

ORIGINAL ARTICLE

Causal Role of the Dorsolateral Prefrontal Cortex in Belief Updating under Uncertainty

Stefan Schulreich¹ and Lars Schwabe¹

Department of Cognitive Psychology, Faculty of Psychology and Human Movement Science, Universität Hamburg, 20146 Hamburg, Germany

Address correspondence to Stefan Schulreich, Department of Cognitive Psychology, Universität Hamburg, Von-Melle-Park 5, 20146 Hamburg, Germany.
Email: stefan.schulreich@uni-hamburg.de

Abstract

Adaptive performance in uncertain environments depends on the ability to continuously update internal beliefs about environmental states. Recent correlative evidence suggests that a frontoparietal network including the dorsolateral prefrontal cortex (dlPFC) supports belief updating under uncertainty, but whether the dlPFC serves a “causal” role in this process is currently not clear. To elucidate its contribution, we leveraged transcranial direct current stimulation (tDCS) over the right dlPFC, while 91 participants performed an incentivized belief-updating task. Participants also underwent a psychosocial stress or control manipulation to investigate the role of stress, which is known to modulate dlPFC functioning. We observed enhanced monetary value updating after anodal tDCS when it was normatively expected from a Bayesian perspective. A model-based analysis indicates that this effect was driven by belief updating. However, we also observed enhanced non-normative value updating, which might have been driven instead by expectancy violation. Enhanced normative and non-normative value updating reflected increased vs. decreased Bayesian rationality, respectively. Furthermore, cortisol increases were associated with enhanced positive, but not with negative, value updating. The present study thereby sheds light on the causal role of the right dlPFC in the remarkable human ability to navigate uncertain environments by continuously updating prior knowledge following new evidence.

Key words: belief updating, decision-making, DLPFC, tDCS, uncertainty

Introduction

Making optimal decisions in the face of uncertain or incomplete information poses a common problem in everyday life. Imagine traveling to another country in an unfamiliar climate zone. Before leaving your hotel on the first day, you are uncertain if it would rain or not and whether it is therefore wise to take an umbrella with you. After 5 days of intermittent heavy rain, you likely think it is wise to do so. Adaptive decision-making in such an environment critically depends on learning from outcomes to reduce uncertainty about environmental states. Now compare this to the decision whether to gamble on the toss of a fair coin with known probabilities of 50% for each possible—but still uncertain—outcome. If you observe 5 “heads” in a row, this may be surprising, but adaptive decision-making requires here to

disregard these outcomes since they do not provide any new information on the a priori known probabilities.

These examples demonstrate that optimal decision-making requires taking into account the nature of uncertainty. Leaving aside differences in autocorrelation (which is typically given for weather but not for random coin tosses), the first example (weather) describes a type of uncertainty often termed “ambiguity”, referring to uncertain outcomes with probabilities that are unknown due to imprecise beliefs about the state of the environment (also referred to as “estimation uncertainty”), whereas the second example (coin toss) illustrates another type of uncertainty often termed “risk”, referring to uncertain outcomes with known probabilities—a long-standing distinction in the decision-making literature (Knight 1921;

Ellsberg 1961; Payzan-LeNestour and Bossaerts 2011). While the observation of outcomes provides critical new information to resolve ambiguity by informing a probability estimate, risk cannot be reduced by such observations.

There is growing evidence that humans are sensitive to the nature of uncertainty. For instance, a recent study reported that people typically take the reducibility of uncertainty into account when updating their beliefs after being presented with new information (Kobayashi and Hsu 2017). More specifically, participants only updated subjective values of ambiguous gambles when ambiguity is reduced, but did not update values of risky gambles—a pattern that closely matched the quantitative predictions of an optimal Bayesian model of belief formation and valuation. This study showed further that neural activity in lateral frontoparietal regions such as the dorsolateral prefrontal cortex (dlPFC) tracked belief updating, in line with other reports (Gläscher et al. 2010; Nour et al. 2018; Tomov et al. 2018). Within this frontoparietal network, the right dlPFC might be particularly linked to ambiguity resolution, since its activity was found to track individual preferences for ambiguity, in contrast to the left dlPFC and parietal regions (Huettel et al. 2006). Furthermore, the reducibility of uncertainty modulates the functional connectivity of these belief-updating regions with value-updating regions such as the ventromedial prefrontal cortex (vmPFC), consistent with enhanced interregional communication under ambiguity resolution relative to risk (Kobayashi and Hsu 2017). Together, these data suggest a model postulating that context-dependent value updating results from an interaction of belief-updating processes with valuation processes, in which the right dlPFC is assumed to play a key role.

This model, however, is built on neuroimaging evidence that is correlational by nature and provides thus no information about the “causal” contribution of a brain area to a process. Insights into causal brain-behavior relationships come from brain stimulation techniques, such as transcranial direct current stimulation (tDCS). tDCS is a method for noninvasive stimulation of the human brain by means of weak electric currents (Nitsche et al. 2008) that has already been successfully used for demonstrating the causal involvement of specific brain areas in decision processes (Ruff et al. 2013; Bogdanov et al. 2017). The primary aim of the present study was to leverage tDCS to investigate whether the right dlPFC—which has been repeatedly suggested as a neural correlate of belief updating (Gläscher et al. 2010; Nour et al. 2018; Tomov et al. 2018) that is sensitive to the reducibility of uncertainty (Kobayashi and Hsu 2017)—is causally involved in belief updating under uncertainty.

Previous research found that while anodal tDCS reliably enhances dlPFC activity, inhibitory effects via cathodal stimulation are less robust (Kincses et al. 2004; Jacobson et al. 2012). One potential inhibitor of dlPFC functioning is stress, mediated through the action of catecholamines and glucocorticoids (Arnsten 2009; Qin et al. 2009; Schwabe and Wolf 2013; Bogdanov and Schwabe 2016). Whether stress modulates belief updating under uncertainty, however, is currently unknown. Thus, a secondary aim of the present study was to test whether stress or the stress hormone cortisol interfere with belief updating.

To investigate the causal role of the right dlPFC in belief updating under uncertainty, we applied anodal vs. sham tDCS over the right dlPFC, while human participants performed a belief-updating task (adapted from Kobayashi and Hsu 2017). To investigate the influence of stress, participants underwent a stress manipulation [Socially Evaluated Cold Pressor Test (SECT); Schwabe et al. 2008] or a control condition [Warm Water

Test (WWT)] prior to the belief-updating task (Fig. 1A). Both the tDCS- and the stress manipulation were implemented within a fully-crossed between-subjects design. The belief-updating task allowed us to measure monetary value updating when belief updating was normative (under ambiguity) and when it was not (under risk) from a Bayesian perspective. By leveraging a model-based analysis, we also assessed the degree of Bayesian rationality and whether observed effects could be explained by belief updating or possibly by non-normative effects of mere surprise or expectancy violation, which can be dissociated from belief updating given the task structure and at a neural level (Kobayashi and Hsu 2017).

Based on the postulated causal role of the dlPFC, we hypothesized that stimulation over the right dlPFC would lead to increased belief updating, which translates into stronger value updating when normatively expected (i.e., when ambiguity is reduced and payoff-relevant), but possibly also when normatively not expected (e.g., when updating refers to risk-related and thus payoff-irrelevant information; see Fig. 1B). With respect to stress, we hypothesized impaired belief updating, resulting either in reduced value updating, or, alternatively, in value updating in both normative and non-normative contexts due to a reduced sensitivity to the nature of uncertainty. We also hypothesized that tDCS-induced enhancements in belief updating would (at least partially) counteract potential stress-induced reductions in belief updating. Besides theoretical implications, such a pattern might point to an interesting clinical avenue to prevent stress-induced impairments by neurostimulation.

Materials and Methods

Participants

A total of 105 right-handed volunteers [50 women, 55 men; mean (*M*) age \pm standard deviation (SD): 26.06 \pm 4.97 years] participated in this experiment. Exclusion criteria for participation were checked in a standardized phone interview prior to the experiment and included current physical or mental conditions, substantial under- or overweight [body mass index (BMI) <18.5 or >28.5], medication or drug intake, smoking, hormonal contraception, pregnancy or lactation in women, a life-time history of any neurological or psychiatric disorder as well as any contraindications for tDCS such as metal implants or a history of epilepsy. Furthermore, participants were asked to refrain from physical exercise, meals and caffeine intake within the 2 h before testing.

Fourteen participants had to be excluded from the analysis due to unreliable tDCS (high impedance or repeatedly disconnected cables; *N* = 10), severe problems in task understanding (*N* = 1), clinically relevant depression scores (Beck Depression Inventory score > 30; *N* = 2), and extreme heart rate (*N* = 1 with >100 bpm) at baseline (*Z* = 3.91) as well as pre-task (*Z* = 3.76), thus resulting in a final sample of 91 participants (45 women, 46 men; mean age \pm SD: 26.08 \pm 5.08 years). When including the outliers with high depression scores and tachycardia, our pattern of results remained largely unaffected.

All participants gave written informed consent before the start of testing and received a compensation of 30 Euros plus a possible bonus in the belief-updating task. The study protocol was in line with the Declaration of Helsinki and approved by the ethics committee of the Faculty of Psychology and Human Movement Science of the Universität Hamburg.

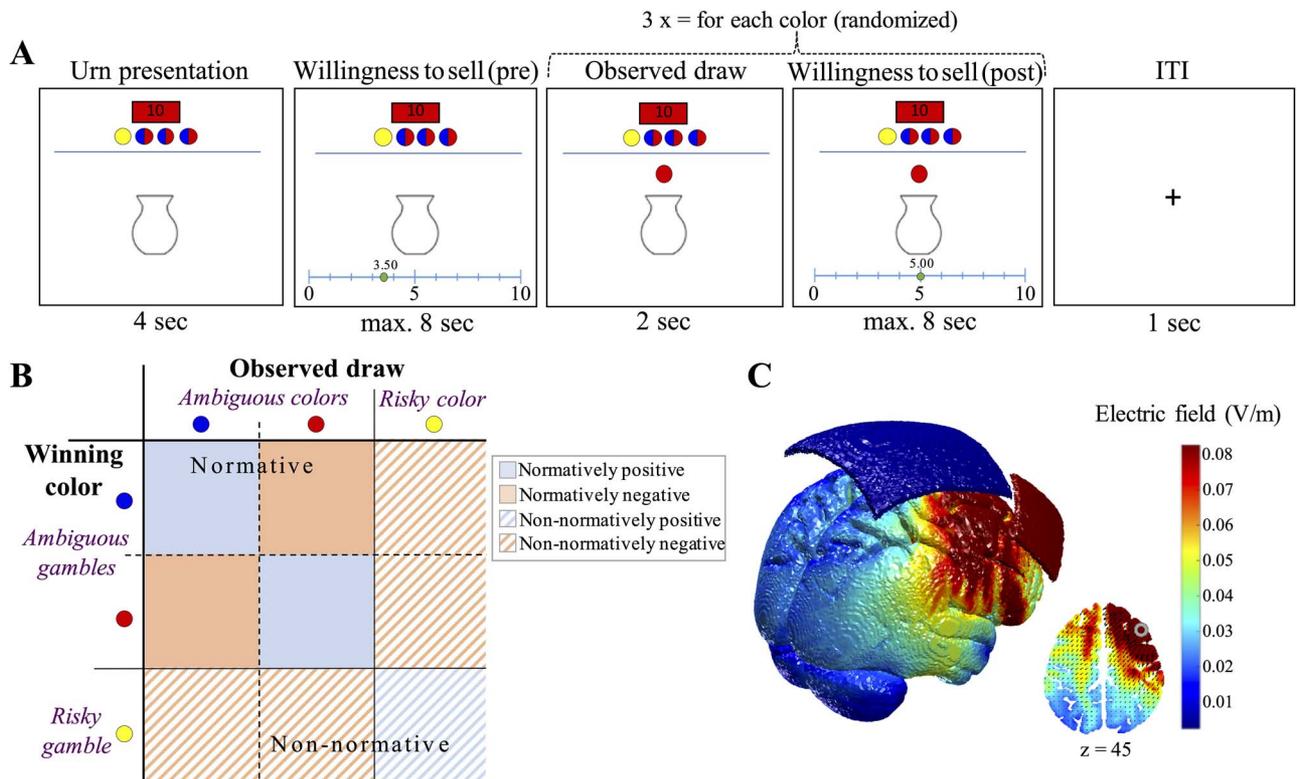


Figure 1. Illustration of the experimental design and tDCS. (A) Belief-updating task. In each trial, participants were presented an urn containing a number of balls of known color (yellow = risky color) and unknown color (blue or red = ambiguous colors) as well as the winning color above the urn. Participants could win €10 if a resolution draw (after the experiment) matched the winning color, and nothing otherwise. They then indicated the subjective value of the given urn gamble, reflected in their willingness to sell (WTS), before they observed draws in each of the three colors, which gave them partial information on the content of the gamble and which should be treated as independent observations. After each observed draw, they again indicated the subjective value of the urn. (B) Categorical combinations of winning colors and observed-draw colors with predictions of positive and negative value updating from a normative and non-normative perspective. Normatively, positive (negative) value updating was only expected after beliefs have been updated following a match (mismatch) in ambiguous-draw and winning color, while zero updating was expected in the other categories. Possible deviations from normativity could be positive value updating when an observed risky-color draw matches the winning color and negative value updating due to color mismatches in the remaining non-normative categories. (C) Electrode positions [anode: F4 (red), cathode: Cz (blue)] and simulated electric field distribution across the brain (see Materials and Methods). The small gray circle in the slice view highlights cortical tissue belonging to the right dlPFC (Brodmann area 8) beneath electrode position F4, with MNI coordinates derived through stereotactic neuronavigation in a previous study (Herwig et al. 2003).

Experimental Design

We used a sham-controlled, fully-crossed between-subjects design with the factors “tDCS condition” (anodal vs. sham tDCS over the right dlPFC) and “stress condition” (SECPT vs. WWT), resulting in four experimental groups to which participants were randomly assigned [sham tDCS/WWT: $N = 21$ (10 women, 11 men), sham tDCS/SECPT: $N = 23$ (12 women, 11 men), anodal tDCS/WWT: $N = 24$ (12 women, 12 men), anodal tDCS/SECPT: $N = 23$ (11 women, 12 men)]. We chose a between-subject over a within-subject design in order to exclude potential sequence or spillover effects.

Transcranial Direct Current Stimulation

The transcranial direct current stimulation (tDCS) manipulation was implemented in a double-blind, sham-controlled procedure using a NeuroConn DC-stimulator (neuroCare Group GmbH). We applied stimulation over the right dlPFC given its involvement in belief updating (Gläscher et al. 2010; Kobayashi and Hsu 2017; Nour et al. 2018; Tomov et al. 2018). In line with previous tDCS studies that targeted the dlPFC (Axelrod et al. 2015; Pope et al. 2015; Bogdanov and Schwabe 2016), we used an EEG cap tailored to head size and the international 10–20 system to

determine electrode positions individually for each participant. A smaller electrode ($5 \times 5 \text{ cm} = 25 \text{ cm}^2$), which served as the anode, was positioned over the right dlPFC (position F4). A larger electrode ($10 \times 10 \text{ cm} = 100 \text{ cm}^2$) was placed centrally on the vertex (position Cz). For an illustration of electrode placement, see Figure 1C.

Different electrode sizes were deliberately chosen so that a more focused and functionally more effective current density was applied over the dlPFC, while cathodal effects were spread over a larger region of the brain and thereby minimized in magnitude (Nitsche et al. 2007; Bogdanov et al. 2017). We applied a current of 1.075 mA for active stimulation. This results in a current density of 0.043 mA/cm^2 for the anode over the right dlPFC and 0.011 mA/cm^2 for the cathode over the vertex, making it much less likely for the larger vertex electrode to induce functional effects on the underlying neural tissue. To better understand the presumed electric field distribution of the used electrode montage, we used the software package ROAST, or Realistic vOlumentric-Approach to Simulate Transcranial electric stimulation (Huang et al. 2019). We used the validated default settings and a T1 image of the sixth-generation MNI-152 head to build a model of the electric field in the brain (Fig. 1C). While this estimation needs to be interpreted with

caution, given individual variability in brain structure and non-neural tissues, it serves as an approximation for the effective electric field distribution in our participants. The estimation results indicate that the electric field in the right dlPFC was substantially modulated [0.116 V/m at the cortical MNI coordinates below electrode position F4 ($x = 39$, $y = 24$, $z = 45$; Herwig et al. 2003)], although areas adjacent to the right dlPFC were likely also stimulated to a degree diminishing with distance. The right dlPFC was stimulated to a substantially stronger degree relative to more distant regions. These include the right intraparietal sulcus that has also been found to track belief updating [0.045 V/m at the reported peak ($x = 30$, $y = -40$, $z = 49$), 38.39% relative magnitude] and the right insula that has been found to track expectancy violation [0.043 V/m at the reported peak ($x = 30$, $y = 20$, $z = -8$), 37.42% relative magnitude] in a previous study (Kobayashi and Hsu 2017). Hence, a functionally effective modulation of brain activity in those areas was considerably less likely or weaker.

A conductive paste (Ten20, Weaver and Company) was used to improve conductivity and to reduce skin irritation. Using a paste rather than a more quickly evaporating sodium-chloride solution, which is a frequent alternative in tDCS studies, allowed for montage prior to the stress manipulation, which was essential given the experimental sequence (see Procedure). Brain stimulation was started with the onset of the task and stopped once the participant had finished the task. The current was applied with an 8-s fade-in and a 5-s fade-out-window at the beginning and the end of the stimulation.

In the sham condition, the initial fade-in-period was immediately followed by the fade-out-period. Subsequently, no current was delivered in the sham condition. This is a common procedure to prevent participants from explicitly understanding to which experimental condition they had been assigned to (Nitsche et al. 2008). The tDCS condition was double-blinded, that is, both the participant and the experimenter were unaware of the experimental condition implemented via the use of pre-programmed codes of the NeuroConn stimulator, which were communicated to the experimenter (trained student assistant) by the first author prior to the experiment.

Stress Manipulation

Participants underwent either the Socially Evaluated Cold Pressor Test (SECPT) or a non-stressful control procedure (Schwabe et al. 2008; Schwabe and Schächinger 2018). The SECPT is a standardized and well-validated laboratory stressor for humans, known to elicit a sympathetic stress response as well as glucocorticoid secretion via the hypothalamo-pituitary-adrenal (HPA) axis. In the SECPT, participants were asked to immerse their right hand including the wrist into ice water (0–2 °C) for up to 3 min (or until they could no longer tolerate it), while they were videotaped and continuously monitored and evaluated by a rather cold, non-reinforcing, and unfamiliar experimenter (different from the experimenter that performed the rest of the experimental procedure). In the control condition [Warm Water Task (WWT)], participants immersed their right hand in warm water (35–37 °C) and were neither videotaped nor monitored, and the experimenter that performed the rest of the experimental procedure also ran the WWT. As a consequence, the experimenter that administered the belief-updating task was not blind to the stress condition. Potential experimenter effects were minimized by using written instructions.

To assess whether the stress manipulation was successful and to determine the individual stress reactivity, measurements of subjective and physiological stress parameters were taken at several time points across the experiment. More specifically, immediately after the stress/control manipulation, participants rated the stressfulness, unpleasantness, difficulty, and painfulness of the SECPT/WWT on a scale from 0 (“not at all”) to 100 (“very much”). In addition, as indicators of sympathetic nervous system activity, blood pressure and pulse were measured using a Dinamap system (Critikon Inc.) before, during, and at several time points after the stress/control manipulation (see Procedure). To assess stress-induced changes in cortisol concentrations, saliva samples were collected from participants at several time points before and after the stress/control manipulation using Salivette collection devices (Sarstedt). Saliva samples were stored at –18 °C and analyzed for cortisol concentrations using a luminescence assay (IBL International) at the end of data collection. Seven subjects had at least one missing cortisol sample, slightly reducing the effective sample size for those analyses that took this stress parameter into account.

Belief-Updating Task

To investigate the effects of tDCS over the right dlPFC and of stress on belief and value updating, we adapted an incentivized (i.e., non-hypothetical) decision-making task that was recently introduced (Kobayashi and Hsu 2017). Participants were presented with several gambles, each consisting of a different number of balls in an urn (see Supplementary Table 1 for urn variants). In each gamble trial, participants knew the exact number of yellow balls (hereafter the “risky color”), but did not know whether the remaining balls were red or blue (“ambiguous colors”). For instance, one particular urn contained four balls—one yellow ball and three in either red or blue (Fig. 1A). Assignment of the colors to the uncertainty domains (i.e., red/blue = ambiguous, yellow = risky) was fixed (for a control analysis of potential color biases, see Supplementary Text 1). The monetary payoff of the gamble was determined by a resolution draw from the urn, after which participants could win €10 if the ball drawn matched a predetermined winning color displayed on top of the urn (e.g., red in Fig. 1A), and nothing otherwise. We call a gamble “ambiguous” when its winning color was one of the ambiguous colors (red or blue), and “risky” when the winning color was the risky color (yellow). Resolution draws and thus monetary outcomes were not revealed before the end of the experiment to prevent outcomes to affect subsequent decision processes.

To assess to what extent participants updated their beliefs and subjective monetary values following environmental signals that either reduce or do not reduce uncertainty, they observed additional ball draws prior to the resolution draw. In each of these observed draws, the subject was presented the color of one ball in the urn before it is returned to the urn. Since participants did not know the composition of ambiguous-color balls (i.e., red and blue balls) in the urn, a draw of an ambiguous-color ball, but not a draw of a risky-color ball (yellow), should have resulted in belief updating if participants rationally integrated prior knowledge about uncertainty with the color of the observed draw (Fig. 1B). In our exemplar urn (Fig. 1A), a red draw normatively updates beliefs because it reveals that the urn holds at least one red ball, increasing the probability of a resolution draw in red, but at the same time decreasing the probability of a resolution draw in blue. On the

other hand, a yellow draw does not carry any new information, because it is already known that the urn contains one yellow ball (for mathematic details on the updating process, see Bayesian Modeling below and the example in [Supplementary Fig. 1](#)). Moreover, from a normative point of view, subjective values should be updated as a consequence of belief updating only in ambiguous gambles, but not in risky gambles, because the probability of a yellow draw is fully specified and unaffected by the observed draw ([Fig. 1B](#)). Subjective values of the gambles were elicited before as well as after the observed draws as willingness to sell (WTS), that is, the amount of money subjects were willing to give up for the opportunity to gamble. A standard Becker-DeGroot-Marschak (BDM) bidding procedure was used ([Becker et al. 1964](#)), in which one randomly chosen gamble was given a randomly determined price at the end of the experiment (uniform distribution between €0 and €10), and participants sold the gamble for its price only if it exceeded their WTS.

In total, 18 gambles were presented in randomized order [6 urn contents ([Supplementary Table 1](#)) × 3 winning colors]. For each gamble, participants indicated their predraw WTS on a slider ranging from €0 to €10 in steps of €0.5 within 8 s, and then draws in red, blue, and yellow (observed draws) were presented in a randomized order ([Fig. 1A](#)). Crucially, participants were carefully instructed to treat each observed draw *independently*. In other words, the three observed draws did not represent incremental information on the urn content but should be regarded as distinct as-if changes in urn content. For instance, a blue ball in the first draw does not mean that—in the course of the second draw—it is now sure that one of the ambiguous balls is now definitely blue (but that it is again ambiguous prior to the next draw). We ran a control analysis to assess potential effects of draw order, which would indicate a non-independent treatment of draws, but found no indication of such an effect ([Supplementary Text 2](#)). After each observed draw, a postdraw WTS was assessed. Thus, four WTSs were obtained in each gamble (1 predraw, 3 postdraw). Hence, 54 postdraw values (and thus pre-post changes) were measured per participant (18 gambles × 3 observed draws)—reflecting effectively 54 (sub)trials. The decision experiment was written in Matlab R2015a (Mathworks) using the Psychtoolbox (3.0.12).

Procedure

Prior to the experiment, participants completed an online survey (implemented via the SosciSurvey platform; [Leiner 2020](#)) at home, which included demographic questions and German versions of the Beck Depression Inventory (BDI; [Hautzinger et al. 2006](#)) and the Trier Inventory of Chronic Stress (TICS; [Schulz and Schlotz 1999](#)).

All experimental sessions took place in the afternoon (12:00–19:00) to control for the diurnal rhythm of cortisol ([Edwards et al. 2001](#)). Upon participants' arrival at the laboratory and their informed consent, the tDCS electrodes were mounted. Subsequently, participants provided a baseline saliva sample and blood pressure as well as pulse were measured. Participants were then instructed to the belief-updating task and underwent the SECPT or control manipulation. To assess stress reactivity, the subjective feeling state was assessed after the stress manipulation and physiological parameters were repeatedly assessed over the course of the experiment (saliva samples at –35, +5, +15, +25, +43, and +54 min relative to stressor/control onset; sympathetic measures at –35, +1, +5, +15, +25, +43, and +54 min). After the stress manipulation, participants

completed three other tasks (Trust Game, Implicit Association Test, and a reinforcement learning task) that were not related to the current research question. Importantly, all task procedures and task order were kept constant across experimental conditions and none of the other tasks was performed under tDCS. Forty-five minutes after the onset of the stressor/control manipulation, when stress-induced cortisol should be significantly elevated, participants were informed that tDCS would be initiated and the belief-updating task started.

Data Analysis

To examine the effectiveness of the stress manipulation, we tested for a difference in ratings of subjective feeling states after the stress manipulation between the stress and control group using t-tests for independent samples. Physiological stress parameters were analyzed using a mixed-design GLM (General Linear Model) with “time” point of measurement as within-subject factor and stress condition and tDCS condition as between-subjects factors.

Monetary value updating served as a proxy for belief updating, as it is a consequence of updated beliefs ([Kobayashi and Hsu 2017](#)) and because (latent) belief updating cannot be directly assessed with choice data alone. Value updating was assessed by 1) calculating the trial-wise difference between predraw and postdraw subjective values (i.e., postdraw WTS—pre draw WTS), and 2) categorizing and averaging these differences according to the prediction of their valence from a normative or non-normative perspective. Trials with missing responses and with response times <200 ms were discarded from analysis (0.55% of all subjective values; max. 5.56% per participant).

We report nine statistical models on value updating: In a first GLM (model 1), we investigated whether participants that did not undergo tDCS or a stress manipulation displayed sensitivity to the nature of uncertainty. To this end, we classified trials according to whether positive, negative, or zero value updating was normatively predicted (within-subject factor “category”) given a specific draw and winning color (see [Fig. 1B](#)), in line with [Kobayashi and Hsu \(2017\)](#). Value updating (i.e., postdraw value—pre draw value) served as the dependent variable.

In a second GLM (model 2), we investigated the effects of tDCS over the right dlPFC and of stress on value updating. Since we hypothesized that participants would deviate from rationality and possibly also update values when not normatively predicted, we dropped here the zero-updating category from the previous model and differentiated between the following trial categories: 1) trials in which participants potentially display non-normatively positive value updating when they observe a color match in a risky gamble (i.e., yellow ball given yellow as winning color), and 2) trials in which participants potentially display non-normatively negative value updating when they observe a color mismatch in risky gambles (i.e., red or blue ball given yellow as winning color) or a color mismatch in ambiguous gambles due to a risky (yellow) draw (see [Fig. 1B](#)). Together, this resulted in a mixed-design model with the two within-subject factors “normativity” (normative vs. non-normative) and “valence” (positive vs. negative) and the between-subjects factors tDCS condition and stress condition. Furthermore, to detect modulations common to both positive and negative value updating and to directly compare the degree of both, we flipped the sign of value updates in the (normatively and non-normatively) negative categories so that larger values in both the

positive and negative categories reflect stronger value updating in the expected direction. Notably, expected valence was still kept as a factor in the model to detect potential valence-specific effects.

To assess updating more formally, we explicitly compared participants' value updates with those predicted by a Bayesian cognitive model of belief and value updating (see Bayesian Modeling below) in another statistical model (model 3). This model-based analysis allows testing the degree of rationality reflected in participants' decisions from a Bayesian perspective, which is the predominant notion of rationality in economics and decision theory (Mas-Colell et al. 2005) as well as a model for human information processing (Knill and Pouget 2004; Behrens et al. 2007). More specifically, we calculated the deviation of observed value updating from the model-based predictions per urn variant and per subject and subjected the mean deviations to a mixed-design GLM with the within-subject factors "normativity" and "valence" and the group factors tDCS as well as stress condition. The sign of the deviations for the negative categories was again flipped for this model, but not in follow-up one-sample t-tests that assessed deviations for individual trial categories.

Another model-based analysis (models 4–8) was used to gain more insight into the potential underlying mechanisms that mediated (changes in) value updating. Specifically, while value updating is driven by belief updating from a normative perspective, expectancy violation might alter valuation in a non-normative manner. A separation of these two factors by design allowed us to regress both the degree of belief updating and of expectancy violation predicted by the Bayesian model on value updating (see Supplementary Table 1 for urn-wise predictions). Mixed models with subjects as random effects and urn-wise belief updating and expectancy violation as predictors were fitted separately for those trial categories in which beliefs should have been updated (i.e., ambiguous draws in ambiguous gambles in the same color [normatively positive], in different color [normatively negative], and ambiguous draws in risky gambles [non-normatively negative]). Other models that included expectancy violation but not belief updating were fitted for risky draws in risky gambles as well as for risky draws in ambiguous gambles, given that no belief updating was normatively expected in these categories. Furthermore, tDCS condition and its interactions with belief updating and expectancy violation were assessed as predictors of value updating. For each trial category, we fitted several models varying in the number of predictors using maximum likelihood estimation (MLE) and formally compared their fit to the data using the Bayesian Information Criterion (BIC; see Supplementary Table 2 for model variants and fits). In the Results section, we report the best-fitting model for each trial category.

In addition to these group-based analyses with respect to tDCS and stress, we also analyzed the association between individual levels of the stress hormone cortisol and value updating. More specifically, we included baseline-to-peak changes in cortisol across groups as a covariate instead of the group factor stress condition in another GLM (model 9) with otherwise identical factors as in model 2. Cortisol effects on value updating were further investigated with bivariate correlations.

Apart from value updating, we also tested for the effect of tDCS condition and stress condition on baseline risk and ambiguity taking, expressed in predraw subjective values, in a two-way GLM. We also assessed whether effects on value updating could be explained by altered baseline risk or ambiguity taking,

expressed in predraw WTS, by adding their mean values as a covariate in the models above as well as by assessing the influence of urn-wise predraw WTS in mixed models (see Supplementary Text 3). Furthermore, we examined whether there were any group differences in several control variables (age, chronic stress, depression, BMI).

Behavioral data were analyzed using Matlab R2018a (Mathworks) and SPSS 22 (IBM). The significance level was set at $P \leq 0.05$. Significant main or interaction effects were pursued by appropriate post-hoc tests if indicated. Significant effects in post-hoc tests survived a Bonferroni-Holm correction for multiple comparisons, unless explicitly labeled via an uncorrected P-value [i.e., "P (uncorrected)"]. In the case of violations of sphericity, Greenhouse-Geisser correction was applied. All reported P-values are two-tailed. Effect sizes are expressed as partial eta-squared (η_p^2) and Pearson correlation coefficients (r). Per convention, effect sizes η_p^2 of 0.01, 0.06, and 0.14, and r of 0.1, 0.3, and 0.5 are considered small, medium, and large effects, respectively (Cohen 1988).

Post-hoc power analyses using the program G*Power (Version 3.1; Faul et al. 2009) revealed that our final sample ($N = 91$) allowed for the detection of medium-sized (i.e., $\eta_p^2 > 0.05$) main effects of tDCS or stress with sufficient statistical power (> 0.80).

Bayesian Modeling

A quantitative Bayesian model adopted from Kobayashi and Hsu (2017) served both as a model of participants' decision processes and as a benchmark for normative decision-making. This cognitive model formalizes two stages, belief formation and valuation. The belief-formation stage models the probability distribution of a future draw's color based on which a rational decision maker would decide. The probability of a future draw in the risky color can be straightforwardly specified as $n_r / (n_r + n_a)$ where n_r is the number of balls in the risky color and n_a is the number of ambiguous balls. However, the probabilities of a future draw in the ambiguous colors cannot, since the number of balls in each ambiguous color was unknown. To generate their unique point estimates, all possible urn contents need to be considered, weighted according to their probability, and averaged. Specifically, we assumed that prior probability P_{pre} (i.e., probability before a potential update after observed draws) over urn contents followed a binomial distribution, that is, the number of balls in one of the ambiguous colors n_{a1} followed

$$P_{pre}(n_{a1}) = \frac{1}{2^{n_a}} \binom{n_a}{n_{a1}}.$$

The probability of a future draw in one ambiguous color can then be obtained as:

$$P_{pre}(a1) = \sum_{n_{a1}=0}^{n_a} P_{pre}(n_{a1}) \cdot n_{a1} / (n_r + n_a).$$

After the observed draw, model-based beliefs were updated according to Bayes' rule: If the observed draw is in one ambiguous color $a1$ (e.g., red), then the posterior probability

$$P_{post}(n_{a1}) = \frac{1}{2^{n_a-1}} \binom{n_a-1}{n_{a1}-1};$$

if the observed draw is the other ambiguous color (e.g., blue), then the posterior probability of the first ambiguous color (i.e., red)

$$P_{\text{post}}(n_{a1}) = \frac{1}{2^{n_a-1}} \binom{n_a-1}{n_{a1}};$$

if the observed draw is in the risky color (i.e., yellow), no belief updating occurs from a normative perspective, that is,

$$P_{\text{post}}(n_{a1}) = P_{\text{pre}}(n_{a1}).$$

For an illustration of the belief-formation process and updating following ambiguous and risky draws in the example urn (Fig. 1A), see [Supplementary Figure 1](#).

In the valuation stage, predraw and postdraw values of gambles were calculated as expected value $EV = 10 \cdot P_w$, where P_w is the probability of the winning color that is multiplied with the possible gain of €10. Normatively, values should only be updated following updates in beliefs, but not following expectancy violation, calculated as $1 - P_{\text{drawcolor}}$, and which is dissociable from belief updating by design (i.e., $r = 0$ across urns within trial categories) and at a neural level ([Kobayashi and Hsu 2017](#)). For a list of the Bayesian-optimal belief- and value updates and expectancy violation per urn variant and gamble- and draw category, see [Supplementary Table 1](#).

Interestingly, this Bayesian account is mathematically equivalent to a more heuristic account, which only considers “effective” urn content (for the mathematical proof, see [Supplementary Material in Kobayashi and Hsu 2017](#)). Under this heuristic, each ambiguous ball is treated as a pair of half (0.5) balls, each half corresponding to one of the two ambiguous colors—identical to the visual representation of the urn content. When an ambiguous-color draw is observed, one of such pairs is replaced with a full ball in the draw’s color. Although we cannot distinguish between a full Bayesian and this heuristic account, in both cases, a match of behavioral observations to their predictions would reflect sensitivity to the (manipulated) reducibility of uncertainty. Notably, this mathematical equivalence only holds for the use of binomial priors. [Kobayashi and Hsu \(2017\)](#) also tested uniform priors and their findings were robust to this alteration, but also found that binomial priors outperformed uniform ones in predicting values and value updates.

Results

Subjective and Physiological Stress Responses

As expected, the SECPT was experienced as significantly more stressful, unpleasant, difficult and painful than the control condition (all $P < 0.001$).

The SECPT also induced profound sympathetic arousal, as indicated by an increase in systolic and diastolic blood pressure as well as pulse in response to the SECPT compared to the control condition [see [Table 1](#); stress condition \times time interaction for systolic blood pressure: $F(4.92, 427.68) = 12.562$, $P < 0.001$, $\eta_p^2 = 0.126$; for diastolic blood pressure: $F(5.01, 435.78) = 16.613$, $P < 0.001$, $\eta_p^2 = 0.160$; for pulse: $F(4.2, 365.48) = 11.986$, $P < 0.001$, $\eta_p^2 = 0.121$], without any differences between the tDCS groups (all $P > 0.356$). Pairwise post-hoc comparisons revealed that systolic and diastolic blood pressure and pulse were significantly elevated during the SECPT relative to the control condition (all

$P < 0.001$), and systolic blood pressure also immediately after the SECPT [+5 min; $P = 0.044$ (uncorrected)], but not at other time points of measurement (all $P > 0.06$), as expected for a transient sympathetic activation.

For salivary cortisol, we did not observe significant increases in glucocorticoid activity after the SECPT, relative to the control condition [see [Table 1](#); stress condition \times time: $F(2.18, 174.78) = 0.674$, $P = 0.524$, $\eta_p^2 = 0.008$], and no main effect of stress condition [$F(1, 80) = 0.914$, $P = 0.342$, $\eta_p^2 = 0.011$], but a significant decline over time in both groups [$F(2.18, 174.78) = 9.578$, $P < 0.001$, $\eta_p^2 = 0.107$], consistent with the typical decline of cortisol levels over time in the afternoon ([Edwards et al. 2001](#)). There were no significant differences between tDCS groups (all $P > 0.408$). The cortisol responder rate (i.e., percentage of participants with a cortisol increase from baseline to +25-min peak of >2 nmol/L; [Schwabe et al. 2008](#)) was modest with 21.7% in the stress group and only by trend larger than in the control group [8.89%; $\chi(1) = 2.885$, $P = 0.089$], which could have been due to habituation to the SECPT experimenter who frequently had to assist with electrode montage (despite keeping the interaction to a minimum), and to the testing environment due to the relatively long preparation period. However, there was considerable interindividual variability in cortisol reactivity (min: -9.39 nmol/L, max: 16.18 nmol/L, range: 25.57 nmol/L).

Value Updating is Sensitive to the Reducibility of Uncertainty

As a first step in our analysis of the choice data, we analyzed whether participants who did neither undergo the anodal tDCS nor the stress manipulation (i.e., sham tDCS/WWT group, $N = 21$) were sensitive to the nature of uncertainty. To this end, we classified trials according to whether positive, negative, or zero value updating was normatively predicted given the draw and winning color (model 1; see [Materials and Methods](#) and [Fig. 1B](#)), in line with [Kobayashi and Hsu \(2017\)](#). We found significant differences in value updating across those categories [$F(1.36, 27.1) = 7.811$, $P = 0.005$, $\eta_p^2 = 0.281$; see [Fig. 2](#)]. Using one-sample t-tests, we found that value updating was significantly more negative than 0 in normatively-negative updating trials [$M = -0.78$ (SD = 0.81), $t(20) = -4.389$, $P < 0.001$, $\eta_p^2 = 0.187$], trend-wise more positive than 0 in normatively-positive trials [$M = 0.81$ (SD = 1.96), $t(20) = 1.882$, $P = 0.074$, $\eta_p^2 = 0.041$], but not significantly different from 0 in normatively-zero updating trials [$M = -0.037$ (SD = 0.64), $t(20) = -0.260$, $P = 0.797$, $\eta_p^2 < 0.001$]. Pairwise comparisons showed that updating was more negative in the normatively-negative category than in the normatively-zero category [$t(20) = -3.292$, $P = 0.004$, $\eta_p^2 = 0.114$], and there was by tendency a larger value updating in the normatively-positive category than in those trials were zero updating was expected [$t(20) = 1.866$, $P = 0.077$, $\eta_p^2 = 0.040$]. As expected, updating in the normatively-positive category was more positive than in the normatively-negative category [$t(20) = 3.318$, $P = 0.003$, $\eta_p^2 = 0.116$]. We also assessed whether the degree of value updating differed between those categories by flipping the sign of updating values of the negative category (as also done in [Fig. 2](#)) and did not observe significant differences [$t(20) = 0.062$, $P = 0.951$, $\eta_p^2 = 0.007$]. Hence, in line with [Kobayashi and Hsu \(2017\)](#), our data indicate that participants were generally sensitive to the nature of uncertainty and able to rationally update beliefs and subjective values.

Table 1 Stress parameters at different times of measurement (in minutes relative to stress-manipulation onset)

	Stress condition		Control condition	
	Mean	SD	Mean	SD
Subjective feelings (+5)				
Stressfulness	37.17**	27.46	5.33	15.02
Unpleasantness	46.74**	26.84	4.89	12.55
Difficulty	45.00**	29.80	7.56	17.86
Painfulness	55.43**	27.30	5.78	16.17
Systolic blood pressure				
−35 (baseline)	131.76	13.21	129.58	12.12
+1 (stress/control)	136.43**	15.42	119.80	13.15
+5	129.33*	13.36	124.09	10.94
+15	128.33	12.96	125.18	10.69
+25	126.67	13.06	125.07	11.58
+43 (pre-task)	128.57	13.50	127.33	11.89
+54 (post-task)	127.07	13.11	123.58	10.93
Diastolic blood pressure				
−35 (baseline)	75.91	9.05	75.76	10.22
+1 (stress/control)	81.04**	11.33	65.80	11.86
+5	73.65	8.28	72.49	10.32
+15	75.13	9.23	75.29	10.29
+25	75.17	10.21	75.22	11.62
+43 (pre-task)	76.43	8.52	74.42	12.05
+54 (post-task)	75.74	7.91	74.89	12.03
Pulse				
−35 (baseline)	74.35	11.86	69.93	10.34
+1 (stress/control)	77.02**	10.66	66.93	8.61
+5	68.67	10.18	68.76	9.14
+15	68.74	10.03	67.80	8.58
+25	68.70	9.92	67.07	9.19
+43 (pre-task)	67.87	9.85	66.11	9.53
+54 (post-task)	70.04	10.64	66.27	8.92
Cortisol				
−35 (baseline)	5.42	3.73	4.55	2.84
+5	4.82	3.80	4.53	2.29
+15	5.51	4.54	4.53	2.96
+25	5.86	5.61	4.44	3.62
+43 (pre-task)	4.30	3.95	3.82	2.73
+54 (post-task)	3.79	3.12	3.36	2.00

Statistically significant effects are already indicated by asterisks (and see table legend). Boldface was used for all means (also non-significant differences) to make them easier visible for readers (next to the standard deviations).

Note: Units of measurement: blood pressure: mmHG; pulse: beats per minute (bpm); cortisol: nmol/L.

*Significant group difference with $P < 0.05$ (uncorrected).

**Significant group difference with $P < 0.001$.

Anodal tDCS over the Right dlPFC Enhances Value Updating

In the next step, we analyzed the whole sample to investigate whether anodal tDCS over the right dlPFC or acute stress modulated value updating. To investigate potential deviations from normativity, we now categorized trials based on normatively and non-normatively positive and (sign-flipped) negative value updating (model 2; see also Materials and Methods and Fig. 1B).

As expected, and identical to our sham-tDCS/WWT subsample analysis, we obtained larger updating in trials in which it was normatively predicted relative to trials in which zero updating would be normative [main effect of normativity: $F(1.87) = 40.825, P < 0.001, \eta_p^2 = 0.319$]. Crucially, we also observed a significant and marginally medium-sized main effect of tDCS condition [$F(1.87) = 4.783, P = 0.031, \eta_p^2 = 0.052$], indicating larger value updating after anodal stimulation over the right dlPFC relative to sham stimulation (Fig. 3; for value updating

in all subcategories, see Supplementary Fig. 1). The tDCS-induced enhancement in value updating was independent of normativity [tDCS condition \times normativity: $F(1.87) = 0.002, P = 0.962, \eta_p^2 < 0.001$] and valence [tDCS condition \times valence: $F(1.87) = 0.770, P = 0.382, \eta_p^2 = 0.009$] or a combination of both [tDCS condition \times normativity \times valence: $F(1.87) = 0.488, P = 0.487, \eta_p^2 = 0.006$], indicating overall enhanced value updating. There were also no other differential effects regarding normativity (all $P > 0.189$) or valence (all $P > 0.108$). Across subjects, normative and non-normative updating was positively correlated [$r(89) = 0.605, P < 0.001$] as well as positive and (sign-flipped) negative updating [$r(89) = 0.366, P < 0.001$].

The effect of anodal tDCS was not modulated by stress [stress condition \times tDCS condition interaction: $F(1.87) = 0.051, P = 0.822, \eta_p^2 = 0.001$] and there was no main effect of stress condition on value updating [$F(1.87) = 0.154, P = 0.696, \eta_p^2 = 0.002$] nor any other stress-related interaction effect (all $P > 0.108$).

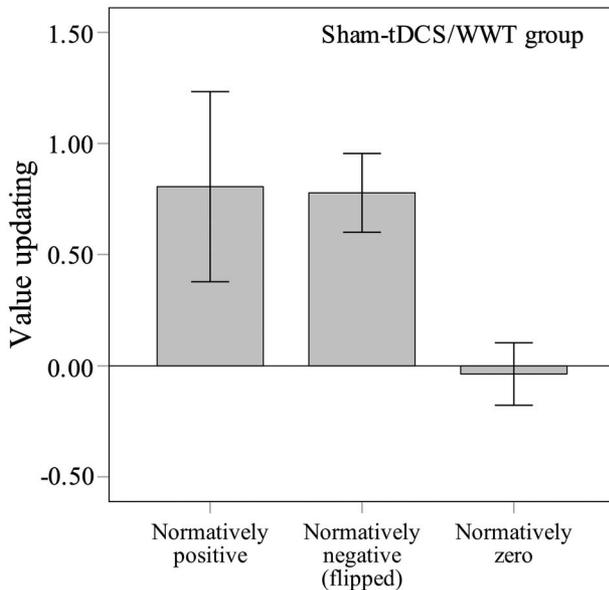


Figure 2. Sensitivity to the reducibility of uncertainty in the sham-tDCS/WWT subgroup ($N = 21$). Participants displayed positive and negative value updating when it was normatively predicted (i.e., when ambiguity was reduced), but zero updating when value updating was not normatively predicted (i.e., in the case of irreducible risk). The sign of the negative-valence category was flipped so that the degree of positive and negative updating can be compared more directly. Error bars represent standard errors of the mean (SEM) and include between-subject variability.

Model-Based Analysis Reveals Domains of Both Increased and Decreased Rationality after tDCS over the dlPFC

To evaluate whether anodal tDCS-induced enhancements of value updating reflected rational behavior more formally, we explicitly analyzed the deviations of participants' value updates from those predicted by an artificial rational Bayesian decision-maker (i.e., our Bayesian model of belief and value updating; see model 3 in Materials and Methods). **Figure 4** shows the mean deviations in the sham and anodal tDCS group, respectively.

Across groups, we found that deviations from Bayesian predictions (sign-flipped for predicted negative updating) were numerically more negative in normative compared to the deviations in non-normative trials [main effect of normativity: $F(1.87) = 105.264$, $P < 0.001$, $\eta_p^2 = 0.547$]. In **Figure 4**, in the top panels, right triangles *above* the 45° line (negative updates here not sign-flipped) and blue triangles *below* this line descriptively reflect less value updating than normatively expected, whereas cyan and magenta cycles deviating from the line at $x = 0$ in all panels descriptively reflect more updating than normatively expected. Hence, the main effect of normativity might be due to underweighting (relative to the Bayesian model) of new evidence in normative trials and overweighting of new evidence in non-normative trials. To interpret whether these deviations truly represented underweighting vs. overweighting of new evidence, however, one has to assess whether they significantly differ from the model predictions (i.e., from zero). Moreover, the degree of underweighting and overweighting was influenced by tDCS over the right dlPFC [main effect of tDCS: $F(1.87) = 4.678$, $P = 0.033$, $\eta_p^2 = 0.051$], consistent with

tDCS-induced enhancements in value updating reported above. Hence, one also has to take this group factor here into account.

For instance, albeit in the expected direction, the degree of updating in normative trials was smaller than normatively expected in the sham group, as indicated by significant deviations from the model-based predictions (i.e., deviations > 0 ; for negative updating here not sign-flipped) in one-sample t -tests [normatively-positive: $M = -0.80$ ($SD = 1.55$), $t(43) = -3.413$, $P = 0.001$, $\eta_p^2 = 0.062$; normatively-negative: $M = 0.75$ ($SD = 0.95$), $t(43) = 5.267$, $P < 0.001$, $\eta_p^2 = 0.136$; also see the deviations from the diagonal in the top left panel of **Fig. 4**]. Due to the tDCS-induced enhancement of value updating, however, the degree of normatively positive and negative value updating for ambiguous gambles more closely matched that predicted by the Bayesian model in the tDCS relative to the sham group, as can be seen in the top right panel of **Figure 4**. In other words, in contrast to updating in the sham group, observed value updating in the anodal tDCS group did not significantly differ from the model-based predictions [normatively-positive: $M = -0.42$ ($SD = 2.09$), $t(46) = -1.367$, $P = 0.178$, $\eta_p^2 = 0.010$; normatively-negative: $M = 0.27$ ($SD = 1.28$), $t(46) = 1.442$, $P = 0.156$, $\eta_p^2 = 0.012$].

There was no significant tDCS \times normativity interaction [$F(1.87) = 0.005$, $P = 0.943$, $\eta_p^2 < 0.001$], indicating that tDCS enhanced value updating and shifted deviation values similarly across normative and non-normative contexts. More specifically, in those trials in which zero updating was normatively expected, the sham group did mostly not deviate from the model-based prediction [risky draws in risky gambles: $M = 0.14$ ($SD = 1.31$), $t(43) = 0.698$, $P = 0.489$, $\eta_p^2 = 0.003$; risky draws in ambiguous gambles: $M = -0.04$ ($SD = 1.24$), $t(43) = -0.188$, $P = 0.852$, $\eta_p^2 < 0.001$; but some degree of negative updating after ambiguous draws in risky gambles: $M = -0.53$ ($SD = 1.32$), $t(43) = -2.652$, $P = 0.011$, $\eta_p^2 = 0.038$]. In contrast, the anodal tDCS group showed significant deviations from model-based predictions in all non-normative categories [risky draws in risky gambles: $M = 0.38$ ($SD = 1.18$), $t(46) = 2.203$, $P = 0.033$, $\eta_p^2 = 0.025$; risky draws in ambiguous gambles: $M = -0.37$ ($SD = 1.13$), $t(46) = -2.267$, $P = 0.028$, $\eta_p^2 = 0.027$; ambiguous draws in risky gambles: $M = -1.42$ ($SD = 2.21$), $t(46) = -4.413$, $P < 0.001$, $\eta_p^2 = 0.094$; see **Fig. 4**]. In other words, from a Bayesian perspective, tDCS-induced enhancements in rationality in the normative trials came at the cost of increased irrationality in trials in which zero updating would be normative.

There was no main effect of stress condition [$F(1.87) = 0.183$, $P = 0.70$, $\eta_p^2 = 0.002$], nor any interaction with tDCS (all $P > 0.101$), in line with our results above.

Normative Value Updating Is Driven by Belief Updating but Non-Normative Value Updating Is Driven by Expectancy Violation

From a Bayesian perspective, value updating should only be driven by belief updating that is sensitive to the nature of uncertainty (i.e., it should only result in value updating after ambiguous draws in ambiguous gambles, see also **Supplementary Table 1**). However, observed draws also violate prior expectations, independent of the nature of uncertainty, and this expectancy violation could theoretically also drive value updating in a non-normative way. To shed further light on these potential underlying mechanisms, we conducted an additional model-based analysis. Specifically, we fitted several models with varying numbers of regressors denoting belief updating or expectancy violation

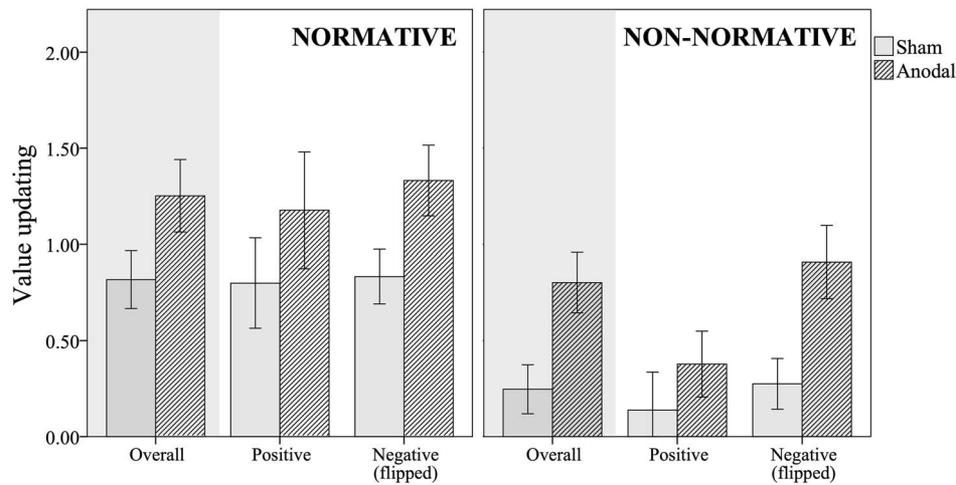


Figure 3. Value updating (collapsed and separately for valence categories) in the normative (left panel) and non-normative trials (right panel) in the two tDCS conditions. The sign of the negative-valence categories was flipped so that the degree of positive and negative updating can be compared more directly. After anodal relative to sham tDCS over the right dlPFC, value updating was overall enhanced. Error bars represent SEM and include between-subject variability.

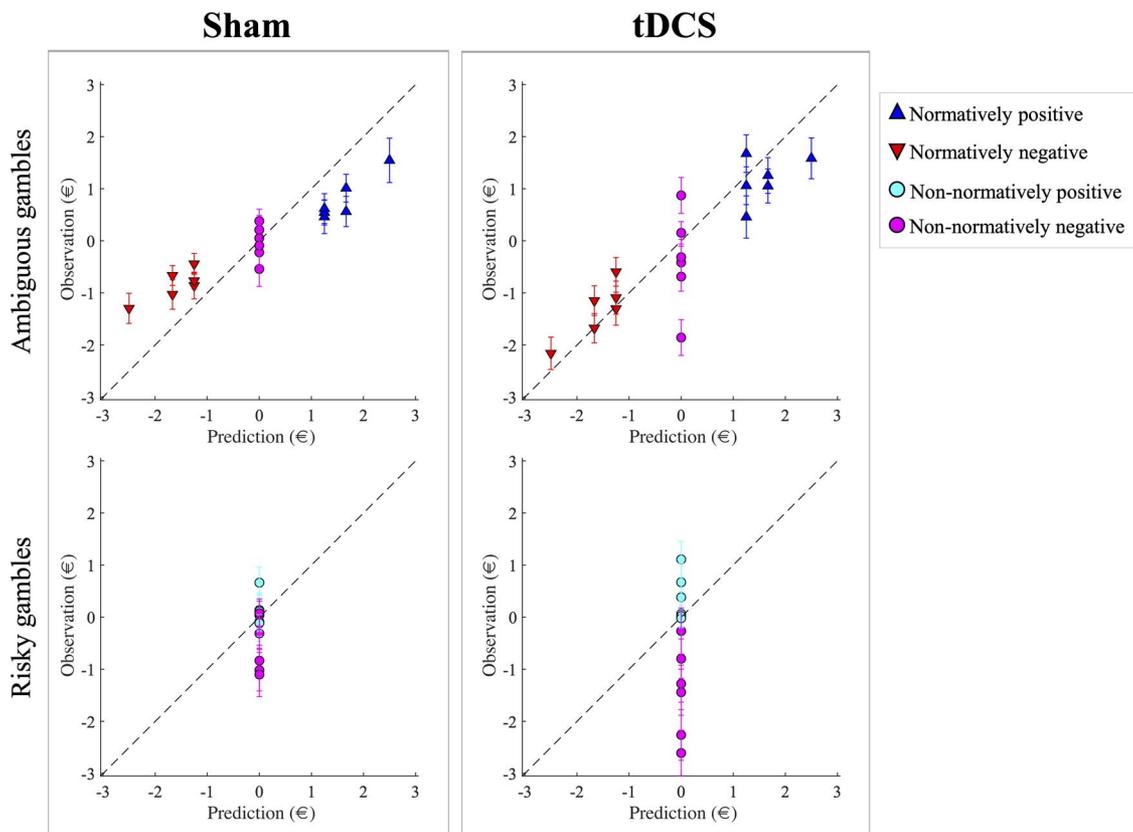


Figure 4. Comparison of observed and model-predicted value updating for each urn variant for the sham (left panels) and tDCS group (right panels) and for ambiguous (top panels) and risky gambles (bottom panels), color-coded with respect to normative and non-normative predictions. “Normatively positive” denotes color-congruent ambiguous draws in ambiguous gambles, “normatively negative” denotes color-incongruent ambiguous draws in ambiguous gambles, “non-normatively positive” denotes color-congruent risky draws in risky gambles, and “non-normatively negative” denotes color-incongruent risky draws in ambiguous gambles as well as ambiguous draws in risky gambles. Negative updates were here not sign-flipped. Error bars represent SEM and include between-subject variability.

as predicted by the Bayesian model, tDCS condition and interactions (see Materials and Methods and [Supplementary Table 2](#) for model variants and fits). In the following, we report the

best-fitting model for each trial category (models 4–8—not identical with the numbers of the best-fitting models in [Supplementary Table 2](#)).

Table 2 Best-fitting models (see [Supplementary Table 2](#) for all models and fits) on the influence of tDCS, belief updating, and expectancy violation on value updating in different trial categories (negative updates not sign-flipped)

	Coefficient	SE	Df	t-value	P-value
Ambiguous draws in ambiguous gambles—same color (normatively positive)					
Constant	0.28	0.36	262.15	0.765	0.445
tDCS	0.36	0.39	89	0.923	0.358
Belief updating	5.57	1.54	453.02	3.627	<0.001
Ambiguous draws in ambiguous gambles—different color (normatively negative)					
Constant	-0.17	0.30	469.39	-0.585	0.559
tDCS	-0.49	0.24	89	-2.039	0.044
Belief updating	-7.23	1.54	454	-4.681	<0.001
Ambiguous draws in risky gambles – (non-normatively negative)					
Constant	3.90	0.80	530.47	4.864	<0.001
tDCS	-0.91	0.38	91.12	-2.403	0.018
Expectancy violation	-7.11	1.01	453.20	-7.038	<0.001
Risky draws in risky gambles (non-normatively positive)					
Constant	-0.34	0.30	438.36	-1.104	0.270
tDCS	0.25	0.26	89.90	0.954	0.343
Expectancy violation	1.42	0.49	450.33	2.896	0.004
Risky draws in ambiguous gambles (non-normatively negative)					
Constant	1.87	0.34	517.01	5.524	<0.001
tDCS	1.10	0.49	517.01	2.273	0.023
Expectancy violation	-4.48	0.58	455	-7.686	<0.001
tDCS × expectancy violation	-2.89	0.84	455	-3.444	<0.001

Statistically significant effects are already indicated by asterisks (and see table legend). Boldface was used for all means (also non-significant differences) to make them easier visible for readers (next to the standard deviations).

Belief updating emerged as a significant predictor of value updating for ambiguous draws in ambiguous gambles (Table 2): Larger (model-predicted) belief updating was associated with a stronger degree of value updating, indicated by a positive slope for positive value updating and a negative slope for negative updating. For normatively-negative trials, we found significantly increased value updating in the tDCS relative to the sham condition, consistent with our previous findings. For normatively-positive trials, we found an effect in the same direction, though not significant. Adding a belief update × tDCS interaction (i.e., a tDCS-induced change in the slope) resulted in a worse model fit (see [Supplementary Table 2](#)) for both trial categories, indicating that the sensitivity to “changes” in belief updates was not modulated, and this interaction was also not significant in the worse-fitting full model. However, the significant tDCS main effect would be in line with a change in the overall “magnitude” of the true latent belief updates.

Interestingly, we observed an entirely different pattern in the non-normative domain. Again, we observed a significant tDCS effect in value updating after ambiguous draws in risky gambles, but instead of belief updating, expectancy violation emerged as a significant predictor (Table 2): Larger (model-predicted) expectancy violation predicted a stronger degree of value updating. Adding belief updating as a predictor resulted in a worse model fit (and was in no case significant), indicating that value updates did not follow belief updates as predicted by the Bayesian model. Furthermore, an expectancy violation × tDCS interaction resulted in a worse model fit, indicating that the sensitivity to “changes” in expectancy violation was not modulated (and the interaction was also not significant in a full model). We also found that expectancy violation predicted value updating in the remaining non-normative categories in which no belief updating (but also no value updating) was

normatively expected, that is, following risky draws in risky gambles and risky draws in ambiguous gambles. The best-fitting models again indicated that expectancy violation predicted non-normative value updating. For risky draws in ambiguous gambles, tDCS also increased the sensitivity to “changes” in predicted expectancy violation, indicated by a significant tDCS × expectancy violation interaction. Together, these results indicate that non-normative value updating in general as well as tDCS-induced changes of value updating in particular might have been driven by expectancy violation rather than by belief updating, which appeared the driving force in those trials in which belief- and value updating were normatively expected.

Notably, the effect of expectancy violation in non-normative updating might also explain why negative updating was larger (i.e., more negative) for ambiguous draws in risky gambles than for risky draws in ambiguous gambles under tDCS [$M = -1.05$, $SE = 0.35$, $t(46) = 3.000$, $P = 0.004$; see also [Supplementary Fig. 2](#)], since mean (predicted) expectancy violation is larger for the former trials (see [Supplementary Table 1](#)).

Cortisol-Related Increases in Value Updating in the Positive Domain

Although there was no group-based effect of stress on value updating, we investigated whether the stress hormone cortisol, known to be a driving force in the modulation of cognition (Joëls and Baram 2009; Vogel et al. 2016) and the concentrations of which varied considerably in our sample, affected value updating processes. To this end, we ran another model with baseline-to-peak changes in cortisol across groups as a covariate instead of the group factor stress condition (model 9).

In this model, the effects of anodal tDCS remained largely identical to those observed in the model with stress condition

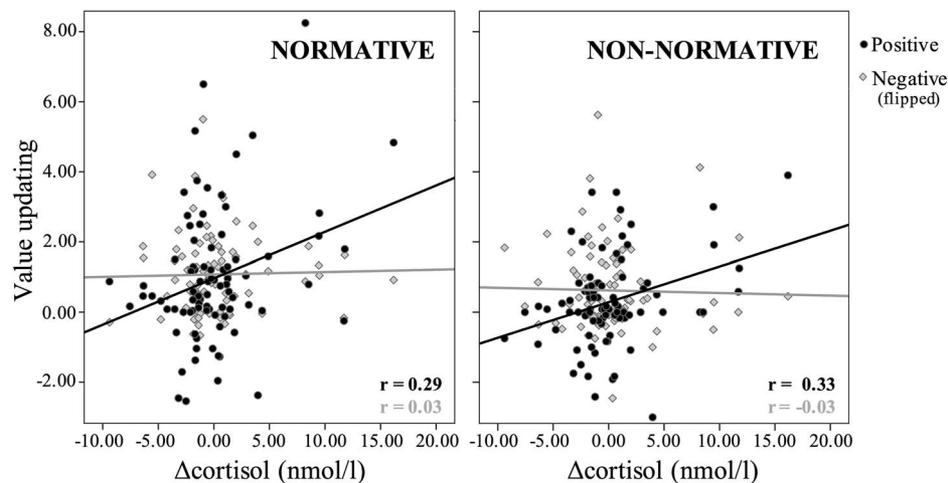


Figure 5. Positive association between cortisol changes (peak—baseline) and positive value updating in normative and non-normative trials (across the whole sample; for the stress- and control group separately, see [Supplementary Fig. 3](#)). No significant association was found for negative updating (sign-flipped in the figure, i.e., more positive values indicate stronger negative updating).

as between-subjects factor. The tDCS main effect emerged even stronger [$F(1.83) = 7.922$, $P = 0.006$, $\eta_p^2 = 0.087$]. However, this additional analysis yielded also a striking cortisol-change \times valence interaction [$F(1.83) = 9.484$, $P = 0.003$, $\eta_p^2 = 0.103$]. Probing this interaction with post-hoc correlations, we found significant positive relationships between cortisol changes and value updating in normatively positive trials [$r(84) = 0.29$, $P = 0.007$, [Fig. 5](#), left panel] as well as in non-normatively positive trials [$r(84) = 0.33$, $P = 0.002$, [Fig. 5](#), right panel] across groups. When comparing the stress and control group, we found similar associations across groups, which showed a trend to significance [normatively positive/stress: $r(40) = 0.30$, $P = 0.054$, normatively positive/control: $r(42) = 0.27$, $P = 0.081$; non-normatively positive/stress: $r(40) = 0.32$, $P = 0.041$ (uncorrected), non-normatively positive/control: $r(42) = 0.39$, $P = 0.009$; see [Supplementary Fig. 3](#) for an illustration]. In other words, the higher the cortisol increase from baseline to peak (+25 min after stressor/control onset), the more positive the value updating when draw color and win color matched—irrespective of whether this update was normative or not. We did not find this association in the negative domain [normatively negative updating (sign-flipped): $r(84) = 0.03$, $P = 0.820$; non-normatively negative updating (sign-flipped): $r(84) = -0.03$, $P = 0.815$; and all $P > 0.354$ for separate groups] and the correlations in the positive domains differed from those in the negative domain (all $P < 0.05$, except $P = 0.058$ for normatively positive vs. normatively negative) according to the Williams' T2 statistic proposed by [Steiger \(1980\)](#). We observed similar relationships when using the cortisol change from baseline to pre-task (+43 min).

We did not observe any significant correlations between value updating and sympathetic reactivity, measured as the difference between each sympathetic measure at baseline and during the SECPT/WWT (all $P > 0.099$), and between value updating and subjective feelings reported immediately after the stress manipulation (all $P > 0.188$), both across stress conditions and separately. Notably, the cortisol-related effects remained significant when controlling for sympathetic reactivity and subjective feelings [normatively positive: $r_{\text{partial}}(77) = 0.32$, $P = 0.004$, non-normatively positive: $r_{\text{partial}}(77) = 0.33$, $P = 0.003$].

Anodal tDCS and Cortisol Modulate Baseline Aversion to Uncertainty

As a complementary analysis, we tested for an effect of tDCS and stress on baseline risk and ambiguity taking (i.e., before belief updating following observed draws), expressed as mean pre-draw subjective values (WTS) in risky and ambiguous gambles, respectively. Higher pre-draw WTS here indicate a higher willingness to take risk or ambiguity. We found significantly increased baseline ambiguity taking after anodal tDCS [$M = 4.04$ ($SD = 1.46$)] over the dlPFC relative to sham stimulation [$M = 3.40$ ($SD = 1.42$); $F(1.87) = 4.516$, $P = 0.036$, $\eta_p^2 = 0.049$], but no significant effect of stress condition [$F(1.87) = 0.035$, $P = 0.853$, $\eta_p^2 < 0.001$] and no tDCS \times stress condition interaction [$F(1.87) = 0.533$, $P = 0.467$, $\eta_p^2 = 0.006$]. There were no significant effects of tDCS or stress group on baseline risk taking (all $P > 0.134$). However, across participants, we found that increases in cortisol were associated with increased baseline risk taking [$r(77) = 0.23$, $P = 0.044$], but we found no significant effect for ambiguity taking, though descriptively in the same direction [$r(77) = 0.10$, $P = 0.371$].

We also ran control analyses to test for the robustness of our main findings once mean baseline risk and ambiguity taking were included as covariates (for a control analysis via urn-wise pre-draw WTS, see [Supplementary Text 3](#)). The tDCS effect remained significant and qualitatively unchanged [$F(1.81) = 5.853$, $P = 0.018$, $\eta_p^2 = 0.067$]. Moreover, the cortisol effect remained significant [$F(1.81) = 5.216$, $P = 0.025$, $\eta_p^2 = 0.06$] with significant partial correlations between cortisol increases and value updating in normatively positive [$r(80) = 0.32$, $P = 0.003$] and non-normatively positive trials [$r(80) = 0.34$, $P = 0.002$]. Hence, the degree of baseline risk and ambiguity taking could not account for tDCS and cortisol effects on value updating.

Control Variables

We also analyzed whether the tDCS and stress-condition groups differed in the following variables: depressive mood (BDI scores), perceived chronic stress (TICS screening score), and Body Mass

Index (BMI = kg/m²). BDI and TICS data were missing for one participant and BMI values were missing for 11 participants (but BMI values were screened to be in the range between 18.5 and 28.5 before the experiment). There were no group differences in any of these variables (all $P > 0.106$; see [Supplementary Table 3](#)). Participants in the tDCS groups were on average slightly older than participants in the control group [$F(1.87) = 5.523$, $P = 0.022$, $\eta_p^2 = 0.06$]. However, even when including age or any of the other covariates into the statistical models, both the tDCS and the cortisol-related effects remained significant.

Discussion

Adaptive performance in uncertain environments depends on the ability to form and update internal beliefs about environmental states. Recent evidence suggests that belief updating is linked to a frontoparietal network, including the dlPFC ([Gläscher et al. 2010](#); [Kobayashi and Hsu 2017](#); [Nour et al. 2018](#); [Tomov et al. 2018](#)). While this previous evidence is based on fMRI data that are correlational by nature, we used here non-invasive brain stimulation via tDCS to probe the “causal” role of the right dlPFC in belief updating. Our results show enhanced monetary value updating after anodal tDCS when it is normatively expected (i.e., under ambiguity). A model-based analysis indicates that this effect is likely driven by belief updating, since belief updating (predicted by the Bayesian model) predicted value updating in the normative context. The present findings thus support the hypothesized causal role of the right dlPFC in belief- and value updating. In addition, we observed a tDCS-induced enhancement of value updating in a non-normative context (i.e., related to risk). Here, our model-based analysis indicates that this effect might be driven by expectancy violation rather than belief updating. Furthermore, we investigated the effect of stress, which is known to be a major modulator of prefrontal functioning ([Arnsten 2009](#); [Schwabe and Wolf 2013](#); [Vogel et al. 2016](#)). We observed that increases in the stress hormone cortisol were associated with enhanced positive, but not negative, value updating in normative and non-normative contexts across participants.

The dlPFC as a Neural Substrate of Belief Updating

Common theoretical frameworks postulate that the dlPFC plays a critical role in working memory ([Petrides 1996](#); [Baddeley 1998](#)) and executive control ([Miller and Cohen 2001](#)), both of which is strongly supported by meta-analytic evidence ([Wager and Smith 2003](#); [Niendam et al. 2012](#); [Rottschy et al. 2012](#)). The concept of working memory relates to the maintenance, monitoring and manipulation of information on a short time scale, with the latter referring to the transformation of representations ([Petrides 1996](#); [Baddeley 1998](#)). Our finding of enhanced normative value updating under tDCS—likely mediated by belief updating—resonates well with this framework, given that the updating of beliefs in our task can be considered as a particular instance of manipulation of short-term information, although the dlPFC plays a critical role in the updating of established episodic memories as well ([Klueen et al. 2019](#)). Theoretically, enhanced value updating might have been mediated by neural mechanisms linked to the manipulation of belief representations per se or, alternatively, related to the input or output of that representational stage. Notably, these possibilities are not mutually exclusive.

Regarding the representational level, it is currently unclear how the dlPFC adjusts representations of posterior probabilities (i.e., the outcome of the belief-updating process). This process may involve a modulation of parietal regions, in which activity also correlates with belief updating ([Kobayashi and Hsu 2017](#)) and tracks relative frequencies of events ([d'Acremont et al. 2013](#)). Regarding the input to the belief-updating system, the proposed transformation of representations through the dlPFC may critically depend on the degree of attention allocated to new observations, which also constitutes one of its proposed functions. The dlPFC has been repeatedly associated with top-down attentional modulation of early sensory cortices ([Egner and Hirsch 2005](#); [Duncan 2013](#); [Erez and Duncan 2015](#); [Gbadayan et al. 2016](#)), where both enhancement of task-relevant and suppression of task-irrelevant information have been observed ([Zanto et al. 2011](#)). From this perspective, it is possible that attentional processes may have increased the influence of new evidence (i.e., the observed draws), thereby supporting the updating of prior beliefs. On a mechanistic level, such effects might be mediated by alpha-band (7–14 Hz) phase coherence in neuronal oscillations, which has been linked to top-down attentional modulation of early visual processing through the prefrontal cortex ([Zanto et al. 2011](#)). As far as the output of belief representations is concerned, regions of the frontoparietal belief-updating network are functionally connected with brain regions that have been associated with valuation processes such as the vmPFC ([Kobayashi and Hsu 2017](#)), consistent with a direct link of reward-related representations in the dlPFC with value-based choice ([Kahnt et al. 2011](#)). Hence, another, not necessarily exclusive possibility is that anodal tDCS might have enhanced this functional connectivity and thereby value updating.

The Algorithmic Level and Bounded Rationality of Belief Updating

In addition to identifying the dlPFC as a key neural substrate that causally contributes to belief updating, our results may advance our understanding of the algorithmic level of belief updating. In line with previous reports ([Behrens et al. 2007](#); [Kobayashi and Hsu 2017](#); [Tomov et al. 2018](#)), our findings show that a Bayesian account—in which new evidence is integrated with prior knowledge according to Bayes' rule ([Bayes and Price 1763](#))—can serve as an approximation of human information processing in some contexts (“Bayesian brain hypothesis,” see [Knill and Pouget 2004](#); [Friston 2012](#)).

However, we also noticed apparent deviations from Bayesian optimality in our model-based analysis, consistent with the notion of bounded rationality ([Gigerenzer and Brighton 2009](#); [Rieskamp et al. 2015](#)). Even under natural conditions (i.e., without tDCS stimulation), participants' value updating was smaller than normatively expected for both normatively positive and negative trials, indicating that they adjust their beliefs less than a fully Bayesian decision-maker would do following new ambiguity-resolving information. In other words, participants overweighed here the prior relative to the new evidence, which is a frequent bias that has been described early in the literature (“conservativeness,” [Edwards 1968](#)) and may be adaptive under some circumstances ([Navon 1978](#)), although another oft-observed bias relates to the overweighing of new information or base-rate neglect ([Kahneman and Tversky 1972](#)). Interestingly, this conservative pattern was also descriptively present to some degree in a recent study (see value updating for ambiguous gambles after draws in ambiguous colors in [Fig. 2C](#) in [Kobayashi](#)

and Hsu (2017)), but significance tests were not reported there. Another study used electroencephalography to investigate the neural mechanisms behind the overweighting of prior information and found that it was linked to an increased lateralized readiness potential in the brain, indicating enhanced response preparation already before new evidence is processed (Achtziger et al. 2014), which might also have played a role in our observations.

Interestingly, following anodal tDCS stimulation over the right dlPFC, the underweighting of new information in the normative-updating trials was reduced and participants' behavior more closely matched that of a fully Bayesian agent.

Our model-based analysis also indicated that normative value updating in general and tDCS-induced enhancements in particular could be explained by belief updating, in line with the view that humans are able to form internal models of the nature of uncertainty. Notably, belief updating could also be explained by a heuristic that only considers "effective" urn content, that is, ambiguous balls are considered as two half balls and replaced by full balls after observed draws. While we cannot differentiate between an approximately Bayesian and this heuristic account, given that they are mathematically equivalent (Kobayashi and Hsu 2017), the expressed degree of (near) optimal vs. bounded rationality would hold for both.

Non-Normative Value Updating Via Expectancy Violation

The mentioned tDCS-induced increase in Bayesian rationality, however, came at the cost of increased deviations from Bayesian rationality in non-normative, risk-related contexts (i.e., when zero updating was normatively expected), as anodal tDCS over the right dlPFC also increased value updating in those trials. Our model-based analysis suggests that this effect might be explained by expectancy violation rather than belief updating, given that only the former emerged as a significant predictor of non-normative value updating in both the tDCS and the sham-control group. Theoretically, beliefs might still have been updated, though not following numerical predictions of the Bayesian model. In any case, this indicates that participants were not able to (fully) ignore surprising, yet irrelevant, signals in the environment, and that tDCS might have enhanced the effect of expectancy violation on valuation.

At the neural level, the anterior insula was recently found to be the only region to track expectancy violation after adjusting for belief updating (Kobayashi and Hsu 2017), consistent with its general role in the processing of surprising and salient information (Uddin 2015; Loued-Khenissi et al. 2020). Given that transcranial stimulation intensity was considerably lower in the anterior insula than in the targeted dlPFC in our study (i.e., an electrical field in the right insula with 37.42% of the magnitude of the field in the right dlPFC), we believe that it is unlikely that these effects were driven by the insula, although we could not completely rule out this possibility. However, when not removing shared variance (present across trial categories) between belief updating and expectancy violation (i.e., not adjusting for belief updating), the dlPFC also tracked the degree of expectancy violation in the study of Kobayashi and Hsu (2017). Hence, tDCS might have modulated dlPFC-mediated processing of expectancy violation in addition to its effects on normative belief updating.

Possible Insights and Limitations of tDCS

We used here tDCS as a noninvasive brain stimulation technique to probe the causal role of the right dlPFC in belief updating in

healthy individuals. However, it is important to note that the spatial precision of this method is limited due to the size of the electrodes and dispersion of electric current (Nitsche et al. 2008), as also indicated by the presented electric field estimation (Fig. 1C). Hence, it is likely that adjacent areas were stimulated as well, albeit to a degree that diminishes with distance. For instance, it is possible that a slightly posterior frontolateral brain region mediated the observed effects, given that a previous study reported a belief-updating cluster that may include the right premotor region and frontal eye field, but which also extended to the right dlPFC (Kobayashi and Hsu 2017). Apart from the effect of passively spreading electric current to adjacent areas, it is also possible that tDCS over the dlPFC modulated functionally connected and possibly also more distant areas, as has been observed before (Weber et al. 2014), which might constitute an important underlying mechanism. Even in this case, however, the dlPFC likely still serves a key role through its functional connectivity. To effectively target the right dlPFC, we chose an electrode position (F4) that has been successfully used in previous studies using tDCS (Axelrod et al. 2015; Pope et al. 2015; Bogdanov and Schwabe 2016) and tDCS combined with fMRI (Weber et al. 2014) or with functional infrared spectroscopy and electroencephalography (Choe et al. 2016), which found that tDCS over this area indeed modulates dlPFC activity. The present experimental findings further converge with a line of correlative studies on belief updating (Gläscher et al. 2010; Kobayashi and Hsu 2017; Nour et al. 2018; Tomov et al. 2018), providing strong evidence that the right dlPFC serves as a key region in belief updating. Building on this, future studies might also target other brain regions such as the left dlPFC to study potential lateralization or parietal regions linked to belief updating (Kobayashi and Hsu 2017) to test for regional specificity. Moreover, future research might also leverage brain stimulation with simultaneous recordings of hemodynamic or electrophysiological activity to further elucidate the causal dynamics in brain activity and functional connectivity.

The Role of Cortisol in Value Updating

These neural dynamics of belief updating may be subject to various neuromodulatory influences. For instance, previous research found that acute stress may impair dlPFC functioning via the modulatory action of glucocorticoids and catecholamines (Arnsten 2009; Qin et al. 2009; Bogdanov and Schwabe 2016). Although we observed here no effect of acute stress per se, we found that increases in the stress hormone cortisol were associated with enhanced value updating in normatively positive trials as well as in non-normatively positive trials. "Enhanced" value updating speaks against the hypothesis of an inhibition of belief updating through stress. However, enhanced "non-normative" updating supports our alternative hypothesis that participants would be less sensitive to the nature of uncertainty with increased levels of glucocorticoids, possibly indicating impaired dlPFC functioning. In contrast to what we expected, the observed effect was valence-specific as only positive but not negative updating was altered, and value updating was enhanced even in normatively positive trials, which could not be explained by the impaired sensitivity to the nature of uncertainty (which only predicts erroneous updating in non-normative contexts). These valence-specific enhancements across contexts might be explained by increases in sensitivity to information signaling increased reward probability. In line with this, previous studies reported cortisol-related enhancements in risk taking (Buckert et al.

2014; Deuter et al. 2017; Kluen et al. 2017; but see Metz et al. 2020). This effect might reflect increased reward sensitivity under stress. Specifically, stress-induced increases in reward-related activity have been observed in the striatum (Oei et al. 2014), which might be associated with stress-induced increases in dopamine release (Pruessner et al. 2004; Scott et al. 2006). The amygdala might also play a role, given that it has been previously found to orchestrate stress-induced shifts towards striatal behavioral control (Schwabe et al. 2013). Both the striatum and the amygdala are sensitive to glucocorticoids through their expression of mineralocorticoid receptors (Arriza et al. 1988; Vogel et al. 2016). These receptors are, however, also present in the dlPFC (Qi et al. 2013), which might also allow for a more direct influence of cortisol on belief-updating processes. Given that the observed cortisol effect is correlational, future studies might leverage a pharmacological manipulation (e.g., via hydrocortisone; Kluen et al. 2017; Metz et al. 2020) to assess whether cortisol, potentially in interaction with catecholamines, causally mediates stress-effects on belief- and value updating.

Apart from the cortisol-related effect, we observed no valence-specific effects or differences in value updating. By contrast, previous studies repeatedly reported an optimistic bias in ego-relevant/self-referential belief updating (Sharot et al. 2011; Korn et al. 2014), which might be adaptive to a certain degree, for instance, by reducing stress and anxiety or by increasing motivation and exploration (see Sharot 2011, for a review). Our findings, however, are in line with recent studies that did not find such a bias in the financial/monetary domain (Coutts 2019; for a direct comparison with the ego-relevant domain, see Barron 2020).

Conclusion

The present study shows that anodal tDCS over the right dlPFC enhances value updating, thereby providing evidence for a causal contribution of the right dlPFC in belief updating under uncertainty. This is corroborated by a model-based analysis that found belief updating to be the driving force of value updating when normatively expected. Putting emphasis on humans' bounded rationality (Navon 1978; Gigerenzer and Brighton 2009), tDCS diminished pre-existing deviations from rationality, but also decreased approximately rational behavior from a Bayesian perspective, depending on whether value updating was normatively expected or not. In contrast to the normative context, non-normative value updating in general and tDCS-induced alterations in particular might be better explained by expectancy violation rather than belief updating. Furthermore, we observed that increases in cortisol were associated with enhanced positive, but not negative, value updating in both a normative and non-normative context. The present findings shed light on the causal role of the right dlPFC in the remarkable human ability to navigate uncertain environments by continuously updating prior knowledge following new evidence. Moreover, they might also help to generate hypotheses on the neural mechanisms underlying mental disorders that have been linked to altered belief updating such as schizophrenia (Adams et al. 2018; Nour et al. 2018; Baker et al. 2019) or depression (Korn et al. 2014).

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Funding

Universität Hamburg.

Notes

We gratefully acknowledge the assistance of Lucie Weber, Susanne Schobel, Rosann Stocker and Kim Löwisch during data collection. We also thank Kenji Kobayashi for providing valuable details on their study and the reviewers of our work for their extremely helpful comments. *Conflict of Interest:* The authors declare that there is no conflict of interest.

References

- Achtziger A, Alós-Ferrer C, Hügelschäfer S, Steinhauser M. 2014. The neural basis of belief updating and rational decision making. *Soc Cogn Affect Neurosci.* 9:55–62.
- Adams RA, Napier G, Roiser JP, Mathys C, Gilleen J. 2018. Attractor-like dynamics in belief updating in schizophrenia. *J Neurosci.* 38:9471–9485.
- Arnsten AFT. 2009. Stress signalling pathways that impair prefrontal cortex structure and function. *Nat Rev Neurosci.* 10:410–422.
- Arriza JL, Simerly RB, Swanson LW, Evans RM. 1988. The neuronal mineralocorticoid receptor as a mediator of glucocorticoid response. *Neuron.* 1:887–900.
- Axelrod V, Rees G, Lavidor M, Bar M. 2015. Increasing propensity to mind-wander with transcranial direct current stimulation. *Proc Natl Acad Sci U S A.* 112:3314–3319.
- Baddeley A. 1998. Recent developments in working memory. *Curr Opin Neurobiol.* 8:234–238.
- Baker SC, Konova AB, Daw ND, Horga G. 2019. A distinct inferential mechanism for delusions in schizophrenia. *Brain.* 142:1797–1812.
- Barron K. 2020. Belief updating: does the 'good-news, bad-news' asymmetry extend to purely financial domains? *Exp Econ.* doi: 10.1007/s10683-020-09653-z.
- Bayes T, Price R. 1763. An essay towards solving a problem in the doctrine of chances. By the late Rev. Mr. Bayes, F.R.S. Communicated by Mr. Price, in a letter to John Canton, A.M.F.R.S. *Philos Trans R Soc London.* 53:370–418.
- Becker GM, DeGroot MH, Marschak J. 1964. Measuring utility by a single-response sequential method. *Behav Sci.* 9:226–232.
- Behrens TEJ, Woolrich MW, Walton ME, Rushworth MFS. 2007. Learning the value of information in an uncertain world. *Nat Neurosci.* 10:1214–1221.
- Bogdanov M, Ruff CC, Schwabe L. 2017. Transcranial stimulation over the dorsolateral prefrontal cortex increases the impact of past expenses on decision-making. *Cereb Cortex.* 27:1094–1102.
- Bogdanov M, Schwabe L. 2016. Transcranial stimulation of the dorsolateral prefrontal cortex prevents stress-induced working memory deficits. *J Neurosci.* 36:1429–1437.
- Buckler M, Schwieren C, Kudielka BM, Fiebich CJ. 2014. Acute stress affects risk taking but not ambiguity aversion. *Front Neurosci.* 8:1–11.
- Choe J, Coffman BA, Bergstedt DT, Ziegler MD, Phillips ME. 2016. Transcranial direct current stimulation modulates neuronal activity and learning in pilot training. *Front Hum Neurosci.* 10:1–25.
- Cohen J. 1988. *Statistical power analysis for the behavioral sciences.* 2nd ed. Associates, L. Hillsdale (NJ): Erlbaum.

- Coutts A. 2019. Good news and bad news are still news: experimental evidence on belief updating. *Exp Econ*. 22:369–395.
- d'Acromont M, Schultz W, Bossaerts P. 2013. The human brain encodes event frequencies while forming subjective beliefs. *J Neurosci*. 33:10887–10897.
- Deuter CE, Wingenfeld K, Schultebrucks K, Hellmann-Regen J, Piber D, Otte C. 2017. Effects of mineralocorticoid-receptor stimulation on risk taking behavior in young healthy men and women. *Psychoneuroendocrinology*. 75:132–140.
- Duncan J. 2013. The structure of cognition: attentional episodes in mind and brain. *Neuron*. 80:35–50.
- Edwards S, Clow A, Evans P, Hucklebridge F. 2001. Exploration of the awakening cortisol response in relation to diurnal cortisol secretory activity. *Life Sci*. 68:2093–2103.
- Edwards W. 1968. Conservatism in human information processing. In: Kleinmütz B, editor. *Formal Representation of Human Judgment*. New York: Wiley, pp. 17–52.
- Egner T, Hirsch J. 2005. Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nat Neurosci*. 8:1784–1790.
- Ellsberg D. 1961. Risk, ambiguity, and the savage axioms. *QJ Econ*. 75:643–669.
- Erez Y, Duncan J. 2015. Discrimination of visual categories based on behavioral relevance in widespread regions of frontoparietal cortex. *J Neurosci*. 35:12383–12393.
- Paul F, Erdfelder E, Buchner A, Lang A-G. 2009. Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behav Res Methods*. 41:1149–1160.
- Friston K. 2012. The history of the future of the Bayesian brain. *Neuroimage*. 62:1230–1233.
- Gbadayan O, McMahon K, Steinhauser M, Meinzer M. 2016. Stimulation of dorsolateral prefrontal cortex enhances adaptive cognitive control: a high-definition transcranial direct current stimulation study. *J Neurosci*. 36:12530–12536.
- Gigerenzer G, Brighton H. 2009. Homo heuristics: why biased minds make better inferences. *Top Cogn Sci*. 1:107–143.
- Gläscher J, Daw N, Dayan P, O'Doherty JP. 2010. States versus rewards: dissociable neural prediction error signals underlying model-based and model-free reinforcement learning. *Neuron*. 66:585–595.
- Hautzinger M, Keller F, Kühner C. 2006. *Beck Depressions-Inventar (BDI-II). Revision*. Frankfurt/Main: Harcourt Test Services.
- Herwig U, Satrapi P, Schönfeldt-Lecuona C. 2003. Using the international 10-20 EEG system for positioning of transcranial magnetic stimulation. *Brain Topogr*. 16:95–99.
- Huang Y, Datta A, Bikson M, Parra LC. 2019. Realistic volumetric approach to simulate transcranial electric stimulation—ROAST—a fully automated open-source pipeline. *J Neural Eng*. 16:056006.
- Huettel SA, Stowe CJ, Gordon EM, Warner BT, Platt ML. 2006. Neural signatures of economic preferences for risk and ambiguity. *Neuron*. 49:765–775.
- Jacobson L, Koslowsky M, Lavidor M. 2012. TDCS polarity effects in motor and cognitive domains: a meta-analytical review. *Exp Brain Res*. 216:1–10.
- Joëls M, Baram TZ. 2009. The neuro-symphony of stress. *Nat Rev Neurosci*. 10:459–466.
- Kahneman D, Tversky A. 1972. Subjective probability: a judgment of representativeness. *Cogn Psychol*. 3:430–454.
- Kahnt T, Heinzle J, Park SQ, Haynes JD. 2011. Decoding the formation of reward predictions across learning. *J Neurosci*. 31:14624–14630.
- Kincses TZ, Antal A, Nitsche MA, Bártfai O, Paulus W. 2004. Facilitation of probabilistic classification learning by transcranial direct current stimulation of the prefrontal cortex in the human. *Neuropsychologia*. 42:113–117.
- Klueen LM, Agorastos A, Wiedemann K, Schwabe L. 2017. Cortisol boosts risky decision-making behavior in men but not in women. *Psychoneuroendocrinology*. 84:181–189.
- Klueen LM, Dandolo LC, Jocham G, Schwabe L. 2019. Dorsolateral prefrontal cortex enables updating of established memories. *Cereb Cortex*. 29:4154–4168.
- Knight F. 1921. *Risk, uncertainty and profit, hart, schaffner, and marx prize essays*. Vol 31. Boston, MA: Houghton Mifflin Company.
- Knill DC, Pouget A. 2004. The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends Neurosci*. 27:712–719.
- Kobayashi K, Hsu M. 2017. Neural mechanisms of updating under reducible and irreducible uncertainty. *J Neurosci*. 37:6972–6982.
- Korn CW, Sharot T, Walter H, Heekeren HR, Dolan RJ. 2014. Depression is related to an absence of optimistically biased belief updating about future life events. *Psychol Med*. 44:579–592.
- Leiner DJ. 2020. SoSci survey (version 3.2.05-i) [Computer software]. <https://www.sosicisurvey.de>.
- Loued-Khenissi L, Pfeuffer A, Einhäuser W, Preuschoff K. 2020. Anterior insula reflects surprise in value-based decision-making and perception. *Neuroimage*. 210:116549.
- Mas-Colell A, Whinston MD, Green JR. 2005. *Microeconomic theory*. New York: Oxford University Press.
- Metz S, Waiblinger-Grigull T, Schulreich S, Chae WR, Otte C, Heekeren HR, Wingenfeld K. 2020. Effects of hydrocortisone and yohimbine on decision-making under risk. *Psychoneuroendocrinology*. 114:104589.
- Miller EK, Cohen JD. 2001. An integrative theory of prefrontal cortex function. *Annu Rev Neurosci*. 24:167–202.
- Navon D. 1978. The importance of being conservative: some reflections on human Bayesian behaviour. *Br J Math Stat Psychol*. 31:33–48.
- Niendam TA, Laird AR, Ray KL, Dean YM, Glahn DC, Carter CS. 2012. Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cogn Affect Behav Neurosci*. 12:241–268.
- Nitsche MA, Cohen LG, Wassermann EM, Priori A, Lang N, Antal A, Paulus W, Hummel F, Boggio PS, Fregni F, et al. 2008. Transcranial direct current stimulation: state of the art 2008. *Brain Stimul*. 1:206–223.
- Nitsche MA, Doemkes S, Karaköse T, Antal A, Liebetanz D, Lang N, Tergau F, Paulus W. 2007. Shaping the effects of transcranial direct current stimulation of the human motor cortex. *J Neurophysiol*. 97:3109–3117.
- Nour MM, Dahoun T, Schwartenbeck P, Adams RA, FitzGerald THB, Coello C, Wall MB, Dolan RJ, Howes OD. 2018. Dopaminergic basis for signaling belief updates, but not surprise, and the link to paranoia. *Proc Natl Acad Sci USA*. 115:E10167–E10176.
- Oei NYL, Both S, van Heemst D, van der Grond J. 2014. Acute stress-induced cortisol elevations mediate reward system activity during subconscious processing of sexual stimuli. *Psychoneuroendocrinology*. 39:111–120.
- Payzan-LeNestour E, Bossaerts P. 2011. Risk, unexpected uncertainty, and estimation uncertainty: Bayesian learning in unstable settings. *PLoS Comput Biol*. 7:e1001048.

- Petrides M. 1996. Specialized systems for the processing of mnemonic information within the primate frontal cortex. *Philos Trans R Soc B Biol Sci.* 351:1455–1462.
- Pope PA, Brenton JW, Miall RC. 2015. Task-specific facilitation of cognition by anodal transcranial direct current stimulation of the prefrontal cortex. *Cereb Cortex.* 25:4551–4558.
- Pruessner JC, Champagne F, Meaney MJ, Dagher A. 2004. Dopamine release in response to a psychological stress in humans and its relationship to early life maternal care: a positron emission tomography study using [¹¹C] raclopride. *J Neurosci.* 24:2825–2831.
- Qi XR, Kamphuis W, Wang S, Wang Q, Lucassen PJ, Zhou JN, Swaab DF. 2013. Aberrant stress hormone receptor balance in the human prefrontal cortex and hypothalamic paraventricular nucleus of depressed patients. *Psychoneuroendocrinology.* 38:863–870.
- Qin S, Hermans EJ, van Marle HJF, Luo J, Fernández G. 2009. Acute psychological stress reduces working memory-related activity in the dorsolateral prefrontal cortex. *Biol Psychiatry.* 66:25–32.
- Rieskamp J, Hertwig R, Todd PM. 2006. Bounded rationality. Two interpretations from psychology. In: Altman M, editor. *Handbook of contemporary behavioral economics. Foundations and developments.* Sharpe, Armonk, p. 218–236.
- Rottschy C, Langner R, Dogan I, Reetz K, Laird AR, Schulz JB, Fox PT, Eickhoff SB. 2012. Modelling neural correlates of working memory: a coordinate-based meta-analysis. *Neuroimage.* 60:830–846.
- Ruff CC, Ugazio G, Fehr E. 2013. Changing social norm compliance with noninvasive brain stimulation. *Science.* 342:482–484.
- Schulz P, Schlotz W. 1999. The trier inventory for the assessment of chronic stress (TICS): scale construction, statistical testing, and validation of the scale work overload. *Diagnostica.* 45:8–19.
- Schwabe L, Haddad L, Schachinger H. 2008. HPA axis activation by a socially evaluated cold-pressor test. *Psychoneuroendocrinology.* 33:890–895.
- Schwabe L, Schächinger H. 2018. Ten years of research with the socially evaluated cold pressor test: data from the past and guidelines for the future. *Psychoneuroendocrinology.* 92:155–161.
- Schwabe L, Tegenthoff M, Höffken O, Wolf OT. 2013. Mineralocorticoid receptor blockade prevents stress-induced modulation of multiple memory systems in the human brain. *Biol Psychiatry.* 74:801–808.
- Schwabe L, Wolf OT. 2013. Stress and multiple memory systems: from “thinking” to “doing”. *Trends Cogn Sci.* 17:60–68.
- Scott DJ, Heitzeg MM, Koeppel RA, Stohler CS, Zubieta JK. 2006. Variations in the human pain stress experience mediated by ventral and dorsal basal ganglia dopamine activity. *J Neurosci.* 26:10789–10795.
- Sharot T. 2011. *The optimism bias.* New York, NY: Pantheon Books.
- Sharot T, Korn CW, Dolan RJ. 2011. How unrealistic optimism is maintained in the face of reality. *Nat Neurosci.* 14:1475–1479.
- Steiger JH. 1980. Tests for comparing elements of a correlation matrix. *Psychol Bull.* 87:245–251.
- Tomov MS, Dorfman HM, Gershman SJ. 2018. Neural computations underlying causal structure learning. *J Neurosci.* 38:7143–7157.
- Uddin LQ. 2015. Salience processing and insular cortical function and dysfunction. *Nat Rev Neurosci.* 16:55–61.
- Vogel S, Fernández G, Joëls M, Schwabe L. 2016. Cognitive adaptation under stress: a case for the mineralocorticoid receptor. *Trends Cogn Sci.* 20:192–203.
- Wager TD, Smith EE. 2003. Neuroimaging studies of working memory. *Cogn Affect Behav Neurosci.* 3:255–274.
- Weber MJ, Messing SB, Rao H, Detre JA, Thompson-Schill SL. 2014. Prefrontal transcranial direct current stimulation alters activation and connectivity in cortical and subcortical reward systems: a tDCS-fMRI study. *Hum Brain Mapp.* 35:3673–3686.
- Zanto TP, Rubens MT, Thangavel A, Gazzaley A. 2011. Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nat Neurosci.* 14:656–663.