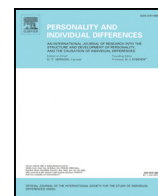




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Cortical alpha asymmetry at central and posterior – but not anterior – sites is associated with individual differences in behavioural loss aversion

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ABSTRACT

Heightened sensitivity to losses, known as loss aversion, is a putative avoidance behaviour, which commonly influences decision-making, particularly in economic scenarios where participants have a 50/50 chance of winning or losing money. Evidence from neuropsychology, EEG and TMS research suggests individual differences in loss aversion may be explained by neural differences in the lateralisation of the right hemisphere. 40 healthy participants underwent an EEG recording during resting state and subsequently performed a behavioural loss aversion task, in which they had an equal chance of winning or losing money. EEG asymmetry in the alpha band at central and posterior sites was associated with individual differences in behavioural loss aversion. This asymmetry was driven by a combination of increased activation in the right hemisphere and decreased activation in the left hemisphere and the site of this asymmetry differed for females and males. These findings are discussed in relation to behavioural avoidance.

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1. Introduction

1.1. Behavioural loss aversion

Human decision making is subject to bias from a range of spurious influences, not least our personality traits and emotional states. Prospect theory (Kahneman & Tversky, 1979) attempts to account for some of these influences and, in turn, individual differences in decision making. A key suggestion of this theory is that individuals are loss averse, that is, we overweight the negative impact of losses in comparison to the positive impact of gains. Research by Kermer, Driver-Linn, Wilson, and Gilbert (2006) indicated that participants overestimated the negative impact of monetary loss on their mood both in the immediate aftermath of the loss and at a later time compared with actual variation in mood following a financial loss. In-keeping with this notion of loss aversion, most people will only accept a 50/50 financial gamble (i.e., a 50% chance of gaining or losing money) if the amount they stand to gain is at least twice as large as that they stand to lose (Kahneman, 2003).

Behavioural loss aversion is traditionally measured using a series of mixed gambles that vary in the magnitude of gains and losses (e.g., Tom, Fox, Trepel, & Poldrack, 2007). Loss aversion is typically calculated by the mathematical parameter Lambda (λ), using the formula: $\lambda = -\beta_{\text{loss}} / \beta_{\text{gain}}$. Both β values are obtained from a logistic regression used to predict the decision made, with gain and loss amounts used as predicting variables. Studies of behavioural loss aversion typically report a λ with a mean value of 2, in-keeping with participants' double-weighting of losses compared to gains (Haigh & List, 2005; Heeren, Markett, Montag, Gibbons, & Reuter, 2016; Johnson & Goldstein, 2003; Post, Van den Assem, Baltussen, & Thaler, 2008; Tovar, 2009). However, slightly lower values have also been observed (e.g., Frydman, Camerer, Bossaerts, & Rangel, 2011; Sokol-Hessener et al., 2009), potentially reflecting methodological variations in the choices offered to participants.

1.2. Loss aversion and the right hemisphere

Neuropsychology research supports the involvement of the right hemisphere in risky decision making, suggesting that individual differences in the neural functioning of the right hemisphere may underpin variation in behavioural loss aversion. Patients with acquired injuries

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to frontal brain areas tend to exhibit a preference for risky decisions with little regard for potential negative consequences, suggesting diminished or absent loss aversion (Rahman, Sahakian, Cardinal, Rogers, & Robbins, 2001). This effect is pronounced for lesions to the right hemisphere, particularly in the right ventromedial prefrontal area (Clark, Manes, Antoun, Sahakian, & Robbins, 2003; Tranel, Bechara, & Denburg, 2002). This involvement receives support from neuroscientific research by Knoch et al. (2006a), who found that healthy participants made riskier decisions on a gambling task after the application of transcranial magnetic stimulation (TMS) to disrupt the right dorsolateral prefrontal cortex (PFC). This effect was not observed when TMS was applied to the left dorsolateral PFC.

1.3. EEG alpha asymmetry and reward sensitive behaviour

Researchers have sought to characterise the source of loss aversion by considering how individual differences in neurobiological traits reflecting reward sensitivity can influence decision making. The hemispheric asymmetry of tonic prefrontal activity, assessed using resting-state electroencephalography (EEG), is thought to be a relatively stable index of behavioural approach and avoidance (Davidson, 2004; Harmon-Jones, Gable, & Peterson, 2010; Tomarken, Davidson, Wheeler, & Kinney, 1992). Tonic cortical activity is typically quantized by measuring the power of alpha-band (8–13 Hz) oscillations (see, e.g., Davidson, 1992). Alpha-band oscillatory activity reflects cortical hypoactivation (Coan & Allen, 2004), such that greater alpha power in one hemisphere (as compared to the other) indicates lower tonic cortical activity in the former (than in the latter). Greater left, relative to right, tonic activity in frontal regions is thought to reflect greater reward approach motivation, whereas greater right (relative to left) frontal activity is thought to reflect avoidance behaviours and disengagement (Davidson, 1992). These asymmetries are thought to arise from the biological processes underlying Gray's (1970) personality systems: the behavioural approach system (BAS), which is sensitive to reward and underlies motivation to approach rewards, and the behavioural inhibition system (BIS), which is sensitive to punishment or fear and can initiate avoidance behaviours (Davidson, 2004; Harmon-Jones, 2004). While a great deal of research has considered frontal alpha asymmetries in relation to psychometric measures of reward sensitivity, particularly Carver and White's (1994) BIS/BAS scales, relatively little work has examined alpha asymmetry in relation to reward related behaviour. Research that has considered reward related behaviour has tended to focus on approach behaviour (e.g. Hughes, Yates, Morton, & Smillie, 2015; Pizzagalli, Jahn, & O'Shea, 2005) and little work has sought to characterise loss aversion specifically.

1.4. EEG asymmetry and avoidance behaviour in infancy

The developmental literature on attachment has consistently linked frontal EEG asymmetries to inhibited/avoidance behaviours in the face of novel / threatening stimuli (see Gander & Buchheim, 2015 for a review). Calkins, Fox, and Marshall (1996) observed greater right (compared to left) frontal activation in 9 month olds, which was associated with increased inhibited exploratory behaviour at 14 months in a group of infants classified as high negative effect, compared to their high positive effect peers. Similarly, Hane, Fox, Henderson, and Marshall (2008) found that four-month-old infants prone to negative reactions were more likely to show avoidance behaviour and reduced approach behaviour in the face of a fearful stimulus at 9 months, which was accompanied by a pattern of greater right (relative to left) frontal EEG asymmetry. Extending this work, Buss et al. (2003) report a link between avoidant behaviours (fear and sadness), relative right asymmetry and higher levels of both basal and reactive cortisol in 6-month old infants in response to a negative affect task.

1.5. Loss aversion and resting state EEG asymmetries

Given the above research, a link between loss aversion, a putative avoidance behaviour, and right frontal alpha asymmetry would be expected. However, research findings in this area have been mixed. Some research has identified a predictive role for right (relative to left) PFC activity in individual risk taking behaviour. Specifically, Gianotti et al. (2009) found that healthy participants with higher resting state activity in the right (compared to the left) PFC showed lower levels of risk averse behaviour on a gambling task. Aversion to risk is generally thought to arise as a result of loss aversion (Kobberling & Wakker, 2005). Similarly, Studer, Pedroni, and Rieskamp (2013) report a relationship between increased right (relative to left) cortical hypoactivity and increased risk-taking behaviour, suggesting diminished loss aversion. Interestingly, they also highlight a relationship between increased BIS scores and decreased risk taking behaviour. Work by Schutter and van Honk (2005), in contrast, has examined the relationship between disadvantageous decision making on the Iowa Gambling Task and the ratio between frontal low-frequency oscillations (indicating cortical inactivity) and high-frequency oscillations (indicating cortical activity) during resting state. While higher values of the frontal EEG ratio were associated with more disadvantageous decision making, this effect was global and was found across both hemispheres. Additionally, the ratio of low- to high-frequency oscillations over posterior cortical regions was most significantly associated with disadvantageous decision making. Finally, Telpaz and Yechiam (2014) found that individuals with stronger left- than right-hemispheric frontal activity showed increased risk-taking on a mixed gambling task, relative to participants characterised by stronger right than left tonic activity.

1.6. Hypotheses

Given the mixed findings represented by the above studies and the links between frontal asymmetry and withdrawal behaviour and punishment avoidance, we sought to investigate the relationship between cortical asymmetry and loss aversion. We predicted that we would find an association between rightward asymmetry (i.e., stronger tonic activity in the right as compared to the left hemisphere) and greater loss aversion, as assessed by the loss aversion parameter λ . We further hypothesised that this effect would be most pronounced in frontal regions, given the neuropsychological and neuroscientific evidence supporting the role of the right PFC in avoidance behaviours. Given the existent inconsistent reports on the location of asymmetry indices, we also considered asymmetry values at central and posterior sites in relation to loss aversion.

2. Methods

2.1. Participants

$N = 41$ healthy participants (23 female; mean age $M = 22.8$ years, $SD = 4.33$ years) volunteered their time in exchange for course credit. One participant was excluded due to excessive data loss during the EEG analysis, leaving a final $N = 40$. All participants were free of past or present neurological or psychiatric disorders. Data from the same participants have already been reported in Voigt, Montag, Markett and Reuter (2015). The study protocol complied with the Declaration of Helsinki and was approved by the local ethics committee of the University of Bonn.

2.2. Electrophysiological recordings

Resting-state EEG was recorded from nine channels (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) with Ag/AgCl electrodes using a BrainProducts System (BrainProducts, Munich, Germany) that consisted of aV-Amp 16 amplifier and VisionRecorder software. AFz was used as a ground electrode.

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