The neural dynamics of reward processing during sealed-bid second-price auctions

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Alice Newton-Fenner

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Table of Contents

Declaration

No part of this work was submitted in support of any other applications for degree or qualification at this or any other university or institute of learning. This thesis is submitted in fulfilment of the conditions for a PhD by published papers. In accordance with the University of Liverpool guidelines and regulations the experimental chapters (Chapters 4 – 6) of this thesis will take the form of journal article manuscripts of which I am the first author, which have either been published during the preparation of this thesis, or are undergoing peer review at a peer-reviewed journal. Specific details regarding the contribution of authors are given at the beginning of each chapter, as required.

Publications relating to the work presented in this thesis:

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List of abbreviations

In alphabetical order:

2AFC	Two-alternative forced-choice
ACC	Anterior cingulate cortex
AI	Anterior insula
ALE	Activation likelihood estimation
ANOVA	Analysis of variance
BDM	Becker-DeGroot-Marschak auction
BESA	Brain electrical source analysis
BOLD	Blood oxygenation level dependent
CT	Computed tomography
dlPFC	Dorsolateral prefrontal cortex
ECG	Electrocardiographic
EEG	Electroencephalography
EMG	Electromyographic
EOG	Electrooculographic
EPI	Echo Planar Imaging
ERP	Event-related potential
EUT	Expected Utility Theory
fERN	Feedback error-related negativity
fMRI	Functional magnetic resonance imaging
FN	Feedback negativity
FPSB	First-price sealed-bid
FRN	Feedback-related negativity
FSN	Fail-safe number
GLM	General linear modelling
GRE	Gradient refocused echo
HRF	Haemodynamic response function
ICA	Independent component analysis
LPP	Late positive potential
MEG	Magnetoencephalography
MFN	Medial-frontal negativity

MNI	Montreal Neurological Institute
MTL	Medial temporal lobe
OA	Open ascending
OD	Open descending
OFC	Orbitofrontal cortex
PCA	Principal component analysis
PCC	Posterior cingulate cortex
PET	Positron emission tomography
PFC	Prefrontal cortex
pgACC	Pregenual ACC
PPC	Posterior parietal cortex
RET	Revenue equivalence theorem
RewP	Reward positivity
RF	Radio frequency
ROI	Region of interest
RPE	Reward prediction error
SD	Standard deviation
SEM	Standard error of mean
sgACC	Subgenual ACC
SNR	Signal to noise ratio
SPSB	Second-price sealed-bid
SV	Subjective value
VA	Vickrey auction
vlPFC	Ventrolateral prefrontal cortex
vmPFC	Ventromedial prefrontal cortex
VPP	Vertex positive potential
VREF	Vertex electrode
VS	Ventral striatum
VTA	Ventral tegmental area
WTA	Willingness to accept
WTP	Willingness-to-pay

List of figures

List of tables

Abstract

During economic decision-making, choice alternatives are evaluated and compared, and the option yielding the greatest expected value is selected. Appraising the resulting decision outcomes, and comparing expected rewards to received rewards, are essential for the updating of subjective values and the adaption of subsequent decision-making behaviours. This thesis synthesised neuroeconomic fMRI research of economic valuation, and examined the spatiotemporal dynamics of value processing in the brain, during incentivised demand-revealing auction environments.

Brain processes related to subjective valuation and reward processing were investigated using the Becker-DeGroot-Marschak (BDM) task, a second-price sealed-bid auction common in fMRI research, and the strategically equivalent Vickrey auction (VA), a socially competitive paradigm popular with online retailers. Three experimental chapters combine a meta-analysis of fMRI studies with two primary EEG studies to exploit the methodologies' respective high spatial and temporal resolutions. A systematic review and activation likelihood meta-analysis was conducted on fMRI studies implementing the BDM task to measure subjective value. Subsequently, EEG recordings and event-related potential (ERP) analysis were used to investigate the neural mechanisms underlying reward processing of decision outcomes.

Findings offer succinct empirical support for the ventral striatum and ventral medial prefrontal cortex as the core structures responsible for automatic formation of economic value, separate from the hedonic aspects of reward. The meta-analysis also provided evidence of the selective involvement of inhibition-related brain structures during active economic valuation. Further, reward-related ERPs were selectively elicited during the auction outcome period for both tasks. A feedback-related negativity was elicited in both auctions, and differentiated between more and less relatively advantageous win outcomes. The P300 component showed

distinct sensitivities to outcome salience, social context, and value, as defined by market price and subjective willingness-to-pay.

The current thesis demonstrated the neural representation of economic valuation and reward processing in incentive-compatible contexts, recorded by means of EEG and fMRI. A subset of the core brain valuation network showed a domain general and automatic increase in BOLD activation in line with willingness-to-pay values. Further, multiple distinct ERPs differentially encoded bid outcomes during the two auction tasks, with distinct cortical responses to valence, motivational significance and social context of auction outcomes.

1. General Introduction

1.1. Economic theory of decision-making

1.1.1. Quantification of value

Value-based decisions are an essential and ubiquitous part of everyday life. Choosing between options – from what to eat for breakfast, to which brand of shampoo to buy, to what career to pursue – requires the weighing of each choice's attributes, benefits and drawbacks, and the conjunction and ranking of option values, before selecting the one considered to be of greatest advantage. In philosophical value theory, every object and event can be characterised as holding either instrumental value, where the item in question has utility that is a means to an end, or intrinsic value, where the item is an end in itself (Olson, 2013). An example of a device with instrumental value is a dishwasher, as if it could no longer wash dishes it would lose its value to the consumer. Conversely, happiness and pleasure are thought to have intrinsic value as they are desirable for their own sake (Weber, 2013). Intrinsic value is adjacent to the concept of aesthetic value, where an item possesses the capacity to elicit pleasure (positive value) or displeasure (negative value) when appreciated or experienced aesthetically (Goldman, 1990, 2018).

The definition of value can vary depending on the context, from the hedonic understanding of gratification and beauty to the utilitarian space of function and economic worth. Subjective valuations (SV) are the private internal states of people's minds, and most are a combination of many different types of value. For example, a luxury car has the financial value of a high retail price, the functional value of high quality performance, the hedonic value of being enjoyable to drive, and the social value of the prestige and status that ownership brings (Wiedmann, Hennigs, & Siebels, 2007).

In practice, the definition of value in any given context is often dependent on the method of measurement, as the methodology and framing of research questions impacts how value is understood. For example, desirability, likeability and pleasantness ratings tasks elicit correlated but distinct results to economic bids and ratings of intention to purchase (Roberts et al., 2018). Additionally, some of the most common methods of eliciting SV, such as preference statements, two-alternative forced-choice tasks (2AFC), attractiveness ratings and liking scales, can also face issues of low reliability and real-world applicability. Research has shown that hedonic scores are not necessarily comparable between participants (Lange, Martin, Chabanet, Combris, & Issanchou, 2002) or appropriate for informing marketing strategies (Murphy, Allen, Stevens, & Weatherhead, 2005; Voigt, Murawski, & Bode, 2017).

In economic contexts, SV is commonly elicited using the metric of willingness-to-pay (WTP): the maximum amount of wealth that a consumer would be willing to part with in exchange for a good or service being sold (Barrot, Albers, Skiera, & Schäfers, 2014; Noussair, Robin, & Ruffieux, 2004; Plassmann, O'Doherty, & Rangel, 2007). In this framework, all decision options can be ranked on the single linear scale of currency, regardless of their sensory properties (e.g. tastes can be compared to sounds), dimensions of value (e.g. the immediacy and probability of rewards can be incorporated into the singular value) and valence (e.g. good and bad outcomes can be directly compared) (Steiner & Hendus, 2012). WTP is often used in economic and psychological studies examining valuation processes, where a participant’s stated WTP is recognised as a direct and public declaration of their private SV.

WTP can be measured directly or indirectly, and can ascertain a consumer's real or hypothetical WTP. Direct measures include auctions and open-ended questions, whereas indirect methods include choice-based conjoint analysis and discrete choice experiments (Bijlenga, Bonsel, & Birnie, 2011; Schmidt & Bijmolt, 2020). Real WTP measures entail a financial commitment, while hypothetical measures of WTP do not impose any financial consequences for participants’ decisions but instead pose the hypothetical question: “if given the opportunity to buy this product, how much would you pay for it?”. An implicit assumption of any value-based decision-making research is for the lab-based findings to accurately reflect real-world SV attribution (Plassmann et al., 2007). Meta-analyses of WTP paradigms have shown that hypothetical purchasing scenarios produce consistent behavioural overestimations of WTP in comparison to that of real WTP measures: this phenomenon is called the hypothetical bias (Foster & Burrows, 2017; List & Gallet, 2001; Little, Broadbent, & Berrens, 2012; Murphy et al., 2005; Schmidt & Bijmolt, 2020). Furthermore, this hypothetical bias is considerably stronger in indirect measures of WTP compared to direct methods (Schmidt & Bijmolt, 2020).

Finally, even within the domain of direct measures of real WTP, some methods can still produce unreliable results due to being not incentive-compatible (Breidert, 2007; Breidert, Hahsler, & Reutterer, 2015). If the parameters of a methodology do not induce truth telling in the participants through appropriate incentives (such that it would be strategically disadvantageous to under or over state their WTP), researchers cannot be certain that the WTP values are representative of SV and are not altered by the participant’s private strategy (Acquisti, Brandimarte, & Loewenstein, 2015; Wertenbroch & Skiera, 2002). The most widely used direct and incentive-compatible measures of real WTP are the Vickrey auction (VA) (Vickrey, 1961) and the Becker-DeGroot-Marschak auction (BDM) (Becker, DeGroot, & Marschak, 1964) (see sections 2.1.1 and 2.1.2).

1.1.2. Expected Utility Theory

Expected Utility Theory (EUT) is a normative economic model of rational choice under risk and uncertainty (Von Neumann & Morgenstern, 2007). EUT dictates that in conditions where one is not certain of the outcomes which will result from one's actions, the rational option is to choose the action with the highest expected utility (Grant & Van Zandt, 2007; Mongin, 1998). The utility of each available action option is calculated as a weighted average of the utility value x of the given outcome i and the probability p of outcome i occurring, such that the expected value of an outcome can be expressed as $x_i \cdot p_i$. The resulting expected utilities of all possible actions are ranked, and the choice option(s) with the greatest expected utility value is executed.

There are several intrinsic axioms central to the predictions of EUT: completeness, transitivity, independence and continuity. Completeness dictates that for any two options A and B, either one must be preferred over the other, or the decider must be indifferent between them. Transitivity states that if option A is preferred to option B, and option B is preferred to option C, then option A must be preferred to option C. The axiom of independence posits that if the decider is indifferent between two options A and B, they will remain indifferent between them regardless of context. Finally, continuity posits that "for any A, B and C, if A is preferred to B, and B is preferred to C, there exists a probability distribution of receiving either A or C, which is equivalent to receiving B with certainty"; this is designed to disallow a discontinuous jump in preferences between options (Caplin & Leahy, 2001; Grant & Van Zandt, 2007; MacCrimmon & Larsson, 1979).

EUT serves as a useful reference guide in theoretical economics for situations where decision makers are uncertain of respective payoffs of choice options. However, it assumes an accurate mental representation of respective outcomes' statistical likelihoods (Hampton, 1994). There are many cases of real-world decision-making where this is not the case. For instance, it is widely observed that individuals over-weigh the probability of unlikely events occurring and under-weigh the probability of nearly certain events occurring (Friedman, Isaac, James, & Sunder, 2014): examples of overestimating the probability of unlikely events include playing the lottery and fears of plane crashes and shark attacks. Inconsistent behaviour such as this cannot be explained by EUT. As a result, the investigation of apparently irrational behaviours of decision makers was subsequently developed into Prospect theory.

1.1.3. Prospect Theory

The foundations of neuroeconomics lie in Prospect theory and the pioneering experiments of Daniel Kahneman and Amos Tversky. Prospect theory is a descriptive behavioural model that describes how people weigh up uncertain probabilistic options when decision-making under risk (Kahneman & Tversky, 2013; Tversky & Kahneman, 1992). It introduces the concept of a ‘probability weighting function’ (Morewedge & Giblin, 2015), where the SVs of the decision outcomes depend on the individual’s reference point, and are weighted by a nonlinear function of the objective probabilities (Kahneman & Tversky, 2013). Prospect theory replaces the utility function of EUT with a value function over gains and losses which are relative to a subjective reference point rather than absolute outcomes (van Osch, van den Hout, & Stiggelbout, 2006). The reference point is viewed as the status quo, or a zero-reference point (e.g. current wealth), and so any outcome that is less than the status quo is perceived as a loss, and an outcome that is greater than the status quo is perceived as a gain. The dependence on reference points can create framing effects, in which different values are assigned to the same prospect depending on which reference point is cognitively prominent (Rangel, Camerer, & Montague, 2008). Framing effects are illustrated in thought experiments such as the Allais paradox (Kühberger & Gradl, 2013), where two logically equivalent scenarios are presented descriptively differently, causing contradictions in people's choices (Tversky & Kahneman, 1989).

In Prospect theory, the value function is S-shaped, being concave in the gain domain and convex in the loss domain, as can be seen in Figure 1.1.1.1. The curvature of the value function implies different reactions to risk in the two domains, with risk aversion behaviours being seen more often in the gain domain, and risk-seeking behaviours seen in the loss domain (H. Levy & M. Levy, 2002; Levy, 1992; M. Levy & H. Levy, 2002). Risk attitude is an individual's stated preference between the options of a guaranteed outcome and a (potentially more/less profitable) gamble (Kahneman & Tversky, 2013; Tversky & Kahneman, 1992). For example, in the gain domain, people are more likely to accept a guaranteed outcome of £80 than select an 80/20 gamble of £100, whereas in the loss domain, people are more likely to select an 80/20 gamble of £100 loss than accept a guaranteed loss of £80.

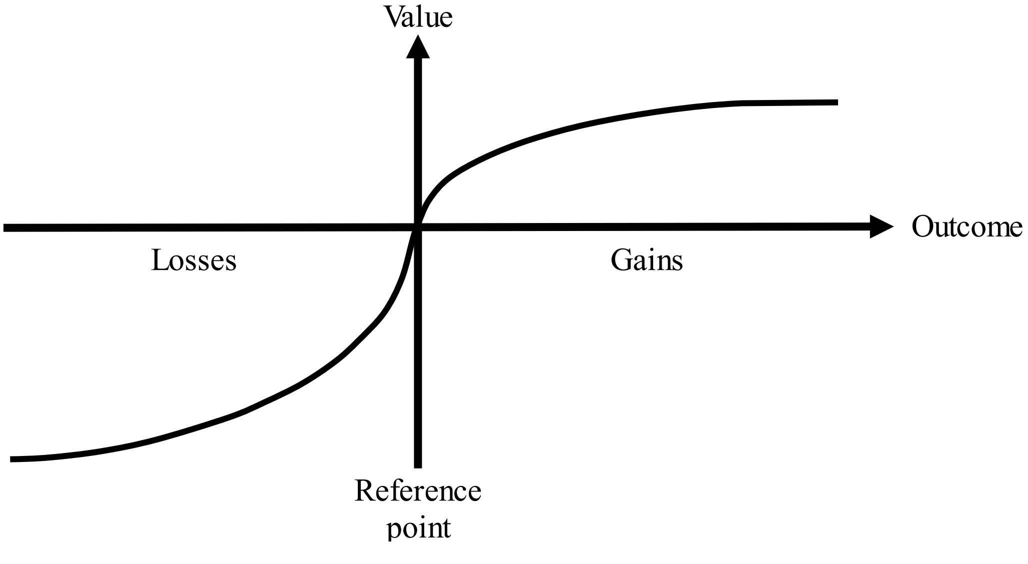

Figure 1.1.1.1 Graphical representation of the Prospect theory value function.

Furthermore, the value function exhibits the psychophysics of diminishing sensitivity: the impact of a marginal change in value becomes less cognitively impactful the further away it occurs from the original reference point (Schwartz, Goldberg, & Hazen, 2008; Werner &

Zank, 2019). For example, the difference between a gain or loss of £50 and a gain or loss of £100 is more cognitively impactful than the difference between a gain or loss of £10,050 and a gain or loss of £10,100. As can be seen in Figure 1.1.1.1, the value function curve is also steeper in the loss domain than in gains, eliciting a cognitive bias called loss aversion. Loss aversion occurs during mixed gain/loss risky decisions, where the disutility of a potential loss is more cognitively prominent than the utility of a potential gain of equal (or comparable) value. It is encapsulated in the expression "losses loom larger than gains" (Kahneman & Tversky, 2013). For example, people will typically choose a guaranteed outcome of £0 over a 50/50 gamble of winning/losing £100. Loss aversion is an individual difference parameter, as levels of loss aversion attitudes vary between individuals.

A common manifestation of loss aversion is the cognitive bias known as the endowment effect: the ascription of greater value to items in one's possession merely because of ownership (Marzilli Ericson & Fuster, 2014). The endowment effect is shown experimentally through a difference between the amount individuals are willing to purchase an item for versus the amount they would be willing to sell an equivalent or identical item for (Kahneman, Knetsch, & Thaler, 1990). The property of ownership (and even pseudo-ownership in some cases) adds utility to the item, increasing its economic value to the owner. The endowment effect violates the EUT axiom of independence, as the ownership context shifts the individual's reference points and influences valuations (Krigolson, Hassall, Balcom, & Turk, 2013). In addition to perceived ownership, utility can also be derived from social cues, such as how one's performance fairs against others (Fehr & Schmidt, 1999), and the maintenance of a good social image (Bénabou & Tirole, 2006). Prospect theory suggests that individual preferences are subjective and context dependent, with values of items changing between people and within people over time (Jones, Childers, & Jiang, 2012). Expected utilities are continuously being updated to keep up with changing environments and preferences.

1.1.4. Auction Theory

Auction theory is an applied branch of economics which deals with how people behave in auction markets, and how this behaviour is determined by the properties of auction parameters (Klemperer, 1999; Krishna, 2009). Auctions are defined as public transactions with a specific set of rules pertaining to resource allocation (goods, services or property) according to participant bids. There are many sets of rules and designs for auctions, and areas of study typically revolve around the efficiency of a given auction design, optimal and equilibrium strategies of the players, price discovery and revenue comparison (Milgrom & Weber, 1982). Auctions are a common paradigm used in many industries, such as real estate sales (Quan, 1994), oil drilling rights (Hendricks & Porter, 1988), privatisation of public sector companies (López-de-Silanes, 1997), and the sale of licences for the use of the electromagnetic spectrum (Madden, Sağlam, & Morey, 2010).

Auctions are characterised as games with incomplete information, as each bidder will possess the private information related to how much she values the item for sale, which is deliberately not shared with the other bidders or the seller. Private information can be referring to SVs of a given auction item, such as how much a person likes a house, or knowledge of objective valuations of the auction item, such as confidential surveys of the property (Kagel & Levin, 1993; Milgrom & Weber, 1982). Most auction items have both private and common values: for example, the bid value submitted for a painting may be a combination of how much a bidder likes it (private value) and the resale value or prestige of owning it (i.e. how much others like it).

Auctions come in many different types, each with their own set of rules, iterations and corresponding optimal strategies. There are four standard single unit auction types (1 – 4), and two further more peculiar mechanisms (5 & 6) (Milgrom & Weber, 1982):

1. **Open ascending auction** (OA) – examples include the English auction. Players offer bids of increasing value until all but one player has dropped out, at which point the last remaining player pays the amount equal to their final bid. No payments are required for other players. The OA auction is the most well-known auction format, commonly used to sell antiques and art.
2. **Open descending auction** (OD) – examples include the Dutch auction. Starting at a high asking price, the price is lowered incrementally by the auctioneer until a player bids, and at that point they commit to paying the current price. No payments are required for other players. The OD format is most commonly used to sell perishable goods, such as flowers and fish.
3. **First-price sealed-bid auction** (FPSB) – also known as a blind auction. All players simultaneously and privately submit a single bid, all bids are compared and the player with the highest bid wins and pays the price equal to their bid. No payments are required for other players. The FPSB format is typically used for estate sales.
4. **Second-price sealed-bid auction** (SPSB) – examples include the Vickrey and BDM auctions (see sections 2.1.1 and 2.1.2). All players simultaneously and privately submit a single bid, all bids are compared and the player with the highest bid wins but pays the price of the second highest bid. No payments are required for other players. The online auction giant eBay uses a modified version of a SPSB format.
5. **Reverse auction** – multiple sellers compete for the business of a single buyer, all players placing bids of decreasing value for the price at which they are willing to sell their goods/services. The seller offering the lowest price wins the auction and sells their good for the price they bid. No payments are required for other players. The reverse auction format is commonly used by large corporations and governments as a competitive procurement method for raw materials, supplies, and contracts.

6. **Bidding fee auction** – also known as a penny auction, bidding fee auctions are similar to OA formats, except all players must pay a non-refundable fee to place a bid. The seller therefore profits from the payment of the winning bid and the fees charged to place each bid.

With the wide variety of auction paradigms available, sellers naturally want to ascertain which type will yield the highest sale for their goods. The first formal application of Game theory principles to auction settings was conducted by Willian Vickrey in the 1960's, with the development of the Revenue Equivalence theorem (RET) (Myerson, 1981; Riley & Samuelson, 1981; Vickrey, 1961). The RET posits that, if a given number of risk-neutral bidders have independent valuations that are drawn from a common distribution, all four of the standard auction types will produce the same final sales price (Klemperer, 2000; Myerson, 1981; Riley & Samuelson, 1981). Bidders will learn to adapt their behaviour depending on the paradigm, such as bidding less than their true SV, referred to as bid 'shading' (Milgrom & Weber, 1982; Vickrey, 1961).

Auction paradigms bring together intellectual and affective demands on the players, with cognitive workload and emotional arousal both influencing bidding behaviour (Adam, Astor, & Krämer, 2016; Adam, Krämer, & Müller, 2015; Agarwal & Malhotra, 2005; Lieberman, 2007; Turel, Serenko, & Giles, 2011; van den Bos et al., 2008). In the open auctions (1 & 2), the behaviour of other bidders can be observed by everyone else. For the OD auction, the maximum willing to pay value of each player is revealed when they drop out, while for the OA auction, incremental opponent bids indicate common values, especially if several players bid the same value at the same time. Conversely, in the sealed-bid auctions (3 & 4), each player has no information about the other players' behaviour during the auction. It is only through repetitions of the auctions that players learn about their competitors. Social competition can change how people make decisions and evaluate outcomes. Defeating the competition to win an auction, and the satisfaction that comes with the win, holds its own utility termed the "joy of winning" (Astor, Adam, Jähnig, & Seifert, 2013), which adds to the overall utility of the item (Chen, 2011). The bidders are also not in a situation of isolated decision-making, but their choices impact other bidders' payoffs, and vice versa. In auctions with back and forth bidding or multiple rounds of auctions on similar items, competitors' bids can be used as a valid social signal as an indication of each bidder's individual private value, and collectively pointing to the good's common value (Toelch, Jubera-Garcia, Kurth-Nelson, & Dolan, 2014). Bidders can update their SVs accordingly, where low competition typically reduces WTP values and high competition increases WTP values. Importantly, this adaption of behaviour is specific to social situations: van den Bos et al. (2008) showed that auction participants submitted significantly higher bids when competing against other humans, but not if the opponents were computers.

The introduction of competition into auction-like environments evokes greater emotional responses. These can influence decision-making, often resulting in suboptimal strategies (Adam et al., 2015; Chen, 2011; Flynn, Kah, & Kerschbamer, 2016; Toelch et al., 2014). Increasing the number of bidders (and therefore increasing the level of social competition) results in participants bidding more aggressively (Delgado, Schotter, Ozbay, & Phelps, 2008). Emphasis on competition during an auction can boost overbidding (Park & Bradlow, 2005) and bid frequency (Kamins, Noy, Steinhart, & Mazursky, 2011). The effect of competition and resulting spite from losing can lead to deviations from logic and can result in monetary losses and opportunity costs (Kagel & Levin, 1993; Kagel, Levin, Battalio, & Meyer, 1989; Ku, Malhotra, & Murnighan, 2005). Suboptimal bidding strategies and outcomes such as the 'winner's curse' have been widely seen in auctions, being a persistent phenomenon even with experienced and professional auction participants (Dyer, Kagel, & Levin, 1989; Garvin & Kagel, 1994). The 'winner's curse' refers to when, due to emotions or incomplete information, the winning bid in an auction exceeds the intrinsic value or true worth of an item. The winner therefore ends up winning the auction but making a loss overall. The ‘winner’s curse’ has been observed in auctions for oil drilling rights in the Gulf of Mexico (Capen, Clapp, & Campbell, 1971), 3G spectrum auctions (Binmore & Klemperer, 2002) and baseball free agency (Blecherman & Camerer, 1998), as well as in industries such as book publishing (Dessauer, Dunbar, Brownstone, & Franck, 1982), construction (Dyer & Kagel, 1996), and corporate takeovers (Roll, 1986).

Most auction houses have now moved online. Beyond the pragmatic benefits of lower operational costs, no geographical limitations and reaching a wider population of potential bidders, this shift to an online marketplace has also shifted the dynamics of auctions themselves. No longer can a bidder ‘eye up the competition’, physically examine the items they are about to bid on, or be caught up in the competitive and fast-paced atmosphere in the room. Furthermore, the information available is commonly limited and publicly available, and the auction itself can last several days or even weeks (Huang, Wu, Wang, & Boulanger, 2011). These factors all have influences on variables critical in auction theory, such as symmetry of information, risk neutrality, independence of bids and common/private valuation (Klemperer, 1999, 2000). The social influences and competitive behaviour dynamics is clearly an important aspect of these situations, but this area has not yet received much attention in neuroeconomics.

1.2.Neuroeconomics and decision-making in the brain

The primary objective of neuroeconomics is to combine the disciplines of microeconomic theory, computational neuroscience and the psychology of decision-making in pursuit of answering fundamental questions regarding the representation and processing of preferences in the brain. In neuroeconomics, SV is defined as an averaged firing rate of certain neuronal populations coding behavioural preferences. Therefore, it follows that the level of neuronal activity in such regions would be proportional to the participant- and stimulus-specific SV amount obtained using a given SV measuring task (Clithero & Rangel, 2014; Rangel et al., 2008). Accordingly, many neuroeconomic studies seek to isolate SV neural mechanisms from the rest of the choice circuitry, such as that involved in choice cost valuation, arousal, motor preparation and attention processing (Maunsell, 2004).

The majority of behavioural and computational models of decision-making assume there to be five distinct stages: representation, valuation, action selection, outcome evaluation, and learning (Rangel et al., 2008). Neuroeconomic investigation often focuses on how SV and reward processing are impacted by contextual factors, or 'value modulators', such as risk level, time delays, social situation, pharmacology, personality and emotion (Rangel et al., 2008). The scope of this thesis focuses on the valuation and outcome evaluation stages under conditions of risk and uncertainty, specifically economic value within the goal-directed valuation system in Chapter 4, and reward processing during outcome evaluation in socially competitive auctions in Chapters 5 and 6.

1.2.1. Dopamine and reward prediction error

When there is a difference between an obtained reward and the expected reward, be it positive or negative, the brain quantifies the reward prediction error (RPE), and updates SVs accordingly (Gazzaniga, Ivry, & Mangun, 2013; Gehring, Goss, Coles, Meyer, & Donchin, 1993). The neurotransmitter dopamine has been hypothesised as the neural marker of RPE in reward-based learning (Paulus & Stein, 2006; Schultz, 1998, 2002). In this model, dopamine is a teaching signal that represents the 'violation of expectation', and the activation of dopaminergic neurons is dependent on the size of the subjective violation of the expectation of the reward, and not on the objective size of the reward itself (Dayan & Balleine, 2002; Dayan & Niv, 2008).

Anatomically, the dopamine reward system is vast: dopaminergic cells are found throughout the midbrain, and have axonal projections to several cortical and subcortical areas. The substantia nigra pars compacta and the ventral tegmental area (VTA) are two of the primary loci of dopaminergic neurons (Gazzaniga et al., 2013). From these brainstem nuclei, dopaminergic neurons project through two pathways: the mesolimbic and the mesocortical pathways (Fields, Hjelmstad, Margolis, & Nicola, 2007). The mesolimbic pathway connects the VTA to structures involved in emotional processing, including the nucleus accumbens of the basal ganglia, the amygdale, the hippocampus, and the anterior cingulate cortex (ACC). The mesocortical pathway projects to the neocortex, and is particularly strongly connected to the medial portions of the frontal lobe and the orbitofrontal cortex (OFC) (Papageorgiou, Baudonnat, Cucca, & Walton, 2016). In nonhuman animal studies, dopamine neurons have been shown to encode RPEs (Schultz, 1998, 2022), decreasing in activity when an expected reward is delayed (Roesch, Calu, & Schoenbaum, 2007; Roesch & Olson, 2004) or omitted (Bayer & Glimcher, 2005; Schultz, 1998).

1.2.2. The brain valuation system

Multiple reviews (Delgado, 2007; Grabenhorst & Rolls, 2011; Kable & Glimcher, 2009; Knutson & Cooper, 2005; Kringelbach & Rolls, 2004; Kuhnen & Knutson, 2005; Montague & Berns, 2002; O’Doherty, 2004, 2014; Padoa-Schioppa & Conen, 2017; Peters & Buchel, 2010) and functional magnetic resonance imaging (fMRI) meta-analyses (Bartra, McGuire, & Kable, 2013; Clithero & Rangel, 2014; Jauhar et al., 2021; Lebreton, Jorge, Michel, Thirion, & Pessiglione, 2009; Levy & Glimcher, 2012; Luo, Eickhoff, Hetu, & Feng, 2018; Martins et al., 2021; Morelli, Sacchet, & Zaki, 2015; Oldham et al., 2018; Silverman, Jedd, & Luciana, 2015) have identified a large and diverse network of brain regions thought to be responsible for various aspects of value-based decision-making. The brain valuation system incorporates structures in the occipital, temporal and parietal cortices, including the ventral striatum (VS) and the ventromedial prefrontal cortex (vmPFC), as well as the posterior cingulate cortex (PCC), dorsolateral prefrontal cortex (dlPFC), OFC, anterior insula (AI), hippocampus, amygdala, insula, and ACC.

Bartra and colleagues (2013) demonstrated two distinct patterns of regional blood-oxygen-level-dependent (BOLD) signal changes during SV: a non-linear, ‘U-shaped’ function where brain activity increases with the level of arousal independent of valence, and a linear function where brain activity monotonically increases in line with SV over the entire value range. The two proposed patterns can be seen in Figure 1.2. In their meta-analysis, the bilateral AI, dorsal medial PFC, thalamus and the dorsal and posterior striatum exhibited U-shaped response profiles during valuation tasks, suggesting their role in salience, motor preparation and attentional processing. Conversely, the vmPFC, the anterior VS and the PCC consistently showed positively signed effects between SV and BOLD activity, suggesting that these areas are critically involved in the computation of SV for both appetitive and aversive stimuli. Further, the vmPFC and the VS independently responded to SV when choice options were presented and also when outcomes were delivered, suggesting a core role in both the initial valuation and outcome evaluation stages of decision-making. It is hypothesised that the representation of SV during these two stages of decision-making is computed similarly, as the predicted value of a choice option is needed in order to compute a RPE, and the value of received outcomes are used to establish SVs for future decisions (Kable & Glimcher, 2009). The findings from these meta-analyses therefore implicate a common set of brain regions in the evaluation of choice options and choice outcomes, and propose that the vmPFC and VS form a 'core valuation system' in the brain (Bartra et al., 2013).

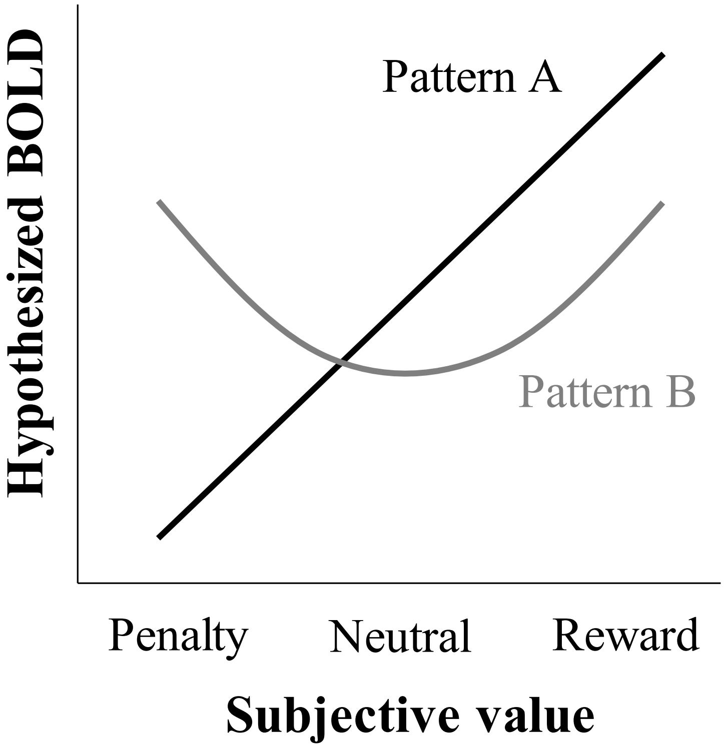

Figure 1.2. Two hypothetical profiles for regional BOLD activity as a function of SV. Figure from Bartra et al. (2013).

There is also converging evidence that the brain valuation system is automatic and domain general, with similar patterns of vmPFC and VS activation in the absence of value-based choices (Lebreton et al., 2009; Levy, Lazzaro, Rutledge, & Glimcher, 2011), and for both primary rewards (such as food) and secondary rewards (such as money or social praise) (Delgado, 2007; Grabenhorst & Rolls, 2011; Kable & Glimcher, 2009; Knutson & Cooper, 2005; Levy & Glimcher, 2012; Montague & Berns, 2002; O'Doherty, 2004; Peters & Buchel, 2010). These findings are in line with the common neural currency hypothesis, which purports that a unitary system represents a 'general-purpose' SV across different types of stimuli, allowing for the cross-category comparison of choice options (Brosch & Sander, 2013; Chib, Rangel, Shimojo, & O'Doherty, 2009; Kim, Shimojo, & O'Doherty, 2011; Levy & Glimcher, 2012).

1.2.3. Risk and uncertainty

Most decisions involve some level of risk. For some choices, the probabilities of each of the outcomes are known, such as a 50/50 coin flip gamble, and so the decision is one of pure and static risk. However, in many instances in real life, decision makers do not have complete information regarding the risk parameters: the choices are ambiguous, or the respective probabilities of the outcomes are unknown, and so they are in a situation of uncertainty. During choice, the brain incorporates the respective perceived likelihoods of receiving each option into the computations of their distinct value signals. Behavioural studies have shown that people generally avoid choices that are ambiguous in comparison to certain outcomes (Camerer & Weber, 1992). It therefore follows that level of risk or uncertainty in a given choice option could modulate the computation of the choice value signal in the brain (Levy, Snell, Nelson, Rustichini, & Glimcher, 2010).

Neuroimaging evidence investigating the neural encoding of the level of known risk of a given outcome, separate from the SV of that outcome, has found increased activation in line with increasing risk level in the lateral OFC and ventrolateral prefrontal cortex (vlPFC) (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Huettel, 2006; Huettel, Song, & McCarthy, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006; Tobler, O'Doherty, Dolan, & Schultz, 2007), the bilateral VS (Diekhof, Kaps, Falkai, & Gruber, 2012; Preuschoff, Bossaerts, & Quartz, 2006; Tom, Fox, Trepel, & Poldrack, 2007; Yacubian et al., 2007), AI (Huettel et al., 2005;

Kuhnen & Knutson, 2005), and posterior parietal cortex (PPC) (Huettel et al., 2005). Activity in the vmPFC and VS (Tom et al., 2007), the AI (Weller, Levin, Shiv, & Bechara, 2009), and amygdala (Sokol-Hessner, Camerer, & Phelps, 2013) are associated with level of individual loss aversion at the time of outcome receipt. Further, in line with Prospect theory, when participants are presented with explicit probabilities the inverted S-shaped nonlinear weighting of outcome probabilities (Figure 1.1.1.1) is reflected in striatal activation (Hsu, Krajbich, Zhao, & Camerer, 2009) as well as in the vmPFC and the left dlPFC (Tobler et al., 2007).

Conversely, neuroimaging studies examining decision-making under ambiguity (unknown risk) have pointed to the lateral OFC and vlPFC as playing a major role in ambiguity processing. The lateral OFC shows greater activity for ambiguity compared to risk processing, and this difference correlates with individual level of ambiguity aversion (Hsu et al., 2005). VlPFC activity is also associated with ambiguity aversion, with greater activation levels found when ambiguity is resolved (Bach, Hulme, Penny, & Dolan, 2011; Huettel et al., 2006).

1.2.4. Social context

Much of everyday decision-making incorporates some form of social component, whether in the form of social norms and expectations, or in interactions with others (such as comparison, cooperation, or competition). However, decision-making in social contexts has received comparatively little attention in neuroeconomics. When performing a task with another player, judgement of one’s own performance can become relative, depending on the immediate counter example of the other player. A meta-analysis exploring downward (being better than others) and upward (being worse than others) social comparison identified greater levels of BOLD activity within the VS and vmPFC for downward comparisons, and greater levels of BOLD activity within the AI and dorsal ACC for upward comparisons (Luo et al., 2018). The AI has also been associated with bad outcomes resulting from unfair offers in the Ultimatum Game (Sanfey, 2007; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), and betrayal in the Trust Game (King-Casas et al., 2005), suggesting a sensitivity to social rules.

With regards to competitive auction tasks, Delgado, Schotter, Ozbay and Phelps (2008) conducted a two-player FPSB auction fMRI study investigating the ‘winner’s curse’. The inclusion of social competition produced a more pronounced BOLD response to loss in the striatum, and greater behavioural overbidding correlated with the magnitude of this activity. Further, van den Bos, Talwar and McClure (2013) conducted a multiplayer FPSB auction fMRI study, and found that participant RPEs correlated with activity in the VS and vmPFC, indicative of reinforcement learning (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008). Additionally, individual differences in social preferences were related to activity in the temporal-parietal junction and AI. Both studies concluded that the players derive utility from winning and disutility from losing an auction, independent of monetary outcome (Delgado, Schotter, et al., 2008; van den Bos, Talwar, & McClure, 2013). Therefore, the decision-making process was influenced by the intrinsic value of winning the auction, irrespective of the intrinsic value of the item won: suggesting an influence of the “joy of winning” (Astor et al., 2013). Van den Bos and colleagues further argue that the social context (e.g., the number of players and the expertise of the competition) may mediate the interaction between socio-emotional and reward areas to bias competitive decisions. It is clear that comparing one’s performance against someone else’s plays a role in outcome evaluation, even in cases where another individual doing well has no impact on one’s own performance (Fliessbach et al., 2007; Kedia, Mussweiler, & Linden, 2014). While preliminary, this evidence suggests that during socially competitive situations, the brain valuation system cares about not only rewards themselves, but also how the rewards have been obtained.

1.3.Temporal dynamics of reward processing

The following section describes the spatiotemporal characteristics of feedback evaluation mechanisms during risky decision reward processing. The high temporal resolution of electroencephalography (EEG, see section 2.2) makes it well equipped to isolate and examine reward processing in the brain during the outcome phase of decision-making. The most extensively researched reward-related potential components during the outcome period, and focus of the EEG studies in this thesis, are the feedback-related negativity (FRN) (Hauser et al., 2014) and the P300 component (Glazer, Kelley, Pornpattananangkul, Mittal, & Nusslock, 2018).

1.3.1. FRN

The FRN is the difference waveform between averaged potentials time-locked to the presentation of probabilistic gain and loss outcomes (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Walsh & Anderson, 2012). It has a frontocentral scalp distribution and is measured approximately 200 – 300ms after feedback onset from electrodes in the midline frontal-central area (e.g. Cz, FCz or Fz in the 10-20 system, see Figure 2.2.1) (Gehring & Willoughby, 2002; Glazer et al., 2018; San Martin, 2012). A visual representation of the FRN can be seen in Figure 1.3.1. First identified during a time estimation task by Miltner et al. (1997) and then during a monetary gambling task conducted by Gehring and Willoughby (2002), the FRN has become one of the most extensively studied event-related potentials (ERPs) in the reward processing literature (Gehring & Willoughby, 2002; Miltner, Braun, & Coles, 1997; Walsh & Anderson, 2012).

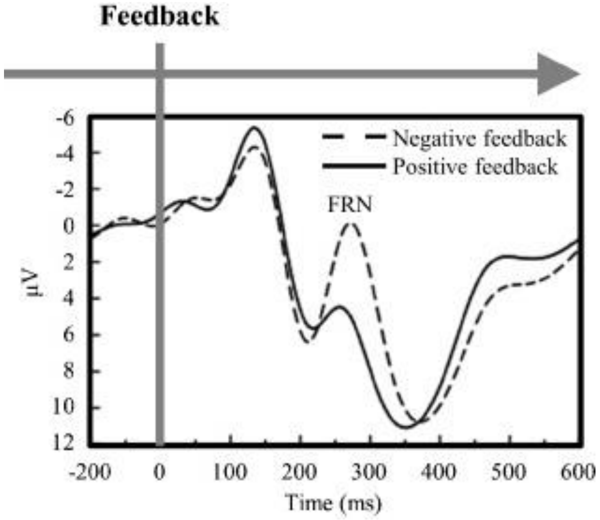

Figure 1.3.1. The time course and amplitude of the FRN, given by the difference waveform between averaged potentials time-locked to the presentation of gain and loss outcomes. This figure was taken from Walsh and Anderson (2012).

It should be noted that within the literature, the FRN is also referred to as the feedback negativity (FN), the medial-frontal negativity (MFN), feedback error-related negativity (fERN) and the reward positivity (RewP). Conventionally, the FRN has been considered a medial-frontal negative deflection in response to adverse outcomes, which is absent in good outcomes. However, there is a growing body of evidence that suggests that this component is actually modulated by positive feedback, and should be characterised as a positive fronto-central deflection in response to reward that is absent or suppressed following non-reward (Proudfit, 2015). The visual negativity in the waveform is due to a N200 component, which has very similar latency and scalp distribution, being elicited automatically as a baseline response (Baker & Holroyd, 2011). Therefore, the positive deflection for reward outcomes is cancelled out by the N200 and has the appearance of an absence of activation, while non-reward outcomes have the appearance of greater negative activation (Holroyd, Pakzad-Vaezi, & Krigolson, 2008; Proudfit, 2015; Yaple, Shestakova, & Klucharev, 2018). The RewP difference waveform is the antonym counterpart of the FRN, and is calculated by subtracting losses from gains, while the FRN is calculated by subtracting gains from losses (Proudfit, 2015). In the experimental chapters of this thesis, this component is referred to as the FRN in Chapter 5 and the RewP in Chapter 6.

Several theoretical accounts of the role of the FRN have been proposed (Yeung, Botvinick, & Cohen, 2004), the most influential being the Reinforcement Learning theory, which posits that the FRN reflects reinforcement learning RPE processing (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Falkenstein et al., 1991; Holroyd & Coles, 2002). In the Reinforcement Learning theory, the ACC, midbrain dopamine system and basal ganglia form a reinforcement learning system within the medial-frontal cortex (Schultz, 2002). Short-latency, phasic reward signals resembling RPEs are known to be encoded by mesencephalic dopamine neurons projecting to the striatum and frontal regions (Schultz, 2002). The FRN potential is generally thought to originate from midbrain dopaminergic projections to the ACC (Bellebaum & Daum, 2008; Cohen & Ranganath, 2007; Gehring & Willoughby, 2002), but there is also evidence of involvement from the PPC (Cohen & Ranganath, 2007; Donamayor, Marco-Pallares, Heldmann, Schoenfeld, & Munte, 2011) and the striatum (Carlson, Foti, Mujica-Parodi, Harmon-Jones, & Hajcak, 2011; Foti, Weinberg, Dien, & Hajcak, 2011). Decreases in phasic dopaminergic firing disinhibit ACC neurons, resulting in a more negative FRN, while increases in phasic dopaminergic firing inhibits ACC neurons, resulting in a more positive FRN. Each time there is a difference between an expected outcome and the received outcome, i.e. a prediction error, RPE signals are emitted signalling the inadequacy of expectations. It is hypothesised that RPE signals reinforce actions associated with positive outcomes and punish actions associated with negative outcomes, in order to guide action selection and future learning (Paulus & Frank, 2006).

There is a large body of evidence that the FRN is primarily modulated by outcome valence (Hajcak, Holroyd, Moser, & Simons, 2005; Hajcak, Moser, Holroyd, & Simons, 2006;

Holroyd & Coles, 2002; Holroyd, Nieuwenhuis, et al., 2004; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Nieuwenhuis, Holroyd, Mol, & Coles, 2004; Ruchsow, Grothe, Spitzer, & Kiefer, 2002; Yeung & Sanfey, 2004), and that elicitation occurs regardless of modality of feedback (e.g. visual, auditory or tactile) (Miltner et al., 1997) and whether the feedback comprises primary reinforcers (e.g. performance feedback) or secondary reinforcers (e.g. monetary gain/loss) (Foti et al., 2011; Hajcak et al., 2005; Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004; Yeung, Holroyd, & Cohen, 2005). FRN amplitude has also been found to be modulated by outcome probability, with greater amplitudes for improbable (unexpected) than for probable (expected) negative outcomes (Bellebaum & Daum, 2008; Bellebaum, Polezzi, & Daum, 2010; Cohen, Elger, & Ranganath, 2007; Hewig et al., 2007; Holroyd & Krigolson, 2007; Holroyd, Krigolson, & Lee, 2011; Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003; Kreussel et al., 2012; Martin & Potts, 2011; Martin, Potts, Burton, & Montague, 2009; Potts, Martin, Burton, & Montague, 2006; Walsh & Anderson, 2011).

Conversely, reports of FRN sensitivity to reward magnitude have been inconsistent. Some studies report a reward magnitude effect (Bellebaum et al., 2010; Kreussel et al., 2012; Nieuwenhuis, Holroyd, et al., 2004), while others report only a binary good/bad outcome differentiation (Goyer, Woldorff, & Huettel, 2008; Hajcak et al., 2006; Masaki, Takeuchi, Gehring, Takasawa, & Yamazaki, 2006; Osinsky, Walter, & Hewig, 2014). A meta-analysis reported a strong main effect of magnitude, where high magnitude outcomes produced larger FRNs than low magnitude outcomes (Sambrook & Goslin, 2015). Therefore, discrepancies in reward magnitude sensitivity may be due to heterogeneity in paradigm parameters or inconsistencies in how the FRN is measured.

In line with the Prospect theory notion of a reference point, there is evidence that the FRN is dependent on the contextual domain of a given task, as what constitutes a good or bad outcome is determined by the alternative option (Gu et al., 2011; Holroyd, Larsen, & Cohen, 2004). For example, in a 50/50 gamble between a £10 win and £0 outcome, the £0 is perceived as the bad outcome, whereas in a 50/50 gamble between a £10 loss and £0, £0 is the good outcome. Linked to this idea, a central part of decision-making under risk and uncertainty is 'counterfactual thinking' (Roese & Epstude, 2017; Roese & Olson, 1993), when the obtained outcome is compared with the other 'roads not taken'. In this way, the FRN may not code for objectively 'good' and 'bad' outcomes, but instead reflect a subjective 'worse than expected' error signal (Holroyd, Larsen, et al., 2004; Miltner et al., 1997; Nieuwenhuis, Holroyd, et al., 2004; Yu & Zhou, 2009).

Similarly, the FRN is also sensitive to the contextual framing of options. For example, when given an initial endowment of £100 and then asked to choose between losing £40 (negative frame) and keeping £60 (positive frame), negative frames were encoded as losses and positive frames were encoded as gains (Yu & Zhang, 2014). Interestingly, when participants received an initial £100 debt, and then chose to either save £60 or still lose £40, no FRN was elicited. The lack of FRN in the loss domain suggests the FRN does not reflect 'better than expected' positive RPE, and suggests a negativity bias or a greater sensitivity to potential losses than potential gains (Nieuwenhuis, Holroyd, et al., 2004; Yu & Zhang, 2014). To this point, the FRN also appears to be an index of loss aversion: using a 2AFC monetary gambling task, Kokmotou et al. (2017) found a positive correlation between individual level of loss aversion and FRN amplitude during choice outcome evaluation (Canessa et al., 2013; De Martino, Camerer, & Adolphs, 2010; Kokmotou et al., 2017).

Finally, the inclusion of a social context has been shown to impact the FRN, with greater amplitudes in response to social (thumbs up and thumbs down) vs. non-social stimuli (+/- signs) (Pfabigan, Gittenberger, & Lamm, 2019). Furthermore, the FRN is sensitive to differences in social status (Boksem, Kostermans, Milivojevic, & De Cremer, 2012), can be elicited by watching someone else perform a gambling task (Yu & Zhou, 2006), and is modulated by empathy (Liu, Hu, Shi, & Mai, 2018) and by relationship (Leng & Zhou, 2014; Wu, Leliveld, & Zhou, 2011) when decision-making for others and processing vicarious rewards. FRN amplitudes are also greater when a player's outcomes are worse than another's in the Ultimatum Game, signalling a sensitivity to social fairness (Boksem & De Cremer, 2010; Hewig et al., 2011; Mussel, Hewig, Allen, Coles, & Miltner, 2014; Osinsky et al., 2014; Polezzi et al., 2008; Riepl, Mussel, Osinsky, & Hewig, 2016).

Conversely, evidence of FRN sensitivity to direct social comparison in other contexts is mixed. Boksem et al. (2011) found that when participants received a bad outcome, FRN amplitudes were smaller when another participant also received a bad outcome compared to a good outcome. However, these results were not replicated by two other studies (Qiu et al., 2010; Wu, Zhang, Elieson, & Zhou, 2012). Further, Luo et al., (2015) found larger FRN amplitudes during social comparison for non-conforming outcomes than conforming outcomes, regardless of valence. A sensitivity to conformity could indicate that amplitude modulation was due to social inequality as opposed to having better or worse outcomes than another person, suggesting a prosocial value orientation (Boksem et al., 2012; Hu, Xu, & Mai, 2017; Luo et al., 2015). Social fairness could also inform an individual's expectations, as they may anticipate that they should perform as well or receive as much reward as another player, and so any deviations from this expectation would impact the RPE signal (Bismark, Hajcak, Whitworth, & Allen, 2013; Boksem, Kostermans, & De Cremer, 2011).

Of course, the situation is slightly different in cases of direct competition, where each player competes for the maximization of their personal benefit, to the detriment of the other players. During outcome evaluation of competitive tasks, such as an auction, opponents' behaviour can still be a barometer of expected performance or common values, but is most saliently a direct signal of personal failure or success (Sheremeta, 2013; Toelch et al., 2014). Competitive decision-making has received comparably less attention in neuroeconomics than collaborative and comparative behaviours, but there is some evidence that the FRN is sensitive to competitive contexts. When passively viewing a partner's (co-operative) and an opponent's (competitive) gambling outcomes, the same gain or loss feedback given to both players evokes the opposite FRN modulations, as an opponent's success is processed as the viewer's failure (Itagaki & Katayama, 2008; Marco-Pallarés, Krämer, Strehl, Schröder, & Münte, 2010). The topography and polarity of the FRN (loss-minus-win) for a partner's outcomes and the player's own reward outcomes is the same, but the polarity is reversed for the opponent's outcomes (win-minus-loss) (Czeszumski, Ehinger, Wahn, & Konig, 2019).

Taken together, the FRN is posited to be involved in evaluating the motivational impact of outcomes, incorporating the value, likelihood and size of potential outcomes, as well as the framing of a given context, in order to characterise their relevance for future learning (Gehring & Willoughby, 2002; Walsh & Anderson, 2012; Yeung & Sanfey, 2004). Conventionally, the FRN is purported to reflect a coarse, binary differentiation of good versus bad outcomes (Hajcak et al., 2006; Yeung & Sanfey, 2004). However, there is a growing body of evidence that the FRN is reflective of a general salience prediction error that is sensitive to the unsigned, absolute size of a prediction error and not its valence (Hird et al., 2022; Sambrook & Goslin, 2015; Talmi, Atkinson, & El-Deredy, 2013). Indeed, in the case of social contexts, it is possible that the FRN is dependent on the motivational and affective evaluation of outcomes, as well as the comparison of oneself to others as a valid social reference point signalling expected performance (Czeszumski et al., 2019; Toelch et al., 2014). Therefore, more research is needed on this topic in order to fully characterise the FRN in situations of complex and competitive value-based decision-making.

1.3.2. P300

The P300 is a positive-polarity deflection peaking over midline parietal sites, most commonly Pz, CPz and Cz (Luck, 2014; Polich, 2007, 2012), occurring at approximately 300 – 500ms following a feedback stimulus (Glazer et al., 2018; Nieuwenhuis, Aston-Jones, & Cohen, 2005), and is composed of two distinguishable subcomponents: the early, frontally distributed P3a and the late, parietally distributed P3b (Polich, 2007). During decision-making, the P300 is thought to be central to context updating and the integration of new information with existing mental schema in order to maximise future rewards (Bellebaum & Daum, 2008; Donchin, 1981; Duncan-Johnson & Donchin, 1977; Duncan-Johnson & Donchin, 1982; Nieuwenhuis, Aston-Jones, et al., 2005; Polich, 2007; Schuermann, Endrass, & Kathmann, 2012; Sutton, Braren, Zubin, & John, 1965). As one of the most well-established and well-documented ERPs, the P300 is also referred to as the P3, or the late positive potential (LPP), and in reward feedback specific contexts the Rew-P3 or FB-P3. A visual representation of the P300 can be seen in Figure 1.3.2. In this thesis, the component is referred to as the P300 in Chapter 5 and the P3 in Chapter 6.

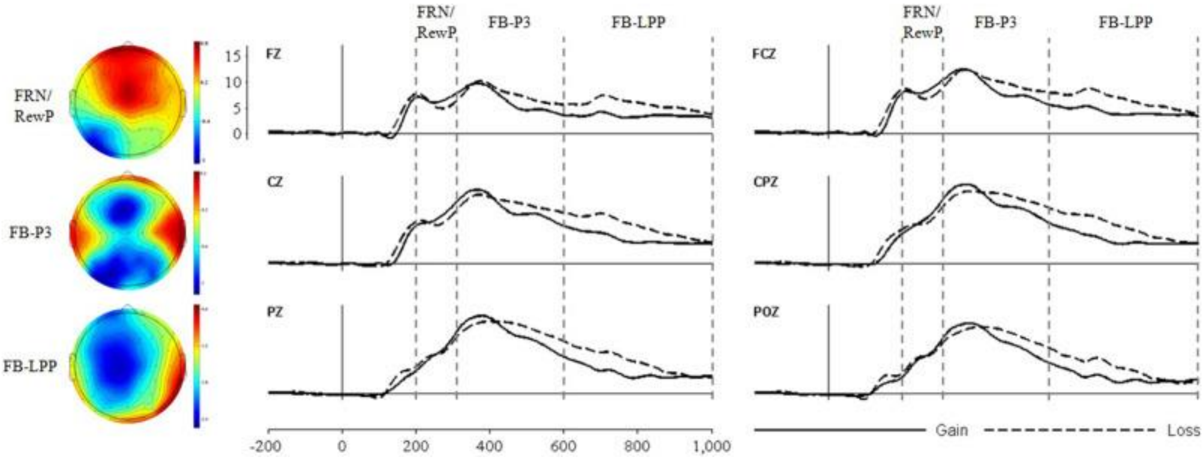

Figure 1.3.2. The time course, amplitude and topography of the P300 component, referred to here as the FB-P3, demonstrating the relationship between the FRN and P300. Figure from Glazer et al. (2018).

The P300 is highly sensitive to the motivational significance of stimuli, such as a target stimulus in visual search tasks, and the probability of outcomes, such as infrequent stimuli in oddball tasks (Duncan-Johnson & Donchin, 1977; Duncan-Johnson & Donchin, 1982; Pritchard, 1981). The amplitude of the P300 increases as a function of the decreasing probability of the occurrence of the target stimulus (Duncan-Johnson & Donchin, 1977; Duncan-Johnson & Donchin, 1982; Polich, 2007). During reward-related feedback processing, surprise at unexpected outcomes (outcomes which are statistically unlikely or subjectively deemed improbable) elicit stronger P300 amplitudes compared to expected outcomes (Bellebaum & Daum, 2008; Cohen et al., 2007; Hajcak et al., 2005; Hajcak, Moser, Holroyd, & Simons, 2007; Holroyd & Krigolson, 2007; Holroyd et al., 2003).

The P300 is typically sensitive to reward evaluation (i.e. sensitivity to incentive vs. neutral feedback), showing larger amplitudes for reward-related feedback (Glazer et al., 2018). However, there is inconsistent evidence on whether the P300 is outcome valence dependent, with some reporting greater positivity for gain compared to loss feedback (Bellebaum et al., 2010; Cano, Class, & Polich, 2009; Conroy & Polich, 2007; Hajcak et al., 2005; Hajcak et al., 2007; Holroyd, Larsen, et al., 2004; Leng & Zhou, 2010; Wu & Zhou, 2009; Yeung et al., 2005), while others reporting no effect (Sato et al., 2005; Yeung & Sanfey, 2004) or reporting greater positivity for loss feedback (Frank, Woroch, & Curran, 2005). Furthermore, emotionally salient stimuli elicit larger P300 amplitudes, regardless of being positive or negative (Johnston, Miller, & Burleson, 1986; Keil et al., 2002). Conversely, the P300 has consistently been shown to encode the absolute magnitude of the reward feedback , with larger rewards eliciting more positive amplitudes than smaller rewards, and larger losses eliciting more positive amplitudes than smaller losses (Bellebaum et al., 2010; Gu et al., 2011; Sato et al., 2005; Wu & Zhou, 2009; Yeung & Sanfey, 2004). Pertinently, Tyson-Carr et al., (2018) found that high value products evaluated during a BDM task produced increased P300 amplitudes during the initial valuation period.

Taken together, it has been suggested that the P300 reflects an attentional resource allocation mechanism, evaluating the functional significance of feedback stimuli, driving the categorisation of salient outcome-related information and streamlining mental model or updating processes (Donchin & Coles, 1988; Hajcak et al., 2005; Kramer, Wickens, & Donchin, 1985; Polich, 2007, 2012; San Martin, 2012; Sato et al., 2005; Toyomaki & Murohashi, 2005; Wickens, Kramer, Vanasse, & Donchin, 1983; Yeung et al., 2005; Yeung & Sanfey, 2004). Linked to this, there is evidence that the relative amplitudes of the P300 subcomponents, P3a and P3b, predict individual differences in gain maximization and loss minimization (P3b) and the subsequent behaviour change (P3a) (San Martin, Appelbaum, Pearson, Huettel, & Woldorff, 2013). Under the attention-allocation mechanism understanding, the P300 is not a valuation mechanism, but during decision-making highly valuable stimuli may be perceived as more motivationally significant than the alternatives.

It is thought that the addition of a social dimension to the decision-making context induces enhanced stimulus salience and processing ease in comparison to equivalent non-social feedback (Alexander & Brown, 2011; Bellebaum & Daum, 2008; Gehring & Willoughby, 2002; Pfabigan et al., 2019; Pfabigan & Han, 2019). In line with this, there is evidence that a social context, reflected in social stimuli (e.g. thumbs up or a smiley face), enhances the P300 amplitude, independent of outcome (Pfabigan et al., 2019; Pfabigan & Han, 2019). In situations of social comparison and competition, P300 amplitudes are modulated by individual differences in trait empathy for other players (Hu et al., 2017; Lyu et al., 2022), social acceptance feedback (Van der Molen et al., 2014; van der Veen, van der Molen, Sahibdin, & Franken, 2014), and interpersonal relationships (Hu et al., 2017; Leng & Zhou, 2010; Wang et al., 2014; Wang et al., 2017; Zhang et al., 2021).

Experiments using the Ultimatum Game have shown that P300 amplitudes are greater when participants have better outcomes than another player (Qiu et al., 2010; Wu, Leliveld, et al., 2011; Wu, Zhou, van Dijk, Leliveld, & Zhou, 2011), and when players receive unfair offers (Falco, Albinet, Rattat, Paul, & Fabre, 2019; Liang et al., 2015; Qu, Wang, & Huang, 2013; Wu, Hu, van Dijk, Leliveld, & Zhou, 2012). The modulation of the P300 may be rooted in the primary social motivations of a given task (Zhang et al., 2021). For instance, in competitive situations, the primary focus of a player is to outperform other players and protect one's self-interests. Meanwhile, in co-operative situations, social inclusion, reciprocation and fairness are prioritised (Cinyabuguma, Page, & Putterman, 2005; Falco et al., 2019; Maier-Rigaud, Martinsson, & Staffiero, 2010; Masclet, Noussair, Tucker, & Villeval, 2003).

2. General Methods

2.1. Auction Tasks

2.1.1. BDM auction

The BDM paradigm is a popular method of measuring SV through the metric of WTP (Becker et al., 1964). In auction contexts, WTP can be thought of as the bidder's reservation price or point of indifference (Padoa-Schioppa, 2011). Under the BDM, a single player submits a single bid for a given item. A random number generator then produces a price, and the player's bid is compared to this price. If the bid is above the price, the player receives the item and pays the randomly drawn price. If the bid is below this price, the individual pays nothing and receives nothing. The BDM is designed to incentivise people to report their true maximum WTP by bidding exactly their SV of a given item. To bid more than one's SV risks overpaying, while to bid less than one's SV risks losing the auction and not purchasing the item for less than they were willing to. Because of this, the BDM is referred to as a demand revealing mechanism. The weakly dominant strategy in this scenario is 'truth-telling', meaning that bidding one's true maximum WTP is the optimal strategy regardless of the opponent(s) strategy profile, and so is independent of risk attitudes (Noussair et al., 2004). The formal argument is laid out in Figure 2.1.1. In practice, bid values elicited from BDM tasks have been shown to more accurately reflect consumer WTP at point of purchase than hypothetical or non-incentive-compatible methods (Foster & Burrows, 2017; Penn & Hu, 2018; Schmidt & Bijmolt, 2020; Wertenbroch & Skiera, 2002)

The research presented in this thesis used the BDM paradigm as a measure of individual SV in a fMRI meta-analysis reported in Chapter 4 and through primary research with EEG reported in Chapter 6. Individual reported WTP bidding values were correlated with changes in neural activity recorded by the two neuroimaging techniques.

Scenario:

Suppose there is a single player in a BDM auction for a single item. The player – denoted i — is given an endowment and asked to submit a bid b_i. *Simultaneously, a random number* b_r *is generated.*

The allocation rule is:

i. *if* $b_i > b_r$: *player i buys the item at price* b_r;

ii. *if* $b_i < b_r$: *player i keeps the endowment;*

iii. *if* $b_i = b_r$: *either (i) or (ii) is implemented with equal probability.*

Strategy:

Suppose that player i's valuation of an item is v_i, *and the auction has a reserve price R. If* $b_i > b_r$, *the payoff for player i is* $v_i - b_r$. *If* $b_i < b_r$, *the payoff for player i is 0.*

a. *When* $v_i < R$

Player i does not want to win the auction because they would have to pay at least R, which will cause them to make a loss. Hence, bidding $b_i = v_i$ *is optimal since they will end up not winning the auction.*

b. *When* $v_i >= R$

Player i has three options, $b_i > v_i$, $b_i < v_i$ *and* $b_i = v_i$

i. *Consider a deviation* $b_i > v_i$:
It is possible that $b_i > b_r > v_i$, *in which case player i will win the auction with a negative surplus* $v_i - b_r$.

ii. *Consider a deviation* $b_i < v_i$:
It is possible that $b_i < b_r < v_i$, *in which case player i loses the auction with a payoff of 0, whereas they could have won it with a positive payoff of* $v_i - b_r$ *if they had bid* $b_i = v_i$.

Hence bidding $b_i = v_i$ *is the weakly dominant strategy.*

The payoff strategy of the BDM is as follows:

$$\begin{cases} v_i - max_{r \neq i} b_r & if\, b_i > max_{r \neq i} b_r \\ 0 & Otherwise \end{cases}$$

Figure 2.1.1. Formal proof of the Dominant Strategy in BDM Auctions.

2.1.2. Vickrey auction

The VA was derived by William Vickrey in 1961 and its impact was a major contributor to his 1996 Nobel prize in economics (Vickrey, 1961). The academic study of VA has great ecological relevance, as the VA format is used by the popular online auction website eBay (Barrot, Albers, Skiera, & Schäfers, 2010). During a VA, multiple players simultaneously and privately put forward bids to purchase a given good. The single highest bidder wins, but the winner will only pay the value of the bid submitted by the second highest bidder (Barrot et al., 2014; Milgrom & Weber, 1982; Vickrey, 1961). The formal argument is laid out in Figure 2.1.2.

In a VA with fully rational players with standard preferences, the weakly dominant strategy is for a bidder to bid their SV. The optimal behaviour is posited to be impervious to the risk attitude of all bidders, the number of bidders involved in the VA, the strategies of other players, and whether the value distributions across players are symmetrical or even correlated. Further, the dominant strategy of bidding one's true SV also holds if bidders have non-standard risk preferences, such as anticipated regret (Filiz-Ozbay & Ozbay, 2007) or ambiguity aversion (Chen, Katuščák, & Ozdenoren, 2007).

The BDM is formally strategically equivalent to a VA against a single unknown bidder, who bids her valuation, and whose value is drawn from the same distribution of valuations as that of the BDM prices (Klemperer, 2000). The only difference in paradigm is that in the VA the participant interacts with other players, whereas the BDM places participants in a situation of individual choice. The normative predictions from Game theory suggest that both paradigms should elicit the same bid responses in players, as there is no incentive to changes one's bid based on the opponent's behaviour (Klemperer, 2000).

However, several significant differences have been found in practice. Many studies have found significant heterogeneity in bidding behaviour in the VA compared to the BDM (Flynn et al., 2016; Irwin, Mcclelland, Mckee, Schulze, & Norden, 1998; Kagel & Levin, 1993; Noussair et al., 2004). Despite clear instructions and an understanding of the paradigm, underbidding and overbidding relative to valuations are common. Flynn, Kah and Kerschbamer (2016) found consistent deviations of bids from SVs in VAs during a direct experimental comparison of the two mechanisms. In the BDM participants were true to their WTP, whereas during VAs participants fell into one of three patterns of behaviour. Firstly, a portion of the participants never found an incentive to deviate from self-interested behaviour and bid their SV as predicted. Secondly, some participants exhibited what was labelled as 'altruistic' behaviour, where they tended to underbid relative to their SVs in the VA. Finally, a third group exhibited the opposite behaviour, overbidding on items in the VA relative to their SV, and were termed 'spiteful' participants. The deviations from the logical optimal strategy suggests that the inclusion of a second player introduces corresponding social dynamics which impact valuation processing. The desire to beat rivals can lead participants to overpay, exceeding the intrinsic worth of an item (Bartling, Gesche, & Netzer, 2017). Similarly, the inclusion of another person can encourage pro-social behaviours for better group relationships, or induce less aggressive behaviours in risk averse individuals. The evidence of three divergent behaviour patterns suggests a role of individual differences in how players react to social competition.

Similarly, Noussair, Robin and Ruffieux (2004) found that the payoff functions for the two mechanisms diverged over repeated games of bidding for objects of induced value. They suggested that outcome feedback (leading participants to adjust their bids in the direction of the optimum) is more powerful in the VA than in the BDM. In a VA, it is costlier to deviate from bidding one's valuation, and there is more to be gained from improvement of a given suboptimal strategy in the VA than in the BDM. Though strategic uncertainty about other players' actions in the VA does not affect the optimal strategy, it does affect the expected cost of deviating from it.

The experience of defeating the competition to win an auction and the satisfaction that comes with the win holds its own value, which adds to the overall value of the item (Adam et al., 2016; Astor et al., 2013; Cooper & Fang, 2008; Morgan, Steiglitz, & Reis, 2003). This is not the case in a BDM when the player is competing against a random number generator (van den Bos et al., 2008). Furthermore, the bidder's decision-making process is made in isolation in the BDM, and the outcome only has consequences for the decision maker. Conversely, in the VA, the bidding behaviour of both players affects the monetary outcome for both parties involved.

The VA tasks reported in the experimental Chapters 5 and 6 of this thesis were modified versions of the two-player VA: a computer opponent was used instead of a human competitor, and the tasks involved participant deception for them to believe they were playing an online VA against another human. In Chapter 5, the computer was programmed to bid so that the participant would lose one third of the trials, win by a small margin for a third of the trials, and win by a large margin for a third of the trials. In Chapter 6, the computer bidding behaviour was randomised so to match the BDM. In both experimental chapters, individual reported WTP bidding values were correlated with changes in patterns of neural activity recorded by EEG.

Scenario:

Suppose there are two players in a VA for a single item. The players— denoted i and j with $i \neq j$—are each given an endowment and asked to submit bids b_i and b_j.

The allocation rule is:

iv. *if $b_i > b_j$: player i buys the item at price b_j, while player j keeps the endowment;*
v. *if $b_i < b_j$: player j buys the item at price b_i, while player i keeps the endowment;*
vi. *if $b_i = b_j$: either (i) or (ii) is implemented with equal probability.*

Strategy:

Suppose that player i's valuation of an item is v_i, and the auction has a reserve price R. If $b_i > b_j$, the payoff for player i is $v_i – b_j$. If $b_i < b_j$, the payoff for player i is 0.

a. *When $v_i < R$*

Player i does not want to win the auction because they would have to pay at least R, which will cause them to make a loss. Hence, bidding $b_i = v_i$ is optimal since they will end up not winning the auction.

b. *When $v_i >= R$*

Player i has three options, $b_i > v_i$, $b_i < v_i$ and $b_i=v_i$

iii. *Consider a deviation $b_i > v_i$:*
  It is possible that $b_i > b_j > v_i$, in which case player i will win the auction with a negative surplus $v_i - b_j$.

iv. *Consider a deviation $b_i < v_i$:*
  It is possible that player j submits a bid higher than bid b_i, but still lower than v_i. In which case player i loses the auction with a payoff of 0, whereas they could have won it with a positive payoff of $v_i - b_j$ if they had bid $b_i = v_i$.

Hence bidding $b_i = v_i$ is the weakly dominant strategy.

The payoff strategy of the VA is as follows:

$$\begin{cases} v_i - max_{j \neq i} b_j & if\, b_i > max_{j \neq i} b_j \\ 0 & Otherwise \end{cases}$$

Figure 2.1.2. Formal proof of the Dominant Strategy in VA Auctions

2.2.EEG

2.2.1. Physiological basis of the EEG signal

EEG is a non-invasive method of recording electrical brain activity distributed across the scalp. Electrical signals are conducted along billions of neurons in the human brain (Azevedo et al., 2009; Lent, Azevedo, Andrade-Moraes, & Pinto, 2012; Sanei & Chambers, 2009). Each neuron consists of a cell body, axon, and excitatory or inhibitory axon terminals known as dendrites. Neurons communicate information via action potentials, which are discrete voltage spikes generated in the cell body that travel along the axon fibre to the dendrites. An action potential is a momentary reversal of membrane potential voltage where the intracellular potential suddenly decreases (depolarisation) producing a spike in membrane potential, and then quickly returns to the resting membrane potential (repolarisation) (Sanei & Chambers, 2009). This process is mediated by the exchange of sodium, potassium, calcium, and chloride ions through voltage-gated ion channels, where the release and binding of neurotransmitters alter the permeability of the postsynaptic cell membrane to specific ions (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). The resulting change in potential results in a dipole: a pair of positive and negative charges separated by a short distance. The fields generated by action potentials have a latency of between 1 and 2 milliseconds (Koester, 1991), a very limited potential field (Rowan & Tolunsky, 2003), and are generally not synchronous with nearby neuronal firing. Therefore, any voltage generated by action potentials is normally cancelled out and undetectable by electrodes on the scalp (Buzsáki, Anastassiou, & Koch, 2012; Speckmann, 1993).

Instead, EEG measures postsynaptic potentials originating from the extracellular current flow, also known as field potentials (Luck, 2014; Mulert & Lemieux, 2010; Niedermeyer & da Silva, 2005). This occurs when there is a build-up of electrical potentials across the cell membrane, caused by neurotransmitters being released into the synaptic cleft and interacting with the corresponding receptors on the postsynaptic membrane (Buzsáki, Traub, & Pedley, 2003; Luck, 2014; Mulert & Lemieux, 2010). These potentials have a considerably longer duration (50 – 200 ms), a larger potential field (Rowan & Tolunsky, 2003), and stem from the summation of large populations of neurons firing in synchrony, with the same polarity and in spatial alignment (Buzsáki et al., 2012; Speckmann, 1993; Speckmann, Caspers, & Andersen, 1979). Due to the macroscopic organisation of dendrites, thousands of field potentials may occur in a similar location and orientation during a coherent response (Fisch & Spehlmann, 1999). The summation of these potentials can be detected and measured as voltage fluctuations on the scalp using EEG (Lopes da Silva, 1998; Nunez & Silberstein, 2000).

2.2.2. EEG signal acquisition and processing

An EEG recording consists of the measurement and amplification of fluctuating electrical field potentials in the brain across time (Kamp, Pfurtscheller, Edlinger, & Lopes da Silva, 2005; Maus, Epstein, & Herman, 2011). For EEG data collection, electrodes are positioned on the scalp in predetermined locations, and a suitable conducting gel, paste or liquid is applied alongside the electrodes to achieve low impedance levels (Teplan, 2002).

To ensure consistent positioning of electrodes on the scalp across studies and laboratories, electrodes are placed in accordance to a standardised system such as the 10-20 system (Jasper, 1958) or the Geodesics EGI System arrangement (Magstim EGI, UK). These systems use internationally recognised anatomical landmarks on the skull: the nasion, inion, and left and right mastoids (Jasper, 1958; Klem, Lüders, Jasper, & Elger, 1999; Pizzagalli, 2007). This standardised electrode placement ensures consistency of recordings between labs which may use different EEG acquisition systems, and allows for the comparison and summation of EEG findings. EEG studies in this thesis used a 129-electrode sponge-based geodesic sensor net and a saline solution as the conducting medium (Magstim EGI, UK). Figure 2.2.1 illustrates the locations of electrodes on the head using this system. The high-density system gives coverage of the whole head including the forehead and suborbital regions of the face. As can be seen in Figure 2.2.1, many sensors in geodesic arrangements (such as electrodes 24, 33 and 45) have corresponding electrodes in the International 10–20 System (Luu & Ferree, 2005).

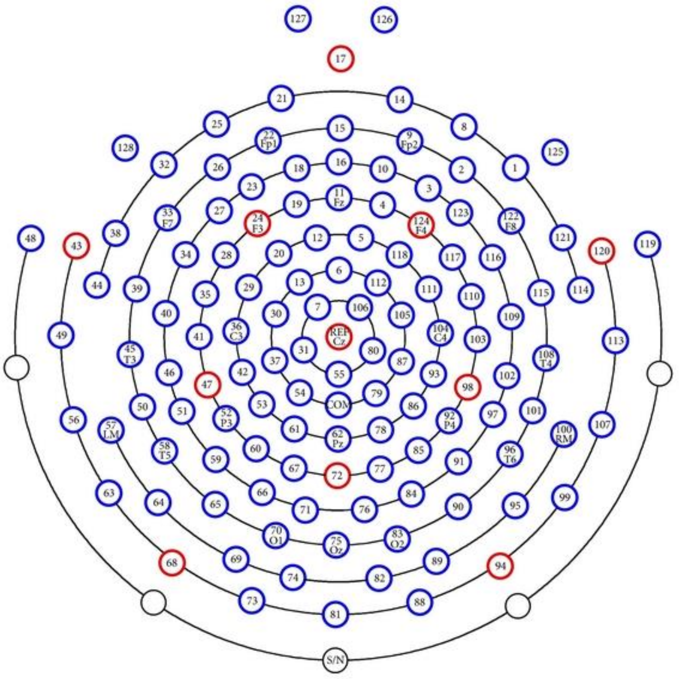

Figure 2.2.1. Distribution of the 129 electrodes across the scalp for the sponge-based EGI Geodesic sensor net.

The raw EEG signal amplitudes from a typical adult scalp are very small, approximately 10 – 100 μV (Aurlien et al., 2004), and so require signal amplification for accurate measurement (Luck, 2014). Once amplified, the resulting voltage fluctuations are digitized and transformed into graphic representations for display, storage and analysis (Luck, 2014; Rowan & Tolunsky, 2003). An important part of this amplification process is establishing reference electrodes. Each individual electrode signal represents the voltage potential difference between an active electrode and a reference electrode signal, meaning that the scalp potentials are reference-dependent (Luck, 2014). Reference electrodes are most commonly the vertex electrode (VREF, commonly referred to as Cz) or the average of the bilateral mastoid electrodes (57 and 100). However, singular electrodes chosen as the reference site can be differentially affected by volume conduction effects of combinations of neuronal generators (Luck, 2014). Furthermore, as there are no inactive (also referred to as 'silent' or 'infinite') recording sites on the scalp, the choice of any single electrode as the reference is inherently arbitrary (Kayser & Tenke, 2015). Therefore, it is common practice to use a technique to obtain reference-free data, such as the common average reference method, which represents the mean signal of all electrodes (Lehmann, 1987; Lehmann, Ozaki, & Pal, 1987).

The common average reference method relies on the principle that electrical events produce both positive and negative poles. The integral of these potential fields in a conducting sphere sum to zero when signals are collected from a spherical object such as the head. Only signals that are common to all sites remain in the common average reference, while isolated signals from singular electrodes are cancelled out. In this way, the reference signal will not be impacted by extreme maximal or minimal potential values in the same way that a single reference electrode would be. Subtracting the resulting common average reference from each electrode channel will result in reference-free EEG signals (Michel et al., 2004; Nunez et al., 1997). The common average reference method is invaluable for inverse solution methods, where the intracranial sources of surface recorded data are reconstructed according to a common average reference. During source localisation, it is necessary to remove the constant potential value caused by the reference electrode prior to applying an inverse solution in order to avoid violating the assumption that the total net source activity occurring in the brain at any one timepoint sums to zero (known as quasi-stationarity) (Murray, Brunet, & Michel, 2008).

An alternative to the common average reference method is to use Laplacian modelling, which is a comparison between each electrode and the weighted average activity of the immediately surrounding electrodes (Carvalhaes & De Barros, 2015; Kamp et al., 2005; Nunez et al., 1997). The Laplacian transformation involves calculating the second spatial derivative of the potential field in the local curvature of each electrode and its neighbours. Surface Laplacian modelling is attenuated to the volume conducted influence of more remote sources in the brain, and so has the benefit of incorporating contributions of volume conduction within the plane of the scalp into the mathematical transformation applied to the EEG potentials (Kayser & Tenke, 2015; Murray et al., 2008).

During EEG data acquisition and cleaning, the waveforms also undergo filtering according to their frequency (Luck, 2014). Low-pass filters are used to remove high-frequency signals such as muscular artefacts. High-pass filters are used to attenuate undesirable low frequency potentials resulting from movement (Litt & Cranstoun, 2003). A notch filter is also employed to remove the narrow range of frequencies generated by line currents, approximately 50/60 Hz (Edgar, Stewart, & Miller, 2005; Luck, 2014). For EEG studies in this thesis, the vertex electrode was chosen as the initial reference, and the COM electrode, was used as the common/ground electrode. During recording, electrode-to-skin impedances were kept below 50 kΩ, and a high-pass filter of 0.01 Hz and a low-pass filter of 1000 Hz were employed.

2.2.3. Artefact rejection

In addition to electrocortical potentials, the EEG system also records extracerebral artefacts, which includes electrooculographic activity (i.e. eyeblinks and saccades; EOG), electrocardiographic activity (i.e. heartbeats; ECG), electromyographic activity (e.g. muscles movement or chewing; EMG), and respiration (Luck, 2014; Rowan & Tolunsky, 2003). Artefacts can also have non-physiological origins, such as poor electrode-to-skin contact, or electronic noise from nearby alternating current electrical appliances (Luck, 2014). These sources of noise contaminate the recordings and must be removed in order to isolate the cortically generated signal. Experimenters should also strive to minimise the creation of artefacts during data acquisition, such as instructing the participants to remain as still as possible, asking participants to not blink at certain intervals during recording (where appropriate), and proper use of a Faraday cage.

During data cleaning, regularly occurring artefacts such as eye movements and heartbeats can be removed from the data using approaches such as principal component analysis (PCA) (Berg & Scherg, 1994) and independent component analysis (ICA) (Jung et al., 2000). PCA uses a spatial filter approach, delineating artefacts that are defined by a systematic topography from the continuous electroencephalographic data. PCA can be implemented in software such as Brain Electrical Source Analysis (BESA, GmbH), whereby artefacts in question can be manually tagged and then removed using adaptive artefact correction (Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002). In addition to this, all trials are visually inspected and any that contain further, unsystematic artefacts can be manually discarded. A potential limitation of the adaptive artefact correction method is that it relies on the researcher being able to accurately tag an artefact topography with a high signal-to-noise ratio, and so rigorous training is necessary. In this thesis, all EEG data was cleaned using BESA software.

Alternatively, ICA can be employed, where mathematical algorithms are used to isolate the average EEG signal component responsible for a specific artefact. The data is decomposed into a temporally independent, linear combination of brain and artefact activities, and the artefact component is subtracted from the rest of the EEG signal to leave behind ‘clean’ data (Ille et al., 2002; Lagerlund, Sharbrough, & Busacker, 1997; Luck, 2014). ICA is implemented in software such as the EEGLAB toolbox (Delorme & Makeig, 2004). However, the ICA method is limited in that the quality of decomposition is dependent on the quality of data (Makeig, Debener, Onton, & Delorme, 2004).

2.2.4. Event-related potentials (ERPs)

During EEG recording, ongoing spontaneous voltage fluctuations are continuously captured by electrodes. ERPs are time-locked waveforms evoked by the onset of a stimulus, which are in addition to the ongoing EEG activity (Niedermeyer & da Silva, 2005). ERPs reflect specific sensory, motor, or cognitive processing triggered by the presentation of an experimental stimulus (Curran, Tepe, & Piatt, 2006; Fabiani, Gratton, & Federmeier, 2007; Friedman & Johnson Jr, 2000; Lopes da Silva, 1998; Sanei & Chambers, 2009). ERPs need to be delineated from ongoing spontaneous EEG activity, often referred to as stationary noise, so that the neural responses to specific stimuli or events between experimental groups or conditions can be compared (Lopes da Silva, 1998). However, ERP responses are small voltages (1 – 30 µV) and cannot be reliably isolated from single trials. Therefore, a large number of trials are required for averaging in order to generate a robust mean ERP waveform with positive and negative voltage deflections, which reflect independent underlying or latent components (Luck, 2014; Niedermeyer & da Silva, 2005). Standard nomenclature for ERP components is the waveform polarity (P for positive or N for negative) followed by either the post-stimulus latency or order of the component: for example, the P300 is a positive deflection appearing approximately 250 to 500 ms post-stimulus onset (Luck, 2014).

Averaging over many trials improves the signal-to-noise ratio of the data by minimising the contribution of deflections that are not time-locked to the event of interest (Boudewyn, Luck, Farrens, & Kappenman, 2018). The EEG signal-to-noise ratio improves as a function of the square root of the trial number (Luck, 2014). However, this averaging technique has two drawbacks. Firstly, deflections which are not phase-locked to an event may be cancelled out during averaging, in which case time-frequency analyses may be more appropriate (Tallon-Baudry et al., 1996). Secondly, the large trial number requirement can cause participants to become fatigued, uncomfortable or bored from the repetition of each condition. Therefore, experimenters must balance establishing a robust waveform with logistical concerns when determining the number of trials for an ERP experiment: taking into account factors such as quality of the data, sample size, effect size under investigation and the amount of time required for data to be collected (Boudewyn et al., 2018).

The averaging process occurs after data cleaning and artefact removal have been completed. Epochs of a fixed length are characterised around the experimental trigger and extracted from the clean continuous data. These epochs typically involve a baseline period of 100 – 300 ms duration prior to the stimulus presentation, and a period of 500 – 1000 ms duration post-stimulus presentation (Luck, 2014). The baseline period is used to correct for voltage offsets and slow data drifts by subtracting the mean baseline voltage from the entire waveform (Luck, 2014). The single-trial waveform epochs for each condition are then aggregated by summing together all of the trials and then dividing them by the number of trials. This produces the grand average waveforms for each condition.

2.2.5. Quantitative evaluation of ERPs

ERP components are typically investigated using quantitative comparisons between experimental conditions of latency (i.e., the time point in ms at which peak occurs), amplitude (i.e., the size of the positive or negative deflection in µV), or scalp distribution (i.e., the pattern of voltage gradient across the scalp and over time) (Luck, 2014). Any resulting differences in component attributes between conditions can be used as evidence of the different temporal characteristics of neurophysiological processes between or within populations (Duncan et al., 2009; Handy, 2005).

The traditional method of quantifying the magnitude and timing of monophasic deflections was by ascertaining the amplitude and latency of peak voltage within a predefined time window (Donchin, 1979). This was the simplest approach to measuring ERPs prior to modern computing; however, it has now been superseded by the superior approach of quantifying the mean voltage amplitude over a given time window (Luck, 2014). By calculating the area under the waveform curve, the results are not impacted by latency jitter caused by other spatially and temporally overlapping components, high-frequency noise, or variations in peak latency across electrode sites, experimental conditions, and participants.

2.2.6. Statistical handling of ERP data

Conventional ERP analysis consists of constructing an averaged ERP waveform at each electrode site in each condition for each participant and measuring the ERP of interest on each waveform curve; these values then undergo statistical analysis. An analysis of variance (ANOVA) statistical analysis is the dominant approach in the majority of ERP experiments, with the hypotheses concerned with a main effect or an interaction in a crossed factorial design.

However, the rich datasets collected from EEG recordings can lead to implicit and explicit multiple statistical comparisons, increasing the probability of type 1 error (finding a false positive). With high-density EEG systems, the large number of electrode sites makes it highly likely that statistically significant differences between conditions will be found at a few electrode sites simply due to random noise. For example, with the 129-electrode system used in this thesis, one would expect statistically significant results in 6–7 electrodes under randomly produced data if each electrode was analysed separately. If not carefully controlled for, EEG experiments can report falsely significant results which lack replicability (Button et al., 2013).

In order to minimise the probability of type 1 error, there are several steps researchers can take. Firstly, stringent parameters can be applied prior to statistical analysis through predetermined and specific a priori hypotheses (Luck, 2014). In this way, statistical analysis can be limited to a well-justified latency range at a reasonably small number of electrode sites. This is appropriate in cases of well-established ERP components, such as the P300, where the component is characterised through extensive previous research (Donchin & Coles, 1988; Duncan-Johnson & Donchin, 1982; Duncan et al., 2009; Johnson Jr, 1993; Polich, 2007, 2012). Secondly, the significance thresholds of the p-value can be adjusted relative to the number of comparisons being made through the Bonferroni correction (Maris & Oostenveld, 2007) or the False Discovery Rate (FDR) Correction (Benjamini & Hochberg, 1995). However, this may not be sufficient in under-researched topic areas or for more exploratory research questions.

When there is insufficient justification for analysing a component at a single or small number of electrodes, a mass univariate approach, such as statistical parametric mapping (SPM), or the related permutation approach, offer alternative whole scalp analyses which control the Type I error rate while optimizing statistical power (Maris, 2004, 2012; Maris & Oostenveld, 2007). Originally developed for fMRI analysis (see section 2.3.2), SPM constitutes a voxel-based approach employing classical inference to interpret regionally specific responses to experimental factors (Friston, 1994; Kiebel & Friston, 2004; Worsley, 2003). SPM creates 3D volumes incorporating amplitude, latency and electrode, where the statistic value at each voxel represents level of evidence against the null hypothesis (Friston, 1994). Similarly, permutation analysis is a related nonparametric statistical framework, where randomised subsets of the observed data set are repeatedly calculated comparing conditions at each time point for each electrode site to determine the distribution of t values that would be expected by chance (null distribution). By using many iterations, researchers can ascertain how big a t-value must be in order to exceed what would be expected by chance. This is based on the assertion that if the null hypothesis is true, then the averaged waveforms for two conditions will be equivalent (excluding noise). Both approaches offer valid, robust and data-driven analyses with only minimal a priori assumptions, which is especially advantageous when investigating exploratory research questions (Achim, 2001; Galán, Biscay, Rodríguez, Pérez-Abalo, & Rodriguez, 1997; Guthrie & Buchwald, 1991; Karniski, Blair, & Snider, 1994; Kiebel & Friston, 2004).

2.2.7. Advantages and limitations of EEG

The main advantage of EEG as an investigative tool is that it has excellent temporal resolution, being able to detect electrical changes in the order of milliseconds (Schneider & Strüder, 2012). This allows for the direct understanding of the neural processing of stimuli in real time (Luck, 2014), as opposed to other neuroimaging methods such as fMRI and positron emission tomography (PET) (Hari, Parkkonen, & Nangini, 2010) which use haemodynamic function as a proxy measure, and have a poor temporal resolution in the magnitude of several seconds (Luck, 2014). In addition, EEG can also be used in tandem with other complementary methods which have superior spatial resolution, such as fMRI and magnetoencephalography

(MEG) (Chowdhury et al., 2015; Ding & Yuan, 2013; Ebersole & Ebersole, 2010; Henson, Mouchlianitis, & Friston, 2009).

There are also considerable practical advantages to EEG. It is a non-invasive technique and is incredibly safe to use, with virtually no risks to participants. Advancements in mobile EEG technology has also allowed for recordings to be conducted in a wide range of environments: EEG systems can be transported to clinical patients when their mobility is an issue, and it can be used in naturalistic settings to increase the ecological validity of findings. Furthermore, in comparison to fMRI, EEG is relatively cheap to run, is silent when recording, is less likely to induce claustrophobia in participants, and does not require the use of strong magnetic fields that exclude participants with ferromagnetic implants.

However, EEG also has some limitations. Fundamentally, it has limited spatial resolution in comparison to other neuroimaging methods such as fMRI or MEG (Burle et al., 2015; Ferree, Clay, & Tucker, 2001; Hämäläinen et al., 1993). As EEG uses electrodes placed on the scalp, the electrical fields recorded are attenuated by the various tissues it has to pass through, such as white and grey matter, meninges membranes and cerebrospinal fluid (Nunez et al., 1997). In addition, the resistance in the skull results in smearing of the electrical signal (Hämäläinen et al., 1993). This smearing results in issues with identifying the location(s) of the source of neuronal activity in the cortex from the EEG data, commonly referred to as the inverse problem. Source analysis methods have been developed to reconstruct potential intracranial origins for a given EEG signal; however, these are not definitive as they are limited by the accuracy of conductivity models and brain templates utilised to subjective data (Schneider & Strüder, 2012).

Further, EEG is not without its practical disadvantages. EEG is susceptible to contamination by non-neural artefacts such as myogenic activity from eye blinks, saccades, jaw and neck movements, cardiographic signals, and spontaneous bad electrode connections. A typical EEG task will ask participants to remain as still as possible to minimise some of these artefacts, which can be effortful and uncomfortable to experience, and can potentially reduce the ecological validity of the results. Oculographic and cardiographic artefacts are removed during data cleaning through a standard pipeline such as principal components analysis (Berg & Scherg, 1994), but some of the trials will likely need to be rejected, and so the number of trials initially collected must take that into account. Separate to the issue of non-neural artefacts, EEG tasks generally require a great number of trials for each experimental condition in order to elicit reliable event-related components due to a high signal-to-noise ratio (Hauk, 2013; Luck, 2014). Taken together, this can result in long, repetitive and boring tasks for the participant, which can induce fatigue or disengagement.

2.3.fMRI

2.3.1. Physiological basis of fMRI recordings

fMRI is a non-invasive medical imaging technique used to measure brain activity over time for clinical and research purposes (Mandeville & Rosen, 2002). fMRI experimental designs can be task-based, where regional neural activation is triggered by a stimulus, or resting state, which investigates the functional architecture of the brain. Unlike EEG, fMRI is an indirect method of measuring brain activity, as it relies on the coupling of neuronal activation with changes in cerebral blood flow.

The physical basis of MRI experiments is from the interaction of nuclear spins and magnetic fields. During scanning, a strong magnetic field causes a new alignment of hydrogen in the brain tissues that are otherwise randomly oriented within water nuclei, a process called longitudinal magnetisation (Mandeville & Rosen, 2002; Narasimhan & Jacobs, 2002; Pooley, 2005). Short radio frequency (RF) pulses are delivered perpendicular to the static magnetic field at a specific frequency called the Larmor frequency, which targets hydrogen nuclei. The RF pulse knocks the proton spins out of alignment with the main magnetic field, and induces transverse magnetisation (Mandeville & Rosen, 2002; Pooley, 2005).

The RF pulse also causes hydrogen nuclei spins to precess in phase about the applied magnetic field. When the RF pulse finishes, the excited hydrogen nuclei spins realign with the external magnetic field, a process called longitudinal relaxation, and also move out of phase, known as transverse relaxation. The time it takes for net longitudinal relaxation and net transverse relaxation are referred to as T1 and T2, respectively. The transverse magnetisation that arises from the RF pulse induces an electrical current that can be detected by the radio frequency coils in the MRI setup; this is known as the magnetic resonance (MR) signal (Deichmann, Nöth, Merola, & Weiskopf, 2022; Hendee & Morgan, 1984). T1-weighted and T2-weighted scans are the most common sequences used in fMRI, highlighting the differences in the T1 and T2 relaxation times of tissues, respectively.

Brain tissue cannot store oxygen or glucose, and so is highly dependent on a reliable and locally adaptable blood supply to constantly replenish energy levels for normal functioning to occur. As a region of the brain becomes more active, more energy is needed to resupply the cells, and so vasodilators are released and the volume of blood being directed to that local area increases. The neural tissue is unable to absorb all the excess oxygen being carried by haemoglobin molecules in the blood. Therefore, there is a localised increase in the ratio of oxygenated to deoxygenated haemoglobin in that area of the brain (Attwell & Iadecola, 2002; Logothetis, 2008). Oxygenated and deoxygenated haemoglobin have different MR signal characteristics: deoxyhaemoglobin is weakly magnetic in the presence of a magnetic field (paramagnetic) due to having 4 unpaired electrons, whereas oxyhaemoglobin is virtually resistant to magnetism (diamagnetic) and is indistinguishable from brain tissue by MRI.

In high concentrations, deoxyhaemoglobin causes field inhomogeneity and susceptibility artefacts from the rapidly de-phasing protons, which decreases the local MR signal, and modulates the intra- and extra-vascular blood's T2 and T2* relaxation times (Kim & Bandettini, 2010; Mandeville & Rosen, 2002). Here, deoxyhaemoglobin acts as an endogenous paramagnetic contrast agent that attenuates the MR signal, and so can be used to evaluate blood flow (Kim & Bandettini, 2010; Mandeville & Rosen, 2002; Narasimhan & Jacobs, 2002). fMRI studies typically use a gradient refocused echo (GRE) MRI pulse sequence sensitive to T2 and T2* contrasts, where the areas with high levels of deoxyhaemoglobin appear darker on a T2 weighted image compared to areas with high levels of oxyhaemoglobin. As the resulting fMRI signal resolution between active and resting neurons is based on the relative concentration of oxyhaemoglobin in the downstream venules, fMRI images show areas with increased neuronal activity as appearing brighter. This value is referred to as the BOLD signal (Glover, 2011; Kim & Ogawa, 2012; Ogawa, Lee, Kay, & Tank, 1990).

2.3.2. fMRI signal acquisition and processing

fMRI studies measure the time course of changes in the BOLD contrast in order to make inferences regarding task-related changes in localised cortical activation of brain structures. During an fMRI experiment, a series of high-resolution 'snapshot' anatomical images are acquired, typically using an Echo Planar Imaging (EPI) method (Poustchi-Amin, Mirowitz, Brown, McKinstry, & Li, 2001; Schmitt, Stehling, & Turner, 2012). Complete cross-sectional two-dimensional images are recorded approximately every 50–100 ms, with whole brain scans (known as sequential volumes) comprised of approximately 32 images completed every 2 seconds. Slices are typically a few millimetres spaced apart, or collected in an interleaved fashion, in order to prevent crosstalk between protons bordering the edges of slices, which would reduce the contrast (McRobbie, Moore, Graves, & Prince, 2017). The 2D slices are then time corrected to bring all slices in a sequential volume to the same timepoint reference. The complete sequential volumes are then modelled across time as a 4D space containing around 100,000 cubic volumes of equal size, known as voxels, with each voxel defined by x y z coordinates and containing its time series across the scan. Each voxel corresponds to a spatial location on a uniform grid of data points and has an array of values that represents its intensity (Lindquist, 2008).

EPI has the advantages of high imaging speed and BOLD contrast sensitivity, but is also susceptible to inherent artefacts and diminished image quality (Poustchi-Amin et al., 2001; Schmitt et al., 2012). fMRI is vulnerable to extraneous noise signals such as head motion, respiration and cardiovascular functions, variations in baseline neural metabolism, thermal sources in the participant and electronics, and random voltages within the fMRI coils and recording equipment. Due to artefact interference, sequential volumes may differ from each other even when there is no change in brain state. Indeed, noise signals can sometimes be larger than the signal of interest. Therefore, fMRI datasets are submitted to standardised pre-processing corrections, such as motion co-registration, spatial smoothing, and low- or high-pass temporal filtering, to improve the signal to noise ratio (SNR). Most importantly, fMRI is registered to the T1 structural image, and the structural image is registered to standard Montreal Neurological Institute (MNI) space, and so any changes in BOLD signal intensity are viewed on the normalised structural image. Following this, rigorous statistical analysis is performed to ensure that the changes in BOLD signal intensity between the 3D maps over time can be used to make inferences regarding task-related localised cortical activation of brain structures (Lindquist, 2008).

The most common method of statistically analysing fMRI data is through general linear modelling (GLM), though cross-correlation with a modelled regressor or a data-driven approach such as independent components analysis (ICA) are also used (Friston et al., 1994). GLM assumes that a given dataset can be modelled as a linear combination of differently weighted regressors, with any discrepancies between the model and the data being labelled as residuals. In GLM fMRI analysis, the BOLD response is convolved with a haemodynamic response function (HRF) to give the regressors, which are then summarised in a design matrix along with known sources of variance, to produce a statistical parametric map with associated parameter estimates for each experimental condition over time (Lindquist, 2008). The resultant BOLD activation maps are a function of the probability of condition-specific differences in brain activation patterns.

2.3.3. Meta-analyses and Activation Likelihood Analysis

Due to the often small sample size of neuroimaging experiments, individual studies can be underpowered; the results have low reliability (Raemaekers et al., 2007) and the findings are often not replicated in other studies (Eklund, Nichols, & Knutsson, 2016; Wager, Lindquist, Nichols, Kober, & Van Snellenberg, 2009; Woo, Krishnan, & Wager, 2014). Further, with the popularity of fMRI as a methodology, it can also be difficult to keep up with the vast number of studies published every year, and discern which effects from individual studies are robust and generalisable (Radua et al., 2012). Pooling data from multiple experiments which investigate the same, or similar, set of research questions is an important step for consolidating the literature (Müller et al., 2018). Performing meta-analyses allows for the identification of consistent brain activations across studies in a systematic and unbiased way (Eickhoff et al., 2009; Laird et al., 2005).

The two main approaches to the computation of fMRI data are image-based and coordinate-based meta-analyses. Image-based meta-analyses require the full statistical images of the individual studies, as it uses hierarchical mixed effects models that incorporate intra- and inter-study variance (Salimi-Khorshidi, Smith, Keltner, Wager, & Nichols, 2009). Conversely, coordinate-based meta-analysis is based only on the published activation maxima *x y z* coordinates of statistically significant results reported in the papers in standardized anatomical space, which is comparatively a very sparse representation of the results. However, this has the advantage of integrating the maximum number of results across the entire published literature, as one does not need to contact the original authors. This avoids the bias of only collating primary data from researchers who are known, or respond, to the authors, and lessens the bias of preferentially reporting more recent results as older findings are less likely to have been stored in their entirety (Poldrack et al., 2008). For this reason, image-based meta-analysis is not recommended for the majority of research questions (Müller et al., 2018).

Activation likelihood estimation (ALE) (Eickhoff et al., 2009; Eickhoff et al., 2016; Laird et al., 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002) is the most widely used coordinate based meta-analysis approach. ALE provides a measure of activation location consistency, being performed to determine whether a spatial convergence of foci or local maxima across a group of independent studies is larger than can be expected by chance. This is done by treating the peak activation foci locations reported in neuroimaging studies as spatial probability distributions centred at given coordinates. Every reported coordinate across all studies are then replaced with 3D Gaussian probability distributions modelling the associated spatial uncertainty (Eickhoff et al., 2016). The size of these Gaussian kernels is dependent on the sample size of the corresponding study, with larger samples having greater statistical power and less spatial uncertainty, and therefore producing smaller distributions. Simulated statistical parametric images, referred to as Modelled Activation (MA) maps, are created for each foci group from the 3D probability distributions and anatomically mapped to locations on standard atlases such as the MNI (Collins, Neelin, Peters, & Evans, 1994) or Talairach (Talairach, 1988) three-dimensional space.

Once the ALE scores are established in the form of the MA maps, the map values are tallied into histograms and the bins are divided by the total number of voxels in an MA map, in order to determine the null distribution of the ALE statistic (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). This method removes spatial information and establishes the P values of finding each given ALE score value in a MA map. The P values are combined to create a P value image, which undergoes significance thresholding. A permutation analysis compares the modelled activation probabilities to a hypothetical null distribution of random spatial association for each voxel in the brain (Müller et al., 2018; Turkeltaub et al., 2002). This algorithm computes the likelihood that the convergence of foci clusters in the MA maps are not due to chance, and experimenters can set their threshold values to be more or less conservative based on their assumptions about the data (Eickhoff et al., 2012; Eickhoff et al., 2016; Müller et al., 2018; Nichols & Hayasaka, 2003). The resulting ALE statistic reports the probability of activation being present at that given voxel for all studies in the analysis.

In this thesis, a systematic review was conducted to identify journal articles investigating economic value with fMRI methods. Coordinates were then extracted from accepted research articles and subjected to an ALE meta-analysis using BrainMap GingerALE v3.0.2 (http://brainmap.org/ale), where the ALE algorithm is implemented (Eickhoff et al., 2012; Eickhoff et al., 2009; Eickhoff et al., 2016). The results of the systematic review and meta-analysis are discussed in Chapter 4.

2.3.4. Advantages and limitations of fMRI

There are several advantages to using fMRI. To begin, it is safe to use, as it does not involve use of injections, surgery, the ingestion of substances, or exposure to radiation like X-rays, computed tomography (CT) and PET scans require. It is therefore very low risk for patients, and can evaluate the entirety of the brain safely and noninvasively. Further, the vast majority of studies follow standardised techniques for pre-processing (cleaning) data, individual statistical analysis, and group-level results analysis, without the need to adjust the analysis parameters each time. Importantly, fMRI has the best spatial resolution of any non-invasive neuroimaging method, as it can examine a spatial range from millimetres to centimetres. A typical voxel in a 3D map contains a few million neurons and tens of billions of synapses, and so can provide an insight into how populations of neurons fire together.

However, fMRI also has several limitations. Firstly, it is classified as an indirect measure of neuronal activity, as the level of regional activation is inferred from the intensity of the BOLD signal (Mandeville & Rosen, 2002). Changes in blood flow are modulated much more slowly than neuronal events, with the BOLD response being observed typically 6 – 10 seconds after a stimulus presentation. Simultaneous fMRI and EEG recordings have established that synaptic and haemodynamic activity are closely related, with strong correlations between local field potentials and BOLD signal (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Ogawa et al., 2000; Rees, Friston, & Koch, 2000). However, the delay in the vascular response means that fMRI cannot separate feedback and feedforward active neural networks in a brain region, as the BOLD signal is the summation of the whole region’s activity. This low temporal resolution of haemodynamic responses makes fMRI ill-suited for investigating the temporal course of brain activity in comparison to EEG.

Further, much of the quality of the fMRI images rely on participant co-operation. Participants can experience claustrophobia and stress from being confined by the head coil and the narrow scanner space. They are also required to remain incredibly still for long periods of time throughout scanning in order to capture high quality images, which can be uncomfortable and limit task duration. Additionally, fMRI necessitates a very careful screening process to ensure that participants do not have any potential MRI-unsafe implants or any ferromagnetic debris (Huettel, Song, & McCarthy, 2009). Finally, as a research method, fMRI is significantly more expensive relative to EEG (Crosson et al., 2010). Due to this, fMRI studies often recruit small samples of participants (Szucs & Ioannidis, 2020), which can result in low reliability and low reproducibility of a single study’s findings (Raemaekers et al., 2007).

3. Research problems and Hypotheses

3.1. Research problems

The neural structures underpinning the automatic and domain-general brain valuation system have been well characterised through a wealth of fMRI studies (see section 1.2.2). However, many meta-analyses have chosen to make their inclusion parameters intentionally broad in the interest of including as many studies as possible in the final cohort (Bartra et al., 2013). While this has some advantages, such as statistical power and robustness of results, the heterogeneity of task paradigms can muddy the proverbial waters. Many of the experiments in the neuroeconomics literature have not utilised an incentive-compatible design, and so the veracity of reported results is reliant on the assumption of participant goodwill, and may be distorted by hypothetical bias (Schmidt & Bijmolt, 2020) and question framing effects (Kühberger & Gradl, 2013). Therefore, there is potential for doubt as to how realistically the participants' behavioural reports of value match their true SVs.

In addition to this, having differing, vague or implicitly defined understandings of value leaves experiments vulnerable to participant interpretation and thereby outside of the researcher's control. Moreover, multiple definitions of SV, such as instrumental, intrinsic, hedonic, utilitarian and aesthetic characterisations, may be amalgamated into a single meta-analysis. In fMRI research, this can lead to confounds with brain areas demonstrating greater BOLD responses during valuation tasks, as researchers are unable to disentangle which definition or aspect of the valuation process the neural substrates are involved in.

Furthermore, the poor temporal resolution of fMRI leaves it unable to isolate the spatiotemporal dynamics of the neural structures in the brain valuation system that are engaged on a scale of milliseconds (Luck, 2014; Schneider & Strüder, 2012). The inferior temporal resolution of fMRI may also lead to ambiguity over which neural substrates are involved with which stage of decision-making: for example, the valuation period may blur into action selection (Rangel, 2008). The use of high-temporal resolution methods such as EEG allows for the elaboration of the temporal features of valuation processes. While the BDM is a popular method of measuring SV in fMRI research, its use in EEG studies to date has been scarce. The few EEG studies which have performed a BDM task have focused on the initial valuation period of value-based decision-making (Roberts et al., 2018; Tyson-Carr et al., 2018; Tyson-Carr et al., 2020). To the best of this authors knowledge, none have investigated the outcome processing period in incentive-compatible contexts such as second-price sealed-bid auction tasks.

The VA is a popular auction method in ecommerce and in the behavioural economics field (Lucking-Reiley, 2000), but the spatiotemporal neural dynamics underlying value-based decision-making during this task have yet to be investigated. Previous research suggests that feedback processing is facilitated by the presence of another person, and that impact of the social context interacts with both initial valuation and outcome salience (van den Bos et al., 2008; van den Bos et al., 2013). It remains unknown whether reward-related brain components measured by EEG are elicited in the VA context at the time of receiving an auction outcome. Moreover, if the FRN and P300 are elicited, it is unclear to what extent this feedback processing is modulated by the socially competitive context. A direct comparison of the BDM and VA paradigms would afford the opportunity to isolate the SV of winning or losing against another player, and its impact on the time course of RPE processing in the brain.

3.2. Hypotheses

H_1 – Economic value, as defined by WTP, will elicit brain activation in the core areas associated with SV in the brain valuation system, such as the VS and vmPFC.

H_2 – Economic valuation processes in the brain will be performed automatically.

H_3 – Reward processing related ERPs, such as the FRN and P300, will be elicited at the time of receiving an outcome in a VA task.

H_4 – During outcome processing in the VA, the FRN amplitude will be positively correlated with individual differences in loss aversion.

H_5 – The inclusion/exclusion of a socially competitive dimension in the second-price sealed-bid auction context will be differentially encoded by reward processing related ERPs.

3.3. Thesis chapters outline

Chapter 4 examines the neural correlates of economic value processing in the human brain by conducting a systematic review and meta-analysis of the fMRI literature. Experiments using a BDM task procedure (either before, during or after scanning) to elicit WTP values as a measure of SV were identified and underwent coordinate-based ALE analysis. It was anticipated that using the BDM paradigm would allow the delineation of the neural substrates involved in economic valuation from brain areas which are involved in other aspects of subjective valuation, such as hedonic processing (H_1). A secondary contrast analysis was also performed to evaluate whether there is a difference in patterns of brain activation between studies which perform a BDM outside of the fMRI scanner and those that perform the BDM during fMRI scanning (H_2).

Chapter 5 describes an ERP study utilising EEG and the VA paradigm to investigate the spatiotemporal characteristics of outcome processing during value-based economic decision-making in the human brain. It was anticipated that outcome related ERPs such as the FRN and P300 would be elicited in this incentive-compatible task in a comparable fashion to that seen in previous decision-making tasks, such as 2AFC paradigms (H_3). The experiment also employed a separate behavioural monetary gambling task measuring participants individual levels of loss aversion, thus allowing the investigation of the impact of loss aversion on reward-related ERPs in this socially competitive auction context (H_4).

Chapter 6 extends the findings from Chapter 5 by comparing reward-related ERPs elicited during the outcome receipt period of the VA and BDM auction paradigms using EEG. Directly comparing two strategically equivalent demand-revealing mechanisms affords the opportunity to isolate the impact of social environment on how good and bad outcomes are computed in competitive, risky decision-making. The experiment increased the market price range of auction items in an effort to examine reward-related neural responses to winning or not-winning high-SV items. It was anticipated that outcome related ERPs would be differentially sensitive to SV, opponent and feedback parameters (H_5).

Chapter 7 comprises a summary and general discussion of all experimental findings. The implications of the findings are discussed in terms of theoretical and practical impact within the field of neuroeconomics. Finally, the limitations of the current work and possible future directions of research are considered.

4. Economic value in the Brain: A Meta-Analysis of Willingness-to-pay using the Becker-DeGroot-Marschak Auction

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This study investigated the neural correlates of economic value during BDM auctions using the fMRI meta-analysis technique activation likelihood estimation analysis. This paper is currently undergoing peer review for publication at PLOS One.

The format of the text has been altered to match the style of the thesis.

The roles of the co-authors are summarised below:

Myself and Andrej Stancak, Olga Gorelkina, Yiquan Gu, Nick Fallon, Carl Roberts and Timo Giesbrecht contributed to the development of the experimental design, hypotheses and planning of the current project. I carried out the preliminary and formal database searches and the article screening process. Jessica Henderson, Danielle Hewitt and Andrej Stancak assisted with the data screening process as second reviewers. Decisions regarding final article inclusion were determined by discussion with Andrej Stancak. I extracted the relevant coordinate data from the final data pool, and these were cross-checked by Carl Roberts. I was responsible for the GingerALE analysis, with the assistance of Tyler Mari. I produced the final written manuscript, which all co-authors read and provided feedback for.

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest.

Data and code availability statement

An a priori protocol for this meta-analysis was preregistered at The Open Science Framework: https://osf.io/vpt3d. The datasets generated and analysed in the current study are available from the Supplementary Materials. To facilitate future research, ROIs created using the resultant unthresholded meta-analytic clusters have been made available via NeuroVault (https://neurovault.org/collections/IBLCLBYH/images/785459/).

4.1.Abstract

Forming and comparing subjective values (SVs) of choice options is a critical stage of decision-making. Previous studies have highlighted a complex network of brain regions involved in this process by utilising a diverse range of tasks and stimuli, varying in economic, hedonic and sensory qualities. However, the heterogeneity of tasks and sensory modalities may systematically confound the set of regions mediating the SVs of goods. To identify and delineate the core brain valuation system involved in processing SV, we utilised the Becker-DeGroot-Marschak (BDM) auction, an incentivised demand-revealing mechanism which quantifies SV through the economic metric of willingness-to-pay (WTP).

A coordinate-based activation likelihood estimation meta-analysis analysed twenty-four fMRI studies employing a BDM task (731 participants; 190 foci). Using an additional contrast analysis, we also investigated whether this encoding of SV would be invariant to the concurrency of auction task and fMRI recordings. A fail-safe number analysis was conducted to explore potential publication bias.

WTP positively correlated with fMRI-BOLD activations in the left ventromedial prefrontal cortex with a sub-cluster extending into anterior cingulate cortex, bilateral ventral striatum, right dorsolateral prefrontal cortex, right inferior frontal gyrus, and right anterior insula. Contrast analysis identified preferential engagement of the mentalizing-related structures in response to concurrent scanning.

Together, our findings offer succinct empirical support for the core structures responsible for the formation of SV, separate from the hedonic aspects of reward and evaluated in terms of WTP using BDM, and show the selective involvement of inhibition-related brain structures during active valuation.

4.2.Introduction

In human decision-making, where an individual compares their options and select the course of action with the highest SV, the construction of SV of potential outcomes is critical (Rangel et al., 2008). Previous theories of decision-making have highlighted rational expectations (Mongin, 1998; Moscati, 2018; Von Neumann & Morgenstern, 2007) and reference points (Kahneman & Tversky, 2013; Tversky & Kahneman, 1989) as prominent factors in SV formation. A set of regions have been identified as comprising the brain valuation system, including the ventromedial prefrontal cortex (vmPFC) (Kim, Hwang, & Lee, 2008; Lebreton et al., 2009; Winecoff et al., 2013), ventral striatum (VS) (Delgado, Locke, Stenger, & Fiez, 2003; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Levy et al., 2010; Peters & Buchel, 2009), anterior insula (AI) (Bartra et al., 2013; Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007; Kuhnen & Knutson, 2005; Sescousse, Caldú, Segura, & Dreher, 2013), posterior parietal cortex (PPC) (Glimcher, 2003; Platt & Glimcher, 1999), orbitofrontal cortex (OFC) (De Martino, Kumaran, Holt, & Dolan, 2009; Padoa-Schioppa & Assad, 2006; Plassmann et al., 2007), amygdala (Basten, Biele, Heekeren, & Fiebach, 2010; Cardinal, Parkinson, Hall, & Everitt, 2002; De Martino et al., 2010; Holland & Gallagher, 2004; Lebreton et al., 2009) and anterior cingulate cortex (ACC) (Botvinick et al., 2001; Shenhav, Cohen, & Botvinick, 2016; Vassena, Deraeve, & Alexander, 2020; Walton, Croxson, Behrens, Kennerley, & Rushworth, 2007).

Subjective valuation is a complex process requiring the amalgamation of an individual's perceptions, prior knowledge, and reward expectations of a given stimulus. It has often been implicitly defined through differing methodology; such as liking scales, unpleasantness ratings and binary forced choice decisions in monetary gambling tasks. However, this heterogeneity in methodology can have the consequence of implicitly defining varying conceptualisations of value under the umbrella term of SV, with the potential to conflate SV with other closely related concepts. For example, hedonic understandings of attractiveness (Rangel et al., 2008) and pleasure (Jiang, Soussignan, Schaal, & Royet, 2014), can be understood as distinct from utilitarian concepts of worth (Moscati, 2018), willingness to exert effort or a motivation to take on costs (Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009). Further, there are established differences in the brain circuitry involved in the liking, wanting, and pleasantness of a reward, in particular in subregions of the VS (Berridge, 2009; Berridge & Kringelbach, 2015; Berridge & Robinson, 2016; Kühn & Gallinat, 2012). Whereas finding a reward pleasant or likeable refers to an emotional state and its experiential qualia, the wanting of a reward refers more to the underlying motivational processes and is linked to decision utility (Morales & Berridge, 2020). In this way, heterogeneity in the definitions of SV and task paradigms may confound the findings to date and it is likely that the range of brain regions associated with SV is smaller than indicated by available meta-analyses owing to SV being estimated by hedonic measures. For example, in the interest of maximising the pool of viable studies, Bartra *et al.* (2013) used simple search parameters of “fMRI” AND “reward”. However, as receiving a reward entails multiple other processes in addition to the representation of the SV of the object, such as the pleasantness of positive feedback, the perceived attractiveness of the object, and other hedonic processes, it is not known which part of the brain valuation system would specifically encode SV.

In behavioural economics and neuroeconomics, valuation consolidates multiple determinants of a goods’ value into a singular figure of a given currency (Padoa-Schioppa, 2011; Padoa-Schioppa & Conen, 2017). Methodologically, this has several advantages. Firstly, one can assign an economic value to any type of outcome stimulus, such as food, music, pain, or lottery tickets (De Martino et al., 2009; Plassmann et al., 2007; Salimpoor et al., 2013; Winston, Vlaev, Seymour, Chater, & Dolan, 2014). In this way, experiences in different mediums can all be translated into monetary worth that is subjective to the individual.

Secondly, multiple facets of reward receipt, such as the outcomes' temporal immediacy and probability of reward, can be integrated into a single discounted SV, and so complex options can be compared against each other. Thirdly, economic valuation is applicable to both rewards and punishments: tasks can explore paying for the opportunity to receive a good outcome or to avoid a bad one (Delgado, Li, Schiller, & Phelps, 2008), which allows the relationships between loss and gain to be explored. Fourthly, as monetary scales are linear, the relative relationships of a theoretically infinite number of outcomes can be compared and ranked. Finally, it is intuitive to participants, as individuals are well-versed in weighing up purchasing decisions to maximise their utility in their everyday lives.

WTP is the standard measure of value in economics, and is defined as the maximum amount of currency a customer is willing to part with in order to purchase a product or service. There are several methods that can estimate WTP, either directly or indirectly, and ascertain a consumer's hypothetical or actual WTP (Miller, Hofstetter, Krohmer, & Zhang, 2011). However, most methods, such as two-alternative forced-choice tasks (2AFC), open-ended questions ("what would you be willing to pay for this item?") or choice-based conjoint analysis ("pick one item from this list of options") can produce unreliable results (Breidert, 2007; Breidert et al., 2015). This is due to a lack of incentive to induce truth-telling: within the parameters of these mechanisms, participants are not appropriately compensated for revealing the private information of their SVs. Therefore, they may not wish to do so, and the responses may be arbitrarily chosen or due to other motives, reporting SVs that they do not necessarily hold or would act upon. As the participants responses do not hold real consequences, such as a purchasing commitment, their choices may not reflect their true preferences. Consequently, researchers cannot rely on the values participants provide (Acquisti et al., 2015; Wertenbroch & Skiera, 2002).

Furthermore, hypothetical purchasing scenarios has been shown to produce consistent behavioural overestimations of WTP in comparison to that of real purchasing scenarios, termed the Hypothetical Bias (Foster & Burrows, 2017; List & Gallet, 2001; Little et al., 2012; Murphy et al., 2005). This effect is strongest in indirect measures, such as in 2AFCs, leading to consistent overestimation of WTP values (Schmidt & Bijmolt, 2020). Crucially for this work, valuation areas of the brain are also differentially activated by hypothetical and real choices, with greater activity for real purchasing decisions in the orbitofrontal cortex, and conflicting evidence of activation in the ventral striatum for hypothetical choices (Bray, Shimojo, & O'Doherty, 2010; Kang, Rangel, Camus, & Camerer, 2011).

In contrast, the auction paradigm Becker-DeGroot-Marschak mechanism (BDM), also known as a second-price sealed-bid auction, is an incentivized experiment (Becker et al., 1964). During a BDM, a player submits a single bid for a given item. Their bid value is compared to a randomly generated price, and if the player's bid exceeds or equals this price they win the item and pay the random price. If the player's bid does not exceed that of the random number generator, they win nothing and lose nothing. As the player's bid value is used to produce the outcome directly affecting the player, bidding one's true SV is the dominant strategy. If the player underbids, they only risk not winning the item for a price that they would be willing to pay, and if the player overbids, they only risk winning the item for more than they are willing to pay. In this way, their bid value can also be thought of as their reservation price, or indifference point (Padoa-Schioppa, 2011). Formal proof of the dominant strategy in BDM Auctions can be seen in Figure 2.1.1.

The present study proposed to compare brain activations associated with SV as defined by WTP through a BDM by employing a coordinate based meta-analysis with activation likelihood estimation (ALE) (Eickhoff et al., 2012; Eickhoff et al., 2009). A single paradigm was utilised, therefore avoiding the confounding effects of task heterogeneity. The BDM has become increasingly popular in neuroeconomics in recent years, in no small part to its use in the seminal paper by Plassmann, O’Doherty and Rangel (2007), so that there now exists a sufficient body of work to conduct a meta-analysis of fMRI studies evaluating WTP using the BDM.

Activation in the brain valuation system tends to increase when considering the SV of the available options during choice, as well as with the value of the reward received, and responds to both primary and secondary forms of reward (Peters & Buchel, 2010; Sescousse et al., 2013; Sescousse, Li, & Dreher, 2015). This suggests that a domain-general system in the brain is responsible for the encoding of SV across multiple decision stages and reward types (Levy & Glimcher, 2012). Furthermore, evidence for automaticity in value attribution has been provided in a number of previous studies (Grueschow, Polania, Hare, & Ruff, 2015; Lebreton et al., 2009; Padoa-Schioppa, 2013; Polanía, Krajbich, Grueschow, & Ruff, 2014; Tyson-Carr et al., 2018). For instance, the brain valuation system scales the SV of objects even if participants are asked to make value-irrelevant judgements, such as perceptual discernment of stimuli characteristics (Grueschow et al., 2015; Motoki, Sugiura, & Kawashima, 2019; Tyson-Carr et al., 2018). To investigate automaticity of economic valuation, we also compared the WTP contrasts in studies for which WTP was elicited during fMRI scanning (concurrently) or outside of the scanner (consecutively). We posited that the brain regions encoding WTP would be invariant to the concurrency of the BDM auction session and fMRI recording, as the WTP values would be automatically invoked during passive viewing of objects even in absence of choice selection.

4.3.Methods

An a priori protocol for this meta-analysis was preregistered at The Open Science Framework: https://osf.io/vpt3d.

4.3.1. Information sources and search strategy

The formal search strategy consisted of systematically examining 3 electronic databases (PubMed, Scopus, PsycINFO) through August 2022 using the MeSH search terms (fMRI OR functional magnetic resonance imaging OR neuroimaging) AND (willing to pay OR willing-to-pay OR willingness to pay OR willingness-to-pay OR WTP OR BDM OR Becker–DeGroot–Marschak OR Becker DeGroot Marschak OR economic valuation). Searches were restricted to terms found in the title or abstract of the articles. No date limit was set for the searches.

During the search process, the authors noticed that several potentially eligible papers did not refer to the task as a BDM auction; for example, one article in the final corpus cites Plassmann, O'Doherty and Rangel (2007) and not Becker, DeGroot and Marschak (1964) as the task originators (Verdejo-Roman, Vilar-Lopez, Navas, Soriano-Mas, & Verdejo-Garcia, 2017). Therefore, for completeness, a comprehensive manual search of the reference sections and citation lists of identified articles was conducted to supplement the formal searches. Previous meta-analyses of fMRI studies on human reward (Bartra et al., 2013; Clithero & Rangel, 2014; Liu, Hairston, Schrier, & Fan, 2011; Morelli et al., 2015) were also screened for additional articles.

4.3.2. Article selection and extraction of data

Formal database searches were conducted by ANF, as were supplementary and manual searches. One author (ANF) was responsible for assessment of articles for inclusion, with three authors (AS, JH and DH) conducting 2nd reviews of 10% of the collected articles each (totalling 30% of the initially identified articles). Decisions regarding final article inclusion were determined by discussion. One author (ANF) extracted the relevant coordinate data, and these were cross-checked by a second author (CR).

4.3.3. Eligibility criteria

The criteria for inclusion were 1) any human fMRI studies published through to August 2022; 2) original English language articles; 3) published in a peer-reviewed journal; 4) used a Becker-DeGroot-Marschak task to elicit WTP; 5) computed the correlation of Blood Oxygenation Level Dependent (BOLD) activity to the WTP value; 6) coordinates were reported in the article or supplementary material in Montreal Neurological Institute (MNI) (Evans et al., 1993) or Talairach space (Talairach, 1988); 7) data were obtained from a healthy population (systemic disease-free); 8) whole-brain analysis were reported with thresholding of (or equivalent to) $P < 0.001$ uncorrected voxelwise throughout the whole brain with at least $p < 0.05$ cluster level correction (or equivalent) declared (Müller et al., 2018).

4.3.4. Additional handling of data

We excluded papers which only reported region of interest (ROI) analysis, which may bias results towards more established or accepted regions (Turkeltaub et al., 2012). One of the studies in the final sample, Chib et al. (2009), reported three separate activation maps for the computation of WTP for three different categories of goods: money, trinkets and snacks. In the interest of including a wide variety of stimuli, the activation map for trinkets was selected for inclusion in the meta-analysis. Studies that reported coordinates in Talariach space were converted into MNI coordinates using GingerALE (Brainmap GingerALE version 3.0.2; Research Imaging Institute; http://brainmap.org) (Eickhoff et al., 2009).

4.3.5. Activation likelihood estimation meta-analysis

A primary ALE meta-analysis was conducted for experiments using BDM paradigms to elicit WTP measures, contrasting increasing WTP with increasing BOLD responses. Decreasing activations in line with increasing WTP were not investigated. See Table 1 for data on the included studies. Subsequently, an exploratory secondary analysis was performed on the same dataset, split by concurrency of BDM task with fMRI scanning, with 16 BDM tasks performed inside the scanner (concurrently) and 8 BDM tasks performed outside the fMRI scanner (consecutively).

To determine consistency in reported regions of neural activation, for our primary analysis we conducted a coordinate-based ALE meta-analysis (single dataset analysis). The analysis was performed using Brainmap GingerALE version 3.0.2. Standardized procedures and default parameters for performing ALE using GingerALE were followed, as outlined in the GingerALE user manual (Research Imaging Institute; http://brainmap.org) and Eickhoff et al. (2016).

The concordance of ALE values throughout the brain for WTP were evaluated in comparison to random distributions using permutation analysis (Maris & Oostenveld, 2007) with 10,000 permutations. An initial cluster forming threshold (uncorrected $p < .001$) was implemented followed by cluster-level Family-wise error (FWE) correction ($p < .05$) to identify relevant ALE regions as previously recommended (Eickhoff et al., 2016; Turkeltaub et al., 2012). Multi-image analysis GUI (http://ric.uthscsa.edu/mango) was used to overlay ALE maps onto an anatomical image using MNI coordinates.

Resulting ALE maps for WTP for concurrency of BDM task were compared using conjunction and contrast analyses. The same protocol as previous ALE meta-analyses conducted in our lab was followed (Fallon, Roberts, & Stancak, 2020; Roberts et al., 2020). Again, permutation analysis was first performed on the concurrent/consecutive sub-groups with 10,000 permutations, an initial cluster forming threshold (uncorrected $p < .001$) and a cluster-level Family-wise error (FWE) correction of $p < .05$. For cluster analysis, an uncorrected threshold of $p < 0.05$ and a minimum cluster size of 200 mm^3 was adopted as previously recommended (Eickhoff et al., 2009; Eickhoff et al., 2016; Gan et al., 2022; Hoffman & Morcom, 2018; Papitto, Friederici, & Zaccarella, 2020).

To facilitate future research, ROIs created using the resultant unthresholded meta-analytic clusters are available via NeuroVault (https://neurovault.org/collections/IBLCLBYH/images/785459/).

4.3.6. Fail-Safe N analysis

Co-ordinate-based meta-analyses can be affected by publication bias, where unpublished null results may alter or invalidate findings: known as the "file drawer problem" (Rosenthal, 1979; Rothstein, Sutton, & Borenstein, 2005). The fail-safe N (FSN) analysis addresses this issue, assessing the robustness of ALE clusters by introducing null pseudo-studies as noise to the ALE cohort to calculate the amount of contra-evidence that the ALE can tolerate (Acar, Seurinck, Eickhoff, & Moerkerke, 2018). It is posited that the number of unpublished fMRI studies is lower than behavioural studies due to their greater expense and time-demands. Recent estimations propose that for every 100 published fMRI studies, there are between 6 – 30 unpublished studies which report no local maxima (Samartsidis et al., 2020). Using the upper bound, an estimate for the number of unpublished WTP studies using BDM used in the FSN analysis (minimum FSN) was set at 7 null pseudo-studies (Pando-Naude, Patyczek, Bonetti, & Vuust, 2021). Further, to ensure that no single study is driving the ALE scores of each cluster, a maximum FSN was set at 146, requiring at least a 10% contribution from the cohort studies (Eickhoff et al., 2016).

4.4.Results

Figure 4.4.1 illustrates a flowchart indicating the study selection steps. A total of 8065 records were returned from initial searches. Of these, 1940 were duplicates from repeated searches and removed in the first step. A further 5791 articles were removed following the initial review of titles and abstracts. Studies excluded at this stage included: those that were not reported in English (7) those where it was clear and obvious that no suitable (i.e. healthy, human adult) population was reported (291), where it was clear and obvious that they did not utilize a WTP task (2560), not an experimental report (e.g. review articles) (732), not fMRI method (2201). Furthermore, following full-text review a further 309 articles were removed including those which exhibited an inappropriate contrast (e.g. donation task) (287), or which only reported ROI analyses (22), leaving a total of 24 studies for the analyses of WTP (Table 1).

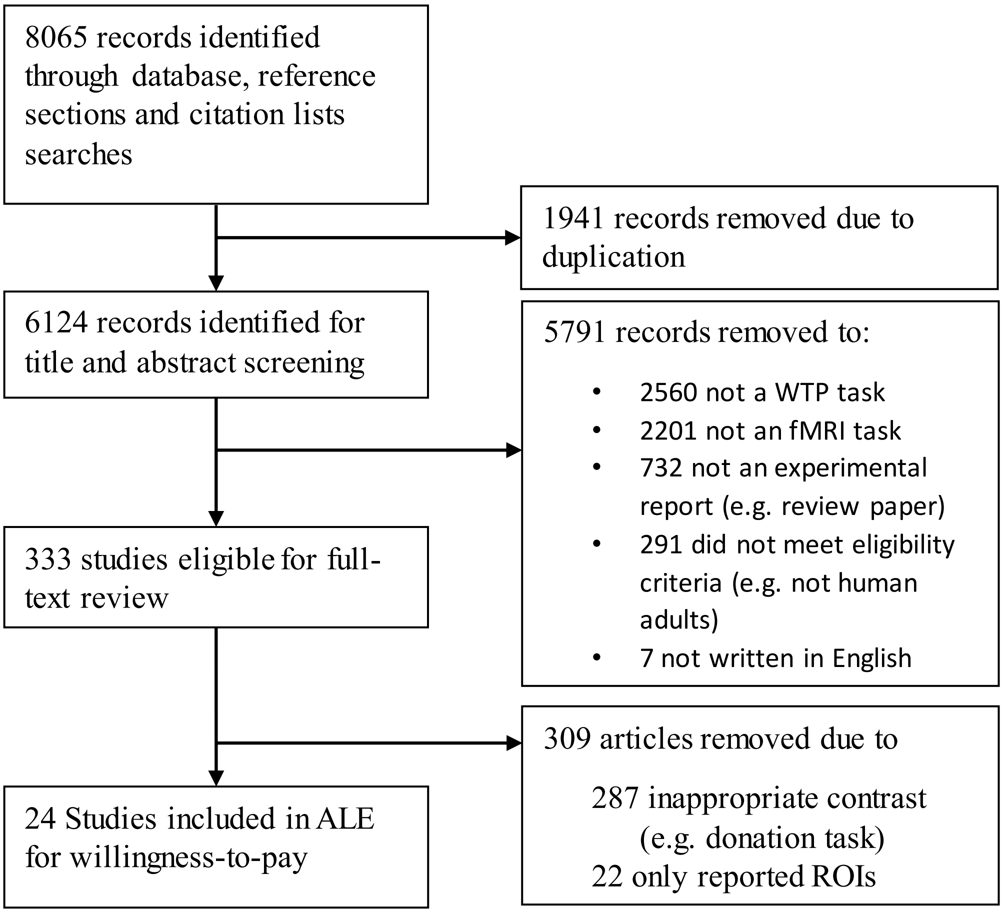


Figure 4.4.1. Flow chart outlining the formal search and eligibility screening process.

Table 1. Studies and experiments included in ALE meta-analyses on willingness-to-pay in human adults

Authors	**Year**	**Title**	**N (men)**	**Mean age (SD)**	**Concurrency of recordings**	**Main Findings**
Chib *et al.*	2009	Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex	32 (25)	23	Consecutive	Common currency mechanism for decision, outcome and anticipatory values encoded in the vmPFC
De Martino *et al.*	2009	The neurobiology of reference-dependent value computation	18 (10)	22.2 (3.1)	Consecutive	OFC and dorsal striatum encoded absolute WTP, VS indexed endowment effect
De Martino *et al.*	2013	Confidence in value-based choice	20 (NA)	24.24	Consecutive	VmPFC encodes SV comparisons and subjective confidence in decisions
Enax *et al.*	2015	Nutrition labels influence value computation of food products in the ventromedial prefrontal cortex	25 (11)	23.3 (4.4)	Concurrent	VmPFC, ACC, caudate nucleus and putamen encode WTP. vmPFC modulated by the inferior frontal gyrus / dorsolateral prefrontal cortex (dlPFC) when rating unhealthy foods, and by the posterior cingulate cortex (PCC) when rating healthy foods
Gluth *et al.*	2015	Effective Connectivity between Hippocampus and Ventromedial Prefrontal Cortex Controls Preferential Choices from Memory	30 (12)	26.1 (3.9)	Consecutive	VS, vmPFC and hippocampus encode the value of the chosen option, vmPFC encodes the value of the unchosen option
Grueschow *et al.*	2015	Automatic versus Choice-Dependent Value Representations in the Human Brain	26 (13)	RG 20-28	Consecutive	Medial PFC and VS activity correlated with SVs during purchasing but not perceptual decisions. PCC activity correlated with both

Hare *et al.*	2008	Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors	16 (9)	24.1, RG 19-38	Consecutive	Goal values correlated with medial OFC activity, decision values correlated with central OFC activity, and prediction errors correlated with VS activity
Hutcherson *et al.*	2012	Cognitive regulation during decision making shifts behavioral control between ventromedial and dorsolateral prefrontal value systems	26 (17)	22, RG 19-28	Concurrent	VmPFC and dlPFC correlated with WTP, indulging upregulated vmPFC signals, behavioural control modulation increased dlPFC contribution
Janowski *et al.*	2013	Empathic choice involves vmPFC value signals that are modulated by social processing implemented in IPL	32 (32)	22.8 (3.9)	Concurrent	Playing in a BDM for others engages vmPFC, modulated by activity from inferior parietal lobule (IPL)
Linder *et al.*	2010	Organic labeling influences food valuation and choice	30 (15)	26.03, RG 23-38	Concurrent	Activity in VS increased with WTP for organic foods
Mackey *et al.*	2016	Greater preference consistency during the Willingness-to-Pay task is related to higher resting state connectivity between the ventromedial prefrontal cortex and the ventral striatum	19 (9)	31.5 (11)	Concurrent	Ventral precuneus, vmPFC and PCC activity increased with WTP
McNamee *et al.*	2013	Category-dependent and category-independent goal-value codes in human ventromedial prefrontal cortex	13 (8)	22.1 (3.6)	Concurrent	Medial PFC implements a goal-value code independent of stimulus category, medial OFC and vmPFC contain category dependent value codes

Medic *et al.*	2014	Dopamine modulates the neural representation of subjective value of food in hungry subjects	47 (23)	23.8 (3.2)	Concurrent	Infusion of dopamine agonist increased the inferior parietal gyrus/intraparietal sulcus response to WTP
Merchant *et al.*	2020	Neural Substrates of Food Valuation and Its Relationship With BMI and Healthy Eating in Higher BMI Individuals	93 (16)	39.25 (3.5)	Concurrent	vmPFC, anterior VS, bilateral AI, and the ACC activity correlated with WTP, vmPFC activity linked to valuation of healthy (vs unhealthy) items
Motoki *et al.*	2019	Common neural value representations of hedonic and utilitarian products in the ventral stratum: An fMRI study	27 (21)	20.37 (1.15)	Concurrent	Values of hedonic and utilitarian goods are similarly processed in the VS during BDM
Plassmann *et al.*	2010	Appetitive and aversive goal values are encoded in the medial orbitofrontal cortex at the time of decision making	20 (15)	23.25, RG 19-34	Concurrent	Medial OFC and the dlPFC correlated with appetitive and aversive goal values
Plassmann *et al.*	2007	Orbitofrontal cortex encodes willingness to pay in everyday economic transactions	19 (16)	25.45, RG 18-46	Concurrent	Medial OFC and the dlPFC correlated with WTP
Rihm *et al.*	2019	Sleep deprivation selectively upregulates an amygdala–hypothalamic circuit involved in food reward	32 (32)	26.13 (3.8)	Consecutive	WTP increased when sleep deprived. Upregulation of hypothalamic valuation signals and amygdala– hypothalamic coupling after sleep deprivation
Seak *et al.*	2021	Single-Dimensional Human Brain Signals for Two-Dimensional Economic Choice Options	24 (11)	25.4, RG 19 - 36	Concurrent	Activity in striatum, midbrain, and OFC correlated with revealed preference across choice indifference curves
Setton *et al.*	2019	Mind the gap: Congruence between present and future	25 (10)	22.52 (2.79)	Concurrent	VS activity positively correlated with level of prospection bias towards food items

		motivational states shapes prospective decisions		RG 18 - 30		
Tang *et al.*	2014	Behavioral and neural valuation of foods is driven by implicit knowledge of caloric content	29 (NA)	(NA)	Concurrent	Activity in the vmPFC linked with caloric density of auction food items
Verdejo - Román *et al.*	2017	Brain reward system's alterations in response to food and monetary stimuli in overweight and obese individuals	81 (38)	33.35 (6.28)	Concurrent	Obese group showed greater activation in VS and dorsal striatum than overweight and normal weight groups
Waskow *et al.*	2016	Pay what you want! A pilot study on neural correlates of voluntary payments for music	25 (13)	35.08 (17.71)	Concurrent	Compared “Pay What You Want” (PWYW) to fixed price condition of BDM. OFC, medial PFC and ACC activity correlates with WTP in BDM, no correlation for PWYW found
Zangemeister *et al.*	2019	Neural activity in human ventromedial prefrontal cortex reflecting the intention to save reward	22 (NA)	NA	Consecutive	vmPFC activity correlates with value and one’s intention to save during sequential economic choices

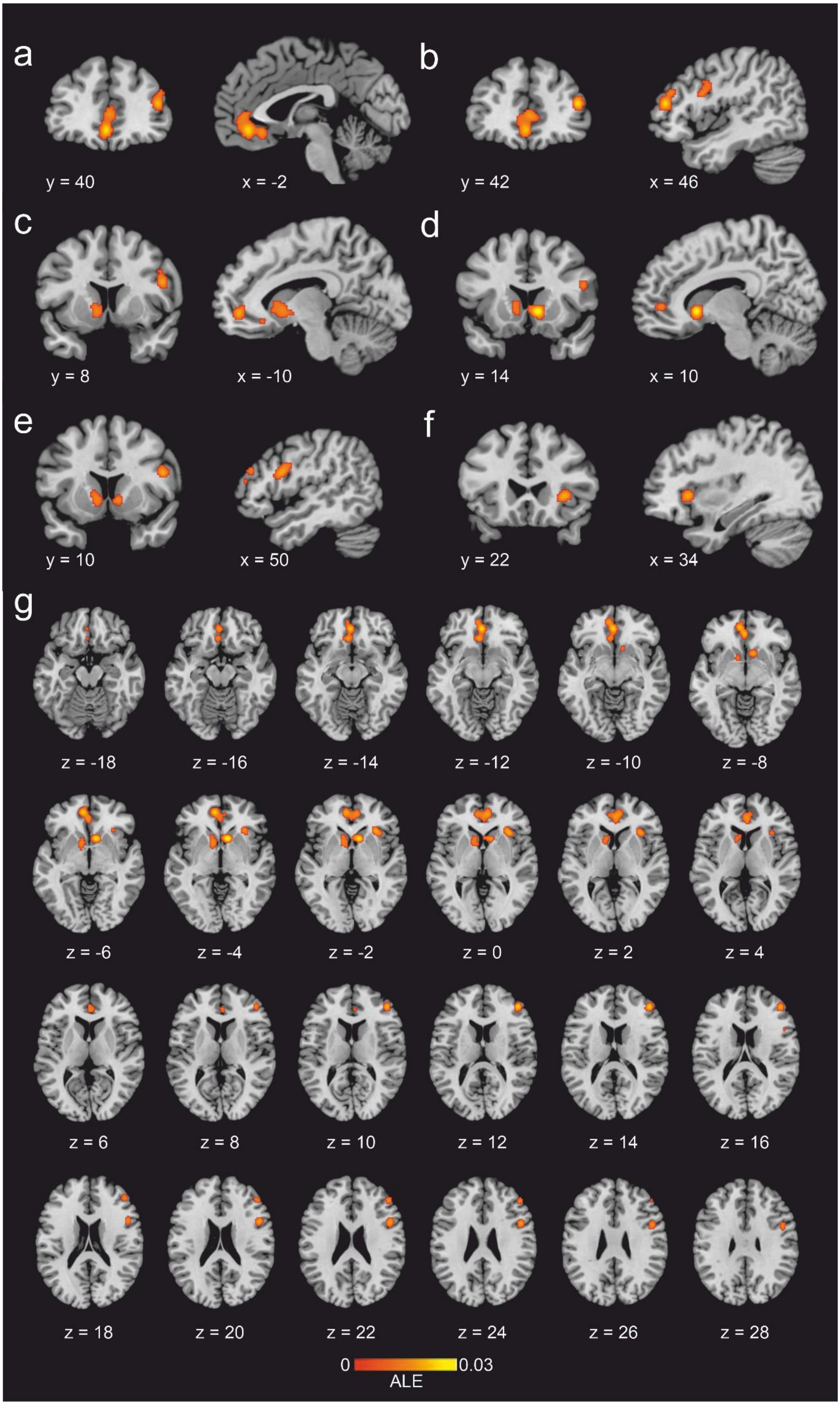
4.4.1. Significant ALE clusters for WTP

The WTP ALE meta-analysis pooled data from a total of 731 participants and 190 reported foci from the 24 studies. The results (see Table 2) revealed six significant clusters, where ALE values represent consistent spatial activations which increased in line with WTP. The largest cluster was elicited in the vmPFC (Brodmann areas 10 and 32) centring on the medial prefrontal gyrus and extending into the left subgenual ACC (sgACC, Brodmann area 32) and right pregenual ACC (pgACC, Brodmann areas 24 and 32). Further clusters were found encompassing the bilateral VS, in the right dorsolateral prefrontal cortex (dlPFC) (Brodmann areas 45 and 46), the right inferior frontal gyrus (IFG) (Brodmann area 44) and the right AI (Brodmann area 13). We found satisfactory robustness of our results against publication bias, with all but the right AI cluster showing an FSN above the minimum imposed, indicating an overall robust convergence of foci. Figure 4.4.2 illustrates the location of significant ALE clusters from the meta-analysis of WTP.

4.4.2. Contrast and conjunction analyses

To investigate to what extent the relationship between brain activation and reported WTP is automatically engaged, a contrast analysis was conducted comparing the ALE maps of concordant activations for concurrency of BDM performance and fMRI recording. Data was pooled from the entire cohort of 24 studies, with a total of 16 studies (535 participants and 158 reported foci) for concurrent recording and 8 studies (196 participants and 32 reported foci) for consecutive recordings. The contrast analysis revealed 3 clusters indicative of increased activation likelihood estimates for concurrent scanning relative to consecutive scanning. These regions were in the right IFG, right dlPFC and right caudate (Table 3, Figure 4.4.3).

Additionally, given the likelihood of an extended network of reward processing, a conjunction analysis was conducted to establish commonalities in activation profiles between the two types of recording. The results highlighted an overlap of activation likelihood coordinates in two clusters, in the left vmPFC and the left OFC (Table 3, Figure 4.4.3).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b
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c
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e
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g
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z = -10
z = -8
z = -6
z = -4
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Figure 4.4.2. The location of significant ALE clusters from the meta-analysis of concordant activations for WTP. A – F show coronal and sagittal slices at the cluster peak in: (A) vmPFC with sub-cluster in the ACC, (B) right dlPFC, (C) left VS, (D) right VS, (E) right IFG and (F) right AI. (G) shows all clusters in axial orientation. Results are displayed overlaid onto a standardized MNI template anatomical brain. ALE scores are indicated by the colour bar.

Table 2. Locations of significant clusters from the ALE map of WTP

Cluster	*Label*	*Volume (mm^3)*	*# Studies (foci)*	*ALE peak*	*Brodmann area*	*MNI co-ordinates (x, y, z)*	*Talairach co-ordinates (x, y, z)*
1	vmPFC L	4584	17 (19)	0.02463	10/32	-2, 40, -12	-2, 35, -12
	vmPFC L			0.02412	10/32	-8, 48, -6	-8, 43, -6
	Subgenual ACC L			0.01898	32	-4, 28, -12	-4, 24, -10
	Pregenual ACC R			0.01955	10/32	6, 46, 0	5, 41, 0
2	dlPFC R	1072	5	0.02479	45/46	46, 42, 12	45, 41, 13
	dlPFC R			0.01652	45/46	48, 38, 22	47, 38, 22
3	VS L	1056	5	0.01670	n/a	-10, 8, -4	-10, 5, 0
4	VS R	1008	4 (5)	0.02956	n/a	10, 14, -4	9, 11, 0
5	IFG R	968	6	0.01982	44	50, 10, 20	48, 9, 21
6	AI R	784	4	0.02132	13	34, 22, 0	32, 19, 3

L, left hemisphere; R, right hemisphere.

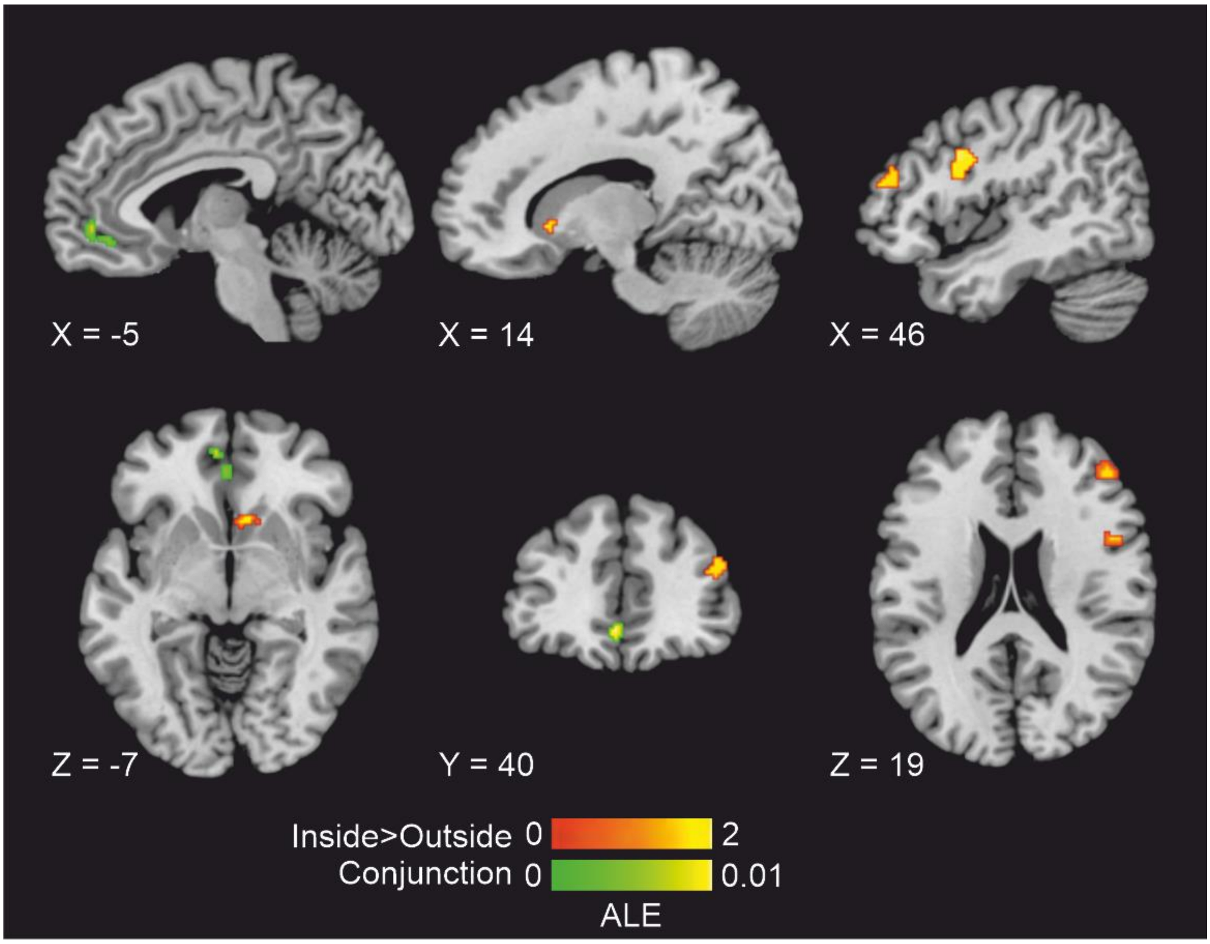

Figure 4.4.3. **The location of significant clusters from conjunction and contrast analyses of ALE maps for concurrent (inside) and consecutive (outside) recordings. Results are displayed overlaid onto standardized MNI template anatomical brain in as a montage of sagittal, coronal and axial slices through the clusters. ALE scores are indicated by the colour bars.**

Table 3. Locations of significant clusters from conjunction and contrast analyses of WTP for concurrent and consecutive recordings

Cluster	Label	Volume (mm^3)	ALE peak	Brodmann area	MNI co-ordinates (x, y, z)	Talairach co-ordinates (x, y, z)
Conjunction Analysis						
1	OFC L	192	0.0100	11	-2, 40, -10	-2, 35, -10
2	vmPFC L	104	0.0096	10/32	-6, 50, -4	-6, 44, -5
Contrast Analysis – Concurrent > Consecutive						
1	IFG R	864	0.0173	6	43, 4, 31	42, 4, 31
	IFG R		0.0328	44	45, 8, 26	43, 8, 26
	IFG R		0.0328	44	50, 6, 24	48, 5, 25
2	dlPFC R	336	0.0333	10	46, 45, 16	45, 45, 16
	dlPFC R		0.0494	10	46, 40, 20	45, 40, 20
3	Caudate R	272	0.0246	n/a	14, 18, -4	13, 15, 0
	Subgenual ACC R		0.025	25	4, 18, -4	3, 15, -1
	Caudate R		0.0265	n/a	10, 18, -6	9, 15, -2

L, left hemisphere; R, right hemisphere.

4.5. Discussion

Performing subjective valuation judgements, and carrying out choices based on these valuations, is an integral part of everyday life. In no case is this more pertinent than in economic purchasing decisions. The present meta-analysis was conducted to identify the core brain valuation system subserving computation of SV as determined by an incentive-compatible WTP metric. The primary ALE analysis identified the locations of positive effects of SV on BOLD activity, where positive effects elicited larger BOLD responses increasing with WTP. The largest concordant activation to WTP was located in the left vmPFC, with a sub-cluster of activation extending into the right pgACC and left sgACC. Additionally, the bilateral VS, right dlPFC, right IFG and right AI also demonstrated significant levels of consistent spatial activation for WTP. Secondary contrast and conjunction analysis established distinct and overlapping neural substrates underlying value-related activations according to concurrency of BDM and fMRI recordings, contrary to our hypothesis. As the pool of studies used a wide range of stimuli types, this analysis shows that the regions elicited play a central role in the encoding of decision values in a wide number of economic settings. Critically, by using an experimental design that allowed us to identify areas that encode for WTP, we were able to isolate those involved in economic choice from other areas that are related to hedonic aspects such as arousal or familiarity.

The results from this meta-analysis confirm the vmPFC as a core brain area of SV computation, with 71% of the pool of studies contributing to the vmPFC cluster in the main analysis. Notably, activations in vmPFC and bilateral striatum are in good agreement with a previous fMRI meta-analysis (Bartra et al., 2013) which highlighted these regions, alongside the PCC, ACC, pre-supplementary motor area and insula, as parts of the brain valuation system. The role of vmPFC in the construction of SV also corroborates with positron-emission tomography studies (Diekhof et al., 2012), as well as single-cell recordings (Strait, Blanchard, & Hayden, 2014), lesion (Fellows, 2011; Henri-Bhargava, Simioni, & Fellows, 2012) and animal studies (Lopatina et al., 2016; Tremblay & Schultz, 1999). Further, our conjunction analysis showed that the vmPFC is the only region to display consistent spatial activation regardless of concurrency of explicit valuation responses and fMRI recording. This suggests that the vmPFC may be the principal region responsible for SV processing in the brain.

The activation shown in the vmPFC extended into the rostral portions of the ACC. Typically, ACC activations are linked to emotions (Phan, Wager, Taylor, & Liberzon, 2002; Vogt, 2005); resting-state fMRI studies show that the ACC is most functionally connected with areas implicated in affective processing, with pgACC having more widespread connections than sgACC (Stevens, Hurley, & Taber, 2011). Both the pgACC and sgACC have also been shown to be modulated by an overestimation of probabilities of good outcomes (Blair et al., 2013), and sgACC activity in particular positively correlates with expected value of an outcome (Beckmann, Johansen-Berg, & Rushworth, 2009; Grabenhorst & Rolls, 2011). Further to this, ACC neurons in non-human primates encode the values of the chosen options during decision-making (Cai & Padoa-Schioppa, 2012; Hosokawa, Kennerley, Sloan, & Wallis, 2013; Kennerley, Dahmubed, Lara, & Wallis, 2009). It may be that activity found in the ACC is due to the uncertainty implicit in the BDM, with the risk of good and bad outcomes being directly linked to the participant's expressed expected values.

The VS is also frequently cited as a primary region of reward processing (Clithero & Rangel, 2014; Filimon, Nelson, Sejnowski, Sereno, & Cottrell, 2020; Hare et al., 2008; Strait, Sleezer, & Hayden, 2015). Both the vmPFC and striatum are key dopaminergic areas, receiving dopaminergic projections from the midbrain (Rutledge, Dean, Caplin, & Glimcher, 2010), and are well established to be involved in option valuation and comparison (Camille, Griffiths, Vo, Fellows, & Kable, 2011; Deserno et al., 2015; Lim, O'Doherty, & Rangel, 2011). Single-cell recordings in rhesus macaques show extensive similarities in neuron firing patterns in the VS and vmPFC during risky reward-based choice (Strait et al., 2015). Activity in the VS has been shown to be mediated by the magnitude of expected reward in both humans (Diekhof et al., 2012; Tom et al., 2007; Yacubian et al., 2007) and non-human primates (Cromwell & Schultz, 2003; Strait et al., 2015). Our findings confirm that the vmPFC and VS have signals that are directionally related to SV in a similar way as they both scale in activity with WTP.

The delineation of activation patterns between concurrent and consecutive execution of task and fMRI scanning in the current context is related to the concepts of task relevance, and the automaticity of value processing (Grueschow et al., 2015; Lebreton et al., 2009; Tyson-Carr et al., 2018). In line with previous studies demonstrating task-irrelevant underlying value-related neural computations, we hypothesised that areas of the brain valuation system would be activated in proportion to WTP regardless of the task being performed in the scanner. However, activation in the right dlPFC and IFG also scaled with WTP, and showed preferential activation in concurrent over consecutive scanning. Both the dlPFC and IFG are known to be central to executive functioning, attention and cognitive control (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Aron, Robbins, & Poldrack, 2004, 2014; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010; Hare, Camerer, & Rangel, 2009; Miller et al., 2011; Staudinger, Erk, & Walter, 2011). Previous work has linked the dlPFC to behavioural restraint and delayed reward (McClure, Laibson, Loewenstein, & Cohen, 2004), demonstrating that individuals who successfully inhibit their value responses during self-control tasks exhibit greater dlPFC activity than those who did not (Chen, He, Han, Zhang, & Gao, 2018; Hare et al., 2009). The IFG is involved in the overweighting of private vs public information (Huber, Klucharev, & Rieskamp, 2014) and conflict resolution (Jarcho, Berkman, & Lieberman, 2010) during decision-making. While not being integral members of the brain valuation system, such as that described by Bartra et al. (2013), the dlPFC/IFG may instead modulate valuation activity in the vmPFC to induce behavioural restraint (McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; McClure et al., 2004). This is supported by the contrast analysis, as the dlPFC/IFG would only be engaged during active bidding and not non-incentivised tasks or passive viewing. It is possible that during the BDM, the dlPFC/IFG acts as a self-control mechanism interacting with the valuation system to optimise bidding outcomes (Hare et al., 2009).

As noted earlier, previous investigation has found a large network of brain areas involved in the formation and updating of subjective valuation (Bartra et al., 2013; Clithero & Rangel, 2014). To this point, a key finding of this meta-analysis is the notable absence of some of these areas in the patterns of consistent activation. For instance, we found no correlation with WTP in the PPC or the amygdala, both of which have been implicated in reward processing (De Martino et al., 2010; Huettel et al., 2006; Raggetti, Ceravolo, Fattobene, & Di Dio, 2017). Most notably, previous fMRI meta-analyses of SV using other tasks have found larger clusters in the vmPFC incorporating the medial OFC (Gottfried, O'Doherty, & Dolan, 2003; Hare et al., 2008; Levy & Glimcher, 2012), whereas the vmPFC cluster found in our main analysis did not. Neural activation in the OFC has been consistently linked to subjective pleasantness of various stimuli (see supplementary materials of Grabenhorst & Rolls, 2011 for review). The delineation of SV of an object from its hedonic pleasure in the present meta-analysis suggests that the OFC may be involved with evaluation of subjective liking as opposed to WTP (Kringelbach, O’Doherty, Rolls, & Andrews, 2003). Finally, the present meta-analysis also showed activation in the right AI in line with SV, but did not reach the statistical criterion of the FSN analysis. This brain region has considerable functional heterogeneity, being involved in a wide variety of functions such as interoception (Craig, 2009; Naqvi & Bechara, 2009), emotion processing (Bechara & Damasio, 2005; Critchley, 2005) and arousal (Quartz, 2009). With regards to reward processing, the AI is extensively connected to dopaminergic regions such as the vmPFC, amygdala and ventral striatum (Namkung, Kim, & Sawa, 2017), and is implicated in loss prediction (Paulus & Stein, 2006), aesthetic appraisal (Brown, Gao, Tisdelle, Eickhoff, & Liotti, 2011) and in economic uncertainty (Mohr, Biele, & Heekeren, 2010; Platt & Huettel, 2008; Rutledge et al., 2010). The AI has been proposed as a candidate for generalized uncertainty processing, as the perception of risk and uncertainty involves integrating both external probability computation and the internal qualia of emotions (Loued-Khenissi, Pfeuffer, Einhäuser, & Preuschoff, 2020; Sescousse et al., 2013). It is possible that the size of the final cohort was insufficient to reliably shed light on the role of the AI in this context.

The present study is not without its limitations. It should be acknowledged that the BDM has been found to be not incentive compatible in certain circumstances, such as when the object being valued is a lottery (Karni & Safra, 1987). There is also evidence that bid values in second-price sealed bid auctions can be impacted by subjective perceptions of uncertainty (Horowitz, 2006) and social competition (Newton-Fenner et al., 2023). Furthermore, the decision to focus on the BDM task, while allowing a clean analysis of SV computation without the confounding effects of task heterogeneity, resulted in a smaller final cohort. This meta-analysis exceeded the recommendation of at least 17 independent studies for ALE analysis in order to be confident that the results are not biased by any individual experiment from the cohort (Eickhoff et al., 2016). However, due to the subsequent split into two subgroups for recording concurrency, it may be premature to draw strong conclusions from the secondary contrast and conjunction analysis. These preliminary distinctions between the effects of concurrency of recordings on SV representation would benefit from clarification by more, higher powered experiments. This would also afford the opportunity to better disentangle any neural differences between passive viewing, binary choice and bid value activation patterns. Here, the aim was to focus on concordance of activations across studies which utilized whole-brain analyses and robust statistical thresholding to reveal the core regions of the brain which demonstrate subjective valuation activations regardless of existing bias. Permitting less stringent search methods would have been detrimental to the integrity of the present investigation. Many other WTP tasks are not sufficiently incentivised, and therefore the WTP values are not reliable indicators of SV (Waskow et al., 2016; Wertenbroch & Skiera, 2002). We should also note that all but one of the clusters (right AI) in the main analysis passed the FSN analysis for potential publication bias, indicating their stability. With the growing popularity of the BDM, a follow up investigation utilizing a larger cohort would further enhance the robustness of these results.

To conclude, we used ALE analyses to map consistent patterns of cerebral activations involved in SV as determined by the behavioural-economic tool of BDM, which pinpoints SV as WTP. The findings document both overlap and dissociations of valuation regions engaged by concurrency of task and scanning. The BDM paradigm has the ability to differentiate economic value from other factors that contribute towards subjective valuation, such as emotional processing, autonomic responses, associative learning, perceptual attention and motor control. We believe that the present meta-analysis represents the most succinct evidence to date of the core brain regions that encode consumers' economic valuations of goods. Knowledge of the distinct and overlapping roles of these brain areas offers unique insights for both theoretical and applied neuroeconomic research.

5. Bid outcome processing in Vickrey auctions: an ERP study

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The format of the text has been altered to match the style of the thesis.

The roles of the co-authors are summarised below:

Myself and Andrej Stancak, Olga Gorelkina, Yiquan Gu and Timo Giesbrecht contributed to the development of the experimental design and planning of the current project. Myself, John Tyson-Carr and Hannah Roberts contributed to the development of the stimuli and materials. MATLAB scripts were created by Andrej Stancak. John Tyson-Carr, Hannah Roberts, Jessica Henderson, Danielle Hewitt and Adam Byrne assisted with the data collection. I carried out the data acquisition, pre-processing and analysis of the Vickrey auction data. Yuxin Xie and Athanasios Pantelous contributed to the analysis of the Loss aversion task data. I was responsible for the synthesis and analysis of the two tasks, as well as figure creation and production of the final written manuscript, which all co-authors read and provided feedback for.

5.1.Abstract

Online retailers often sell products using a socially competitive second-price sealed-bid auction known as a Vickrey auction (VA), an incentivised demand-revealing mechanism used to elicit players' subjective values. The VA presents a situation of risky decision-making, which typically implements value processing and a loss aversion mechanism. Neural outcome processing of VA bids are not known; this study explores this for the first time using EEG.

Twenty-eight healthy participants bid on household items against an anonymous, computerised opponent. Bid outcome event-related potentials were predicted to differentiate between three conditions: outbid (no-win), large margin win (bargain) and small margin win (snatch). Individual loss aversion values were evaluated in a separate behavioural experiment offering gains or losses of variable amounts but equal chances against an assured gain.

Processing outcomes of VA bids were associated with a feedback-related negativity (FRN) potential with a spatial maximum at the vertex (251–271 ms), where bargain win trials resulted in greater FRN amplitudes than snatch win trials. Additionally, a P300 potential was sensitive to win versus no-win outcomes and to retail price. Individual loss aversion level did not correlate with the strength of FRN or P300.

Results show that outcome processing in a VA is associated with FRN that differentiates between relatively advantageous and less advantageous gains, and a P300 that distinguishes between the more and less expensive auction items. Our findings pave the way to an objective exploration of economic decision-making and purchasing behaviour involving a widely popular auction.

Keywords: ERPs, FRN, P300, vickrey auction, reward

5.2.Introduction

As electronic commerce continues to dominate retail markets, it is vital to understand decision-making in online purchasing contexts (Cinar, 2020; Nguyen, de Leeuw, & Dullaert, 2018; Rose, Hair, & Clark, 2011). In value-based decision-making research, subjective valuations are often quantified in the form of willingness-to-pay (WTP), where a person assigns a monetary unit to the value of obtaining a good or experience. This has the advantage that valuations within and across domains (such as food, pain, people and experiences) can be compared on the linear scale of a given currency. Auction paradigms are widely used to quantify WTP in neuroeconomics research; the most well-established of these being the Becker-DeGroot-Marschak (BDM) auction (Becker et al., 1964; Peters & Buchel, 2010; Plassmann et al., 2007; Roberts, Tyson-Carr, Giesbrecht, & Stancak, 2022; Roberts et al., 2018; Tyson-Carr et al., 2018; Tyson-Carr et al., 2020). Further, several multinational auction websites utilise a format that is strategically equivalent to the BDM: the Vickrey auction (VA) (Barrot et al., 2010).

The VA and BDM share the same basic paradigm: players put forward a single bid privately, the highest bidder wins and pays the value of the second highest bid. All other players win nothing and lose nothing. In both auctions, the game-theory dominant strategy, that is, the best reply to every strategy profile of all other players, is to bid the maximum amount one is willing to pay (Vickrey, 1961). Therefore, the VA and BDM allows for the inference of the participant's subjective values of items whilst manipulating the behaviour of their opponent and therefore the auction outcomes (Noussair et al., 2004).

The VA and BDM are both demand-revealing mechanisms, but differ in two major respects: the identity of the bidder's opponent(s) and the amount of outcome feedback (Noussair et al., 2004). In a BDM, the player bids against a random number generator and is told whether they won or lost; whereas in a VA the players are aware of competing with other anonymous, human players, and the winner is also told the final price paid. This price is wholly dependent on the bid of the losing player (or in the case of multiple opponents the second highest bidder) and therefore, the winner receives information about their opponents' subjective values, and whether their values align.

Furthermore, by revealing the final price paid in winning trials, wins can be divided into more- and less-advantageous outcomes. If there is a large difference between the bids, the winner will pay significantly less than they were willing; an outcome hence referred to as a bargain trial. Meanwhile, if both players place similar bids, the final price paid will be much closer to the winner's WTP; an outcome hence referred to as a snatch trial. Both outcomes are considered 'good' as the participant pays less than their WTP, but the margin of difference between their bid and the final price paid can be controlled. This is a unique advantage of the VA, as it allows for intermediate outcomes on a scale of relative good–bad in the win domain, so that some wins can be more extreme than others. Previous behavioural studies of economic decision-making have also demonstrated that subjective value is sensitive to social factors, such as how one's performance fairs against others (Fehr & Schmidt, 1999). Therefore, decision-making in the VA could employ different reward processing mechanisms to the BDM, by virtue of social context information and the competitive environment (Chen, 2011; Malhotra & Bazerman, 2008; van den Bos et al., 2013).

In EEG research, the most prominently investigated event related component connected to outcome evaluation in decision-making tasks involving uncertainty is the feedback related-negativity (FRN) (Walsh & Anderson, 2012). Also referred to as the feedback error related negativity, (fERN) (Holroyd & Coles, 2002), the medial frontal negativity (MFN) (Gehring & Willoughby, 2002), feedback negativity (FN) (Hajcak et al., 2006), and most recently the reward positivity (RewP) (Proudfit, 2015), is a suppressed or otherwise obliterated negative deflection elicited by win outcomes approximately 200 – 300 ms post-feedback onset, which is not present in loss outcomes. It is typically measured from a single electrode in the midline frontal-central area (Glazer et al., 2018), and has been posited to reflect a reinforcement learning reward prediction error (Holroyd & Coles, 2002), consistently differentiating between context-dependent favourable and unfavourable outcomes (Hajcak et al., 2006; Holroyd, Larsen, et al., 2004). It was initially theorised to reflect a subjective "worse than expected'' error signal (Hajcak et al., 2007; Nieuwenhuis, Holroyd, et al., 2004). However, current research suggests that the apparent negativity of the FRN waveform is produced by a conflation of the N200 potential with the RewP component, where all outcome feedback elicits an N200, but a RewP suppresses this N200 in gain outcomes in this time range (Holroyd et al., 2008; Proudfit, 2015). Here, we define the FRN as the difference waveform between averaged potentials time-locked to gain and loss outcome-feedback. As VA involves outcome uncertainty, it is likely that feedback processing of auction outcomes entails an FRN.

Additionally, the P300 event related component – in particular the P3b sub-component – is also thought to be involved in outcome evaluation. The P3b has a positive-going amplitude which occurs approximately 300 – 500 ms after stimulus onset, and typically peaks at its maximum amplitude at parietal electrode sites, most commonly Pz, CPz and Cz (Polich, 2007, 2012). While the P300 is typically produced by non-frequent target stimuli interspersed among frequent standard stimuli (Duncan-Johnson & Donchin, 1977; Polich, 2012; Polich & Margala, 1997), it also has well established sensitivities to outcome magnitude, particularly in purchasing and social contexts (Bellebaum et al., 2010; Jones et al., 2012; Pfabigan & Han, 2019; San Martin, 2012; Schaefer, Buratto, Goto, & Brotherhood, 2016; Yeung & Sanfey, 2004). Recent literature has also shown that the P300 is modulated by social feedback in economic contexts (Mussel, Weiß, Rodrigues, Heekeren, & Hewig, 2022; Weiß, Mussel, &

Hewig, 2020), with a larger positivity for positive and unexpected feedback. The P300 is also modulated by outcome probability, with studies utilising gambling paradigms demonstrating that unexpected rewards elicit stronger P300 amplitudes compared to expected rewards (Cohen et al., 2007; Hajcak et al., 2005; Hajcak et al., 2007). Taken together, we postulated that a series of VA trials would elicit a P300 potential, differentiating between win and no-win outcomes.

Research into reward processing typically investigates decision-making in conditions of risk and uncertainty, most commonly using a variant of a gambling task (Chandrakumar, Feuerriegel, Bode, Grech, & Keage, 2018). These scenarios also often engage loss aversion: a greater sensitivity to potential losses than potential gains (Kahneman & Tversky, 2013). For example, loss aversion is correlated with greater autonomic responses to losses (Sokol-Hessner et al., 2013; Stancak et al., 2015) and stronger activation in the amygdala in the outcome period during gambling tasks (Canessa et al., 2013; Sokol-Hessner et al., 2013). Most relevantly, Kokmotou et al. (2017) found a positive correlation between loss aversion and FRN amplitude in the outcome evaluation period of a monetary gambling task. Most gambling tasks have known probabilities of outcomes (e.g. a 50:50 gamble) whereby participants can quantify the static risk level and behave accordingly (Kokmotou et al., 2017). During a VA, by using an anonymous opponent with an unknown strategy, the players are put into a situation of unpredictable uncertainty. This allows investigation of the role of uncertainty in decision-making as a separate entity to risk. A secondary aim of the current study was to investigate loss aversion implementation in this real online purchasing scenario.

To date, no studies have explored the neural mechanisms implemented during a VA, despite its widespread use in online retail. Unlike other decision-making tasks under uncertainty, no outcome in a VA can be classified as a financial loss, and so it is unclear whether processing outcomes in a VA would be associated with FRN and a P300. This study examined for the first time the FRN and P300 components of ERPs elicited by receiving outcomes of bids in a VA, and explored the nuance of ERP responses to different types of wins in a win vs no-win context (e.g. high retail value wins vs low retail value wins, and bargain wins vs snatch wins). It was hypothesised that processing outcomes in a VA will be accompanied by the FRN and P300 ERP components. Further, we predicted that the relatively advantageous win outcomes (bargain) will show greater FRN than the relatively disadvantageous (snatch) win outcomes. Finally, given the presence of FRN in the data, we also postulated a positive association between individual loss aversion levels and the strength of FRN.

5.3.Method

5.3.1. Participants

Twenty-eight healthy participants (12 male, 25 right handed) with a mean age of 25.9 ± 6.9 years (mean ± SD), took part in the current study. Three participants (two male) were removed from subsequent analyses due to excessive muscle artefacts in EEG recordings. One participant (male) was excluded due to not bidding in 65% of trials. All had normal or corrected-to-normal vision. All participants were screened for psychological/psychiatric disorders. A post hoc sensitivity analysis confirmed that the one-way within-subjects ANOVA with 24 participants across three outcome conditions would be sensitive to effects of $\eta p^2 = 0.21$ with 80% power ($\alpha = .05$). The experimental procedures were approved by the Research Ethics Committee of the University of Liverpool. All participants gave written informed consent in accordance with the Declaration of Helsinki. Participants were reimbursed for their time and travel expenses.

5.3.2. Procedure

The study was carried out in a single session. Participants completed an EEG experiment involving a computerised VA task, and a behavioural computerised monetary gambling task to measure loss aversion. The purpose of the experiment and instructions for the tasks were explained to participants at the beginning of the session. All experimental procedures were carried out in a dimly lit, sound-attenuated Faraday cage. Both tasks were displayed on a 19-inch LED monitor using MATLAB (Mathworks, Inc., USA), with Cogent software 2000 (Cogent, www.vislab.ucl.ac.uk/Cogent/).

5.3.2.1. VA Task

Participants received an initial endowment of £18 and were instructed to use it to purchase items during the VA task. They were informed that two items from winning trials would be randomly selected and the price that they won the items for would be deducted from their endowment; they would receive the remaining amount of their endowment and the two items as reimbursement for their participation. After application of the EEG net, participants were led into the Faraday cage to complete the task. Participants were seated in front of the computer and rested their dominant hand on a computer mouse.

The protocol for the VA task was adapted from previous studies (Kokmotou et al., 2017; Roberts et al., 2018; Tyson-Carr et al., 2018; Tyson-Carr et al., 2020) which used a BDM paradigm. The trial structure is shown in Figure 5.3.1. The order of item presentation was randomised between participants, and each item was presented once, resulting in a total of 300 auction trials. The stimuli comprised 300 everyday household products such as kettles, batteries and mugs, valued in the ranges £3 – 5 (low value) and £7 – 9 (high value; n=150 in each range), with a mean value of £6.04 ± £2.19 (mean ± SD) obtained from a shopping catalogue. The items were chosen for their ubiquity, utility and price point, as we wanted the participants to be familiar with the type of items they were bidding on and view them as desirable. Each auction trial began with a resting interval during which participants viewed a white fixation cross on a black background for 2 s. The participants were then presented with an item to bid on, using a sliding scale from £0 – £9 in increments of 25p, giving a total of thirty-seven options. Participants were asked to bid the maximum amount they would be willing to pay for each item, and to select their bid value by clicking on the scale, and submit the bid by clicking on a white square in the bottom right-hand corner. There was no time limit on bid submission and participants could click on the scale as many times as they wished before submitting the bid.

After bid submission, the trial outcome was determined randomly by the computer, with three equally likely outcomes: (1) the participant is outbid (no-win condition); (2) the participant has won by a small margin, paying 70 – 90% of the value of their bid (‘snatch’ condition); (3) the participant has won by a large margin, paying 10 – 30% of the value of their bid (‘bargain’ condition). In outcome (1), the value of the participant’s bid plus a 25p increment appeared in the centre of a red square for 2 s. In outcome (2) and (3), prices were rounded to the nearest 25p and displayed at the centre of a green square for 2 s.

The task consisted of a total of 300 trials, split into three blocks of 100 trials each. Trials were presented in random order for each participant. Participants were given a short break in between blocks to limit fatigue. The duration of each block was approximately 15 minutes. After the VA task was complete, participants were given a short break and the EEG system was removed.

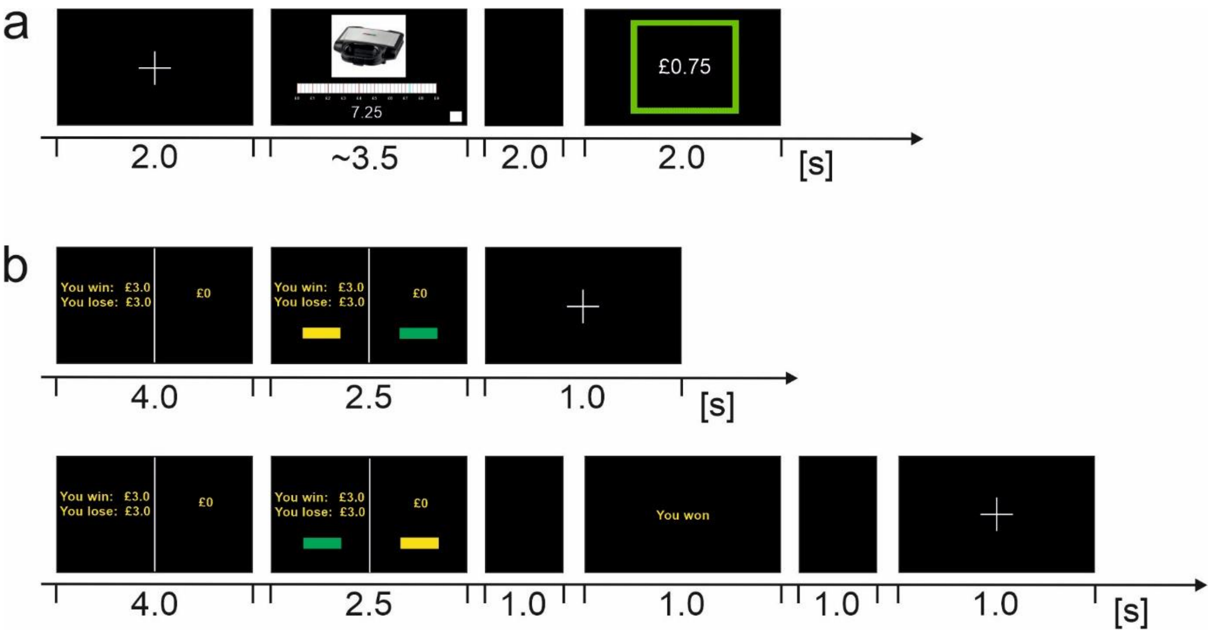

Figure 5.3.1. a) Trial structure of Vickrey Auction task in the bargain condition. Each trial began with a fixation cross for 2 s, followed by the auction item and a sliding scale from £0 – £9 in increments of 25p on which to select their bid. Participants were instructed to select their bid on the scale, and once they were happy with their decision submit the bid by clicking on a white square in the bottom right-hand corner. The screen was blank for 2 s before presenting the outcome of the trial. If the participant won the trial (presented) a green square appeared with the amount they won the item for in the centre of the square. If the participant lost the trial, 25p more than their bid value was shown at the centre of a red square. b) Trial structure of loss aversion task. Top panel: Declined gambles. Bottom panel: Accepted gambles. Each trial began with a fixation cross, followed by the presentation of two possible choices, which were displayed on the screen for 4 s. Half of the screen showed the gamble option (e.g., “you win £3.0, you lose £3.0”) with a 50:50 chance of winning or losing the displayed amount of money. The other half of the screen showed the value of a sure outcome. In the next 2.5 s, the options stayed on the screen and two yellow rectangles appeared at the bottom of the screen. Participants were instructed to choose between the two options by pressing the left or the right mouse button corresponding to the side of the screen they preferred. If the participants selected the sure outcome, a fixation cross appeared on the screen and the next trial started after 1 s. If participants selected the risky gamble option, a black screen was displayed for 1 s

after the 2.5 s response period, and feedback about the gamble outcome was shown for 1 s ("You won" or "You lost"). A 1 s black screen served as a resting period before the next trial.

5.3.2.2. Loss aversion task

The loss aversion task was adapted from previous studies (Kokmotou et al., 2017; Stancak et al., 2015). Participants were given £10 as an initial endowment to use during the task. They were told that 10% of the final amount of money gained or lost during the task would be added to or subtracted from the endowment, and the remaining amount would be given as compensation for their travel costs and time.

The task consisted of 100 two-alternative forced choice monetary gamble trials. In 80 of those trials, participants chose between a 50:50 gamble and a sure zero outcome. The gamble options comprised of 8 possible gain amounts (£1.00, £2.00, £3.00, £3.50, £4.50, £5.00, £5.50, £6.00) and 10 possible loss amounts, which were devised by multiplying the given gain value with a number between 0.2 – 2.0 in 0.2 increments. All possible permutations were presented in the task trials (8 gains × 10 losses). In the other 20 trials, participants chose between a gain-only gamble and a sure smaller gain. In these trials, the gain-only gambles presented a 50:50 chance to win a certain gain amount or a zero outcome. The list of assured gains was identical to our previous study (Stancak et al., 2015). Trial order was randomized for each participant.

The trial structure of the loss aversion task can be seen in Figure 5.3.1.

At the beginning of each trial a fixation cross appeared on screen for 1 s, followed by the two alternative options for 4 s. One side of the screen showed the gamble option (e.g., "you win £2.0, you lose £1.5"), and the other side of the screen showed the sure outcome option.

Participants were told that the gamble option had a 50:50 probability of winning or losing. They were told to make their selection by pressing the left or right mouse button as it corresponded to their choice on the monitor. When the participant chose the gamble option, outcome feedback appeared on screen for 1 s (“you won” or “you lost”). The task took approximately 10 minutes to complete.

5.3.3. EEG recordings

EEG was recorded continuously using a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. This system allows full head electrode coverage as it includes electrodes positioned over lower scalp regions and face, which is essential for identification of deep cortical sources, such as those located in the orbitofrontal cortex (Luu, Poulsen, & Tucker, 2009; Luu et al., 2001; Sperli et al., 2006; Tucker, 1993). The sensor net was aligned with respect to three anatomical landmarks: two preauricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ and at equal levels across all electrodes, as recommended for the system (Ferree, Luu, Russell, & Tucker, 2001; Luu et al., 2003; Picton et al., 2000). The recording band-pass filter was 0.001 – 200 Hz with sampling rate of 1000 Hz. The electrode Cz served as the reference electrode.

5.3.4. ERP analysis

The ERP analysis of the outcome period served to evaluate the individual feedback-related potentials FRN and P300. EEG data were pre-processed with the BESA v. 7.0 program

(MEGIS, Munich, Germany). EEG signals were spatially transformed to reference-free data using the common average reference method (Lehmann et al., 1987). This spatial transformation restored the signal at electrode Cz for use in further analyses.

During pre-processing, EEG data were filtered (0.5 – 70 Hz with a 50 Hz notch filter) for viewing both slow, for example, movement or pressure pulse, and high-frequency, for example, EMG, artefacts. Ocular artefacts and, when necessary, electrocardiographic artefacts were removed with principal component analysis based on averaged artefact topographies (Berg & Scherg, 1994; Ille et al., 2002). Data were also visually inspected for the presence of atypical electrode artefacts. In rare cases where an electrode signal was continually affected by artefacts, the electrode signal was interpolated. Continuous data were sectioned into epochs of 900 ms duration each with a baseline interval ranging from -300 ms to 0 ms relative to feedback onset.

The average number of accepted trials in each condition were: no-win, 96.8 ± 15.8 (mean ± SD); bargain win, 89.9 ± 11.4; snatch win, 85.0 ± 10.0. Paired t-tests revealed that the average number of accepted trials differed between the snatch win and other conditions ($p < .05$) but did not differ between no-win and bargain win conditions ($p > .05$) or between number of accepted trials in low value and high value conditions (low = 135.3 ± 9.4, high = 136.4 ± 9.1; $p > .05$). Data were filtered from 0.5 – 30 Hz. ERPs in response to outcome feedback were computed separately for each condition by averaging respective epochs in the intervals ranging from -300 ms to 600 ms post feedback-onset. The FRN potential was quantified by subtracting ERPs of no-win trials from ERPs of bargain/snatch trials (analogous to a win-minus-loss difference waveform).

In the VA task, EEG epochs were averaged for each type of outcome (snatch, bargain and no-win) and for both market value categories (high and low). Based on visual inspection of scalp topographies and previous research (Glazer et al., 2018; Hauser et al., 2014; Krigolson, 2018; Meadows, Gable, Lohse, & Miller, 2016; Walsh & Anderson, 2012), the Cz electrode was selected for statistical analysis. Intervals of interest were selected based on visual inspection and a permutation test involving 4000 permutations and implemented in the *statcond.m* function of the EEGLAB toolbox (Delorme & Makeig, 2004; Maris & Oostenveld, 2007). The time windows of interest chosen were 251 – 271 ms (FRN) and 354 – 374 ms (P300) post feedback-onset. Graphical representations of these intervals can be seen as grey bars in Figures 5.4.2b and c for FRN, and 5.4.3b for P300.

5.3.5. Statistical analysis

5.3.5.1. Behavioural data

For the VA task, trials in which the participant did not bid were excluded due to lack of engagement in the trial and the resulting outcome. Response times were uninformative as judgements were not time limited. A one-way repeated measures ANOVA was conducted to examine the effect of market value category on bid value.

As outcome probabilities were fixed, the participant was pre-determined to win two thirds of the trials. While participants were instructed that the dominant strategy was to bid one’s true subjective value, the true dominant strategy was to bid the smallest amount possible: 25p per trial. In order to test for any implicit learning during the task, we conducted a Pearson’s correlation between the trial number and bid value to test for a general trend of lowering of bids as the task progressed.

For the loss aversion gambling task, Shapiro-Wilk tests were conducted to confirm normal distributions across loss aversion, risk aversion and choice sensitivity parameters.

5.3.5.2. ERP data

For the FRN, in line with previous studies (Chandrakumar et al., 2018; Glazer et al., 2018; Walsh & Anderson, 2012), win trials were subtracted from no-win trials in order to establish the difference waveform, and to select the appropriate electrode and latency epoch showing a statistically significant effect. A one-way repeated measures ANOVA was conducted examining outcome condition (no-win, bargain, snatch), and a subsequent 2 × 3 repeated measures ANOVA was conducted comparing the effects of value (high vs. low) and outcome condition (no-win, bargain, snatch) on ERP amplitudes.

For the P300, four electrodes of interest corresponding to Fz, FCz, Cz and Pz in the 10-20 electrode system, numbered 11, 6, 129 and 62 respectively in the HydroCel Geodesic net, were selected to account for the whole positive maximum of the P300 potential. A 4 × 2 × 3 repeated measures ANOVA with factors of electrodes (four electrodes), value (low vs. high) and bid outcome conditions (bargain, snatch, no-win) was carried out. A subsequent 2 × 3 (value × outcome) repeated measures ANOVA was carried out to unpack the relationship between outcome condition and item market value in electrode 6.

In both components, Greenhouse-Geisser corrections were utilised whenever the sphericity assumption was violated. Significant differences outlined in the ANOVA were subjected to pairwise t-tests with Bonferroni corrections and a critical threshold of $p < .05$ was upheld. A 95% confidence level was always employed.

5.4.Results

5.4.1. Behavioural data

5.4.1.1. The VA Task

Participants submitted bids in 94.2% of trials. The maximum bid of £9 was submitted on 2.9% of trials. The overall mean bid value was £3.36 (SD ± 2.5), £2.59 less than the mean market value of the items. Average bid value rose slightly as the task progressed: $r(22) = .63$, $p < .001$.

Figure 5.4.1a shows a statistically significant relationship between participants' mean bid value and the six levels of market value ($F(5,115) = 68.11$, $p < .001$, $\eta p^2 = .75$). Post hoc pairwise comparisons with Bonferroni corrections showed differences across all value levels ($p < .05$) except between the £3 – 3.5 and £4 – 4.02 brackets, and between the three high market value brackets ($p > .05$). The participants were not told the retail price of the auction items so as not to anchor their bids, but the significant relationship between participant bid value and market value validates the use of market value as a proxy measure in the analysis. Additionally, there was a highly significant linear trend ($p < .001$), confirming a linear increase in subjective value with increase in retail price. This suggests that subjective value ratings within the VA reflects the retail prices of the products. The distribution of market price frequencies among the 300 auction item stimuli can be seen in Figure 5.4.1b.

5.4.1.2. Loss Aversion Task - Choice Parameters

Loss aversion ($W(23) = .98$, $p > .05$), risk aversion ($W(23) = .97$, $p > .05$) and choice sensitivity were all normally distributed ($W(23) = .96$, $p > .05$). The mean level of loss aversion (λ) was 1.38 ± 0.10 (mean ± SEM). This value fit well with previous studies of $\lambda = 1.4$ (Sokol-Hessner et al., 2009; Stancak et al., 2015). There was no correlation between loss aversion and risk aversion ($p > .05$).

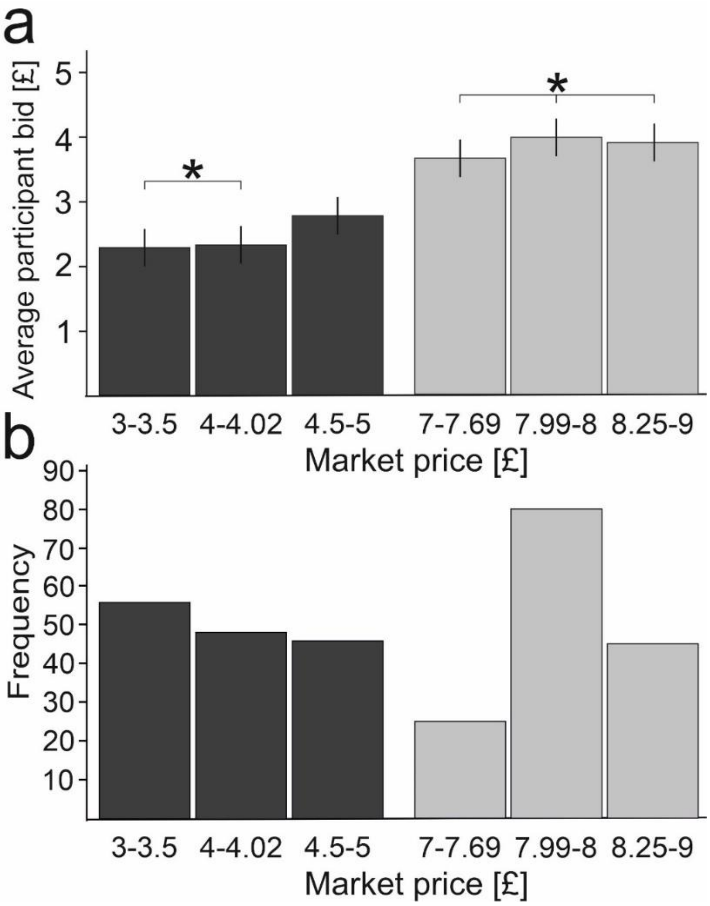

Figure 5.4.1. (A) Bar graph showing mean participant bids in the VA task across 6 levels of market value: three subsections of low value (£3 – 5, dark grey) and high value (£7 – 9, light grey). The subsections were grouped according to frequency of price, as seen in (B). All levels of participants' bid value differed between the six levels of market value except for the brackets highlighted by a *. (B) Bar graph showing the frequencies of market prices among 300 auction item stimuli corresponding to the 6 levels of market value in (A). Efforts were made to distribute prices evenly within the high and low value ranges.

5.4.2. ERP results

5.4.2.1. FRN

An FRN with a spatial maximum at the central midline electrode Cz was found in response to bidding outcomes in VA during the epoch 251 – 271 ms (Figure 5.4.2a).

From visual inspection of the topographic plots, the FRN appeared to be stronger in the right hemisphere, as can be seen on the topographic maps in Figure 5.4.2a. To verify a right lateralisation effect, a repeated measures ANOVA was conducted comparing activity at the Cz electrode with the electrodes on the right and left of Cz (electrodes 36, 31, 80 and 104 were selected). No significant difference was found between electrodes ($p > .05$).

The grand-average ERP waveforms at electrode Cz for win and no-win conditions used to compute the difference wave are shown in Figure 5.4.2b. Figures 5.4.2c and d demonstrate a main effect of condition ($F(2,46) = 16.90$, $p < .001$, $\eta p^2 = .42$) between the win and no-win conditions during the epoch 251 – 271 ms. Significant differences were found between all three outcomes, with bargain trials ($1.84 \pm .38\ \mu V$) resulting in more positive potential amplitudes than snatch trials ($1.61 \pm .39\ \mu V$, $p = .036$) and both bargain and snatch trials resulting in more positive amplitudes than no-win trials ($0.95 \pm .38\ \mu V$, $p < .001$ and $p = .001$ respectively). The subsequent 2 × 3 ANOVA found no statistically significant main effect of value or interaction between values and condition ($p > .05$).

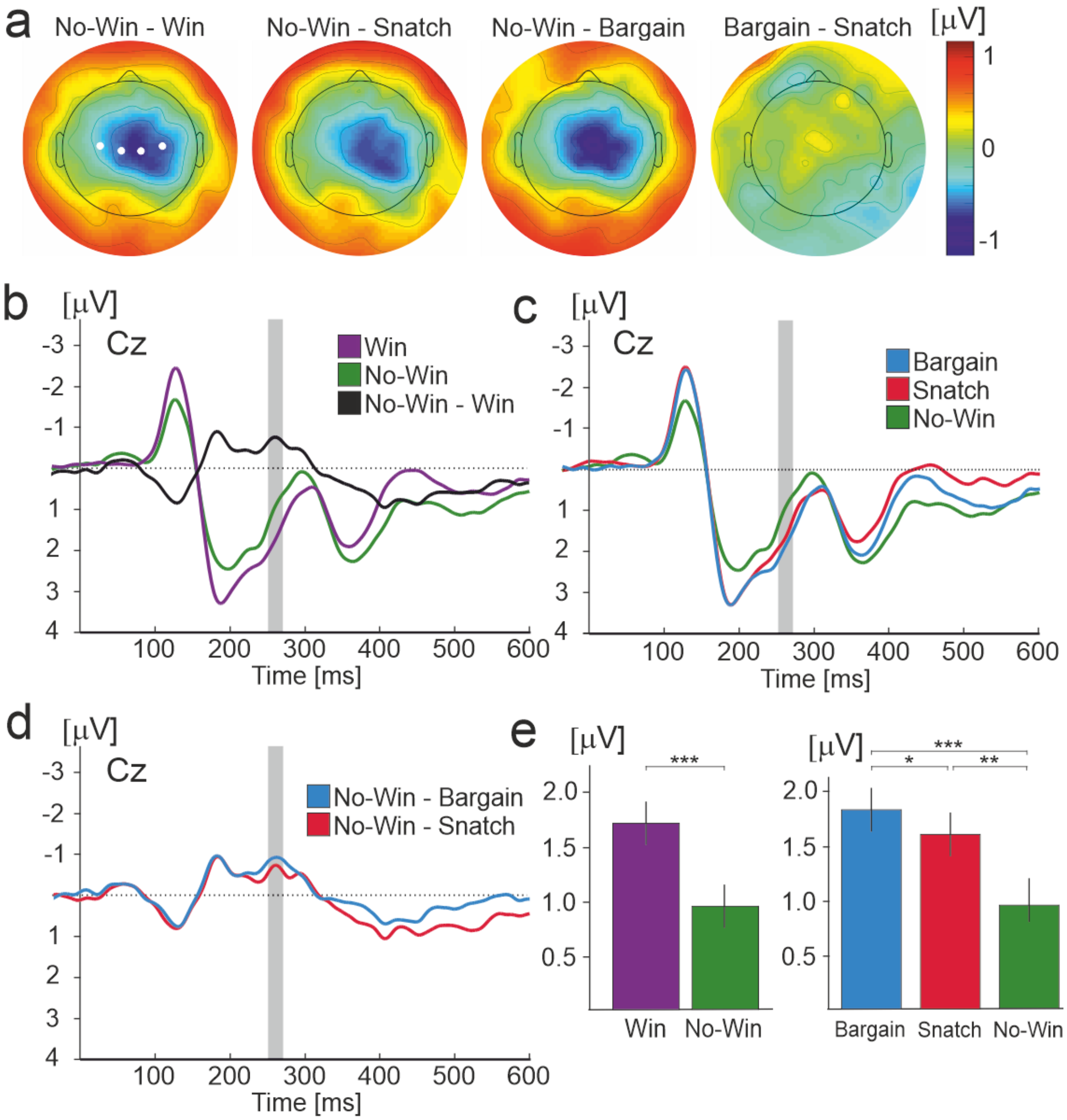

Figure 5.4.2. FRN component. (a) Whole scalp topographic maps displaying differences in grand average ERPs at time point (251 – 271 ms). (b) Grand average ERP waveform across all subjects and product value conditions comparing win (purple), no-win (green) outcome conditions and the no-win minus win difference waveform (black) at electrode Cz. Epoch of interest showing statistically significant differences between win and no-win conditions (251 – 271 ms post feedback-onset) highlighted in grey. (c) Grand average ERP waveform across all subjects and product value conditions comparing the no-win outcome condition (green) to the two types of win condition – bargain (blue) and snatch (pink) at electrode Cz. Epoch of interest (251 – 271 ms post feedback-onset) is highlighted

in grey. (d) Grand average difference ERP waveform across all subjects and product value conditions comparing the no-win minus bargain win (blue) and the no-win minus snatch win (pink) at electrode Cz. Epoch of interest (251 – 271 ms post feedback-onset) is highlighted in grey. (e) Bar graphs showing mean amplitude of ERPs over epoch 251 – 271 ms for (b) and (c). Statistically significant differences are denoted as * for < .05, ** for < .01 and * for < .001. The error bars show the standard error.**

5.4.2.2. P300 Component

Topography of the P300, as can be seen in Figure 5.4.3a, showed bilateral positivity over the parietal electrodes, peaking at 354 – 374 ms. The topographic maps of the P300 component in win and no-win conditions showed spatial maximum at central parietal locations, and the greatest differences between conditions were maximal at midline frontal-central electrodes.

A main effect of electrodes ($F(3,69) = 6.69$, $p = .004$, $\eta p^2 = .225$), value ($F(1,23) = 8.81$, $p = .007$, $\eta p^2 = .277$), and outcome conditions ($F(2,46) = 7.89$, $p = .001$, $\eta p^2 = .255$), and a statistically significant interaction between electrodes and bid outcome conditions ($F(6,138) = 4.19$, $p = .006$, $\eta p^2 = .154$) was found. The main effect of value was due to the larger P300 potential in high- compared to low-value items (high: 1.48 ± .24 μV; low: 1.23 ± .21 μV, mean ± SEM).

Subsequent analysis revealed that the main effect of electrodes was due to significant differences in amplitudes between all electrodes apart from between 62 and 11, and between 129 and 62 ($F(3,69) = 6.61$, $p = .001$, $\eta p^2 = .223$). A stronger positive P300 potential was observed at the electrodes located at vertex (electrode 129: 2.01 ± .35 μV) and in the parietal scalp region (electrode 62: 1.67 ± .43 μV) compared to two electrodes located anteriorly relative to the vertex electrode (electrodes 11: .34 μV ± .20 μV, and 6: 1.37 ± .30 μV; see Figure 5.4.3c). Figure 5.4.3b shows topographical maps of the difference in potential amplitude of the

P300 between conditions. Notably, the topographic maps of the contrast no-win vs. both win conditions revealed that only the anterior part of the P300 potential maximum, represented in electrodes 11 and 6, resolved the bid outcome conditions.

The main effect of bid outcome conditions (F(2,46) = 7.59, p = .001, $\eta p^2 = .248$) was related to a stronger P300 in no-win outcomes (1.64 ± 0.27 µV, mean ± SEM) compared to both bargain (1.28 ± 0.25 µV) and snatch (1.12 ± 0.19 µV) outcomes; the two win outcomes did not significantly differ. The interaction between electrodes and bid outcomes (Figure 5.4.3d) revealed that the amplitudes differed between no-win and both win outcomes in electrodes 11 (bargain: .18 ± .24 µV, p = .009; snatch: .16 ± .20 µV, p = .001; no-win: .66 ± .22 µV,), and 6 (bargain: 1.15 ± .31 µV, p = .001; snatch: 1.01 ± .27 µV, p < .001; no-win: 1.94 ± .39 µV), at electrode 129 no-win differed from snatch but not from bargain (bargain: 2.05 ± .40 µV p > .05; snatch: 1.69 ± 2.8 µV p = .012; no-win 2.29 ± .41 µV), and the outcomes did not differ at all in the parietal electrode 62 (ps > .05), in accordance with the topographic maps of bid outcome contrasts (Figure 5.4.3b). This can be seen in Figure 5.4.3d.

Figure 5.4.3e shows the grand mean ERP amplitudes at electrode 6 in each of three bid outcomes and for high and low-value items, as evaluated in the subsequent 2 × 3 repeated measures ANOVA. A main effect of condition (F(2,46) = 12.03, p < .001, $\eta p^2 = .34$) and of value (F(1,23) = 4.57, p = .043, $\eta p^2 = .17$) was found. There was no statistically significant interaction effect (p > .05). No-win trials (1.94 ± .39 µV) resulted in more positive potential amplitudes compared to both snatch (1.01 ± .28 µV; p < .001) and bargain trials (1.14 ± .30 µV; p = .001; see Figure 5.4.3e). Bargain and snatch trials did not significantly differ from each other (p > .05). High market value trials (1.21 ± .31 µV) resulted in a more positive potential amplitude than low market value trials (1.51 ± .31 µV, p = .043; see Figure 5.4.3e).

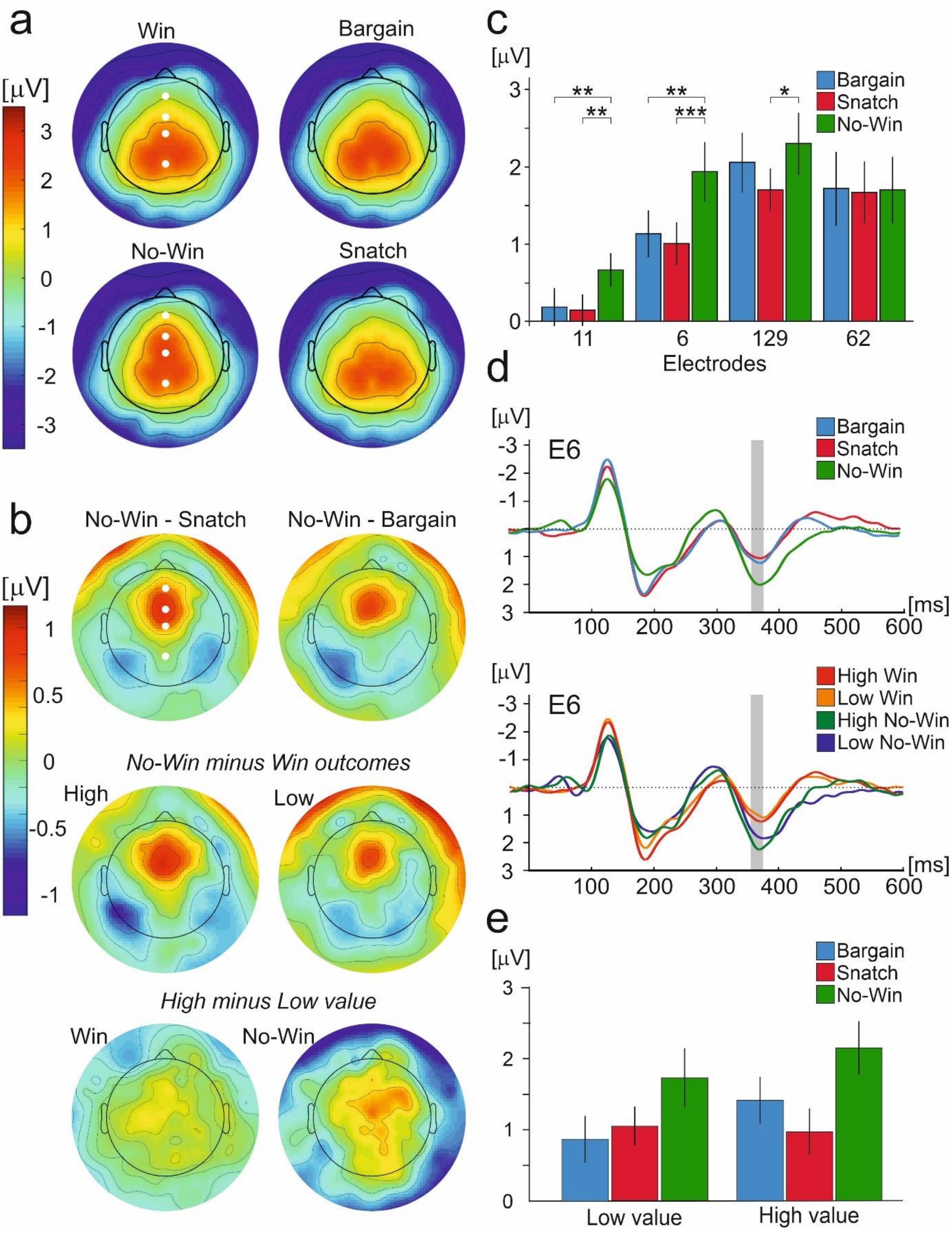

Figure 5.4.3. P300 component (a) Whole scalp topographic maps displaying grand average ERPs for each of the outcome conditions at time point 354 – 374 ms. Four midline electrodes used in statistical analysis, numbered 11 (Fz in 10-20 system), 6 (FCz), 129 (Cz) and 62 (Pz) in HydroCel Geodesic net, are highlighted in white. (b) Whole scalp

topographic maps displaying difference in grand average ERPs between conditions in the latency epoch of 354 – 374 ms. (c) Bar graph showing mean amplitude of ERPs over epoch 354 – 374 ms for all outcome conditions across four midline electrodes 11, 6, 129 and 62, as indicated by white circles on topographic maps in (a) and (b). The error bars show the standard error. Statistically significant differences in the bar graphs are denoted as * for < .05, ** for < .01 and * for < .001. (d) Top: Grand average ERP waveform across all subjects and product value conditions comparing outcome conditions at electrode 6. Bottom: Grand average ERP waveform across all subjects comparing no-win outcomes with high (green) and low (blue) market value to win outcomes with high (red) and low (orange) market value at electrode 6. Epoch of interest 354 – 374 ms post feedback-onset is highlighted in grey. (e) Bar graph showing mean amplitude of ERPs over epoch 354 – 374 ms for all outcomes and market values.**

5.5.Discussion

The present study shows for the first time that FRN and P300 can be elicited during the VA. Both FRN and P300 components differentiated between win and no-win outcomes. Most notably, an FRN potential elicited at the vertex 251 – 271 ms post feedback onset differentiated between less favourable (snatch) and more favourable (bargain) wins – representing two extreme outcomes unique to the VA. In addition, the P300 amplitudes differentiated wins from no-wins and between auction items of high and low retail price.

The production of an FRN demonstrates that VA bid outcomes were processed in a way comparable to outcomes in individual gambling tasks, such as a binary forced-choice monetary gambling task (2AFC) (Gehring & Willoughby, 2002; Hajcak et al., 2007; Kokmotou et al., 2017; Yeung & Sanfey, 2004). Our findings support the involvement of a context-dependent reward prediction error, as the FRN was primarily modulated by outcome valence (Holroyd & Coles, 2002; Holroyd, Larsen, et al., 2004). While the no-win condition was objectively a financially neutral outcome, in the context of winning or 'losing' an auction, it was the most unfavourable result.

The ability of the FRN to differentiate between the two types of win outcomes is also in line with reinforcement learning (Holroyd & Coles, 2002; Holroyd, Larsen, et al., 2004; Nieuwenhuis, Holroyd, et al., 2004). The bargain win condition can be viewed as a reward of greater magnitude than the snatch win, as the difference between the participant's bid and the final price paid is larger. In the VA and BDM paradigms, one's bid value can also be referred to as a reservation price or indifference point, as paying one cent more than one's bid is a bad outcome (Padoa-Schioppa, 2011). Therefore, the participants should be ambivalent towards a price outcome that is equal to their bid, and so the snatch condition is an intermediate outcome between the two extremes of bargain and no-win. The greater FRN amplitude for bargain than snatch outcomes indicates that the FRN is sensitive to the relative value of a win (Holroyd, Larsen, et al., 2004; Meadows et al., 2016).

Violations of expectation may also have contributed to the difference in FRN amplitudes between snatch and bargain outcomes. The probability of each outcome is unknown in a VA task, unlike paradigms such as the 2AFC monetary gambling task, where participants are aware of the 50:50 chance of winning or losing (Gehring & Willoughby, 2002). The uncertainty caused by unknown outcome probabilities in the VA may have induced participants to rely on their own subjective values as an indicator of their opponent's behaviour, and hence a predictor of likely outcomes. Correspondingly, the bargain condition would be considered a less probable win outcome as it indicates the misalignment of the participant's subjective value with that of their opponent. Therefore, the bargain result is the greater deviation from the expected reward magnitude (Bellebaum et al., 2010; Hauser et al., 2014).

In contrast with the previous study (Kokmotou et al., 2017), no correlations were found between any of the ERP components and loss aversion level. During a 2AFC monetary gambling task, loss aversion correlated positively with FRN amplitude at electrodes corresponding to the OFC, indicating a link between loss aversion implemented during risky decision-making and a valuation process occurring in the OFC (Canessa et al., 2013). However, the associations between FRN and loss aversion seen in the study by Kokmotou and colleagues were based on FRN elicited during a task which involved real monetary losses in loss trials. Our findings suggest that the association between loss aversion and the FRN does not occur in the absence of a potential (monetary) loss. Therefore, the subjective framing of no-wins as 'losses' in an auction setting may be inadequate, and an objective risk of real loss is necessary to engage loss aversion mechanisms.

The P300 distinguished between no-win and win outcomes, and between high and low market value results. However, the parameters of the study limits interpretation of the win vs no-win amplitude differences due to the win outcomes being twice as frequent as the no-win outcomes. As the P300 is well established to be sensitive to outcome probability (Polich, 2007, 2012), it cannot be ruled out that this difference impacted the observed win vs no-win amplitudes.

As the P300 is involved in discerning motivational significance of outcomes (Bradley, 2009; Hajcak & Foti, 2020; Pfabigan et al., 2019; Wang, Zheng, Huang, & Sun, 2015), the attentional engagement and cognitive effort shown in auctions may be mediated by the market value of the item being auctioned (Meadows et al., 2016; Tyson-Carr et al., 2018). This is also in line with the broader motivational significance framework (Bradley, 2009). As bid values were linked to market value, participants may have been more invested in the outcomes of items that they appreciated were worth more. This tendency would echo the sunk cost effect, where emotional and cognitive effort is extended in situations of financial commitment (Zeng, Zhang, Chen, Yu, & Gong, 2013; Zeng, Zou, & Zhang, 2013). This would suggest that P300 component was sensitive to retail value as items of a higher retail price are more salient and engaging.

The present study was not without its limitations. Previous work has shown significant relationships between cortical activation changes during initial valuation of products and subsequent purchase decisions (Goto et al., 2017; Schaefer et al., 2016). As the pre-bid period during the VA consists of free viewing of a displayed item, electrophysiological explorations would require recording and analysis of eye-movement related potentials, similar to Tyson-Carr et al. (2020), which was beyond the scope of the present study. A monetary threshold effect may have also impacted the results. As all wins are considered a good economic outcome, the degree of difference between the final price paid and one's bid could be of minor importance. Meanwhile, the social reward of beating an opponent brings another dimension to the outcome, and so "snatching" a win could be perceived as the "better" reward outcome (Chen, 2011).

This interplay of social and financial reward processing is a limitation of the present study, but could be unpacked by directly comparing a VA to a BDM to isolate the effect of a social dimension on reward processing mechanisms. Previous behavioural data has shown that, relative to a BDM, participant bidding behaviour during a VA is more varied and divergent from the economically dominant strategy (Flynn et al., 2016). Further, fMRI studies using first-price auctions have found emotional cue factors, such as risk aversion and loss contemplation, result in higher levels of overbidding and the 'winner's curse' (Delgado, Schotter, et al., 2008; van den Bos et al., 2013). A comparison of the two mechanisms could be valuable for evaluating individual differences in replying on emotional cues during bidding.

Present data provides an initial insight into neural mechanisms underlying evaluation of decision outcomes in VA. Results show that receiving bid outcome information during a VA elicited an FRN potential at a latency and location that were compatible with FRN activity seen in other decision-making tasks. The amplitude of the FRN also differentiated the favourability of VA win outcomes, a specific feature not seen in other demand revealing mechanisms. The VA also elicited a P300 component that encoded salience related to the economic value of the items. Separation of value- and auction-specific cortical responses provides important insight into decision-making processes. Future exploration of the dynamics of Vickrey auctions has the potential for significant contributions to understanding the cognitive and neural systems that support economic decision-making.

6. A Comparison of reward processing during Becker–DeGroot–Marschak and Vickrey auctions: an ERP study

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This study directly compared the spatiotemporal dynamics of reward processing in the brain during BDM and Vickrey auctions. This paper has been accepted for publication in Psychophysiology.

The format of the text has been altered to match the style of the thesis.

The roles of the co-authors are summarised below:

Myself and Andrej Stancak, Olga Gorelkina, Yiquan Gu, Nick Fallon and Timo Giesbrecht contributed to the development of the experimental design and planning of the current project. I carried out the development of the stimuli and materials, as well as the PsychoPy scripts. Danielle Hewitt and Jessica Henderson assisted with the data collection. MATLAB scripts were created by Andrej Stancak. I was responsible for the data acquisition, pre-processing and analysis of the behavioural and neural data. I produced the final written manuscript, which all co-authors read and provided feedback for.

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Data and code availability statement

Data and MATLAB files are available on the open access platform OSF:

https://osf.io/2d7ub/?view_only=995efddf256d4af5ad6f945249eef3e3

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest.

6.1.Abstract

Vickrey auctions (VA) and Becker–DeGroot–Marschak auctions (BDM) are strategically equivalent demand-revealing mechanisms, differentiated only by a human opponent in the VA, and a random-number-generator opponent in the BDM. Game parameters are such that players are incentivised to reveal their private subjective values (SV) and behaviour should be identical in both tasks. However, this has been repeatedly shown not to be the case.

In the current study, the neural correlates of outcome feedback processing during VA and BDM were directly compared using electroencephalography. 28 healthy participants bid for household products which were then divided into high- and low-SV categories. The VA included a human opponent deception to induce a social environment, while in reality a random-number-generator was used in both tasks.

A P3 component peaking at 336 ms over midline parietal sites showed more positive amplitudes for high bid values, and for win outcomes in the VA but not the BDM. Both auctions also elicited a Reward Positivity potential, maximal at 275 ms along the central midline electrodes, that was not modulated by auction task or SV. Further, an exploratory N170 potential in the right occipitotemporal electrodes and a vertex positive potential component were stronger in the VA relative to the BDM.

Results point to an enhanced cortical response to bid outcomes during VA task in a potential component associated with emotional control, and to the occurrence of face-sensitive potentials in VA but not in BDM auction. These findings suggest modulation of bid outcome processing by the social-competitive aspect of auction tasks.

Keywords: P3, RewP, N170, EEG, subjective value, reward, willingness-to-pay

6.2.Introduction

Social comparison and competition have been shown to affect reward-seeking behaviour, subjective valuation, and outcome processing during economic decision-making (Bhanji & Delgado, 2014). Emphasis on competition during an auction can increase bid frequency (Heyman, Orhun, & Ariely, 2004; Kamins et al., 2011), overbidding (Delgado, Schotter, et al., 2008; Teubner, 2013; van den Bos et al., 2008) and the prevalence of the 'winner's curse', where the winning bid exceeds the worth of the auction item (Malhotra, 2010; Park & Bradlow, 2005). However, the neural mechanisms underlying these processes are underexplored.

Vickrey auctions (VA) and Becker–DeGroot–Marschak auctions (BDM) are two of the most widely used demand-revealing mechanisms in experimental economics (Lucking-Reiley, 2000; Noussair et al., 2004), and notably have been adopted by online auction websites such as eBay. In both auctions, the player who submits the highest bid for a given good wins the auction, but pays a price equal to the second highest bid (Vickrey, 1961). The only difference between the two is that in the VA, players compete against other human players, whereas in the BDM a single player bids against a random number generator (Becker et al., 1964). Unlike other auction structures, both the VA and BDM purport dominant strategies of bidding one's true subjective value (SV), as deviating from doing so risks paying more than they believe the item is worth or missing out on the item for a price they were willing to pay. Importantly, these strategies are impervious to the risk attitude of the player and the strategies of other players.

The vast majority of risky decision-making tasks employ monetary gambling paradigms where the participant can win and lose varying amounts of currency. The VA and BDM are different in that, in economic terms, the outcomes are either good (in the case of win) or neutral (in the case of no-win); the degree to which a given win outcome is good depends on the difference between the bid value and the final price paid. In the BDM, outcomes are processed as purely economic rewards and can be ranked on that single dimension. Meanwhile, the VA involves the additional dimension of social value, which is a combination of the validation of shared public values and the value of "winning" as a separate entity to the value of the item won (Ariely & Simonson, 2003; Astor et al., 2013; Delgado, Schotter, et al., 2008; Malhotra, 2010).

Further, the BDM is formally strategically equivalent to a VA against a single unknown bidder, who bids their valuation, and whose value is drawn from the same distribution of valuations as that of the BDM prices. Therefore theoretically, under these conditions, the BDM and VA paradigms should elicit the same responses in players. However, many behavioural studies have found significant heterogeneity in bidding behaviour in the VA compared to the BDM (Irwin et al., 1998; Kagel & Levin, 1993; Kagel et al., 1989; Noussair et al., 2004). Despite clear instructions and a full understanding of the paradigm, underbidding and overbidding relative to SV are common in the VA (Flynn et al., 2016; Georganas, Levin, & McGee, 2017; Rosato & Tymula, 2019). The deviation from logical decision-making has been attributed to several factors, including: feelings of spite induced by competition (Bartling et al., 2017; Kagel & Levin, 1993; Kagel et al., 1989; Ku et al., 2005), the "joy of winning" and the fear of losing (Astor et al., 2013), and differences in risk and uncertainty between the two paradigms (Levy et al., 2010; Noussair et al., 2004). The direct comparison of the VA and BDM under these conditions affords the opportunity to isolate the impact of a social environment and competition on decision-making processes in the brain.

The inclusion of a second player in the VA has several implications. Whereas the BDM places players in a situation of individual choice, in the VA the player is now being observed by a competitor and can utilise their opponent's bid values to inform them about the items' common/public value (Toelch et al., 2014). The items also now have an additional dimension of value, in that the act of winning against another person holds a worth that is separate from the value of the item itself (Noussair et al., 2004). Further, while both tasks place players in a situation of decision-making under uncertainty, in the BDM players are in a situation of static risk, where the computer bid values have equal probability across the entire range. Therefore, participants can quantify the probability of winning any given trial depending on their bid value. However, in the VA, the human opponent is unpredictable, in that opponent bids will not be equally distributed across the entire range of values. As a consequence, the players are placed in a situation of uncertainty, where they cannot gauge the likelihood of a given outcome based on their bid (Levy et al., 2010). Therefore, we would expect there to be a difference in subjective outcome probability expectation between BDM and VA.

Several studies investigating SV and outcome processing during decision-making have found increased arousal and immediate emotional responses in the presence of a human opponent, as evidenced by increased heart rate and skin conductance responses (Adam et al., 2015; Astor et al., 2013; Teubner, Adam, & Riordan, 2015), and stronger activations in brain regions related to emotion processing (Delgado, Li, et al., 2008; Sanfey et al., 2003), social preferences (Sanfey, 2007; van den Bos et al., 2013) and mentalizing (Riedl, Mohr, Kenning, Davis, & Heekeren, 2011).

Reward positivity (RewP), also known as the feedback-related negativity (FRN), is the most widely investigated ERP component in the outcome processing stage (Falkenstein et al., 1991; Walsh & Anderson, 2012). The RewP is maximal at 200 – 300ms post feedback onset over fronto-central sites and reflects a subjective reward prediction error signal. It is characterised by a suppressed negative deflection elicited by win outcomes, that is not present in loss outcomes, giving the appearance of enhanced negativity for bad outcome feedback (Hakim & Levy, 2019; Holroyd, Larsen, et al., 2004; Miltner et al., 1997; Nieuwenhuis, Holroyd, et al., 2004). The RewP is also dependent on the relationship between expected rewards and actual rewards, with increased amplitudes for unexpected compared to expected outcomes (Ferdinand, Mecklinger, Kray, & Gehring, 2012; Hajcak et al., 2005; Hajcak et al., 2007; Pfabigan, Alexopoulos, Bauer, & Sailer, 2011). The RewP is also sensitive to outcome magnitude (Goyer et al., 2008; Gu et al., 2011) and salience (Hauser et al., 2014; Talmi et al., 2013; Walentowska, Severo, Moors, & Pourtois, 2019; Yeung et al., 2005). However, the RewP was not sensitive to reward magnitude in our previous VA study (Newton-Fenner et al., 2022), as characterised by auction item market value.

Notably, while a social dimension adds salience to the context and induces comparison of one's task performance to others (Fehr & Schmidt, 1999; Fliessbach et al., 2007; Kedia et al., 2014), the evidence of an impact on RewP amplitudes is mixed. RewP amplitudes have been shown to be larger for non-conformity when comparing performance to other players during a lottery task (Luo et al., 2015), and for competition compared to cooperation during a perceptual four-alternative forced-choice task (Czeszumski et al., 2019). However, no difference in RewP amplitudes were found comparing non-social, socially comparative and socially competitive conditions during a monetary gambling task (Rigoni, Polezzi, Rumiati, Guarino, & Sartori, 2010). We hope to shed light on this inconsistency, using a context where the participant's optimal strategy to maximize their payoff is the same, regardless of the social context. As the level and type of competition remains the same between tasks, we can delineate the effect of competition from the social environment.

The P3 (or P300) component, a large positive deflection elicited 300 – 450 ms along midline central-parietal electrodes post-feedback onset (Polich, 2007, 2012) is also extensively studied during outcome processing and performance monitoring. The P3 is thought to be central to indexing attention for novel stimuli (Schuermann et al., 2012), mismatch detection and context updating (Martin & Potts, 2011), and is highly sensitive to the motivational significance of stimuli (Nieuwenhuis, Aston-Jones, et al., 2005; San Martin, 2012; Yeung & Sanfey, 2004). Regarding reward processing, positive feedback elicits larger P3 amplitudes compared to negative feedback (Pfabigan et al., 2011), as do reward outcomes associated with higher levels of arousal or task-relevance, reflecting an increased allocation of attention (Nieuwenhuis, De Geus, & Aston-Jones, 2011). The P3 is also sensitive to outcome magnitude, with larger rewards/losses eliciting greater amplitudes (Bellebaum & Daum, 2008; Yeung & Sanfey, 2004). Relevantly, in our most recent study using a VA task, auction outcomes were associated with larger P3 amplitudes for high market value than low market value items, and win outcomes compared to no-win outcomes (Newton-Fenner et al., 2022). Similarly, Tyson-Carr et al., (2018) also found during a BDM task that high-value products produced increased activation in the P3 interval during the initial valuation period.

This study focused on the time course of neural activity during feedback processing upon receipt of the auction outcome. We analyzed the amplitudes of the RewP and P3 components during the outcome processing period to gain insight into the temporal progression of attentional biases and attentional resource assignment, preference encoding, prediction error and motivation during decision-making. We hypothesised that RewP amplitudes would differentiate between the BDM and VA tasks, but not between high- and low-value items as denoted by bid value. The P3 component was predicted to be larger for wins than no-wins, and for high-value than low-value items, in both tasks, in line with our previous findings. In addition to the hypothesized components, during visual inspection of the topographies, we also found an enhanced negative potential in the right occipitotemporal electrodes and a vertex positive potential (VPP) in the latency of 170 – 180 ms during the VA compared to the BDM. The configuration is consistent with the face-sensitive N170 ERP component occurring during viewing human faces (Deffke et al., 2007; Dijkstra, Mostert, Lange, Bosch, & van Gerven, 2018; Rossion, 2014; Rossion & Jacques, 2012; Weiß et al., 2020), and so we performed a post hoc exploratory analysis.

This is the first EEG study to directly compare the neural correlates of decision-making during the VA and the BDM. Contrasting the two paradigms isolates the effect of a competitive environment on ERPs while keeping the paradigm identical in all other respects. This informs work on SV, reward processing, overbidding and competitive arousal.

6.3.Method

6.3.1. Participants

Twenty-four healthy, right-handed participants (14 female) with a mean age of 25.9 ± 5.4 years (± SD) completed the study. Four additional participants (3 female) were removed prior to ERP analysis due to not properly following the study procedure. All participants had normal or corrected-to-normal vision and were screened for psychological/psychiatric disorders. All gave written informed consent and were reimbursed for their time and travel expenses. The experimental procedures were approved by the Research Ethics Committee of the University of Liverpool and were in accordance with the Declaration of Helsinki.

6.3.2. Procedure

The study was carried out over two sessions separated by a minimum of 7 days (mean 10.3). Participants completed computerised VA and BDM tasks, one task per session, while brain activity was recorded with EEG. The order of the tasks was counterbalanced. The purpose of the experiment and instructions for the tasks were explained to participants at the beginning of the session. All experimental procedures were carried out in a dimly lit, sound-attenuated Faraday cage. Both tasks were displayed on a 19-inch LED monitor using PsychoPy software (Peirce et al., 2019). Upon completion of the second session, participants were given the option to receive two auction items (one from each task) for the price that they were won for, or to select two equivalent items from a small selection in the lab. This was done for logistical reasons due to the Covid-19 pandemic to reduce the number of participant visits into the lab.

6.3.2.1. BDM Task

The BDM task protocol can be seen in Figure 6.3.1. At the beginning of the session, participants were informed that they would be bidding against a random number generator in a computerised auction task. If the participant bid higher than the random number, they would win the item and pay the random number as the price; if they bid lower than the random number they would lose the trial, not winning the item and paying nothing. In the case of both bids being equal, the winner was decided randomly.

Participants received an initial endowment of £12 and were instructed to use it to purchase items during the BDM task. To ensure that their behaviour was incentivised, they were informed that at the end of the session one of their winning trials would be randomly selected and the price that they won the item for would be deducted from their endowment; they would receive the remaining amount of their endowment and the item as reimbursement for their participation. After application of the EEG net, participants were led into the Faraday cage to complete the task. Participants were seated in front of the computer and rested their dominant hand on a computer mouse.

The protocol for the BDM task was adapted from previous studies (Roberts et al., 2018; Tyson-Carr et al., 2018; Tyson-Carr et al., 2020). The stimuli comprised 300 everyday household products such as kettles, batteries and mugs, valued in the ranges £3 – 7 (low-value) and £8 – 12 (high-value; n=150 in each range), with a mean value of £7.39 ± £3.12 (± SD) obtained from a shopping catalogue. Efforts were made to distribute retail prices evenly within the two ranges. Each auction trial began with a resting interval where participants viewed a white fixation cross on a black background for 2 s. The participants were then presented with an item to bid on, using a sliding scale from £0 – £12 in increments of 25p. The item was presented for 2 seconds before the sliding scale appeared. Participants selected their bid using the sliding scale and submitted the bid by clicking on a button in the bottom right-hand corner. There was no time limit on bid submission and participants could click on the scale as many times as they wished before submitting their bid. The opponent bid was generated by the random function in Excel (Microsoft, USA) to be between £0 - £12 with matched increments of 25p and compared to the submitted bids. The outcome was displayed on the screen (e.g. “you won! £2.75” or “you lost”) for 2 s.

Participants were instructed, and confirmed that they understood, that there was an equal likelihood of the random number bidding any increment of 25p between £0 - £12, and so their bid directly corresponded to the likelihood that they would win a given trial. For example, if they place a bid of £6 on an item, the likelihood of them winning is 50%. The order of item presentation was randomised, and each item was presented once, resulting in a total of 300 auction trials. The task was broken up into five blocks of 60 trials, and participants were given a short break in between blocks to limit fatigue and to make any necessary adjustments to the EEG system. The duration of each block was approximately 12 minutes.

6.3.2.2. VA Task

The VA task protocol can be seen in Figure 6.3.1. The VA task was identical to the BDM task in all but two respects. Firstly, at the beginning of the session, the participants were informed that they were playing against another human participant as their opponent, who was situated in another room so they would remain anonymous. They were told that for each trial, whoever bid higher would win the item but pay the price equal to their opponent’s bid. In reality, the participants were bidding against the random number generator. Secondly, a jitter of between 0 – 6 seconds was included post-bid submission where the phrase “wait for opponent” and a loading GIF appeared on screen to mimic a human opponent deciding on their bid. Participants were informed of the deception during the debriefing. All participants confirmed that they believed that they were bidding against another person during the VA during an informal exit interview. The same stimuli, trial number and timings were used in the VA task as in the BDM.

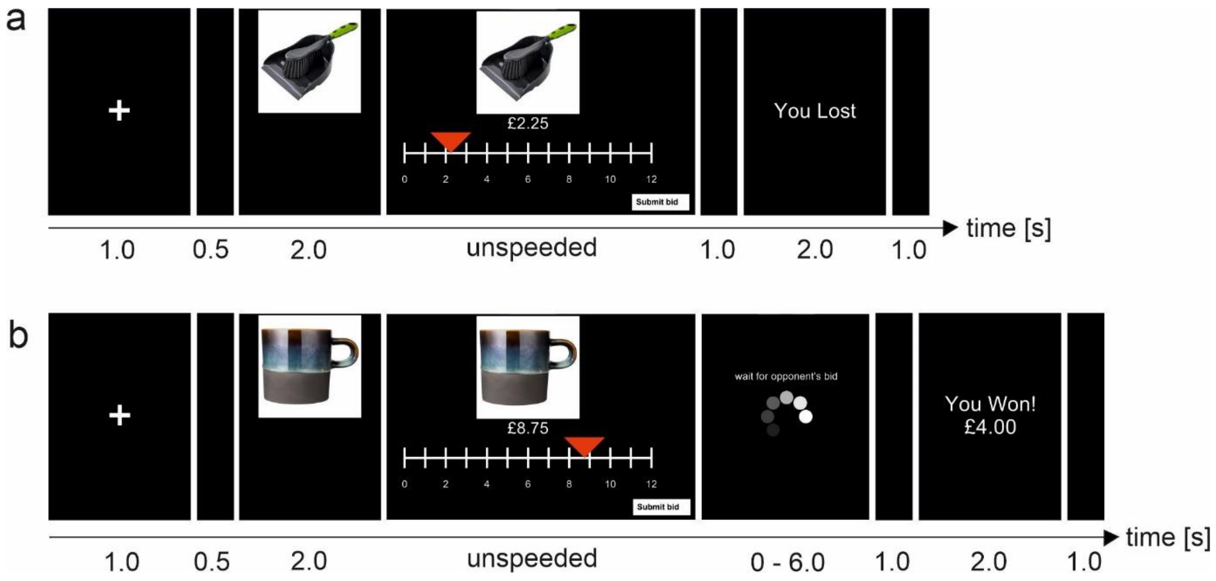

Figure 6.3.1. a) A no-win trial in the BDM task. b) A win trial for the VA task. For both tasks, each trial began with a fixation cross for 1 s, followed by the auction item for 2 s,

which is then joined by a sliding scale from £0 – £12 in increments of 25p on which to select their bid. Participants were instructed to select their bid on the scale, and once they were happy with their decision, to submit the bid by clicking on the button in the bottom right-hand corner. In the VA, in two thirds of the trials, this was followed by the phrase "wait for opponent" and a loading GIF indicating that the other player has yet to submit their bid, which lasted for either 1 – 2 s or 5 – 6 s. This was then followed by a blank screen for 1 s. In the BDM, the screen was blank for 1 s before presenting the outcome of the trial. The outcome of the trial was then presented for 2 s. EEG triggers were synced to the onset of auction feedback.

6.3.3. EEG recordings

EEG was recorded continuously using a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. The sensor net was aligned with respect to three anatomical landmarks: two preauricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ and at equal levels across all electrodes, as recommended for the system (Ferree, Luu, et al., 2001; Luu et al., 2003; Luu et al., 2001; Picton et al., 2000). The recording band-pass filter was 0.001 – 200 Hz with a sampling rate of 1000 Hz. The electrode 129 (corresponding to Cz in the 10 – 10 system) served as the reference.

6.3.4. ERP analysis

EEG data were pre-processed with the BESA v. 7.0 program (MEGIS, Munich, Germany). EEG signals were spatially transformed to reference-free data using the common average reference method (Lehmann et al., 1987). This spatial transformation restored the signal at electrode 129 for use in further analyses.

Ocular and electrocardiographic artefacts were removed using a combination of a pattern-search algorithm and principal component analysis based on averaged eye blinks and artefact topographies (Berg & Scherg, 1994; Ille et al., 2002). Data were also visually inspected for the presence of atypical electrode artefacts, head movement artefacts, and artefacts related to muscle contractions. Continuous data were sectioned into epochs of 1200 ms duration each with a baseline interval ranging from -200 ms to 0 ms relative to feedback onset. Epochs contaminated with artefacts were manually excluded.

The average number of accepted trials after artefact exclusion were 254.2 ± 39.6 (mean ± SD) in the BDM and 260.5 ± 25.6 in the VA. For each condition, the average accepted number of trials were: in the BDM, high 127.7 ± 22.7; low 126.5 ± 18.3, win 101.2 ± 31.2; no-win 153 ± 35.7; and in the VA, high 130,7 ± 15.5; low 129.8 ± 13, win 105 ± 23.6; no-win 155.4 ± 31.6.

Conditions in the auction outcome period were grouped by value or outcome for statistical analysis. Paired t-tests revealed that the average number of accepted trials differed between the win and no-win conditions in both the BDM (win: 101.2 ± 31.2, no-win: 153.0 ± 35.7) and VA (win: 105.0 ± 23.6, no-win: 155.4 ± 31.6) ($p < .001$), but did not differ between high- and low-value conditions for both time periods and both tasks. There were also no differences between the average number of accepted trials when conditions were compared across the two tasks ($p > .05$).

Data were filtered from 0.5 – 30 Hz and exported to EEGLab (Delorme & Makeig, 2004) for further processing. ERPs in response to outcome were computed separately for each condition by averaging respective epochs in the intervals ranging from 200 ms before outcome onset to 1000 ms post feedback onset. EEG epochs were averaged for both tasks (VA and BDM), each type of outcome (win and no-win) and for both subjective value categories (high and low). The RewP potential was quantified as a win–minus–no-win difference waveform in the outcome receipt period. Based on visual inspection of scalp topographies and previous research (Glazer et al., 2018; Hauser et al., 2014; Krigolson, 2018; Meadows et al., 2016; Walsh & Anderson, 2012), the electrodes 129, 55 and 6 for the P3 and RewP components (corresponding to Cz, CPz and FCz in the International 10-10 system respectively), and 101, 100, 99 for the N170 component (electrode 100 corresponding to TP10 in the International 10-10 system) were selected for statistical analysis (Luu & Ferree, 2005). Time intervals of interest were selected based on visual inspection of waveforms in our data and according to the definitions concerning the time windows of each component from previous literature (Glazer et al., 2018; Polich, 2012; Roberts et al., 2019; Tyson-Carr et al., 2018; West, Bailey, Anderson, & Kieffaber, 2014). These time periods were further analysed using repeated measures ANOVAs. To compensate for violations of the sphericity assumption, a Greenhouse Geisser ε correction was used where applicable. Significant differences outlined in the ANOVA were subjected to pairwise t-tests with Bonferroni corrections and a critical threshold of $p < .05$ was upheld. A 95% confidence level was always employed.

6.4. Results

6.4.1. Behavioural Results

The overall mean bid value across the two tasks was £4.61, with VA = £4.66 (SD ± 3.25) and BDM = £4.56 (SD ± 3.25). The mean retail value of the auction items was £7.39. The participants were not told the retail price of the auction items so as not to anchor their bids. A Shapiro-Wilk test confirmed the bid values within the two tasks were normally distributed ($p > .05$). Response times were uninformative as judgements were not time limited. All but three participants showed a strong positive correlation between their bid values in the two tasks ($r =$

.90 – .61; two showed a medium positive correlation (*s* = .431 and .367) and one a weak positive correlation (r = .273, p < .001). To explore effects of high and low SV in subsequent ERP data analysis, the bid values for each participant were divided into low- and high-value by median split, with approximately n=150 each and means of £2.15 (SE = .021) and £7.04 (SE = .039) respectively.

The effect of task order was investigated with paired samples t-tests. Bid values did not significantly differ between the first and second session: *t*(23) = 1.038, *p* > .05. The order of the two tasks were counterbalanced; 10 participants bid more in the first session (6 in the VA and 4 in the BDM) and 10 participants bid more in the second session (5 in the VA and 5 in the BDM).

In order to determine whether participants changed their strategy as the tasks progressed, we correlated the average bid values in each task with the trial number. A small negative trend was observed in VA (*r(*22) = -.118, *p* = .041), suggesting participants tended to decrease their bid as the task progressed. No significant correlation was found in the BDM.

Finally, overbidding or underbidding behaviours in the VA relative to the BDM were explored, however there was no significant difference in bidding behaviour between tasks (paired t-test: t = -.37, df = 23, p > .05). To examine any individual differences in bid behaviour, a series of paired t-tests compared the bid values for matched auction items during both tasks for each participant. 11 participants bid more in the VA, 9 participants bid more in the BDM, and 4 participants' bid differences between tasks were not statistically significant. The overall average bid value across both tasks did not statistically significantly differ between VA > BDM and BDM > VA participants (p =.50). As there was no effect of strategy on the overall bidding behaviour, strategy was not explored in the ERP analysis.

6.4.2. ERP results

Figure 6.4.1 shows a butterfly plot illustrating the ERPs at each electrode site in response to outcome presentation across all conditions and both tasks; ERP components and their corresponding latencies and topographic maps are labelled.

Three distinct ERP components were observed across the epoch. The RewP component was defined as the win–minus–no-win difference waveform and was measured from midline frontal-central electrodes peaking at 275 ms post-feedback onset. The P3 component (Polich, 2012) emerged at approximately 310 ms in a parietal region on the right side of the scalp, before reaching a positive maximum at 331 ms over the midline frontal electrodes.

The N170 component peaked at 182 ms and displayed a bilateral negative potential at occipitotemporal electrodes that was stronger on the right than left side of the head. The prominent negative potential in the right occipitotemporal electrodes was accompanied by a vertex positive potential (VPP) (Figure 6.4.1). In contrast to the VPP seen in VA task, the scalp potentials in the BDM task showed two symmetric positive spatial maxima in occipital regions of the scalp. The topographic maps of the VPP and N170 components overlaid on the 3D volume rendering of a human head are shown in Supplementary materials (Figure 6.6.1).

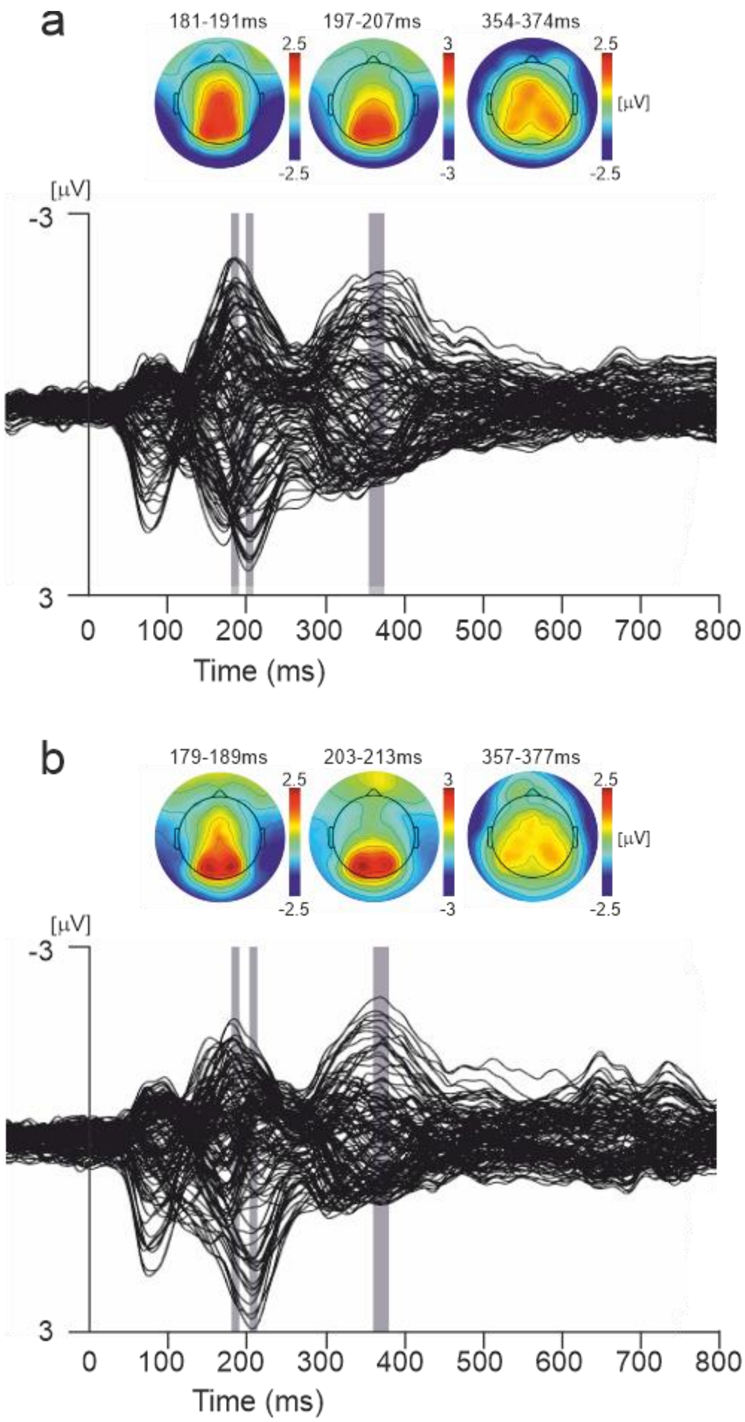

Figure 6.4.1. Butterfly plots of grand average ERPs in response to outcome presentation for (A) VA task and (B) BDM task. Epochs for distinct ERP components, N170, P2 and P3, are highlighted with grey bars, and the corresponding averaged topographies across the selected epochs are shown above.

6.4.2.1. N170 component

For analysis of the N170 component, based on visual inspection of scalp topographic maps (Figure 6.4.2) and previous research (Eimer, 2000; Rossion, 2014; Rossion & Jacques, 2012), the epoch of 172 – 192 ms post-outcome stimulus onset and the occipitotemporal electrodes 99, 100 and 101 (100 corresponding for TP10 in the 10 – 10 system) and the vertex electrodes 129 and 55 (corresponding for Cz and CPz in the 10 – 10 system) were selected for statistical analysis. The ERP waveforms for win and no-win outcomes and for bid value contrasts in both tasks are shown in Figure 6.4.2.

As far as the negative potential in occipitotemporal electrodes is concerned, a 3 × 2 × 2 × 2 repeated measures ANOVA (electrode × task × value × outcome) revealed main effects of electrode ($F(2, 46) = 4.46$, $p = .017$, $\eta p^2 = .16$), outcome ($F(1,23) = 12.48$, $p = .002$, $\eta p^2 = .35$), task ($F(1,23) = 10.34$, $p = .004$, $\eta p^2 = .31$) and value ($F(1,23) = 11.34$, $p = .003$, $\eta p^2 = .33$). No significant interaction effects were found. Electrode 101 (-1.59 ± .23 µV) showed less negative amplitudes than electrode 100 (-2.01 ± .27 µV, $p = .004$); win trials (-2.09 ± .26 µV) resulted in more negative potential amplitudes than no-win trials (-1.53 ± .23 µV); VA trials (-2.11 ± .27 µV) resulted in more negative potential amplitudes than BDM trials (-1.52 ± .23 µV); and high-value trials (-1.93 ± .24 µV) resulted in more negative potential amplitudes than low-value trials (-1.70 ± .23 µV).

Analysis of the VPP using a repeated measures 2 × 2 × 2 × 2 ANOVA (electrode × task × value × outcome) revealed main effects of task ($F(1,23) = 11.53$, $p = .002$, $\eta p^2 = .33$), value ($F(1,23) = 4.39$, $p = .047$, $\eta p^2 = .16$) and outcome ($F(1,23) = 12.94$, $p = .002$, $\eta p^2 = .36$). There was also a significant interaction effect between task and electrode ($F(1,23) = 4.71$, $p = .041$, $\eta p^2 = .17$), and between task and outcome ($F(1,23) = 9.23$, $p = .006$, $\eta p^2 = .29$).

Notably, amplitudes for win outcomes were significantly greater in the VA task than in the BDM (VA win: 2.39 ± .40 µV, BDM win: 1.50 ± .34 µV, $p<.001$), but there was no significant difference between tasks for no-win outcomes (VA no-win: 1.37 ± .26 µV, BDM no-win: 1.03 ± .24 µV, $p=.097$). Amplitudes between the two electrodes also significantly differed during the VA (129: 1.97 ± .34 µV; 55: 1.25 ± .31 µV, $p = .046$) but not during the BDM (129: 1.79 ± .30 µV; 55: 1.28 ± .25 µV, $p = .805$). Further, VA trials (1.88 ± .32 µV) resulted in more positive potential amplitudes than BDM trials (1.26 ± .28 µV); high-value trials (1.71 ± .29 µV) resulted in more positive potential amplitudes than low-value trials (1.43 ± .29 µV); and win trials (1.94 ± .36 µV) resulted in more negative potential amplitudes than no-win trials (1.20 ± .23 µV).

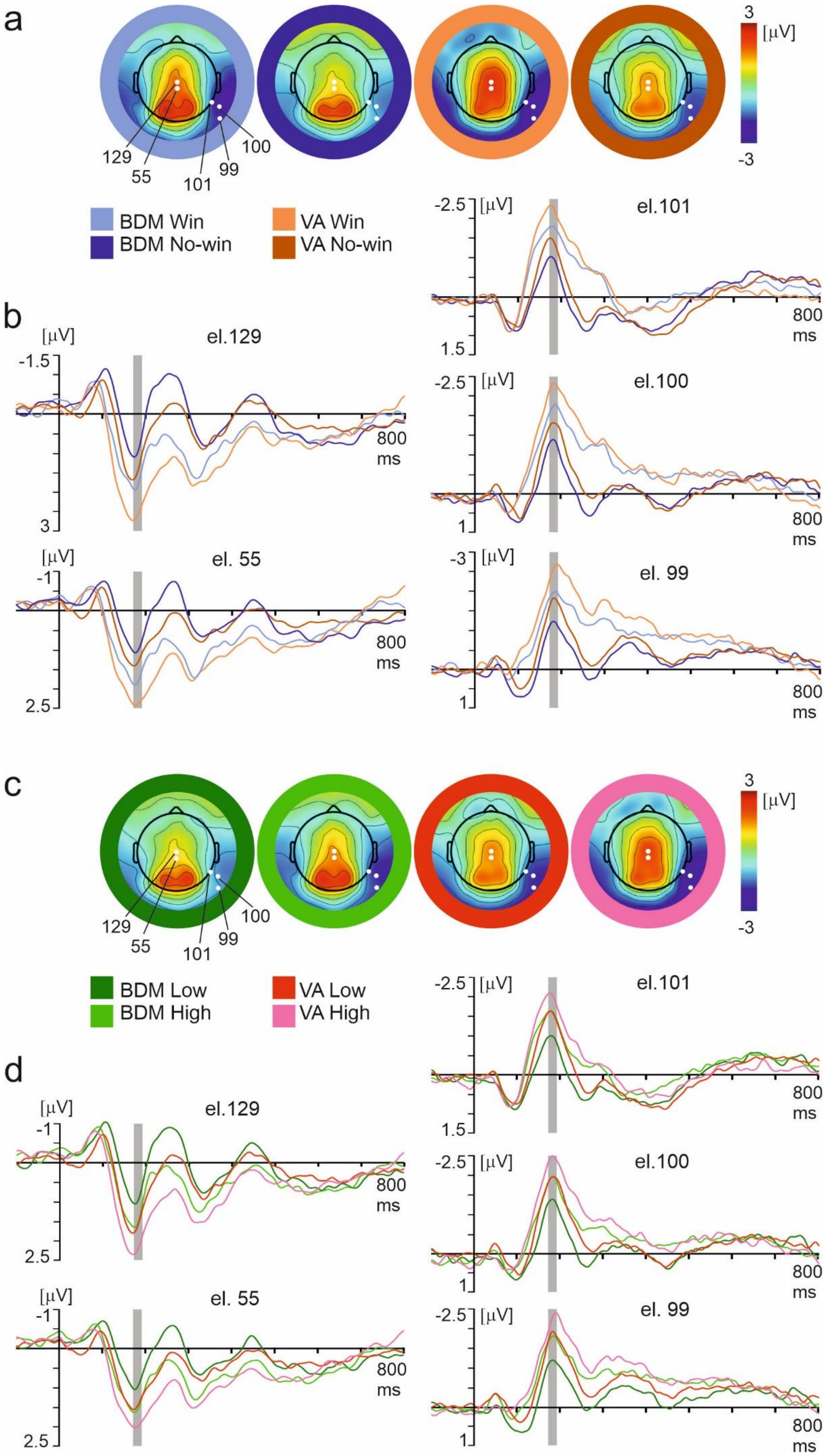
a
3
[μV]
-3
129
55
101
99
100
BDM Win
BDM No-win
VA Win
VA No-win
b
el.129
el. 55
el.101
el.100
el. 99
[μV]
-1.5
3
-1
2.5
-2.5
1.5
1
-3
800
ms
c
BDM Low
BDM High
VA Low
VA High
d
el.129
el. 55
el.101
el.100
el. 99
-1
2.5
-2.5
1.5
1
800
ms

Figure 6.4.2. Win–no-win contrasts (a – b) and high vs. low bid values contrasts (c – d) in BDM and VA tasks for the N170 and the VPP. (a) Whole scalp topographic maps displaying grand average ERPs for each outcome condition at time point 182 ms. Electrodes used in statistical analysis (129, 55, 99, 100, 101) are highlighted in white. (b) Grand average ERP waveforms across all participants and subjective value conditions comparing the four outcome conditions: BDM win (light blue), BDM no-win (navy), VA win (light orange) and VA no-win (dark orange). Epoch of interest (172 – 192 ms post feedback-onset) highlighted in grey. (c) Whole scalp topographic maps displaying grand average ERPs for each value condition at time point 182 ms. (d) Grand average ERP waveform across all participants and outcome conditions comparing the four value conditions: BDM low-value (dark green), BDM high-value (light green), VA low-value (red) and VA high-value (pink).

6.4.2.2. RewP component

A RewP with a spatial maximum at the central midline electrodes was found in response to bidding outcomes in VA and BDM during the epoch 260 – 290 ms. The electrodes 6, 129 and 55 (corresponding to FCz, Cz and CPz in the 10 – 10 system) were selected for statistical analysis. The ERP win–minus–no-win difference waveforms are shown in Figure 6.4.3. A 3 × 2 × 2 repeated measures ANOVA (electrode × task × value) revealed no main effects or interaction effects.

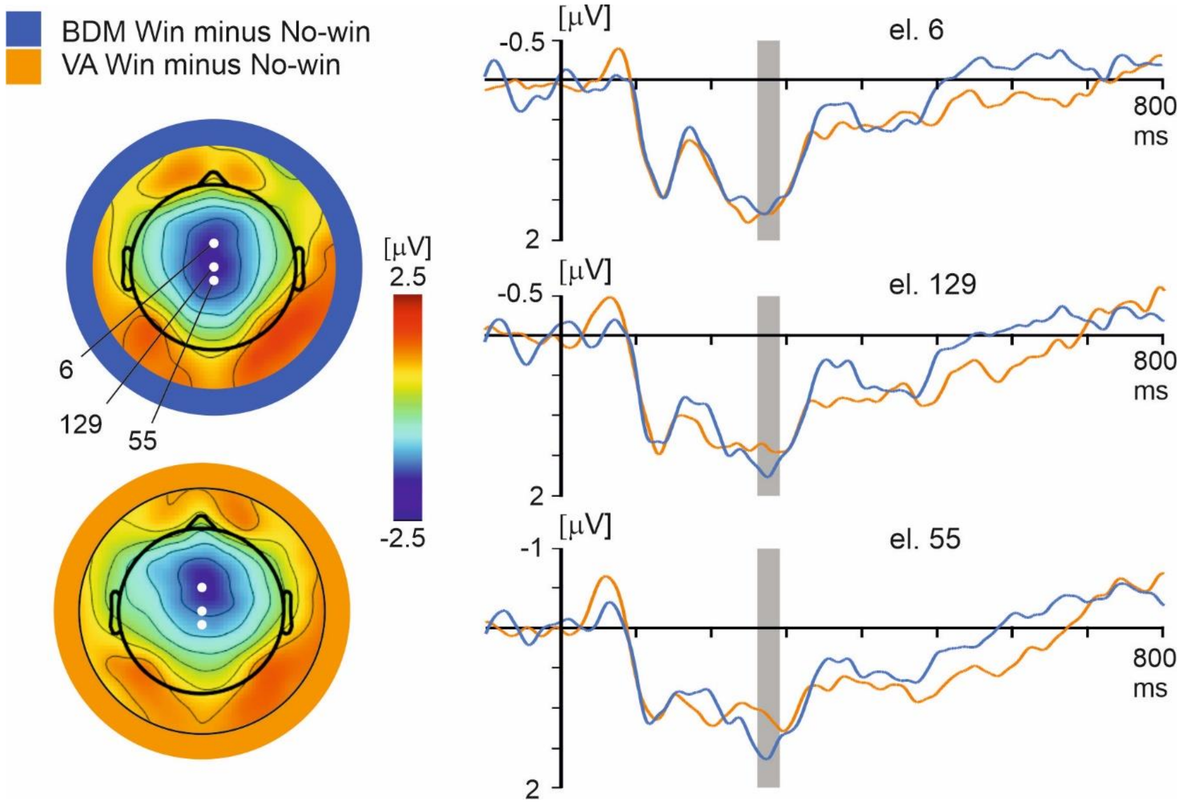

Figure 6.4.3. The Win–No-win contrast in BDM and VA tasks in the RewP component. Left: Whole scalp topographic maps displaying differences in grand average ERPs at time point 275 ms. Three electrodes used in statistical analysis, numbered 6, 129 and 55, are highlighted in white. Right: Grand average win–minus–no-win ERP difference waveform across all subjects and product value conditions comparing BDM (blue) and VA (orange) win–minus–no-win difference waveforms. Epoch of interest, 260 – 290 ms post feedback-onset, highlighted in grey.

6.4.2.3. P3 Component

Topographic maps of the P3 component for the win–no-win contrast and the high vs low-value contrast (Figure 6.4.4) showed a positive potential over the midline parietal electrodes, peaking at 316 – 346 ms. The electrodes 6, 129 and 55 were selected for statistical analysis.

A 3 × 2 × 2 × 2 repeated measures ANOVA (electrode × task × value × outcome) revealed a main effect of value (F(1, 23) = 6.83, p = .016, ηp2 = .23) and outcome (F(1, 23) = 6.52, p =

.018, ηp2 = .22), and, importantly, an interaction effect between task and outcome (F(1, 23) = 6.35, p = .019, ηp2 = .22). No other interaction or main effects were found.

High-value trials (1.33 ± .20 μV) resulted in more positive potential amplitudes than low-value trials (0.99 ± .20 μV), and win trials (1.43 ± .24 μV) resulted in more positive potential amplitudes than no-win trials (0.88 ± .19 μV). As far as the interaction between task and outcome is concerned, amplitudes for win outcomes were significantly greater than no-win outcomes in the VA task (Win: 1.68 ± .26 μV; no-win: 0.85 ± .22 μV, p=.001) but not in the BDM (Win: 1.18 ± .28 μV; no-win: 0.92 ± .25 μV, p=.345) (Figure 6.4.4).

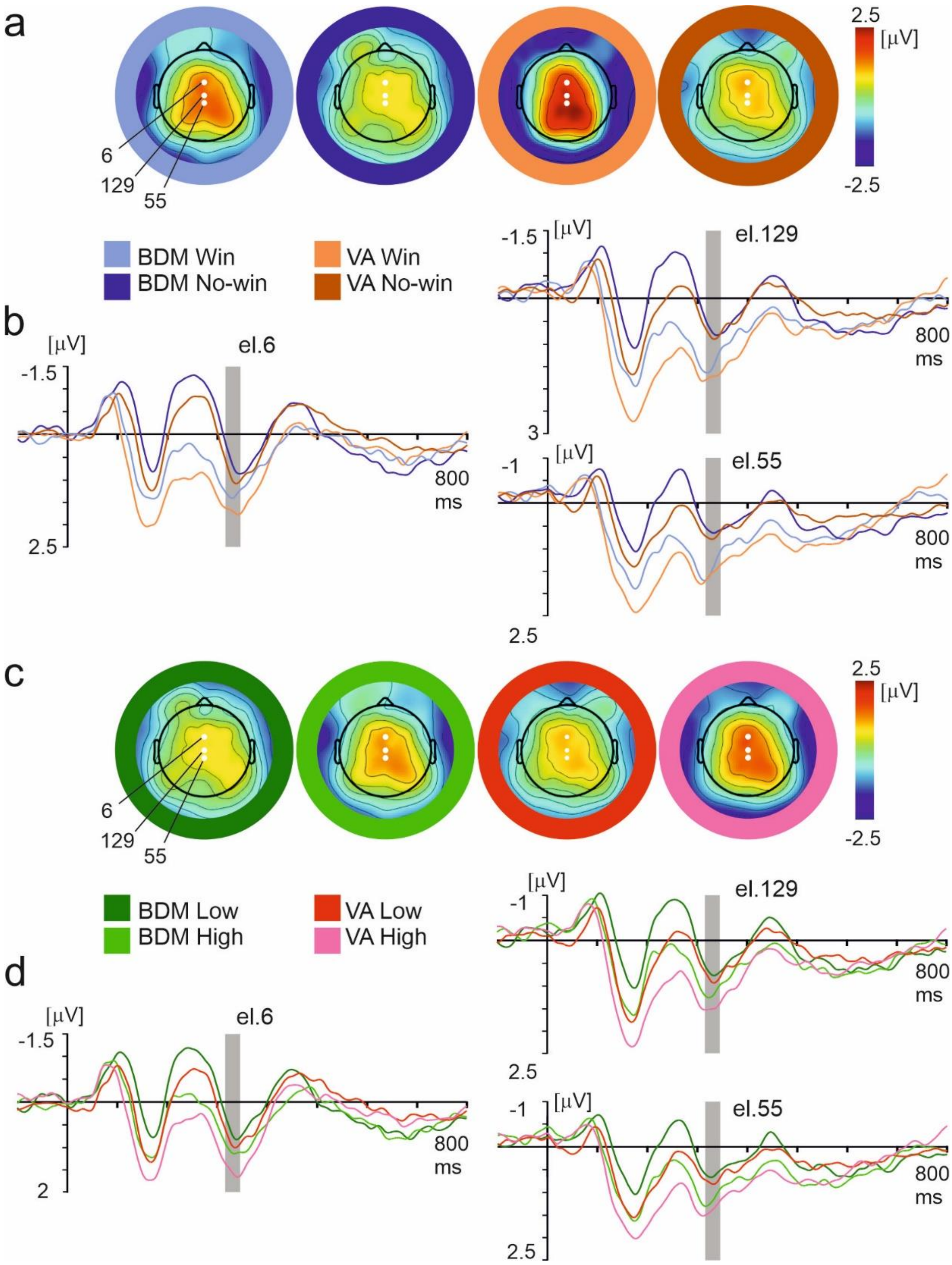

Figure 6.4.4. The win – no-win contrast (a – b) and the high vs low-value bids contrast (c – d) in BDM and VA tasks in the P3 component. (a) Whole scalp topographic maps displaying grand average ERPs for each outcome condition at time point 331 ms. Three electrodes used in statistical analysis, numbered 6, 129 and 55, are highlighted in white. (b) Grand average ERP waveforms across all subjects and product value conditions comparing the four outcome conditions: BDM win (light blue), BDM no-win (navy), VA

win (light orange) and VA no-win (dark orange). Epoch of interest (316 – 346 ms post feedback-onset) highlighted in grey. (c) Whole scalp topographic maps displaying grand average ERPs for each value condition at time point 331 ms. (d) Grand average ERP waveform across all subjects and outcome conditions comparing the four value conditions: BDM low-value (dark green), BDM high-value (light green), VA low-value (red) and VA high-value (pink).

6.5.Discussion

The present study examined the impact of social competition on economic valuation and the cortical representations of outcome processing during risky economic decision-making. Two well-established second-price sealed-bid auction paradigms were utilized to elicit SVs and isolate the impact of a second human competitor on reward-related ERPs. Contrasting the two tasks highlights the impact of a social dimension, while comparing win and no-win outcomes examines the effect of feedback valence, and splitting the data into high and low SV investigates feedback salience. Our results found that the amplitude of the P3 component for win compared to no-win trials was larger in the VA than in the BDM. Further, the VA task, relative to the BDM, was associated with an unanticipated prominent negative potential in the right occipitotemporal electrodes and a VPP in the latency range of approximately 170 – 190 ms, suggesting the modulation of a face-sensitive N170 potential. Both the P3 and N170 were also sensitive to SV, as indexed by bid value, and trial outcome. A RewP, defined as a win–minus–no-win difference waveform, was elicited in both tasks but was not modulated by task or value.

The increased amplitudes of the N170 potential and the VPP in the VA relative to the BDM was not hypothesized. The N170 in the right occipitotemporal electrodes is well established as a face-sensitive component, traditionally posited to reflect early bottom-up visual perception

(Deffke et al., 2007; Itier & Taylor, 2004). The VPP is a frequent companion to the negative N170 potential (Jeffreys, 1996; Joyce & Rossion, 2005; Rossion, 2014), and the two components are thought to be opposing manifestations of the same brain processes (Zhao, Meng, An, & Wang, 2019). There is evidence that the mental imagery of faces recruits the same early processing mechanisms as face perception (Ganis & Schendan, 2008). The N170 has been shown to be elicited by imagining a face (Dijkstra et al., 2018), and modulated by prompted mental imagery (Ganis & Schendan, 2008) and auditory semantic information (Landau, Aziz-Zadeh, & Ivry, 2010) prior to face perception. These enhancement effects reflect the influence of top-down processing pathways on the N170 component, with the mental visualization of a person recruiting additional perceptual processing resources. In the present study, the visual stimuli in the outcome period were words and were identical between the two tasks. Nevertheless, the outcome feedback in the VA was not merely financial information, as in the BDM, but also a valid social signal of their opponents' SV. It is possible that the additional mental visualization of a human opponent during the VA task caused a projection of personhood onto the expected incoming visual stimuli, which enhanced the VPP and N170 component amplitudes through top-down processes. Together, the activations of a prominent VPP and negativity in the occipitotemporal electrodes in the VA present strong evidence that the VA, but not the BDM, activated the fusiform cortices responsible for the N170 face-sensitive component. This is a preliminary finding, and the VPP and the N170 component were not the focus of this study but merit further exploration in future research.

Further, the P3 component activity also differentiated between the two tasks: P3 amplitudes showed an effect of feedback valence in the VA but not in the BDM. Consistent with prior studies, a P3 was elicited in both tasks over central midline sites peaking at 331 ms post outcome feedback presentation, showing a more positive amplitude for win outcomes than no-win outcomes in the VA. The P3 is well established as sensitive to outcome probability

(Duncan-Johnson & Donchin, 1982; Polich, 2007, 2012; Polich & Margala, 1997; Rosenfeld, Biroschak, Kleschen, & Smith, 2005) and so a main effect of outcome was expected, as in both tasks no-win outcomes were more probable than win outcomes. The task parameters of both auctions prescribe that the participants are in control of the likelihood of win/no-win outcomes. As the bid value directly dictates the outcome probabilities (for example, in this experiment a bid of £3 designates a 25% probability of winning), we were unable to control the respective quantities of win/no-win trials. However, the overall win/no-win probabilities in both tasks were comparable, with the average likelihood of winning being 38.83% and 38% for VA and BDM respectively. The P3 component is central to the allocation of attentional resources based on motivational significance (Nieuwenhuis, Slagter, von Geusau, Heslenfeld, & Holroyd, 2005), therefore the observed difference in amplitudes between outcomes during the VA which is absent in the BDM can also be interpreted as reflecting the enhanced motivational salience of social compared to non-social feedback stimuli (Bellebaum & Daum, 2008; Gehring & Willoughby, 2002; Pfabigan et al., 2019). The final price paid in VA win trials is the only source of information about the opponent and their SVs, and so can be utilized as a valid social signal for the participant to learn about the public, shared values of items. Comparatively, the win outcome in the BDM (final price paid) does not provide any insight into the opponent strategy or can be used to predict future behavior.

No other ERP component in the present study differentiated between VA and BDM tasks. Specifically, the lack of RewP component sensitivity to the social domain in this competitive context is interesting when compared to previous research. In the present study, the level of competition remained the same, but the source of competition was changed. In previous studies where RewP amplitudes were modulated in social competitive scenarios (Czeszumski et al., 2019; Luo et al., 2015), the level or type of competition (e.g. direct or indirect) was altered while the social context remained the same. Our results align with those found by Rigoni et al.

(2010), where the RewP amplitudes did not differ between a non-social and a socially competitive context. Together, these results suggest that the type of competition, e.g. comparison vs direct competition, is the modulating factor in RewP amplitude. Further studies could more comprehensively unpack the relationship between competition/comparison type and social context to elucidate the respective contributions to RewP activity.

The amplitudes of the N170 and P3 components, but not the RewP, were modulated by SV in both types of auctions, with greater amplitudes for high- than low-value auction items. The insensitivity of the RewP to SV as dictated by bid value is in line with findings from our previous VA study, where the RewP was indifferent to the market value of the auction items (Newton-Fenner et al., 2022). The more positive P3 amplitude potentials following high SV outcomes compared to low SV items may be linked to attentional engagement (Nieuwenhuis, Aston-Jones, et al., 2005; San Martin, 2012; Yeung & Sanfey, 2004). Our results indicate that high-value item trials were deemed more salient and consequently garnered greater attentional resources in the outcome processing period. The participants were more invested in the outcomes of the trials where they had bid higher, and this increase in engagement was reflected in the initial neural response.

Finally, it is important to note that, while this study builds on previous research conducted in our lab and provides new insights into outcome processing in risky economic contexts, it is also limited by a potential confound in the outcome stimuli. The additional information when items were won resulted in a luminance difference between win and no-win outcomes. While this was necessary to convey the details of the final price paid to the participant, it may have impacted early low-level visual components. Our previous VA study found an impact of final price paid in win trials on RewP but not P3 amplitude, and so future studies could explore the interaction of social context and final price paid to further understand this information's role as a valid social signal of shared SV.

To conclude, the present study showed that two event-related components differentiated between Vickrey and BDM auctions. An unanticipated N170 component, and P3 amplitudes for high-value items, were enhanced in the VA compared to the BDM. Findings suggest that automatic feedback processing as early as 176 ms post-feedback onset is facilitated by the presence of a human competitor, and that later processing of outcome feedback is modulated by social context and subjective value. Further, our results align with previous investigations that found reward-related components are differentially sensitive to outcome valence and salience. This study progresses the neural characterization of the impact of social context on reward processing in risky environments.

6.6.Supplementary Materials

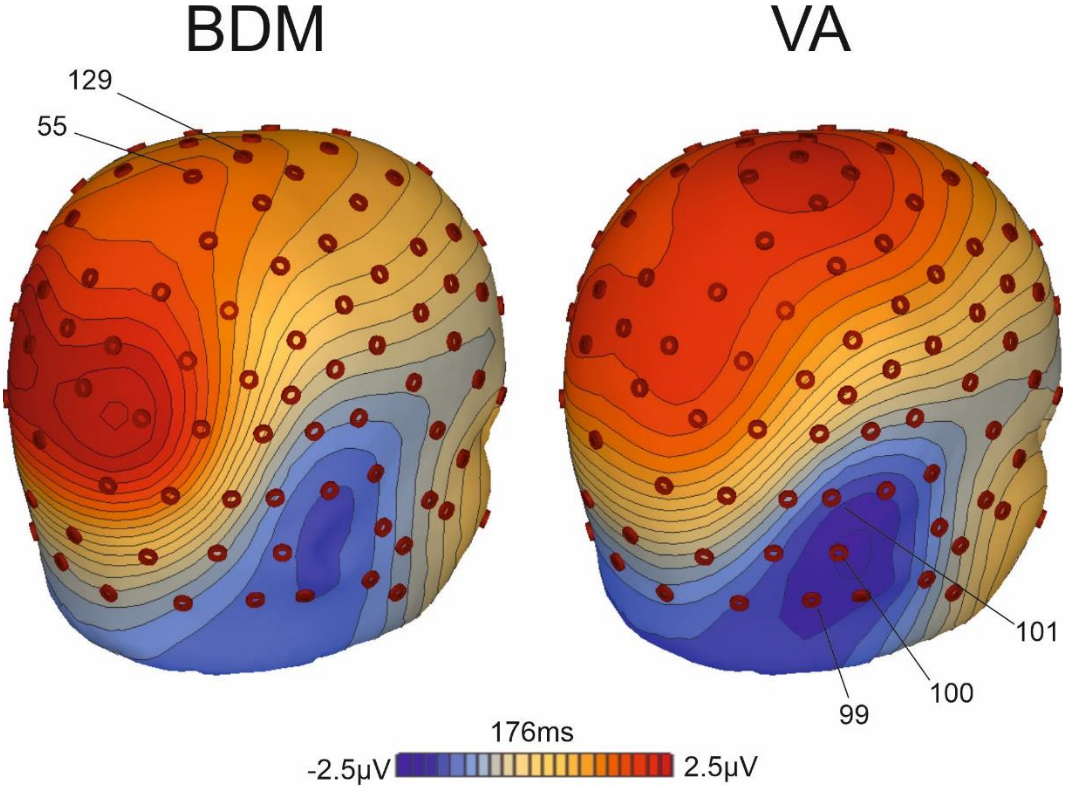

Figure 6.6.1. The topographic maps of the VPP and N170 components overlaid on the 3D volume rendering of a human head, shown at time point 176ms post-feedback onset.

7. General Discussion

Research in the field of neuroeconomics has focused on unpacking the intricacies of complex decision-making representation in the vast dopaminergic brain valuation system, and how the characteristics of this representation align with economic models of consumer behaviour. The overall aim of this thesis was to explore the neural mechanisms of subjective valuation and reward processing in an incentive-compatible economic context. The meta-analysis of fMRI studies and two primary EEG experiments described in the previous chapters used two demand-revealing SPSB auction paradigms, the VA and BDM, to characterise the spatiotemporal characteristics of decision-making involving social competition and risk and uncertainty.

7.1. Summary of findings

- WTP elicited by the BDM positively correlated with BOLD activity in the left vmPFC, bilateral VS, right dlPFC, right IFG, and right AI (Chapter 4).
- The left vmPFC and the left OFC demonstrated consistent activation in line with WTP regardless of task relevance, indicating the automaticity of valuation processing (Chapter 4).
- Meanwhile, the right IFG, right dlPFC and right caudate showed preferential engagement during concurrent (as opposed to consecutive) fMRI scanning and BDM performance (Chapter 4).
- Reward-related ERP components were elicited in the outcome-processing stage of VA and BDM trials (Chapters 5 & 6).

- FRN (RewP) amplitudes differentiated between less favourable (snatch) and more favourable (bargain) wins in the VA (Chapter 5), but were not modulated by retail price, auction task or SV (Chapters 5 & 6).
- P300 (P3) amplitudes were sensitive to value as defined by retail price (Chapter 5) and by bid value (Chapter 6), and differentiated between win and no-win outcomes in the VA but not in the BDM task (Chapters 5 & 6).
- Individual loss aversion level did not correlate with the strength of the FRN during the VA (Chapter 5).
- An N170 and accompanying VPP component exhibited larger amplitudes in the VA than the BDM, and was also sensitive to outcome and SV (Chapter 6).

7.2. Themes of findings

7.2.1. Unitary system of value related processing

Neuroeconomic research using fMRI imaging has found evidence of a domain general valuation network that linearly encodes subjective value across reward types, supporting the hypothesis of a common currency mechanism (Chib et al., 2009; Levy & Glimcher, 2012; Peters & Buchel, 2009; Sescousse et al., 2015). In line with this, across all experimental studies in this thesis there were systematic patterns of brain activity present regarding valuation processing (H_1). It has also been suggested that the representation of SV during the initial valuation and outcome evaluation stages of decision-making is computed by the same neural system incorporating the vmPFC and the VS (Kable & Glimcher, 2009; Rangel et al., 2008). Results from Chapters 5 and 6 confirmed that the temporal characteristics of reward-related neural processing in the VA is comparable to simpler and more constrained paradigms common in the literature, such as 2AFC tasks, validating its use as an investigative tool of SV (H_3).

Furthermore, Chapter 5 and 6 showed that value, as defined by market price or WTP, impacted the amplitude of several ERP components during outcome evaluation, in particular the P300. These findings complement and extend previous work which investigated ERP activity during the initial valuation period of BDM auctions (Roberts et al., 2018; Tyson-Carr et al., 2018; Tyson-Carr et al., 2020). Tyson-Carr et al. (2018) and Roberts et al. (2018) both found that low value items were preferentially encoded during the N2 component latency, with enhanced activation in the AI and OFC, irrespective of task relevance. Conversely, high value products produced increased, and sustained, activation in the P300 latency interval, sometimes referred to as the LPP (Hajcak, Dunning, & Foti, 2009; Hajcak & Foti, 2020). The P300 and LPP have been proposed as indexing preference during product valuation (Hakim & Levy, 2019). In the outcome processing period, the current results align with the role of the P300 as processing stimulus significance, defined as a response of appetitive and aversive motivational systems (Hajcak & Foti, 2020).

In addition to performing value computations during different stages of decision-making, previous studies have highlighted that the brain valuation system automatically encodes value independent of task relevance (Lebreton et al., 2009; Levy et al., 2011). Results from Chapter 4 largely support the proposition of automatic economic valuation processes (H_2): the majority of the activated areas, including the vmPFC and the VS, showed increasing levels of BOLD activity in line with SV regardless of whether the participant was engaged in active valuation. However, it should also be noted that the use of BDM auctions in the meta-analysis in Chapter 4 revealed some distinctions in processing that were modulated by factors such as task relevance. Certain structures were preferentially activated during active valuation processing, namely the right IFG, right dlPFC and right caudate. Previous work has linked the IFG and dlPFC to behavioural control modulation, which is engaged during decision-making to help modulate the decision-making circuitry to regulate choices (Hutcherson et al., 2012). It may therefore be the case that the IFG and dlPFC regulate the influence of parts of the brain valuation system during decision-making, but are not commonly included as part of the valuation system itself in the literature.

7.2.2. The FRN, salience and reward prediction error

The ERP results from Chapters 5 & 6 contribute to a more general literature on reinforcement learning during outcome processing. The results in Chapters 5 and 6 confirm and extend previous findings in situations of direct competition and comparison during independent performance, showing that FRN amplitudes were not sensitive to value (as denoted by either market price or WTP) or social context (Qiu et al., 2010; Y. Wu et al., 2012) when processing auction outcomes. Further, the differentiation of snatch vs bargain conditions in the FRN is opposed to the suggestion that the FRN reflects a binary differentiation between good and bad outcomes (Hajcak et al., 2006; Holroyd, Hajcak, & Larsen, 2006; Yeung & Sanfey, 2004; Yu & Zhou, 2006). The differentiation between a quite-good and a very-good win outcome suggests that the FRN may encode the outcome prediction error on a linear scale, instead of the coarse division of good and bad.

Modulations of the FRN have conventionally been thought to reflect operations underlying reinforcement learning by expressing a binary reward prediction error through dopaminergic projections to the ACC. However, there is a growing discussion in the neuroeconomic literature about whether the FRN actually signals a prediction error regarding motivational salience as opposed to outcome valence (Glazer & Nusslock, 2022; Moser & Simons, 2009; Talmi et al., 2013). Several studies have observed increased RewP amplitudes after unexpected absences in punishment conditions equivalent to that of unexpected gains in reward conditions (Heydari & Holroyd, 2016; Hird, El-Deredy, Jones, & Talmi, 2018; Talmi et al., 2013). Both SV and social context are posited to modulate the motivational salience of the received outcome (Hauser et al., 2014; Pfabigan et al., 2019; Pfabigan & Han, 2019). Therefore, the observed insensitivity of the FRN to these factors does not support the hypothesis of the FRNs role as denoting a salience prediction error. Furthermore, we can understand the distribution of outcome expectations to be different between the two SPSB auctions. With the BDM, there is an equal distribution of likelihood across the entire range of opponent bid values, and this does not change, and so the participant can adapt their expectations of winning or not winning a given trial through their bid value. However, in the VA there is not an equal distribution of outcome likelihoods across the range of bid values. The participant has no information about what the given likelihood of either outcome is, and can only use their own SV as an anchoring figure. Therefore, there is an expectation that their human opponent's SVs will align with theirs to a certain degree, and this will be reflected similar bidding patterns. This has the consequence of the participant having an expectation of a normal distribution of opponent preferences around their own bid value, where the greater deviation of opponent bid from the participant's own results in a greater violation of expectation.

This is a possible explanation for the difference seen in Chapter 5 between bargain and snatch FRN difference waveforms. The Bargain condition was not only a greater financial win, but it was also the more unexpected outcome: this could be explained by the value function in Prospect theory (see Figure 1.1.1.1), where the outcome that is further away from the original reference point is more cognitively impactful (Schwartz et al., 2008; Werner & Zank, 2019).

Salience is linked to probability expectation, and so the insensitivity of the FRN to the differences between tasks is further evidence that the FRN may not purely represent a salience prediction error. However, the interpretation of the present results is limited, as the SPSB auctions operate in the gain domain and so salience prediction errors and reward-prediction errors cannot be fully disentangled. In a similar way to the hypothetical profiles for regional BOLD activity as a function of SV proposed by Bartra and colleagues (see Figure 1.2), salience and reward prediction errors would both increase from neutral to reward outcomes, and so can only be separated through the elicitations of aversive predictions errors.

7.2.3. Social competition impact on outcome ERPs

The research presented in Chapters 5 and 6 sheds light on the differential effects of social competition on outcome processing ERPs. Comparatively little neuroeconomic research has investigated the impact of direct social competition on decision-making, with the majority of social neuroscience focusing on pro-social collaborative behaviours. Behavioural economic research has found that winning against an opponent holds its own utility, which is distinct from the utility of the item or good that has been won, termed the “joy of winning”. fMRI studies have indicated increased activity in the VS and vmPFC in line with the “joy of winning” (Delgado, Schotter, et al., 2008; van den Bos et al., 2013). This added utility often leads to deviations in logical behaviour, such as overbidding, which can result in the ‘winner’s curse’. Despite consistent reports of differentiations between bidding behaviours during the BDM and VA in the economic literature, no overall difference in bidding behaviour was observed between the two auctions in Chapter 6. It is possible that the participant sample size was too small to reliably elicit any group behavioural differences. Despite this, there were robust differences in how the rewards were processed in the brain.

In support of H_5, the inclusion of a socially competitive dimension in the SPSB auction context resulted in differential encoding of reward outcomes in the P300 and an unexpected N170 component. The P300 is thought to reflect motivational significance and attention allocation processing: the findings in the experimental chapters align with this understanding as higher amplitudes were elicited for higher value, which indicates higher salience (Hajcak & Foti, 2020; Polich, 2012; Wang et al., 2015). The results also suggest that this is applicable in situations where value is defined as the internal subjective state and also as the objective market price, which could have significant commercial implications (Schmidt & Bijmolt, 2020).

The N170 is typically posited as an early bottom-up automatic perceptual processing mechanism of facial features (Rossion & Jacques, 2012); however, there is evidence that it is face-sensitive as opposed to face-specific (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Recent studies have associated the N170 with feedback processing in medial temporal lobe (MTL) during immediate and delayed reward feedback (Arbel, Hong, Baker, & Holroyd, 2017; Yin, Wang, Zhang, & Li, 2018). The feedback in VA is a valid social signal, with information which the participant can build a profile about their opponent and use it to predict their future behaviours. In line with this, the enhanced amplitude of the N170 in the VA compared to the BDM may be a potential marker of MTL activation reflecting enhanced active learning (Arbel et al., 2017).

There are two major competing theoretical schemas for how the brain may determine the value of social and non-social factors during decision-making (Ruff & Fehr, 2014). The 'extended common currency schema' assumes that a single neural circuit determines the motivational significance of both social and non-social events, while the 'social-valuation-specific schema' proposes that social aspects of the environment are processed by a separate, specialised neural circuitry. The presence of enhanced N170 and VPP amplitudes in the VA compared to the BDM suggests the selective implementation of the fusiform gyrus and other facial processing brain regions in social contexts (Deffke et al., 2007; Hinojosa, Mercado, & Carretié, 2015; Joyce & Rossion, 2005; Rossion & Jacques, 2012). This is suggestive of a specialised neural circuitry recruited specifically for social value processing. Recent studies have found an inconsistent association of the N170 with delayed feedback processing in the MTL (Arbel et al., 2017; Yin et al., 2018). An unexplored factor in the VA task was the delayed response caused by the “waiting for opponent bid” jitter, which may have led to increased feelings of anticipation of the final outcome. Therefore, interpretation of the unexpected finding of the N170 is limited here, but this potential confound could be explored in future research. Further, the topography and latency of the other ERPs from Chapter 6 were comparable in the social and non-social context, giving evidence of a single neural circuit providing a 'common motivational currency' for social and non-social information.

7.2.4. Risk, uncertainty and Loss aversion

The role of risk as a static and known probability factor in decision-making has been investigated extensively (Dhar & Simonson, 2003; Ernst & Steinhauser, 2017; Kreussel et al., 2012; Little et al., 2012; San Martin, 2012; Yeshurun, Carrasco, & Maloney, 2008). The results from the studies conducted in this thesis add to the understanding of loss aversion computation in the brain, and have begun to unpack the respective influences of conditions of risk and uncertainty on decision-making.

Previous work has found that the FRN amplitude is modulated by individual attitudes to loss aversion in 2AFC monetary gambling tasks (Kokmotou et al., 2017). Despite this, results from Chapter 5 showed no correlation between FRN amplitude and individual differences in loss aversion during outcome processing in the VA, not supporting H_4 of this thesis. It was discussed that as SPSB auctions operate only in the gain domain, it is possible that the incentives were insufficient to engage loss aversion mechanisms. Sokol-Hessner et al. (2009) proposed that loss aversion by default requires the potential of loss outcomes, whereas risk aversion can occur without the prospect of potential loss. In previous research, risk aversion and loss aversion often co-occur and are commonly confounded variables, but they represent distinct properties of Prospect theory and can be isolated.

People are typically risk averse in the gain domain but risk seeking in the loss domain (De Martino, Kumaran, Seymour, & Dolan, 2006). In line with this, the lateralized activation patterns of the IFG and dlPFC, shown in Chapter 4 may be linked to the engagement of risk aversion mechanisms in the SPSB tasks (Levy et al., 2010). Previous fMRI studies have found correlations between individual levels of risk aversion and increasing IFG activity to low risk and safe options during risky decision-making (Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009). Disruptive transcranial magnetic stimulation (TMS) over the right dlPFC has been shown to increase risky decisions and diminishes sensitivity to changes in risk (Fecteau et al., 2007; Knoch, Gianotti, et al., 2006; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006). Additionally, patients with predominantly right-sided prefrontal lesions demonstrate lower levels of risk aversion (Clark, Manes, Antoun, Sahakian, & Robbins, 2003). In the gain domain of SPSB auctions, it may be the case that the dlPFC and IFG engage cognitive regulation mechanisms to regulate risky choices.

Furthermore, the ACC and AI have also been linked to ambiguity and uncertainty processing. Ambiguity and uncertainty are common factors in real-life decision-making, where the respective probabilities of the outcomes are unknown or unclear, but do not typically feature in simple lab-based decision-making tasks such as the 2AFC. Activation in the AI is related to increased subjective uncertainty (Mohr et al., 2010; Platt & Huettel, 2008; Rutledge et al.,

2010) and ACC activation is modulated by the individual's level of risk tolerance during uncertainty (Behrens, Hunt, Woolrich, & Rushworth, 2008; Sanfey et al., 2003). As the ACC is posited to be the neural generator of the FRN, it is possible that the FRN could be modulated by risk attitudes and individuals’ aversion to uncertainty.

7.3.Thesis limitations

The primary limitation of the fMRI meta-analysis in Chapter 5 was the relatively small sample size of the final cohort. Less stringent inclusion and exclusion criteria may have allowed for a larger final cohort. However, the stringent inclusion criteria allowed for the clean definition and investigation of the concepts of interest. Furthermore, the sample was comfortably above the minimum number of 17 advised for ALE analysis (Eickhoff et al., 2016). The sample size was also comparable to those employed in previous fMRI meta-analyses of related issues (Jauhar et al., 2021; Martins et al., 2021; Morelli et al., 2015; Silverman et al., 2015). Nevertheless, it should be acknowledged that analysis of a cohort of this size may not possess the statistical power to perform robust contrast analyses or elucidate weak or subtle effects. Meanwhile, the primary limitation of the EEG research conducted in this thesis, and EEG research generally, is the insufficient spatial resolution necessary to locate the neural generators of reward processing in the brain (Luck, 2014). The gap in the reward literature was identified to be specifically the spatiotemporal aspects of outcome processing in SPSB auctions, and as such EEG was deemed to be the most appropriate method due to its excellent temporal resolution.

Regarding the task parameters of the VA and BDM tasks conducted in this thesis, there were some logistical limitations which should be addressed. Firstly, there is a question of ecological validity in all lab-based tasks. While the SPSB auctions are more complex and more reflective of real-life economic decision-making than many other simplified paradigms such as

2AFC tasks, the constraints of neuroimaging research require some deviations from real-life. For example, participants were required to partake in 300 auctions in one sitting in the EEG studies, and were required to lie supine for the in-scanner fMRI BDM tasks. Secondly, the price range of the auction items in the EEG studies were constrained by budget restrictions. While the market price range of the auction items was deliberately increased for the ERP study in Chapter 6 (from £3 – £9 to £3 – £12), the stimuli items may still have had limited incentive to the participants, and therefore limited the salience of the outcome responses. It would be interesting for future research to expand on the current findings by utilizing a greater price range than what was possible here. Thirdly, the EEG study in Chapter 6 defined high and low SV categories by splitting stimuli into two equally sized conditions according to bid value. The dichotomising of the data was deemed a necessary step, as EEG data is difficult to investigate on a single-trial level due to the restricted signal-to-noise ratio (Luck, 2005). Therefore, transforming SVs from continuous into categorical data was done in an effort to retain the maximum number of trials possible.

Finally, it should be acknowledged that the majority of participants recruited in the two EEG studies were predominantly undergraduate and postgraduate students, and the average ages reported in the meta-analysis cohort indicate a similar participant pool. Thus, findings might not be generalizable to populations of different cultures and ages (Henrich, Heine, & Norenzayan, 2010). In particular, perception of risky decision-making outcomes may be different between those of different socio-economic status, as individual differences in wealth may greatly influence subsequent risk attitudes and reference points for risky decision-making. While a previous study using the BDM did not find an impact of socioeconomic status on bidding behaviour (Roberts et al., 2018), their participant pool was also largely made up of students. The replication of the studies presented in this thesis with different cultural and socioeconomic groups would therefore help to extend, clarify and confirm findings.

7.3.1. Refuting an FRN-N200 confound

N200 is an important confound of FRN, and researchers must ensure that they do not mistake differences in N200 amplitudes as evidence for modulation of the FRN (Glazer et al., 2018; Krigolson, 2018). The difference between an outcome vs a no-outcome trial drives the N200 amplitude, and importantly, supresses or cancels out the positive waveform of the FRN in win conditions, leading to the appearance of a negative deflection in loss outcomes (Holroyd et al., 2008; Proudfit, 2015). In the current thesis, trials where participants bid 0 were treated as a no-outcome trial, as it was reasoned that they were not invested in the auction outcome. However, as in the BDM and VA paradigms a no-win outcome means that the participant wins nothing and loses nothing, it is conceptually very similar to a no-outcome trial seen in other tasks. Therefore, it is plausible that the amplitude of the FRN was modulated by the N200 component, and we must address this concern. In Chapter 5 the probability of win / no-win outcomes were predetermined and not dependent on the bid value of the participant, and this is reflected in comparable average bid values (£3.24 for no-win outcomes and £3.47 for win outcomes). The similarity of the average bid values suggests comparable levels of investment and attention given to the two outcome conditions in this case. In Chapter 6, there was a difference in average bid values between win / no-win outcomes (£3.18 for No-win outcomes and £6.83 for win outcomes), which was to be expected as the bid value altered the likelihood of each outcome. However, the average bid value of no-win outcomes in Chapter 6 is comparable to both the win and no-win average bid values in Chapter 5, and sufficiently distinct from a bid value of 0. From this evidence, we can be confident in participant engagement during the no-win trial outcomes, and that the FRNs found in this thesis were not due to contamination by a N200.

7.4. Suggestions for future research

The data presented in the current thesis characterised the spatiotemporal dynamics underpinning economic decisions in SPSB auctions through two separate neuroimaging methodologies. The inclusion of the meta-analysis of fMRI studies employing a BDM task to the EEG findings in this thesis afforded the opportunity to compare and synthesise findings across methodologies. Future research could formalize and expand on this work by conducting simultaneous EEG-fMRI recordings of decision-making during VA and BDM auctions, allowing the elucidation of the relationship between the haemodynamic correlates and the timing and strength of reward-related ERPs (Mullinger & Bowtell, 2011).

Furthermore, the study presented in Chapter 5 established that the FRN was not impacted by individual differences in loss aversion level during the VA auction. Unlike many gambling paradigms, SPSB auctions are situations of risky decision-making but do not involve the potential for real financial loss. Therefore, it is possible that the monetary gambling task used to establish individual loss aversion levels actually measured the inappropriate metric. In previous decision-making research, risk and loss aversion often co-occur and are frequently confounded (Sokol-Hessner et al., 2013). Furthermore, the majority of the type of uncertainty in real-life decision making is ambiguity, where each given outcome probability is either unknown or an interval estimation (Zhu, Pan, Wang, Li, & Wang, 2019). “Ambiguity avoidance” is a robust phenomenon where known risk is preferred over ambiguity (Bach et al., 2011; Camerer & Weber, 1992). As the two SPSB auction paradigms discussed here are delineated by the type of uncertainty, risk in the BDM and ambiguity in the VA, these paradigms afford the opportunity to dissociate the two. Previous studies have shown that activation in the lateral OFC and vlPFC is greater for ambiguity compared to risk processing, and this difference correlating with individual level of ambiguity aversion (Hsu et al., 2005).

Therefore, future studies could potentially use SPSB auction paradigms to investigate associations between risk aversion and brain data, while disentangling risk aversion, ambiguity avoidance and loss aversion dynamics (Chen et al., 2007).

Future studies could also endeavour to create more realistic experimental SPSB auction paradigms by using real human participants as auction opponents. Previous research has found that interpersonal relationships impact outcome processing in comparative situations (Leng & Zhou, 2010, 2014; Zhang et al., 2021), and that emphasis on competition in first price auctions increases bidding behaviour (van den Bos et al., 2008) and activity in the VS and vmPFC (van den Bos et al., 2013). Therefore, it would be of merit to determine how altering various auction parameters, such as number of opponents or playing against a friend vs. a stranger, can impact the temporal dynamics of outcome processing. Related to this point, another possibility would be to further investigate the behaviour of the N170 in social but non-face viewing settings. The elicitation of a stronger N170 component in the VA than BDM task found in Chapter 6 was not hypothesised, and while interesting it was not the primary focus of the present thesis. It would be interesting to see whether the N170 would be modulated by factors such as real human vs. computer components, particularly if players are told that they are playing against another person in both contexts. Future studies could further explore the dynamics of this component in online or anonymous social contexts to better understand top-down and bottom-up facial or ‘personhood’ processing.

Finally, in acknowledging that the data collected in this thesis came from a fairly homogenous and healthy sample, investigation of reward processing in SBSP auctions would benefit from replications in other populations (Henrich et al., 2010). In addition to different cultural and socioeconomic groups, exploring reward processing in clinical samples may increase understanding of impaired approach and avoidance behaviours and decision-making deficits often seen in disorders such as depression (Hikosaka, 2010; Luo, Jiang, Chen, Zhang, & You, 2019; Proudfit, 2015; Tucker, Luu, Frishkoff, Quiring, & Poulsen, 2003), addiction (Hewig et al., 2010; Kamarajan et al., 2010; Oberg, Christie, & Tata, 2011; Turel et al., 2011) and schizophrenia (Deco, Rolls, Albantakis, & Romo, 2013; Hikosaka, 2010; Horat et al., 2018; Morris, Heerey, Gold, & Holroyd, 2008).

7.5. Concluding remarks

The current thesis advances understanding of the spatiotemporal neural dynamics underpinning economic decision-making under conditions of risk and uncertainty. The superior spatial resolution of fMRI and superior temporal resolution of EEG were combined to holistically investigate the characteristics of economic value-related processes during SPSB auctions.

Despite extensive interest in human computation of value from economists and neuroscientists, the vast majority of neuroeconomic experiments on valuation use non-incentive-compatible paradigms, and ill-defined conceptualisations of value. This can lead to heterogeneity and contradictions in results, and a lack of real-world applicability in marketing and consumer environments. The results presented in this thesis advance our understanding of the involvement of the brain valuation system during risky economic decisions by using a real, demand-revealing purchasing scenario, with the impacts of SV, outcome valence and salience on the FRN and P300 reward-related ERPs discussed. The current research also contributes to the literature concerning the impact of a social dimension on reward processing in the brain. Against the predictions of traditional economic accounts but echoing behavioural findings, the inclusion of a rival elicited greater value related signals across the scalp in the N170 and P300 components, suggesting that the mentalizing of an opponent impacts the salience and valuation given to auction outcomes.

In sum, the findings reported here add important contributions to the existing literature on economic decision-making processing, suggesting that to ensure effective goal-adaptive behaviour there is the swift detection of mismatches between desired and received outcome, mediated by adaptive expectation prediction-error mechanisms. This is succeeded by the updating of subjective motivational action values, necessary to adapt to new contingencies in the social competitive environment and to avoid future errors in behaviour as a result of non-optimal strategies. Finally, these processes are mediated by self-control mechanisms, which are discriminant of risk and uncertainty as separate parameters, and regulate the value computation of choice options in order to maximise the utility of outcomes.

In closing, it is hoped that the methodology and results presented in the experimental chapters of this thesis provide a useful insight and strong foundation for future research into real-world and complex value-based economic decision-making.

8. References

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