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The angular gyrus and visuospatial attention in decision-making under risk

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ABSTRACT

Recent neuroimaging studies on decision-making under risk indicate that the angular gyrus (AG) is sensitive to the probability and variance of outcomes during choice. A separate body of research has established the AG as a key area in visual attention. The current study used repetitive transcranial magnetic stimulation (rTMS) in healthy volunteers to test whether the causal contribution of the AG to decision-making is independent of or linked to the guidance of visuospatial attention. A within-subject design compared decision making on a laboratory gambling task under three conditions: following rTMS to the AG, following rTMS to the premotor cortex (PMC, as an active control condition) and without TMS. The task presented two different trial types, 'visual' and 'auditory' trials, which entailed a high versus minimal demand for visuospatial attention, respectively. Our results showed a systematic effect of rTMS to the AG upon decision-making behavior in visual trials. Without TMS and following rTMS to the control region, decision latencies reflected the odds of winning; this relationship was disrupted by rTMS to the AG. In contrast, no significant effects of rTMS to the AG (or to the PMC) upon choice behavior in auditory trials were found. Thus, rTMS to the AG affected decision-making only in the task condition requiring visuospatial attention. The current findings suggest that the AG contributes to decision-making by guiding attention to relevant information about reward and punishment in the visual environment.

Introduction

Many of the decisions we face in our every-day lives involve some degree of uncertainty and risks. Recent work suggests that the inferior parietal cortex (IPC) might play an important role in guiding choice behavior under risk and uncertainty. Extant neuroimaging studies of economic decision-making tasks consistently found activations in the inferior parietal cortex (for meta-analyses, see Liu et al., 2011; Mohr et al., 2010), and a recent neuropsychological study demonstrated that damage to this area is associated with impaired decision-making (Studer et al., 2013). However – in contrast to other structures within the brain network supporting decision-making such as the striatum or orbitofrontal cortex – the functional role of the human IPC in choices under uncertainty remains largely unstudied. One reason for this gap of knowledge might be that extant research on decision-making has rarely differentiated between IPC subregions. The IPC is an extensive and heterogeneous cortical area, whose subdivisions have different structural connectivity profiles (Uddin et al., 2010) and were found to play distinct functional roles in other cognitive domains (see e.g. Dehaene et al., 2003). The development of a comprehensive model of IPC function in choice behavior is also complicated by the fact that this area has been implicated in a range of other cognitive functions, for instance attentional processes (Husain and Nachev, 2007) and number processing (Dehaene et al., 2003). These cognitive processes often go along with decision-making both in laboratory tasks and in everyday life, making it difficult to assess the contribution of the IPC to the decision process *per se*.

The current study aims to specify the causal role of the angular gyrus (AG), an IPC subregion, in decision-making under risk. Previous neuroimaging studies found that the AG is activated during decision-making (Ernst et al., 2004; Labudda et al., 2008; Vickery and Jiang, 2009) and moreover, showed that hemodynamic responses in this area during the choice process reflect the probability (Bach et al., 2011; Berns et al., 2008; Studer et al., 2012) and variance (Symmonds et al., 2011) of potential outcomes. The AG is also thought to be a key area for visuospatial attention. Lesions to the AG are associated with neglect (Chechlacz et al., 2012), and temporary disruption of AG activity by means of transcranial magnetic stimulation (TMS) affects performance on tasks requiring allocation and reorientation of visuospatial attention (reviewed in Rushworth and Taylor, 2006). Attentional processes interact with decision-making in multiple ways. The attentional focus can influence both the processing of a decision situation and the choice made (Armel et al., 2008; Kovach et al., 2014; Krajbich et al., 2010) decision difficulty is likely to drive general attentional effort

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(Philiastides et al., 2006) and reward-associated features of visual stimuli can attract and capture attention, even when they are no longer relevant (e.g. Anderson et al., 2011; Chelazzi et al., 2013; Hickey et al., 2010). Given the involvement of the AG in the orientation of visuospatial attention, this last relationship might be particularly relevant to the understanding of the role of the AG in decision-making. The vast majority of laboratory decision-making tasks use visual stimuli to represent the probability and magnitudes of potential wins and losses, and many of these stimuli contain spatial feature (e.g. segments on wheel or bar graphs). We thus hypothesize that the AG might be involved in guiding attention within the visual representation of decision information. Alternatively, it is also conceivable that the AG contributes to decision-making independently of its role in the guidance of visual attention.

We used continuous theta burst stimulation (cTBS; Huang et al., 2005) to specify the causal contribution of the AG to decision-making under risk. cTBS is an offline repetitive TMS paradigm that can temporarily inhibit the activity in the target brain area, i.e. induce a 'virtual lesion' (Walsh and Pascual-Leone, 2003). Twenty-eight healthy volunteers were tested with a modified version of the Roulette Betting Task (RBT, Studer and Clark, 2011) in three sessions: without stimulation, following cTBS to the AG bilaterally, and following cTBS to the dorsal premotor cortex (PMC) bilaterally. cTBS to the PMC acted as a control condition to allow separation of effects specific to AG stimulation from general TMS effects. In the RBT, participants are asked to place bets on a roulette wheel with winning and losing segments, and then either win or lose the wagered points. The ratio of winning to losing segments was manipulated across trials. The current task version presented two different trial types, 'visual trials' and 'auditory trials', which were designed to entail high and minimal visuospatial attention demands, respectively. 'Visual trials' displayed the wheel, while in 'auditory trials' a computer voice informed participants about the number of winning and losing segments. This task design allowed us to test whether the contribution of the AG to decision-making is linked to or independent of visuospatial attention: If the AG is involved in guiding visuospatial attention within the decision display, cTBS to the AG should impact decision-making on visual trials only. Meanwhile, if the AG contributes to decision-making independently of visuospatial attention, cTBS to the AG should affect choice behavior in both trial types.

Materials and methods

Participants

Twenty-eight right-handed subjects participated in this study (15 males, 13 female, average age = 25 years, SD = ±5 years) and attended three testing sessions. Subjects had normal/corrected-to-normal vision and no hearing impairments. All participants fulfilled the following TMS safety criteria: No history of neurological or psychiatric conditions, no personal or family history of febrile convulsions and/or epilepsy, no implants with metal components, not currently taking any prescribed medication, no alcohol consumption in the 24 h prior to the experiment, no use of recreational drugs in the last three months. Participants were reimbursed for their time, and received a fixed payment of £10 per hour plus a variable bonus (£0–£10) depending on their earnings in the experimental task. This bonus payment ensured that task decisions had direct financial consequences for subjects. The study was approved by the UCL Research Ethics Committee and was conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent.

Study design and procedure

The study used a within-subject design, and each subject was tested under three different conditions: i) following cTBS to the AG, ii) following cTBS to the PMC (as an active control condition) and iii) without stimulation. These conditions were tested in three sessions, separated by 6–8 days. Condition order was randomly assigned and counterbalanced across subjects. In each testing session, participants were first given the task instructions and completed six practice trials. In the two TMS sessions, cTBS was applied to the AG bilaterally or the PMC bilaterally using neuronavigation. Next, participants completed the experimental task. Each testing session lasted approximately 45–60 min.

TMS parameters and set-up

TMS was delivered with a MagStim Rapid2 stimulator (Magstim, Whitland, UK) using a 70-mm figure-of-eight coil, which was manually held tangentially to the skull (handle orientation: posterior direction, at approximately 45° to the midsagittal line). cTBS was applied sequentially to both hemispheres, with stimulation of the contralateral side immediately following the first stimulation. Laterality order was counterbalanced across participants. An offline cTBS paradigm was used, consisting of bursts of three pulses at 50 Hz repeated at 5 Hz (Huang et al., 2005) for 30 s (450 pulses) per hemisphere. Stimulation intensity was set to 40% of maximum machine output. Based on previous research (Cárdenas-Morales et al., 2010; Huang et al., 2005; Noh et al., 2012), this stimulation protocol is expected to induce an inhibition of the stimulated area lasting for approximately 20 to 30 min.

TMS coil position was defined and monitored on-line with the BrainSight frameless stereotaxy system (Rogue Research, Montreal, Canada). Target sites were individually located for each participant on a previously acquired high-resolution structural MRI, using anatomical landmarks. The posterior part of the AG was defined as the target area. The dorsal PMC was identified as described by Duque et al. (2012). The BrainSight software allows a-posteriori normalizing of individual coordinates with respect to the Montreal Neurological Institute (MNI) brain atlas, by means of an iterative algorithm that searches for an optimal projection of an individual brain to the MNI template. Averaged normalized MNI coordinates were −56, −60, 31 (SD: 3, 4, 2) and 60, −53, 31 (SD: 2, 4, 2) for the left and right AG respectively (Fig.1), in line with parietal activations reported in previous neuroimaging studies of decision-making (Berns et al., 2008; Mohr et al., 2010; Studer et al., 2012). Average normalized MNI coordinates for the left and right PMC were −22, −3, 71 (SD: 2, 2, 1) and 23, −3, 71 (SD: 2, 3, 2), respectively, similar to those used in previous TMS studies (Davare et al., 2010; Duque et al., 2012).

Experimental task

A modified version of the Roulette Betting Task (RBT; Studer and Clark, 2011) was used to assess risk-sensitive decision-making. In this task, participants are presented with a wheel containing winning and losing segments (10 segments in total) and three bet options (10, 50 and 90 points). The ratio of winning versus losing segments (4:6, 5:5, 6:4 or 8:2) reflects the chances of winning (40%, 50%, 60% or 80%). On

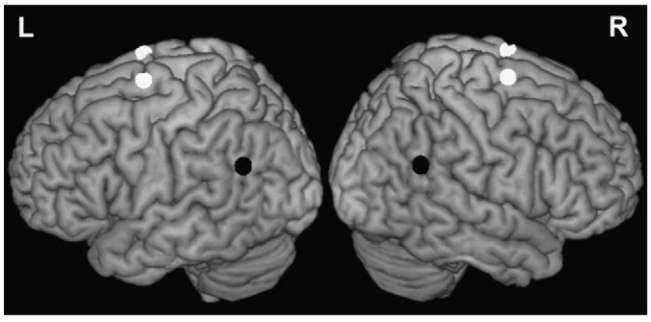

Fig. 1. Stimulation targets. Average normalized stimulation targets in the AG (black) and in the dorsal PMC (white), which was used as a control region.

each trial, participants first select one of the bet options. Then, the wheel spins and eventually stops on either a winning or losing segment resulting in win or loss of the bet, respectively. For this study, we made several important modifications to original RBT: first, we constructed a second trial type, 'auditory trials', in which the wheel was described by a computer voice instead of being displayed. The voice informed participants how many winning versus losing segments the wheel contained. For instance, a wheel with 4 winning and 6 losing segments was described as "four to six". Participants were made familiar with the voice recordings prior to the task. Second, in 'visual trials', the wheel was displayed for a brief period only (350 ms) to boost visuospatial attention demands. Third, bet options were presented horizontally stacked in the middle of the screen to avoid a potential influence of spatial biases upon response selection (see Fig. 2).

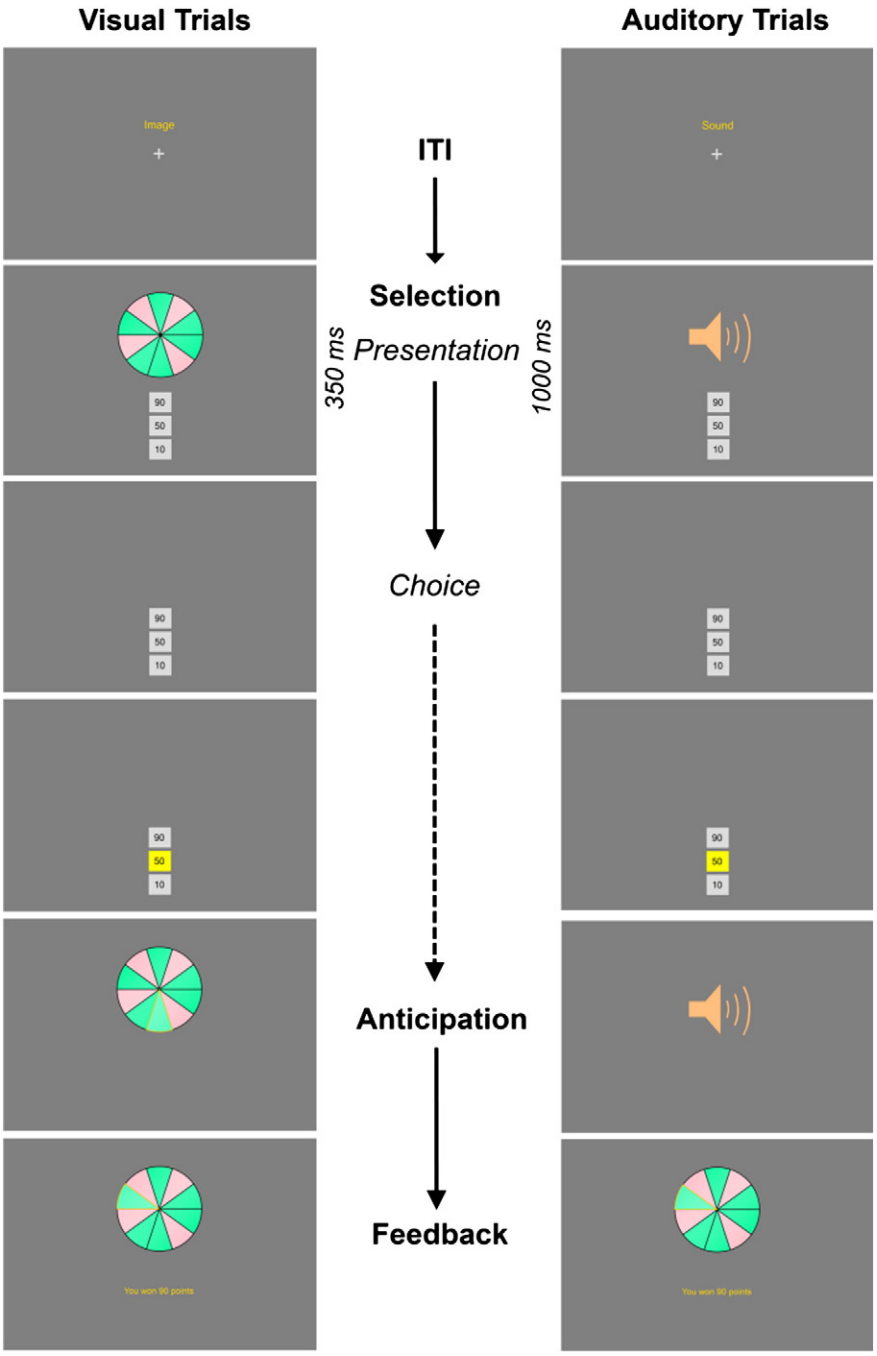

Fig. 2. Experimental task. Participants were asked to place bets on a roulette wheel, containing winning (green) and losing (red) segments. The chances of winning (represented by the ratio of winning to losing segments) varied across trials. Two trial types were used: 'visual trials' (depicted on the left) and 'auditory trials' (depicted on the right). In 'auditory trials', participants were told by a computer voice how many winning and losing segments the wheel contained. Both trial types entailed three phases. In the *Selection* phase, the wheel was presented visually or auditory and participants chose a bet option (10, 50 or 90 points; self-paced). In the *Anticipation* phase, the wheel spun for 1500 ms to 2500 ms (visual spin in visual trials, spinning noise in auditory trials). In the *Feedback* phase (duration: 2000 ms), participants saw whether they won (wheel landed on green) or lost (wheel landed on red) their bet. Trials were separated by an ITI (duration: 1000–2000 ms), in which a fixation cross and information about whether the upcoming trial was a visual ("Image") or auditory trial ("Sound") were presented. The orange sound symbols have been added to this Figure for illustration purposes only.

The two trial types were presented interleaved, and betting choices were made self-paced. Average trial length was 6.9 s (SD = 0.4 s, see Fig. 2 for more details on timings). Participants completed 80 trials of the task, 40 visual trials and 40 auditory trials. Task duration was approximately 9 min on average, and therefore task competition fell within the time window of the assumed effects of our cTBS protocol.

Data analysis

For statistical analysis, decision latencies and two indexes of betting behavior, overall betting and risk adjustment, were extracted for each participant and session. The risk adjustment measure quantifies the degree to which participants vary their bets with the chances of winning, while overall betting reflects the average level of bet sizes (Studer and Clark, 2011; Studer et al., 2013). Data analysis focused on decision-making behavior in trials where the chances of winning were 40%, 50% or 60%.[1] The two indexes of betting behavior were compared across the three stimulation conditions (cTBS to AG, cTBS to PMC, Without Stimulation) using repeated-measures ANOVAs with Stimulation Condition and Trial Type as a within-subject factor. Decision latencies were analyzed using a 3 (Stimulation Condition) × 3 (Chances of winning) × 2 (Trial Type) ANOVA with repeated measures. Since our aim was to assess whether AG involvement in decision-making depends upon the probability information being presented in a visual–spatial manner, our a priori focus was on trial-type specific effects of cTBS to the AG upon the adjustment of betting choices/deliberation times to the chances of winning. Therefore the aforementioned ANOVA models were also run for visual versus auditory trials separately. Greenhouse–Geisser corrections were applied to ANOVAs when sphericity could not be assumed (Mauchly's sphericity test: $p < .05$). All statistical tests are reported two-tailed, and alpha was set at .05. Statistical analysis was carried out in SPSS (Version 20, SPSS Inc., Chicago, IL, USA).

Results

Decision latencies

Decision latencies were modulated by the chances of winning (main effect of Chances: $F(2) = 4.24$, $p = .02$, $\eta p^2 = .14$), and affected by the trial type: Responses were slower in visual trials than in auditory trials (main effect of Trial Type: $F(1) = 80.49$, $p < .001$, $\eta p^2 = .75$). The overall ANOVA model also yielded a significant interaction effect of Stimulation Condition and Chances of Winning ($F(4) = 2.67$, $p = .04$, $\eta p^2 = .09$, main effect of Stimulation Condition: $F(1.47) = 1.33$, $p = .27$, $\eta p^2 = .05$) and a significant interaction effect of Trial Type and Chances of Winning ($F(2) = 6.04$, $p < .01$, $\eta p^2 = .18$, Trial Type × Stimulation Condition: $F(1.56) = 1.51$, $p = .23$, $\eta p^2 = .053$-way interaction: $F(2.99) = .36$, $p = .78$, $\eta p^2 = .01$). Collapsed across the two trial types, decision latencies were sensitive to the chances of winning without stimulation ($F(2) = 6.09$, $p < .01$, $\eta p^2 = .18$) and following cTBS to the PMC ($F(2) = 2.47$, $p = .09$, $\eta p^2 = .08$), but not following cTBS to the AG ($F(2) = .48$, $p = .62$, $\eta p^2 = .02$). Follow-up analysis of the Chances of winning × Trial Type interaction revealed that deliberation times increased linearly with the chances of winning in auditory trials ($F(1) = 4.84$, $p = .03$, $\eta p^2 = .15$); whereas a quadric relationship was found in visual trials ($F(1) = 7.033$, $p = .01$, $\eta p^2 = .21$). Thus, the relationship between the chances of winning and deliberation times (which was of a priori interest) was different for visual and auditory trials. Next, we turn to the results of the 3 (Stimulation Condition) × 3 (Chances of Winning) repeated-measure ANOVAs conducted separately for each trial type.

[1] Trials with a 80% chance of winning were not included in the data analysis, because both pilot data and the current data (from the no-stimulation session) showed that responses in these trials were highly automatic: The vast majority of participants always chose the highest bet and response times were very fast.

In visual trials, a significant interaction between Stimulation Condition and Chances of Winning ($F(4) = 2.75$, $p = .03$, $\eta p^2 = .09$) was found (main effect of Chances of Winning: $F(2) = 5.70$, $p < .01$, $\eta p^2 = .17$, main effect of Stimulation Condition: $F(2) = .67$, $p = .51$, $\eta p^2 = .02$). This interaction effect was driven by a systematic influence of cTBS to the AG: Deliberation times reflected the chances of winning following cTBS to the PMC ($F(2) = 6.42$, $p < .01$, $\eta p^2 = .33$) and without stimulation ($F(2) = 6.29$, $p < .01$, $\eta p^2 = .32$), but not following cTBS to the AG ($F(2) = .58$, $p = .57$, $\eta p^2 = .04$, see Fig. 3A). That is to say, following cTBS to the AG deliberation times in visual trials was no longer modulated by the chances of winning.

In contrast, no systematic effect of cTBS to the AG (or to the PMC) upon decision latencies in auditory trials was found. Response times were sensitive to the chances of winning ($F(2) = 3.75$, $p = .03$, $\eta p^2 = .12$), but not significantly influenced by the stimulation condition (main effect of Stimulation Condition: $F(2) = 1.76$, $p = .18$, $\eta p^2 = .06$, interaction term: $F(4) = 1.13$, $p = .34$, $\eta p^2 = .04$, see Fig. 3B).

Betting behavior

Betting behavior was not systematically influenced by cTBS to the AG. No significant main effect of Stimulation Condition was found for either risk adjustment ($F(2) = .76$, $p = .47$, $\eta p^2 = .03$) or overall betting ($F(2) = .58$, $p = .92$, $\eta p^2 = .01$). Betting behavior was similar in visual and auditory trials: No significant main effect of Trial Type (risk adjustment: $F(1) = .02$, $p = .89$, $\eta p^2 = .01$, overall betting: $F(1) = .14$, $p = .71$, $\eta p^2 = .01$) or Trial Type * Stimulation Condition interaction effects (risk adjustment: $F(2) < .89$, $p = .41$, $\eta p^2 = .03$, overall betting: $F(2) = 1.05$, $p = .36$, $\eta p^2 = .04$) were found for either index (see Fig. 4).

Discussion

Previous neuroimaging studies showed that multiple areas within the IPC are activated during the performance of economic choice task (see Liu et al., 2011; Mohr et al., 2010), yet to-date little is known about the specific contributions of these areas to the decision process. We used cTBS to investigate whether the AG subregion of the IPC is causally involved in decision-making under risk, and to test whether the contribution of this area to the decision process is independent from visuospatial attention. We compared choice behavior of healthy subjects on a modified version of the RBT under three conditions: without stimulation, following cTBS to the AG and following cTBS to the PMC (as an active control condition). The task contrasted decision-making behavior in two trial types. *Visual trials* presented the probability of winning visually and posed a high demand for visuospatial attention, while *auditory trials* provided the same information without a visuospatial component. cTBS to the AG significantly and systematically affected decision-making behavior in visual trials. Without stimulation, and following cTBS to the control region, deliberation times reflected the chances of winning (see also Studer et al., 2012; Studer and Clark, 2011), however, this was no longer the case following cTBS to the AG. Inhibitory TMS to the AG thus disrupted the relationship between decision latencies and the probability of winning/losing. In contrast, we found no systematic effect of cTBS to the AG upon decision-making in auditory trials. We note that average decision latencies were overall higher in visual than auditory trials. Could the differential effect of cTBS in auditory versus visual trials have arisen as a consequence of a higher task difficulty in visual trials? If this was the case, a global increase in the decision latencies in visual trials following cTBS to the AG would be expected, which we did not find. Rather, our results indicate that the AG is particularly involved in decision making when encoding of visuospatial representations of decision information is required. In many laboratory decision paradigms, such encoding is necessary to compute an internal representation of the decision situation, which is defined as the first stage of the decision process in

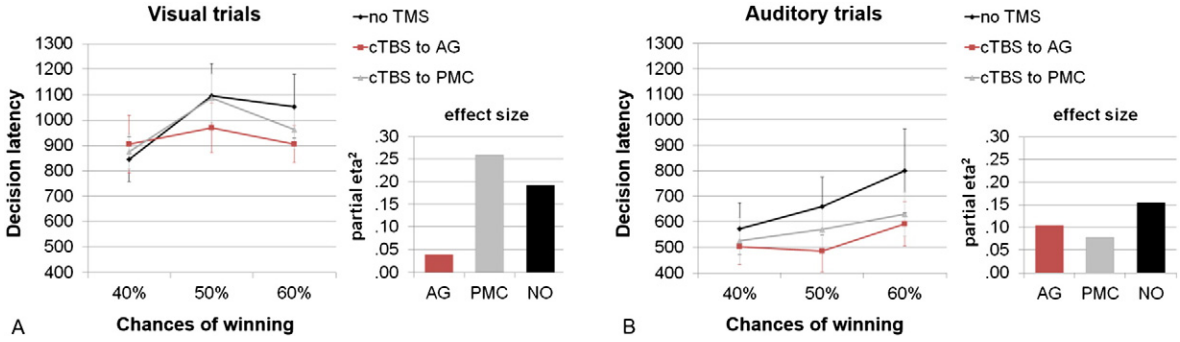

Fig. 3. Modulation of decision latencies by the chances of winning. A — cTBS to the AG significantly affected decision behavior on visual trials. Decision latencies were sensitive to the chances of winning following cTBS to the PMC and without stimulation, but not following cTBS to the AG. The panel on the left shows the average deliberation time for each condition and chance level. Error bars represent SEM. The small panel on the right displays the effect size for each stimulation condition (quadratic contrast). B — No significant effects of cTBS to the AG or the PMC upon decision latencies in auditory trials were observed. The panel on the left shows the average deliberation time for each stimulation condition and chance level. Error bars represent SEM. The graph on the right displays the effect size of the modulation by chance level for each stimulation condition (linear contrast).

psychological and neuroeconomic models (e.g. Rangel et al., 2008). Drawing on an extensive body of research on attentional functions of the AG, we propose that the AG contributes to this subprocess of decision-making by guiding attention to relevant information in the decision display, or more generally speaking, to signals of reward/punishment in the visual environment. The key role of the AG in visuospatial attention outside of a decision-making context is well established. For instance, TMS-induced disruption of AG activity affects performance on visuospatial search tasks (e.g. Göbel et al., 2001; Taylor et al., 2011) and cued attention orientation paradigms (Chen et al., 2012; Heinen et al., 2011), potentially by altering goal-directed salience representations (Zenon et al., 2010). A recent meta-analysis of neuropsychological studies on neglect by Chechlacz et al. (2012) furthermore revealed that damage of the AG is associated with impaired control of attention within objects. The current results suggest that the AG is also responsible for the guidance of visuospatial attention in a decision-making context.

While cTBS to the AG affected decision latencies in the visuospatial condition, we did not find a significant effect upon choice behavior itself. The quality of decision-making thus remained intact. One potential explanation for this result could be that the effect observed for decision latencies was a non-specific consequence of TMS stimulation and that the AG does not in fact contribute to the decision process. This, however, is highly unlikely. First, a non-specific effect of TMS would be expected to manifest in both stimulation conditions; however, the disruption of decision latencies was specific to cTBS to the AG and not found for cTBS to the control region. Secondly, an assumed general TMS-effect is difficult to reconcile with the fact that cTBS to the AG did not induce a general increase (or decrease) in response times, but rather selectively affected the modulation of decision times by the chances of winning. A more likely explanation for the resistance of choice behavior to AG stimulation relates to the mechanisms of repeated TMS (rTMS), including cTBS. rTMS acts by raising the noise level and perturbing, rather than completely suppressing, neural activity in the target area. Indeed, the finding that rTMS affects response times but not performance accuracy is not uncommon and has been observed for a variety of tasks (e.g. Kaller et al., 2011; Koch et al., 2005; Sandrini et al., 2004; Taylor et al., 2011). An alternative explanation would be that the neural network underlying decision-making can compensate for a temporary loss of an area, at least to the degree that the final choice is not affected. Future research might provide more insight into such functional compensation with the decision-making network by combining TMS with neuroimaging.

Our results provide new insights into the functional significance of IPC activations observed in neuroimaging studies (Bach et al., 2011; Berns et al., 2008; Ernst et al., 2004; Labudda et al., 2008; Studer et al., 2012; Symmonds et al., 2011; Vickery and Jiang, 2009), and suggest that the AG is crucially involved in the guidance of attention to relevant decision information in the visual environment. We note that the IPC consists of multiple cytoarchitectonic subdivisions (e.g. Caspers et al., 2006) with differential structural connectivity profiles (Mars et al., 2011; Uddin et al., 2010). In our view, it is highly likely that different IPC subregions play distinct functional roles in decision-making, as found for other cognitive domains [e.g. numerical cognition (Dehaene et al., 2003), memory (Nelson et al., 2010)]. For instance, in a neuroimaging study employing a dual-task design, Vickery and Jiang (2009)

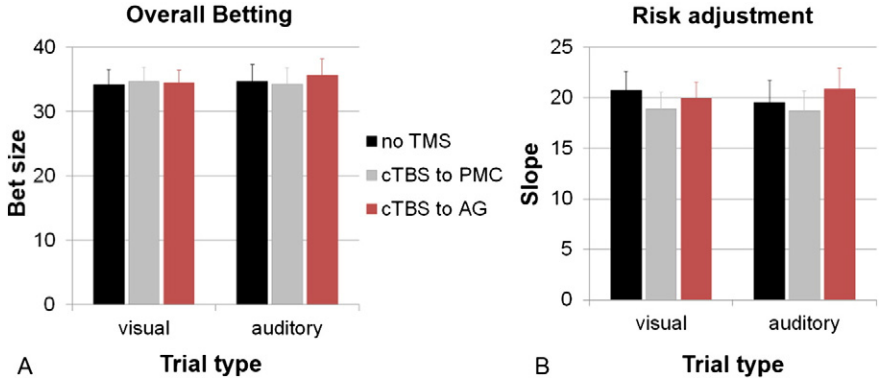

Fig. 4. Betting behavior. No significant effects of cTBS upon the two indexes of betting behavior were found. Graph A displays the overall betting at baseline and following cTBS to the PMC and AG. Graph B shows the average risk adjustment, i.e. the degree to which participants adjusted their bets to the chances of winning, for each stimulation condition. Error bars represent SEM.

found an area in the right IPC – located dorsally to our AG target site – for which activity during a risky choice task could be dissociated from general attentional load. The authors proposed that this area in the right IPC might be involved in integrating past outcomes into the valuation of current choice options. In order to gain a comprehensive understanding of IPC functions in decision-making, it would be valuable for future research to specify the precise contributions of additional IPC subregions.

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