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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

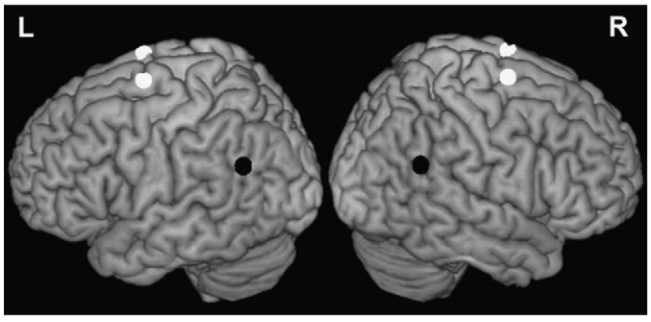

Fig. 1. Stimulation targets. Average normalized stimulation targets in the AG (black) and in the dorsal PMC (white), which was used as a control region.