from a model which did not include transfer choice as parametric modulator. This ROI-analysis yielded a significant negative correlation (Pearson's $r = -0.45$, $p = 0.04$) between participants' beta coefficients and participants' ambiguity preferences. However, when removing one significant outlier (see Panel A in Appendix Figure B11), the results changed substantially (see Panel B in Appendix Figure B11).⁷

⁷ We reran our linear mixed-effects model by excluding this same participant, and this did not change our results.

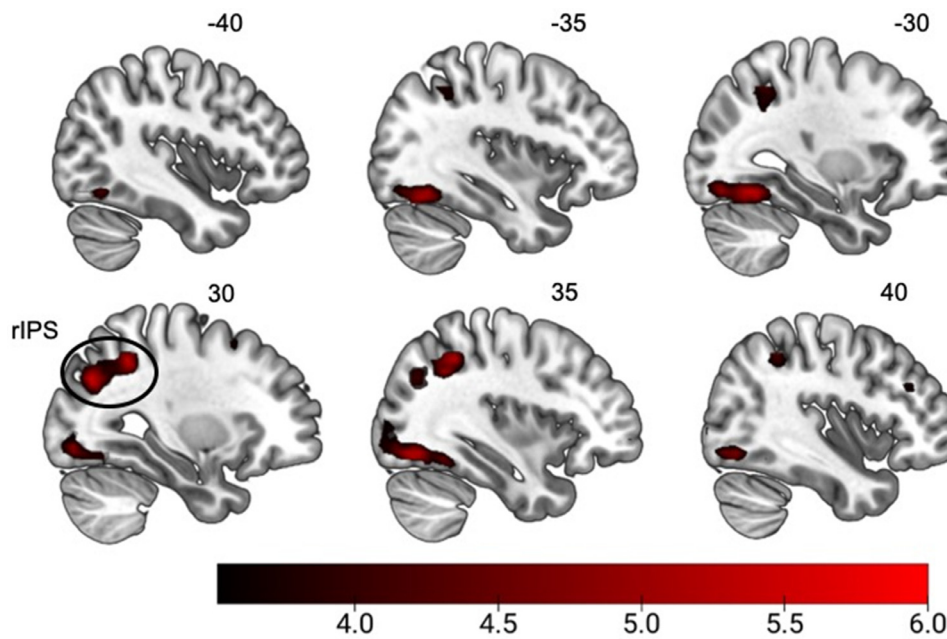


Fig. 6. Neural effect of the interaction of types and sources of uncertainty
The right IPS was more involved when participants decided on their transferred amount in the risky lottery as compared to the ambiguous lottery versus when they invested under social risk as compared to social ambiguity. Results were FWE cluster-corrected with a primary voxel-wise threshold of $p < .001$.

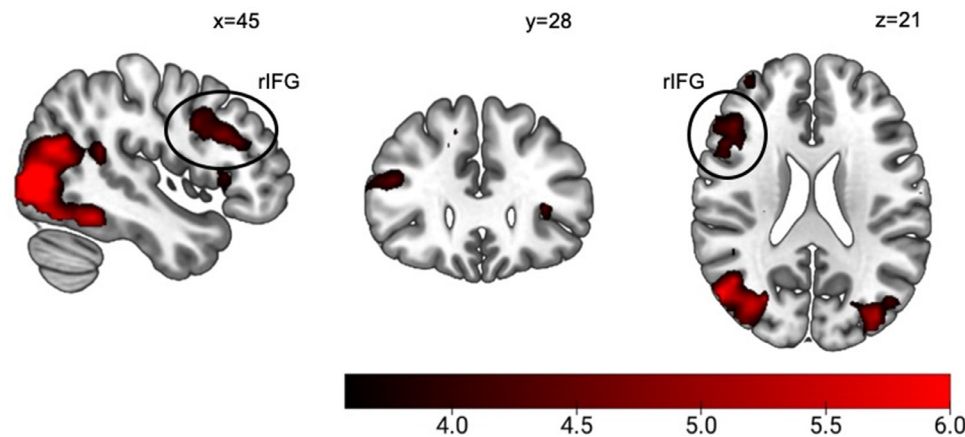


Fig. 7. Neural effect of sources of uncertainty
The right IFG was involved when participants decided under social uncertainty as compared to lottery uncertainty. Results were FWE cluster-corrected with a primary voxel-wise threshold of $p < .001$.

After removing this outlier and regressing participants' beta coefficients from their right IPS activation with the variables participants' beliefs, ambiguity preferences, and the interaction of beliefs and ambiguity preferences, we found a significant effect ($\beta = -1.270$, $p < 0.001$) of this interaction on participants' right IPS activation (see Fig. 8 and Panel C and D in Appendix Figure B11).

This interaction illustrates that as ambiguity aversion increases, the coefficient of participants' beliefs on rIPS brain activation decreases (see Fig. 8). If we unpack this interaction, we can clearly see (1) the pattern in the right IPS on ambiguity preferences between participants who are ambiguity seeking (Panel C in Appendix Figure B11) and ambiguity averse (Panel D in Appendix Figure B11). Furthermore, from the behavioral results we found that (2) participants with higher beliefs regarding the likelihood of reciprocation invest more in the risky conditions than in the ambiguous conditions, resulting in more ambiguity averse behavior. Connecting both insights results in the overall negative correlation between the interaction of beliefs and ambiguity preferences in the right IPS when participants decide on their transfer amounts in the risky conditions as compared to the ambiguous conditions.

In line with some previous work (Platt and Huettel, 2006; Huettel et al., 2006; Ikink et al., 2019), this finding underlines the role of the IPS in ambiguity preferences, with our findings adding the important role of beliefs to this account.

4. Discussion

Previous fMRI research has primarily focused on the distinction between risk and ambiguity in lottery contexts. Our study sought to investigate the interplay of both the types of uncertainty, that is, risk versus ambiguity, as well as sources of uncertainty – lottery versus social – in one well-controlled experimental paradigm. This research question is quite relevant, in that real-life decisions are generally not determined by the flip of a coin or the roll of a die. People often face uncertainty that directly stems from the deliberate choice of another person. Moreover, these social decisions can vary between risky or ambiguous depending on the familiarity the decision-maker has with the interaction partner.

One key difficulty with such an endeavor is to control for participants' naturally occurring social beliefs, which, in contrast to a lottery, cannot be simply 'handed-down' to participants by providing a clear experimental prior. While underlying subjective probabilities can easily be manipulated in a lottery context, people have more organic, idiosyncratic expectations in social environments, built over many years of interpersonal interaction. It is essential to address these individual beliefs in order to allow for meaningful comparisons between the different contexts. We therefore elicited participants' beliefs regarding receivers' reciprocal behavior in the Trust Game and subsequently constructed *belief-corresponding scenarios* for each participant individually.

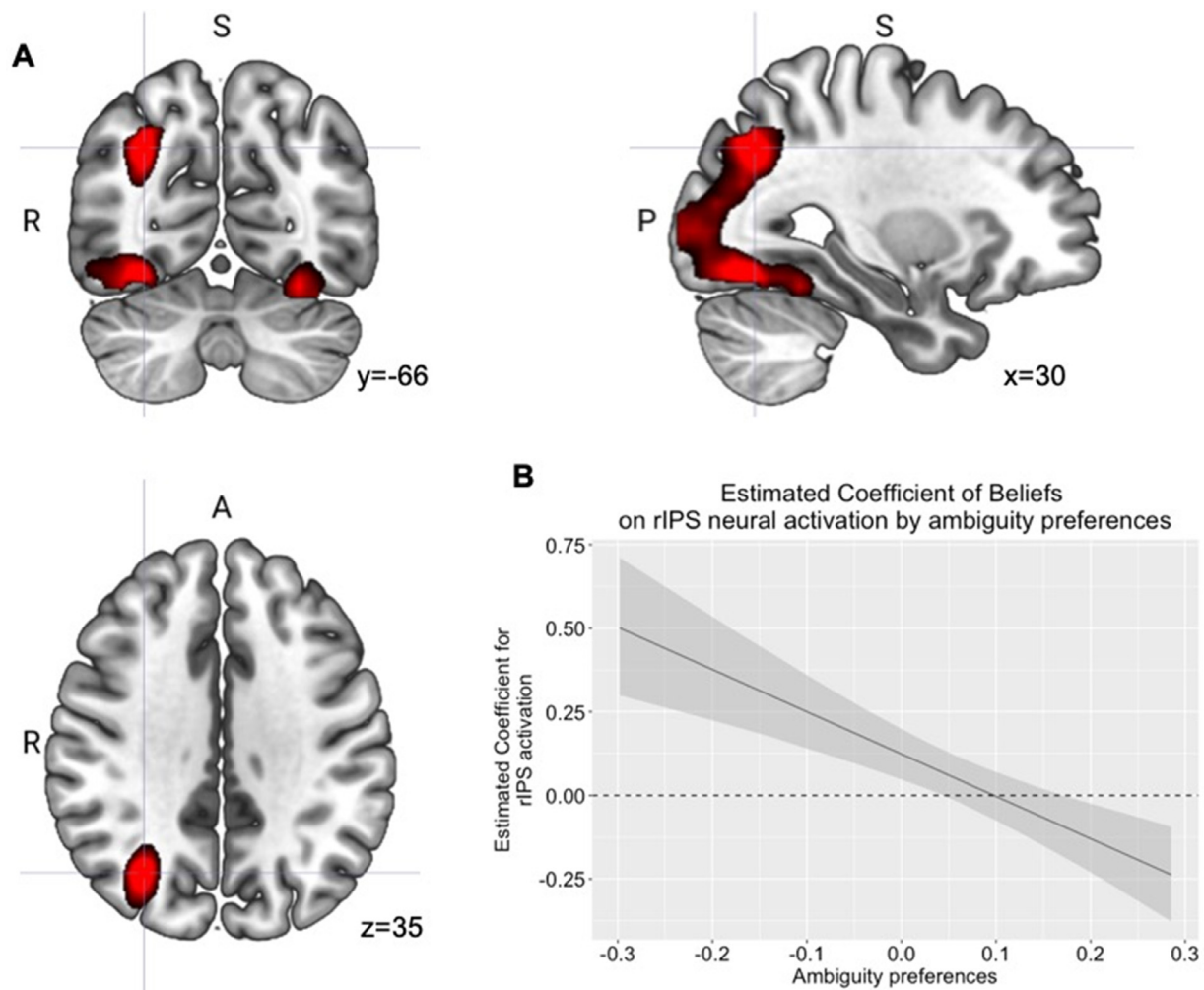


Fig. 8. Ambiguity preferences in the right IPS

In this ROI, we extracted participants' beta coefficients from the right IPS (Panel A) during the time window participants decided on their investment in the risky context versus the ambiguous context and importantly from a model which did not include transfer choice as parametric modulator. We regressed this dependent variable with participants' ambiguity preferences, beliefs and the interaction of beliefs and ambiguity preferences. We found the interaction to be significant, which resulted in a negative correlation with the right IPS, plotted in Panel B by the estimates slope and a simulated 95% confidence interval with the R package Interplot (Solt and Hu, 2015).

By utilizing this approach, we made sure that participants made their investment decisions across contexts which only varied as a function of the relevant experimental conditions.

Results indicated that this strategy to derive and employ belief-corresponding scenarios was crucial, as participants indeed varied widely in their inherent beliefs regarding receivers' reciprocating behavior. Neglecting participants' social beliefs would have resulted in a clear mismatch of underlying likelihoods across our experimental conditions. The protocol to elicit participants' beliefs appeared successful, as participants did invest more in the ATG as a function of higher beliefs regarding receivers' reciprocal behavior, and also invested more in the ALOT after being offered a corresponding number of winning marbles. Again, it is important to note that these beliefs were elicited during the instruction period before any decision-making took place and that the interaction outcomes were not shown during the decision-making part of our experiment, thereby ruling out learning and any role for prediction errors.

We found a general decision-making pattern in line with our expectations, namely that participants invested less when in the ambiguous context than in the risky context, thereby clearly illustrating ambiguity aversion. However, in contrast to our hypotheses, we did not find any indication that participants invested differently between social and

non-social sources of uncertainty, nor was the interaction of types and sources of uncertainty significant. Finally, with regard to our behavioral findings, while ambiguity aversion might have represented the average behavioral pattern in our study, it is far from telling the complete story. Participants' beliefs interacted with their investment behavior across types of uncertainty (but not across sources of uncertainty), which again underlines the importance of taking individuals' beliefs into account: participants who had higher beliefs in receivers' reciprocation likelihoods, demonstrated increased ambiguity aversion, both in the distinction between RLOT and ALOT, as well as between RTG and ATG.

Before we discuss our neuroimaging results, it is useful to provide some context. The finding that individuals' beliefs affect ambiguity preferences relates to a relatively new strand of experimental economic findings which has termed this behavioral phenomenon 'likelihood insensitivity' (Abdellaoui et al., 2011; Kocher et al., 2018). Participants tend to overweigh low subjective probabilities (resulting in ambiguity seeking behavior) and underweight high subjective probabilities (resulting in ambiguity aversion), hence participants do not typically discriminate between subjective probabilities close to 0.5. Put differently, participants do not show sensitivity regarding subjective probabilities around 0.5. These findings are mostly observed in within-subject experimental designs in which participants make choices when the underlying like-

likelihood in the ambiguous context is, for example, 0.1, 0.5 and 0.9. Our results, on the other hand, stemmed from variability across participants in their social beliefs, thereby creating natural contexts whereby participants made choices when likelihoods were generally lower – such as when they believed only 3 out of 9 receivers would reciprocate – and generally higher – such as believing that 6 out of 9 receivers would reciprocate. Moreover, in this study we also showed that likelihood insensitivity is prevalent between risk and ambiguity in the social context, thereby illustrating the generic pattern of this behavioral phenomenon. Thus, to sum up, the current study showed that individual beliefs varied in social interactive situations, and that this had a direct effect on ambiguity preferences, namely that, in line with previous insights from likelihood insensitivity, the higher one's expectation regarding an other-dependent outcome, the more ambiguity aversion was expressed.

The neural correlates of the interaction of individuals' beliefs and level of ambiguity seeking or ambiguity aversion was reflected in increased activation in the right IPS. Our study has thereby highlighted the role of participants' beliefs in neural correlates of ambiguity preferences. Participants' naturally occurring beliefs regarding social and non-social uncertainty can reflect general optimism and pessimism regarding (non-)social interactions under uncertainty (Carleton et al., 2012; Abdellaoui et al., 2011) and this in turn can shape participants' tolerance for uncertainty and how strongly the rIPS is activated. Moreover, as reflected by a significant neural interaction of types and sources of uncertainty, the right IPS was primarily involved when participants experienced risk vs. ambiguity in the lottery context, as opposed in the social context. The parietal cortex, and the IPS specifically, have been related to the general processing of known probabilities – both in adults (Huettel et al., 2005) and adolescents (Blankenstein and van Duijven-voorde, 2019) – as well as unknown probabilities (Huettel et al., 2006; Krain et al., 2006; Ikink et al., 2019). This region has been informally described as “calculative”, which might therefore resonate more with a lottery context than the social context.

Although sources of uncertainty did not seem to impact participants' investment behavior directly, we did find a significant neural activation in the right IFG when participants made investment decisions in the social as opposed to the lottery context. This is in contrast to our hypothesis, which expected that the anterior insula would be related to social uncertainty. The role of the IFG in processing uncertainty in general is well-known, but has not to date been specifically related to social uncertainty. Both Huettel et al. (2006) and Bach et al. (2009) have stressed the importance of the IFG in their explorations of uncertainty. In Huettel et al. (2006) participants could gradually learn the underlying uncertainties across the experiment as the lotteries were resolved after each trial. The authors therefore explicitly related the IFG activation to a process of resolving ambiguity. In Bach et al. (2011), lotteries were resolved via a bowling game during the experiment and, moreover, the lottery setup was framed in a somewhat social manner. Namely, each of 2 bowlers would bowl a different colored ball, with this color indicating the first-order objective probability to win the lottery. Only one of the two bowlers would actually play, and depending on where the ball ended up, participants could indicate which bowler they thought had likely bowled the ball (in order to assess the probability of winning the lottery). Overall, therefore, the IFG is involved when players are making uncertain choices, but specifically when the context requires participants to reflect on the underlying likelihood they face under uncertainty. In the social condition of the present study, participants might be actively trying to figure out the likelihood of receivers' reciprocity. This active engagement was required less in the lottery context of our experiment, as participants had received a prior, namely the number of winning colored marbles (that corresponded to participants' social beliefs).

In addition to these neuroimaging findings, it is also important to address the neural null-effect observed when participants made decisions in the ambiguous versus the risky contexts. Give previous findings, it was somewhat surprising that no significant brain responses emerged

when participants faced ambiguity rather than risk. We suspect that our highly controlled experiment plays a role here. Although our experimental design is precise in capturing types and sources of ambiguity while taking participants' beliefs into account, it arguably suffers from a lack of ecological validity. The studies by e.g. Huettel et al. (2006) and Hsu et al. (2005) are more engaging as participants actually see the outcomes of their decision-making (in Huettel et al. 2006) or are based on many intertwining real-life decision scenarios (in Hsu et al. 2005).

On the other hand, Levy et al. (2009) did not find that the subjective value of ambiguity was represented differently than the subjective value of risk on a neural level. With respect to this latter finding, they noted that the subjective value of both risk and ambiguity represent ‘a unified evaluative system that uses a common currency to represent value under different conditions’ (p. 1046). However, we did find significant areas of activation for risky versus ambiguity conditions, which leads to the question of what might be special about risk versus ambiguity. One possibility is that risk requires a different calculative mindset when making decisions which are guided by the availability of objective probabilities. These objective probabilities are not available when one faces ambiguity, yet in both cases one faces uncertainty regarding the realization of potential outcomes. Therefore, it might be that risk is the exception, or to quote Peter Wakker in his seminal work on uncertainty: ‘It is more efficient, and conceptually more appropriate, to treat risk as a special case of uncertainty’ (2010, p. 44).

Although our experimental design enabled us to study neural effects of sources and types of uncertainty without individual beliefs as confounds, there are several important points to bear in mind regarding the interpretation of our results. For one, we could not directly compare individual differences in lottery ambiguity preferences as we presented participants with different likelihoods of drawing a winning marble, with these probabilities matched with each participant's endogenous belief regarding receivers' reciprocation in the ATG. Also, the procedure to align beliefs between the social and the lottery source necessarily produced a difference in the amount of information across sources. An unavoidable consequence of this is that participants in the ALOT did not have to actively form a prior belief. If participants felt that the ATG was more uncertain as compared to the ALOT, due to differences in information received, we reasoned that they would vary more in their investment choices in the ATG. To the contrary, our results showed that participants expressed higher variability in transfer amounts across the RLOT and ALOT (but not RTG and ATG) as a function of beliefs and experimental conditions. We suspect that participants more easily form multiple priors (Qiu and Weitzel, 2016) in the lottery – a second-order belief (or confidence level) for all potential priors that a participant forms – than is formed in the Trust Game, as participants likely have a clear idea about the possibility of reciprocity in the Trust Game, whereas the lottery is viewed as more random in nature. This is explicit within the field of Economics, where theoretical models assume that a participant forms multiple priors (Gilboa and Schmeidler, 1989; Ghirardato et al., 2004; Maccheroni et al., 2006; Klibanoff et al., 2005). Based on our findings here, we therefore expect that multiple priors play a bigger role within the lottery domain than the social domain, which would be an interesting notion to more formally test in subsequent research.

A further interesting point for future research is the nature of the relationship between the participant and their game partners. While it was beyond the scope of the current study, the specific social relationship the decision-maker might have with another person could of course strongly guide investment decisions. If our participant had different relationship states with different game partners (e.g. romantic partner vs. friend vs. work colleague) this would of course add an interesting additional assessment of both the likely response, and the reaction to, an unexpected decision. Future work could of course explore the nature of the relationship itself, and its impact on social decision-making.

Finally, a point of note is the relatively small sample size in this study. This was partly due to our extensive and time-consuming design protocol, which consisted of pre-collected receivers' data, a pool of re-

participants, and the extensive instruction time each fMRI participant required. The current study should therefore be seen as a first attempt to experimentally investigate both types and sources of uncertainty in the MRI scanner. We hope that our findings, which underline the relevance of measuring participants' beliefs in relation to their ambiguity preferences, inspire future research to broaden the knowledge base regarding the neural correlates of decision-making under uncertainty.

To conclude, the current study extended the general investigation of lottery-induced uncertainty significantly by examining a fourfold pattern of both sources and types of uncertainty, demonstrating the use of belief-corresponding scenarios and showing how beliefs interact with ambiguity preferences.

All data and codes has been available in the repository of the Donders Institute for Brain, Cognition and Behaviour. You can review the data sharing collection with the following url <https://doi.org/10.34973/z3jh-4586>.

Authors' contributions

KF, AS, JV and UW designed research. KF performed research. KF analyzed data. KF and AS wrote the paper. All authors approved the final version of the manuscript for submission.

Funding

This research was partially supported by a European Research Council grant to Alan Sanfey (ERC StG 313454).

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgement

We would like to thank members of the Decision Neuroscience Lab at the Donders Institute for Brain, Cognition and Behaviour and the Experimental and Behavioral Finance group at the Department of Economics at Radboud University for their valuable feedback throughout several stages of this research. Furthermore, we thank conference participants of Society of Neuroeconomics 2013 in Lausanne, Social and Affective Neuroscience 2014 in Denver, Tiber 2014 in Tilburg, European ESA 2014 in Prague, and interactions with the Emotion and social cognition laboratory at Caltech and the Huettel laboratory at Duke for very valuable comments.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.neuroimage.2022.119007](https://doi.org/10.1016/j.neuroimage.2022.119007).

References

Abdellaoui, M., Baillon, A., Placido, L., Wakker, P.P., 2011. The rich domain of uncertainty: source functions and their experimental implementation. *Am. Econ. Rev.* 101, 695–723.

Aimone, J., Houser, D., 2012. What you don't know won't hurt you: a laboratory analysis of betrayal aversion. *Exp. Econ.* 15, 571–588.

Aimone, J., Houser, D., Weber, B., 2014. Neural signatures of betrayal aversion: an fMRI study of trust. *Proc. of the Royal Soc* 281, 1–6.

Bach, D.R., Hulme, O., Penny, W.D., Dolan, R., 2011. The known unknowns: neural representation of second-order uncertainty, and ambiguity. *J. Neurosci.* 31, 4811–4820.

Bach, D.R., Seymour, B., Dolan, R., 2009. Neural activity associated with the passive prediction of ambiguity and risk for aversive events. *J. Neurosci.* 29, 1648–1656.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67, 1–48.

Bellucci, G., Chernyak, S.V., Goodyear, K., Eickhoff, S.B., Krueger, F., 2017. Neural signatures of trust in reciprocity: a coordinate-based meta-analysis. *Hum Brain Mapp* 38 (3), 1233–1248.

Berg, J., Dickhaut, J., McCabe, K., 1995. Trust, reciprocity, and social history. *Games Econ. Behav.* 10, 122–142.

Blankenstein, N.E., van Duijvenvoorde, A.C., 2019. Neural tracking of subjective value under risk and ambiguity in adolescence. *Cognit. Affect Behav. Neurosci.* 19 (6), 1364–1378.

Bohnet, I., Zeckhauser, R., 2004. Trust, risk and betrayal. *J. Econ. Behav. Org.* 55, 467–484.

Carleton, R.N., Mulvogue, M.K., Thibodeau, M.A., McCabe, R.E., Antony, M.M., Asmundson, G.J., 2012. Increasingly certain about uncertainty: intolerance of uncertainty across anxiety and depression. *J. Anxiety Disord.* 26 (3), 468–479.

Chen, X., Hackett, P.D., DeMarco, A.C., Feng, C., Stair, S., Haroon, E., Ditzen, B., Pagnoni, G., Rilling, J.K., 2016. Effects of oxytocin and vasopressin on the neural response to unreciprocated cooperation within brain regions involved in stress and anxiety in men and women. *Brain Imaging Behav* 10 (2), 581–593.

Eklund, A., Nichols, T.E., Knutsson, H., 2016. Cluster failure: why fMRI inferences for spatial extent have inflated false-positive rates. *Proc Natl Acad Sci* 113 (28), 7900–7905.

Ellsberg, D., 1961. Risk, ambiguity, and the Savage axioms. *Q. J. Econ.* 75, 643–669.

Fairley, K., Sanfey, A., Vyrastekova, J., Weitzel, U.G., 2016. Trust and risk revisited. *J. Econ Psychol* 57, 74–85.

Fairley, K., Sanfey, A.G., Vyrastekova, J., Weitzel, U.G., 2019. Subjective beliefs about trust and reciprocity activate an expected rewards signal in the ventral striatum. *Front Neurosci-Switz* 13, 660.

Feng, C., Luo, Y.J., Krueger, F., 2015. Neural signatures of fairness-related normative decision making in the ultimatum game: a coordinate-based meta-analysis. *Hum Brain Mapp* 36 (2), 591–602.

Frackowiak, R.S.J., Friston, K.J., Frith, C.D., Dolan, R.J., Mazziotta, J.C., 1997. *Human Brain Function*. Academic Press, Cambridge, MSUSA.

Ghirardato, P., Maccheroni, F., Marinacci, M., 2004. Differentiating ambiguity and ambiguity attitude. *J. Econ. Theory* 118 (2), 133–173.

Gilboa, I., Schmeidler, D., 1989. Maxmin expected utility with non-unique prior. *J. Math. Econ.* 18 (2), 141–153.

Green, P., MacLeod, C.J., 2016. Simr: an r package for power analysis of generalised linear mixed models by simulation. *Methods Ecol. Evol.* 7 (4), 493–498.

Houser, D., Schunk, D., Winter, J., 2010. Distinguishing trust from risk: an anatomy of the investment game. *J. Econ. Behav. Org.* 74, 72–81.

Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., Camerer, C., 2005. Neural systems responding to degrees of uncertainty in human decision-making. *Science* 310, 1680–1683.

Hu, J., Li, Y., Yin, Y., Blue, P.R., Yu, H., Zhou, X., 2017. How do self-interest and other-need interact in the brain to determine altruistic behavior? *Neuroimage* 157, 598–611.

Huettel, S.A., Song, A.W., McCarthy, G., 2005. Decisions under uncertainty: probabilistic context influences activation of prefrontal and parietal cortices. *J. Neurosci.* 25, 3304–3311.

Huettel, S.A., Stowe, C.J., Gordon, E.M., Warner, B.T., Platt, M.L., 2006. Neural signatures of economic preferences for risk and ambiguity. *Neuron* 49, 765–775.

Ikink, I., Engelmann, J.B., van den Bos, W., Roelofs, K., Figner, B., 2019. Time ambiguity during intertemporal decision-making is aversive, impacting choice and neural value coding. *Neuroimage* 185, 236–244.

Kleiner, M., Brainard, D., Pelli, D., 2007. What's new in Psychtoolbox-3? *Perception* 36 ECVF Abstract Supplement.

Klibanoff, P., Marinacci, M., Mukerji, S., 2005. A smooth model of decision making under ambiguity. *Econometrica* 73 (6), 1849–1892.

Kocher, M.G., Lahno, A.M., Trautmann, S.T., 2018. Ambiguity aversion is not universal. *Eur. Econ. Rev.* 101, 268–283.

Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U., Fehr, E., 2005. Oxytocin increases trust in humans. *Nature* 435 (7042), 673–676.

Krain, A.L., Wilson, A.M., Arbuckle, R., Castellanos, F.X., Milham, M.P., 2006. Distinct neural mechanisms of risk and ambiguity: a meta-analysis of decision-making. *Neuroimage* 32 (1), 477–484.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: tests in Linear Mixed Effects Models. *J. Stat Software* 82 (13), 1–23.

Lauharatanahirun, N., Christopoulos, G.I., King-Casas, B., 2012. Neural computations underlying social risk sensitivity. *Front. Hum. Neurosci.* 6, 1–7.

Levy, I., Snell, J., Nelson, A.J., Rustichini, A., Glimcher, P.W., 2009. Neural representation of subjective value under risk and ambiguity. *J. Neurophysiol.* 103, 1036–1047.

Maccheroni, F., Marinacci, M., Rustichini, A., 2006. Ambiguity aversion, robustness, and the variational representation of preferences. *Econometrica* 74 (6), 1447–1498.

McCabe, K.A., Rigdon, M.L., Smith, V.L., 2003. Positive reciprocity and intentions in trust games. *J. Econ. Behav. Org.* 52, 267–275.

Morey, R.D., 2008. Confidence intervals from normalized data: a correction to Cousineau (2005). *Reason* 4 (2), 61–64.

Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. *Neuroimage* 25 (3), 653–660.

Poser, B.A., Versluis, M.J., Hoogduin, J.M., Norris, D.G., 2006. BOLD contrast sensitivity enhancement and artifact reduction with multiecho EPI: parallel-acquired inhomogeneity-desensitized fMRI. *Magn. Reson. Med.* 55, 1227–1235.

Qiu, J., Weitzel, U., 2016. Experimental evidence on valuation with multiple priors. *J. Risk Uncertain.* 53 (1), 55–74.

Core Team, R., 2013. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.

Rilling, J.K., King-Casas, B., Sanfey, A.G., 2008. The neurobiology of social decision-making. *Curr. Opin. Neurobiol.* 18 (2), 159–165.

Rustichini, A., Dickhaut, J., Ghirardato, P., Smith, K., Pardo, J.V., 2005. A brain imaging study of the choice procedure. *Gam. Econ. Behav.* 52, 257–282.

- Saxe, R., 2006. Uniquely human social cognition. *Curr. Opin. Neurobiol.* 16 (2), 235–239.
- Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2003. The neural basis of economic decision-making in the ultimatum game. *Science* 300 (5626), 1755–1758.
- Schlag, K.H., Tremewan, J., Van der Weele, J.J., 2015. A penny for your thoughts: a survey of methods for eliciting beliefs. *Exp. Econ.* 18, 457–490.
- Solt, F., Hu, Y., 2015. *interplot: plot the Effects of Variables in Interaction Terms*. Available at: The Comprehensive R Archive Network (CRAN).
- Trautmann, S.T., Vieider, F.M., Wakker, P.P., 2008. Causes of ambiguity aversion: known versus unknown preferences. *J. Risk Uncertain.* 36 (3), 225–243.
- Trautmann, S.T., Vieider, F.M., 2012. Social influences on risk attitudes: applications in economics. In: *Handbook of Risk Theory*. Springer, Rotterdam/Netherlands, pp. 575–600.
- Trautmann, S.T., van de Kuilen, G., 2015. Ambiguity attitudes. In: Keren, G., Wu, G. (Eds.), *The Wiley Blackwell Handbook of Judgment and Decision Making*. Wiley-Blackwell, Hoboken, NJ, pp. 89–116.
- Wakker, P.P., 2010. *Prospect Theory For Risk and Ambiguity*. Cambridge University Press, Cambridge.
- Xiong, W., Gao, X., He, Z., Yu, H., Liu, H., Zhou, X., 2020. Affective evaluation of others' altruistic decisions under risk and ambiguity. *Neuroimage* 218, 116996.
- Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Large-scale automated synthesis of human functional neuroimaging data. *Nat. Methods* 8 (8), 665–670.