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# Economic value in the Brain: A meta-analysis of willingness-to-pay using the Becker-DeGroot-Marschak auction

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**Data 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/).

## 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 participating in 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.

## 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 [1].

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Previous theories of decision-making have highlighted rational expectations [2–4] and reference points [5,6] 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) [7–9], ventral striatum (VS) [10–13], anterior insula (AI) [14–17], posterior parietal cortex (PPC) [18,19], orbitofrontal cortex (OFC) [20–22], amygdala [7,23–26] and anterior cingulate cortex (ACC) [27–30].

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 [1] and pleasure [31] can be understood as distinct from utilitarian concepts of worth [3] and a willingness to exert effort or a motivation to take on costs [32]. 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 [33–36]. 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 [37]. 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. 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 [20,21,38,39]. 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 [40], 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 [41]. However, most methods, such as 2 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 [42,43]. 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 [44,45].

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 [46–49]. This effect is strongest in indirect measures, such as in 2AFCs, leading to consistent overestimation of WTP values [50]. 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 [51,52].

In contrast, the auction paradigm Becker-DeGroot-Marschak mechanism (BDM), equivalent to a second-price sealed-bid auction, is an incentivized experiment [53]. 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 [54]. Formal proof of the dominant strategy in BDM Auctions can be seen in Supporting information.

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) [55,56]. 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 [17,57,58]. This suggests that a domain-general system in the brain is responsible for the encoding of SV across multiple decision stages and reward types [59]. Furthermore, evidence for automaticity in value attribution has been provided in a number of previous studies [7,60–62]. 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 [60,61,63]. To investigate automaticity of subjective 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 even in non-incentivized tasks or during the passive viewing of objects even in absence of choice selection.

## Methods

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

## 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 [64]. 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 [16,65–67] were also screened for additional articles.

## 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 2$^{nd}$ 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).

## 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) [68] or Talairach space [69]; 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 [70].

## 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 [71]. 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) [72].

## 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 [94] 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 [71,95]. 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 [96,97]. 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 [72,95,98–100].

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

### 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" [101,102]. 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 [103]. 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 [104]. 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 [105]. 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 [95].

## Results

Fig 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

**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.* [73]** | 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.* [21]** | 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.* [74]** | 2013 | Confidence in value-based choice | 20 (NA) | 24.24 | Consecutive | VmPFC encodes SV comparisons and subjective confidence in decisions |
| **Enax *et al.* [75]** | 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.* [76]** | 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.* [61]** | 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.* [77]** | 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.* [78]** | 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.* [79]** | 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.* [80]** | 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.* [81]** | 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.* [82]** | 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.* [83]** | 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.* [84]** | 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.* [85]** | 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.* [86]** | 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 |

(*Continued*)

Table 1. (Continued)

| Authors | Year | Title | N (men) | Mean age (SD) | Concurrency of recordings | Main Findings |
|---|---|---|---|---|---|---|
| **Plassmann *et al.* [20]** | 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.* [87]** | 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.* [88]** | 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.* [89]** | 2019 | Mind the gap: Congruence between present and future motivational states shapes prospective decisions | 25 (10) | 22.52 (2.79) RG 18–30 | Concurrent | VS activity positively correlated with level of prospection bias towards food items |
| **Tang *et al.* [90]** | 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.* [91]** | 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.* [92]** | 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.* [93]** | 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 |

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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).

## 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. Fig 2 illustrates the location of significant ALE clusters from the meta-analysis of WTP.

**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

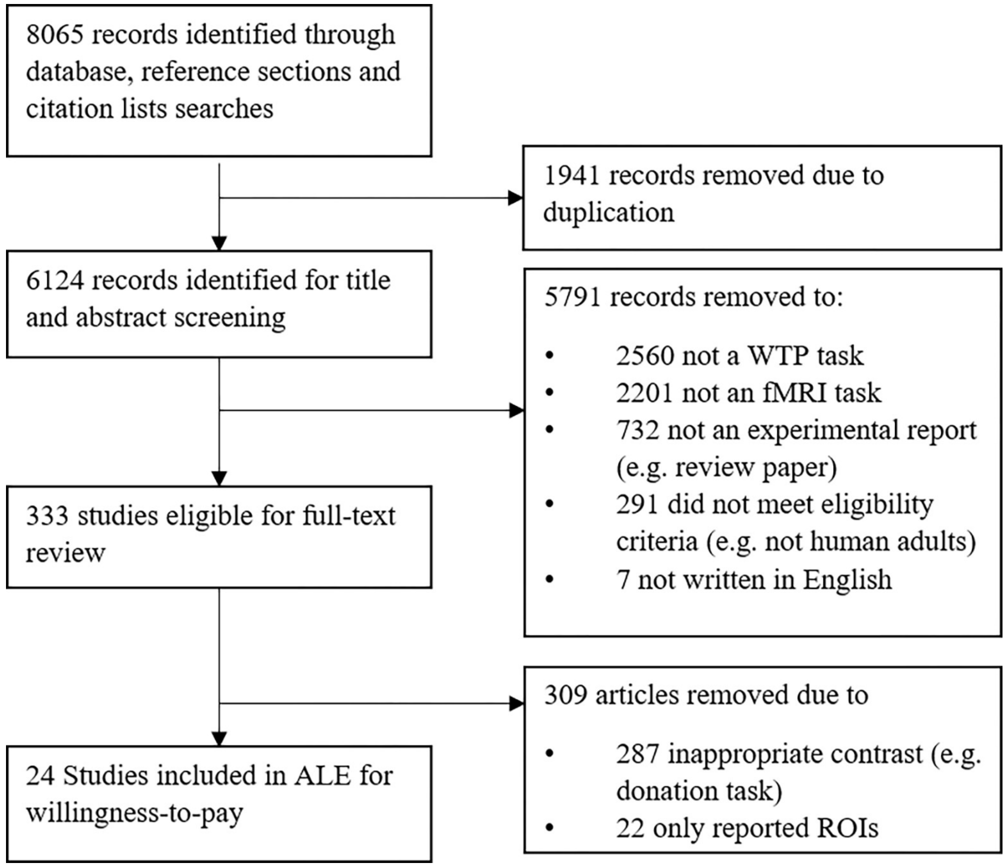


**Fig 1. Flow chart outlining the formal search and eligibility screening process.**

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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, Fig 3).

**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.

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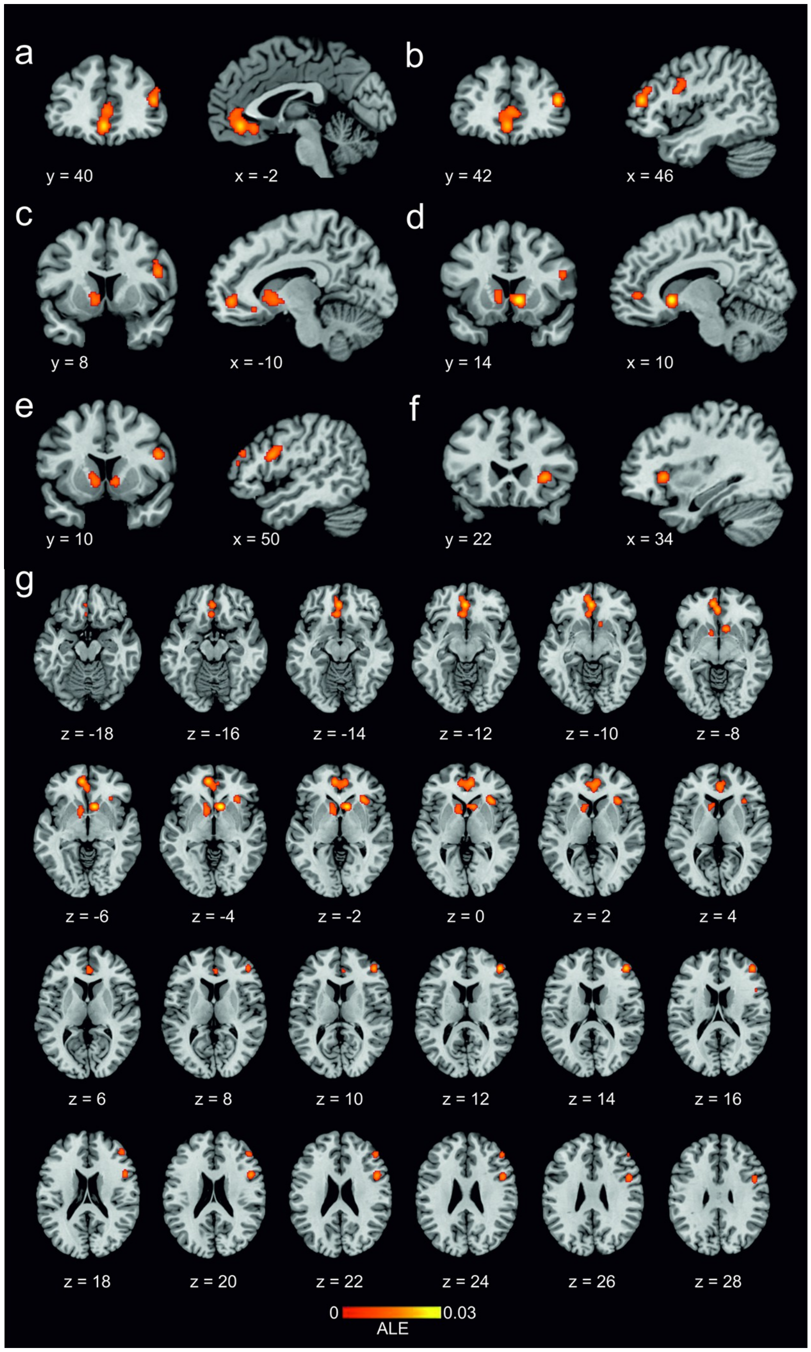


**Fig 2. The location of significant ALE clusters from the meta-*analysis* of concordant activations for WTP.** A–F show coronal and sagittal slices at the cluster peak in: (A) vmPFC with sub-cluster in the ACC, (B) right dlPFC, (C) left VS, (D) right VS, (E) right IFG and (F) right AI. (G) shows all clusters in axial orientation. Results are displayed overlaid onto a standardized MNI template anatomical brain. ALE scores are indicated by the colour bar.

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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, Fig 3).

**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.

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## 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 [16] 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 [106], as well as single-cell recordings [107], lesion [108,109] and animal studies [110,111]. 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 [112,113]; resting-state fMRI studies show that

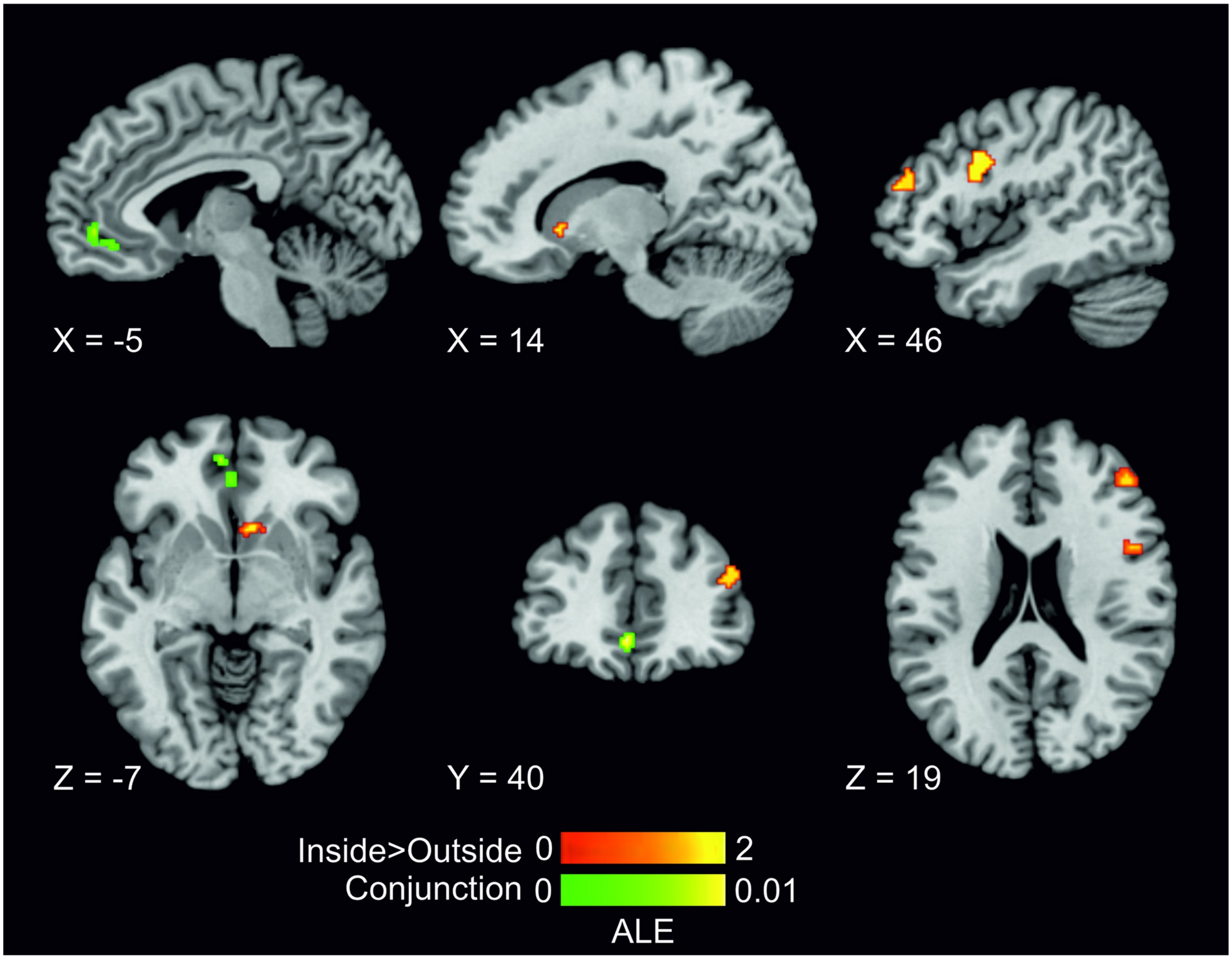


**Fig 3. The location of significant clusters from conjunction and contrast analyses of ALE maps for concurrent (inside) and consecutive (outside) recordings.** Results are displayed overlaid onto standardized MNI template anatomical brain in as a montage of sagittal, coronal and axial slices through the clusters. ALE scores are indicated by the colour bars.

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the ACC is most functionally connected with areas implicated in affective processing, with pgACC having more widespread connections than sgACC [114]. Both the pgACC and sgACC have also been shown to be modulated by an overestimation of probabilities of good outcomes [115], and sgACC activity in particular positively correlates with expected value of an outcome [116,117]. Further to this, ACC neurons in non-human primates encode the values of the chosen options during decision-making [118–120]. 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 [67,77,121,122]. Both the vmPFC and striatum are key dopaminergic areas, receiving dopaminergic projections from the midbrain [123], and are well established to be involved in option valuation and comparison [124–126]. Single-cell recordings in rhesus macaques show extensive similarities in neuron firing patterns in the VS and vmPFC during risky reward-based choice [121]. Activity in the VS has been shown to be mediated by the magnitude of expected reward in both humans [106,127,128] and non-human primates [121,129]. 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 present meta-analysis also showed the right AI was consistently activated by SV. This brain region has considerable functional heterogeneity, being involved in a wide variety of functions such as interoception [130,131], emotion processing [132,133] and arousal [134]. With regards to reward processing, the AI is extensively connected to dopaminergic regions such as the vmPFC, amygdala and ventral striatum [135], and is implicated in loss prediction [136], aesthetic appraisal [137] and in economic uncertainty [123,138,139]. 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 [17,140]. Our findings support this hypothesis, as the parameters of the BDM are such that players are in a situation of static risk: players are presented with potential economic losses if they overbid (see the winner's curse) [141,142] and an increase in likelihood of a social loss if they underbid (in the form of negative feedback such as "you lose").

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 [7,60,61]. 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 scaled with WTP and also 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 [41,143–148]. Previous work has linked the dlPFC to behavioural restraint and delayed reward [149], demonstrating that individuals who successfully inhibit their value responses during self-control tasks exhibit greater dlPFC activity than those who did not [148,150]. The IFG is involved in the overweighting of private vs public information [151] and conflict resolution [152] 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 [149,153]. 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 [148].

As noted earlier, previous investigation has found a large network of brain areas involved in the formation and updating of subjective valuation [16,67]. 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 [24,154,155]. Most notably, previous fMRI meta-analyses of SV using other tasks have found larger clusters in the vmPFC incorporating the medial OFC [59,77,156], 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 117 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 [157].

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 [158]. Furthermore, there is evidence that bid values in second-price sealed bid auctions can be impacted by subjective perceptions of uncertainty [159] and social competition [160]. 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 [95]. 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 [44,92]. 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.

## Supporting information

**S1 File. Formal proof of the dominant strategy in BDM auctions.**
(DOCX)

**S2 File. Literature search and final dataset with co-ordinates for ALE analysis.**
(XLSX)

**S3 File. Completed PRISMA checklist for meta-analysis.**
(DOCX)

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**Visualization:** Alice Newton-Fenner.

**Writing – original draft:** Alice Newton-Fenner.

**Writing – review & editing:** Alice Newton-Fenner, Danielle Hewitt, Jessica Henderson, Hannah Roberts, Tyler Mari, Yiquan Gu, Olga Gorelkina, Timo Giesbrecht, Nicolas Fallon, Carl Roberts, Andrej Stancak.

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