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Research Article

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The Value of Numbers in Economic Rewards

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Abstract

Previous work has identified a distributed network of neural systems involved in appraising the value of rewards, such as when winning \$100 versus \$1. These studies, however, confounded monetary value and the number used to represent it, which leads to the possibility that some elements in the network may be specialized for processing numeric rather than monetary value. To test this hypothesis, we manipulated numeric magnitude and units to construct a range of economic rewards for simple decisions (e.g., 1¢, \$1, 100¢, \$100). Consistent with previous research in numerical cognition, results showed that blood-oxygen-level-dependent (BOLD) activity in intraparietal sulcus was correlated with changes in numeric magnitude, independent of monetary value, whereas activity in orbitofrontal cortex was correlated with monetary value, independent of numeric magnitude. Finally, region-of-interest analyses revealed that the BOLD response to numeric magnitude, but not monetary value, described a compressive function. Together, these findings highlight the importance of numerical cognition for understanding how the brain processes monetary rewards.

Keywords

numerical cognition, value, posterior parietal cortex, orbitofrontal cortex, neuroeconomics, open materials

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The magnitudes of competing values—how much people value competing consumer goods or competing job offers—play a central role in virtually every decision that people make. Over the last decade, cognitive neuroscientists have mapped a network of cortical regions where activity correlates with the magnitude of competing values (Kable & Glimcher, 2009; Liu, Hairston, Schrier, & Fan, 2011). The activity of this cortical valuation network has been of particular interest in neuroeconomic research because the activity of the network in response to external value often mirrors parameters from economic models, such as those related to reward magnitude versus reward probability (Berns & Bell, 2012) and loss aversion (Tom, Fox, Trepel, & Poldrack, 2007). One prominent finding, for example, is that the activity of the cortical valuation network in response to the magnitude of rewards mirrors the compressive utility function inherent to economic models of value, in which subjective utility is roughly a logarithmic function of objective value (Deco & Rolls, 2005).

In previous studies of the cortical valuation network, medial orbitofrontal cortex (mOFC), ventral striatum, anterior and posterior cingulate cortex (ACC and PCC, respectively), and posterior parietal cortex have been identified as having central roles (Glimcher, Fehr, & Poldrack, 2009; Kable & Glimcher, 2009; Liu et al., 2011). Although there is much consensus on the central role of mOFC in the representation of absolute economic value (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Padoa-Schioppa & Assad, 2006, 2008; Plassmann, O'Doherty, & Rangel, 2007; Tom et al., 2007), the role of posterior parietal cortex is not as clear. Usually, the roles of lateral intraparietal cortex (LIP) in monkeys and its homologue intraparietal sulcus (IPS) in humans are described as representing the value of the different available options, with their value represented

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on a relative scale (Clithero, Carter, & Huettel, 2009; Kable & Glimcher, 2009; J. Peters & Bucher, 2009; Platt & Glimcher, 1999).

Previous studies of the cortical valuation network, however, contain a potentially important confound. Namely, as the magnitude of value increases, other magnitudes increase, too: For example, a reward of three M&Ms may be three times as valued as a reward of one M&M, but the neural response to one versus three M&Ms must track both the value of the reward and the number of M&Ms. One reason this confound is particularly relevant is that IPS has been identified as having a central role in processing numeric magnitude, and those magnitudes also are represented in compressive scales (Arsalidou & Taylor, 2011; Dehaene, Piazza, Pinel, & Cohen, 2003; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004), just like the utility function.

Manipulation of monetary rewards provides a unique way to disambiguate the neural correlates of value and numeric magnitude. Because monetary value is represented symbolically as a combination of numbers and currency units, it is possible to test the effects of numeric magnitude and economic value independently (as in Furlong & Opfer, 2009). For example, one can ask whether changing rewards from 3¢ to 300¢ increases neural activity in a given region to the same extent as an economically identical change from 3¢ to $3.

To address this question, we presented participants with real monetary rewards to test whether activation of different brain regions within the valuation network correlated with increases in numeric magnitude (controlling for monetary value) or with increases in monetary value (controlling for numeric magnitude). A key feature of our design included an independent manipulation of numeric magnitudes (i.e., 0, 1, 3, 100, 300) and the units of the monetary rewards (dollars vs. cents), thereby presenting a range of rewards that could disentangle the effects of number and value on cortical activity. In particular, this manipulation allowed us to create rewards that differed in value but not number (e.g., 100¢ vs. $100) or rewards that differed in number but not value (e.g., 100¢ vs. $1).

Method

Participants

Seventeen adults participated (mean age = 22.2 years, range 18–41; 10 female, 7 male). All were right handed, had normal or corrected-to-normal vision, and reported no neurological problems. One participant was excluded for not completing the task because of headaches during scanning. The sample size was comparable with that of similar studies, and we ran as many participants as possible given time and money constraints.

Design and procedure

Participants were recruited to play a lottery game; $15 was guaranteed for playing, plus they had the chance to earn up to $20 more depending on the value of tickets uncovered during the experiment. To win extra money, participants had to choose between two covered tickets (represented as two gray rectangles on a computer screen) by pressing one of two buttons on a button box. After choosing a ticket, the amount of money earned or lost was revealed (Fig. 1). Participants had only 1,000 ms to choose a ticket or the choice was made for them; if 25 tickets were missed during the session, all extra money was forfeit.

Unbeknownst to participants, the sequence of rewards was presented in a pseudorandom order determined by a modified version of a custom MATLAB (The MathWorks, Natick, MA) script (adapted by Bob Spunt from code authored by Russ Poldrack) that optimizes contrast efficiencies of functional MRI (fMRI) event-related designs. The duration of intertrial intervals was jittered randomly from 2,000 ms to 8,000 ms and was derived from a pseudoexponential distribution (mean intertrial interval = 4,000 ms). The optimization routine was created for each of five individual runs, and the order of runs varied randomly among subjects. The amount of money participants received was predetermined.

Critically, values of tickets came from all possible combinations of five numbers (0, 1, 3, 100, 300) and two monetary units (dollars and cents), thereby yielding nine different values: 0, 1¢, 3¢, 100¢, 300¢, $1, $3, $100, and $300. Each of these values could be positive or negative, depending on whether participants picked a winning or losing ticket. To control for the number of digits and position of units, we presented rewards such that valence signs always appeared in the leftmost position, units appeared rightmost, and numbers appeared in the middle and always had three digits and a decimal point (e.g., "+ 1.00 ¢"). To minimize the cost of the experiment, we presented negative tickets with the same range of values, though participants could not actually lose money overall. We present results for these trials for purposes of completeness only, since IPS has not been reliably related to losses in previous research (Liu et al., 2011).

The experiment comprised five fMRI runs of 8 min each. Each run contained 57 trials, that is, 51 trials corresponding to three repetitions each of the 17 different tickets (all eight values presented as wins or losses plus 0) and 6 extra tickets. Extra tickets were added because equal repetitions of all tickets would yield no net gain for participants. Instead, the lottery was rigged so all participants earned $10.50 from the 30 extra tickets distributed randomly over the five runs.

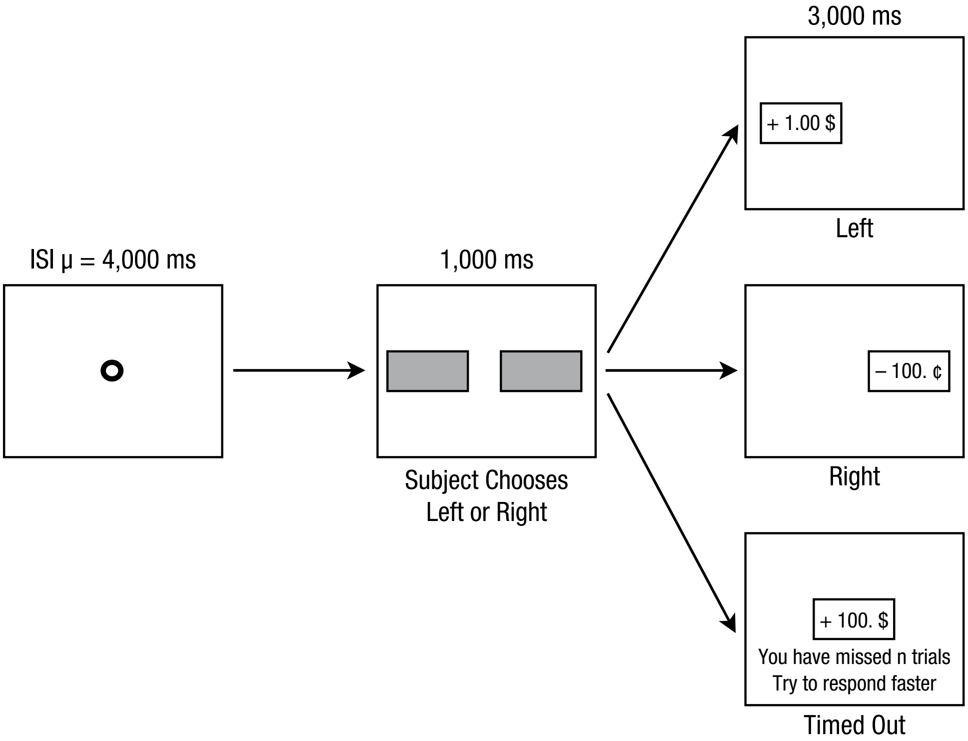

Fig. 1. Experimental procedure. Each trial began with a fixation period (µ = 4,000 ms, randomly jittered). After the fixation period, two gray lottery tickets appeared, one on the left and one on the right side of the screen. Participants had to choose one of the tickets, after which the value earned or lost by the chosen ticket was shown. If participants did not choose a ticket, one was chosen automatically, and a feedback message appeared reminding participants to answer more quickly and stating how many tickets they had missed so far.

The trial sequence began with a fixation period of a randomly jittered duration. Following fixation, two covered tickets were presented for 1,000 ms, during which participants made their response. Tickets remained on screen for 1,000 ms regardless of when participants responded. After this 1,000-ms period, the value of the ticket selected was revealed for 3,000 ms. If participants did not respond in time, a message appeared below the value of the ticket reminding participants to answer faster and tallying up how many tickets they had missed.

fMRI scanning parameters

Imaging data were collected on a Siemens (Erlangen, Germany) Tim Magnetom Trio 3-T MRI scanner. For registration of images, we used a T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE) sequence—repetition time (TR) = 1,900 ms, echo time (TE) = 4.68 ms, field of view (FOV) = 256 mm, sagittal plane, slice thickness = 1 mm, 160 slices. In each run, we acquired 237 whole-brain T2*-weighted echo-planar blood-oxygen-level-dependent (BOLD) contrast images (TR = 2,100 ms, TE = 25 ms, flip angle = 75°, slice thickness = 3 mm, 42 slices, FOV = 240 mm). The first four volumes were discarded to allow for stabilization of the scanner. Parameters of functional scans were selected to minimize susceptibility problems associated with imaging of prefrontal cortex.

fMRI preprocessing

Data from the fMRI scans were analyzed using FMRI Expert Analysis Tool (FEAT; Version 6.00) from the FMRIB Software Library toolbox (www.fmrib.ox.ac.uk/fsl). Preprocessing of data consisted of brain extraction (Smith, 2002), motion correction (Jenkinson, Bannister, Brady, & Smith, 2002), spatial smoothing with a 5-mm (full-width half-maximum) Gaussian kernel, grand-mean intensity normalization of the entire four-dimensional data set by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted, least-squares, straight-line fitting, with σ = 50.0 s), and boundary-based registration to standard Montreal Neurological Institute (MNI) space (Greve & Fischl, 2009; Jenkinson et al., 2002; Jenkinson & Smith, 2001).

Generalized-linear-model (GLM) analysis

Statistical analyses were conducted using a whole-brain GLM parametric analysis in which parametric regressors were created to separately model trials on which participants won and lost money (win trials and loss trials, respectively). We used this approach to account for the different subjective value functions of prospect theory (Kahneman & Tversky, 1979). Specifically, each trial was modeled using monetary units (i.e., dollars = 1, cents = −1) and numeric magnitude (i.e., 1, 3, 100, 300) as regressors. The Numeric Magnitude × Monetary Units interaction corresponded to the objective monetary value of each ticket. The following equations describe this model separately for wins and losses:

$$\begin{aligned}\mathrm{BOLD}_{\mathrm{wins}} = b_0 &+ \text{numeric magnitude}_{\mathrm{wins}} + \text{monetary units}_{\mathrm{wins}} \\ &+ \left(\text{numeric magnitude}_{\mathrm{wins}} \times \text{monetary units}_{\mathrm{wins}}\right)\end{aligned}$$

$$\begin{aligned}\mathrm{BOLD}_{\mathrm{losses}} = b_0 &+ \text{numeric magnitude}_{\mathrm{losses}} + \text{monetary units}_{\mathrm{losses}} \\ &+ (\text{numeric magnitude}_{\mathrm{losses}} \times \text{monetary units}_{\mathrm{losses}})\end{aligned}$$

The two regressors were mean-centered, and whole-brain statistical analyses were performed using a multistage approach to implement a mixed-effects model treating participants as random effects. Regressors were constructed by convolving a boxcar function representing the onset time of the stimulus, the magnitude of the parametric regressor, and its duration with a canonical double gamma (hemodynamic response function). All reported results were assessed for cluster-wise significance ($p < .05$, family-wise-error corrected) using a cluster-defining threshold of $Z > 2.3$.

Region-of-interest (ROI) analyses

For follow-up analyses, we constructed 12-mm-sphere ROIs for IPS and mOFC. To construct the IPS ROIs, we used a previous meta-analysis of number-processing tasks (Arsalidou & Taylor, 2011), and to construct the mOFC ROI, we used a meta-analysis of reward-processing tasks (Liu et al., 2011). For the ROI analyses, instead of using parametric regressors, we constructed new regressors for each condition separately.

Results

Behavioral findings

To ensure that participants were paying attention to the task, we instructed them to choose a lottery ticket within 1,000 ms of the tickets' onset on screen. The typical participant was very attentive and missed only 3.88 of 285 tickets.

Additionally, to test for possible contamination of imaging results by participant behavior, we used Fisher's z transformation on Pearson's correlations, calculated for each participant. This analysis revealed that participants' choices were not correlated with any of the variables of interest—number: $t(16) = 0.68$, $p = .50$; unit: $t(16) = -0.65$, $p = .53$; money: $t(16) = 1.59$, $p = .13$. Thus, we can rule out the hypothesis that imaging results were contaminated by participant choice or motor response.

Imaging results

The experimental design allowed us to examine effects of manipulating numeric magnitude, units, and monetary value on neural activity. We expected that IPS would be more responsive than mOFC to increases in numeric magnitude, whereas mOFC should be particularly responsive to monetary rewards. To test these hypotheses, we used a GLM analysis to first look for brain areas where activity increased parametrically with increases in the values of our variables of interest.

As predicted, we found that bilateral activation of IPS was related to increases in numeric magnitude but not to increases in monetary value (see Fig. 2 and Table 1). Besides IPS, increases in numeric magnitude were associated with increases in activity in adjacent parietal areas, such as superior parietal gyrus, and other adjacent posterior areas, such as lateral occipital cortex and inferior temporal gyrus. Additionally, we found significant clusters in middle and inferior frontal gyrus. These patterns are consistent with findings reported in the literature on number processing (Arsalidou & Taylor, 2011) and show the importance of numeric information in the processing of monetary rewards. Further, these findings contradict the idea that the role of IPS in the valuation network is to compute economic value (Glimcher, Dorris, & Bayer, 2005).

We also found that increases in monetary rewards were associated with increases in brain activity in mOFC, bilateral orbitofrontal cortex (OFC), insula, frontal pole, ACC, and striatum. Notably, none of these areas were significantly associated with increases in numeric magnitude (see Fig. 2). These results are consistent with what is known about neural correlates of absolute value (Kable & Glimcher, 2009; Padoa-Schioppa & Assad, 2008). Other areas associated with increases in monetary value were inferior frontal gyrus, angular gyrus, supramarginal gyrus, and lateral occipital gyrus (Fig. 2 and Table 1).

Activity associated with monetary units (i.e., greater activity for dollars than for cents) was found in areas of mOFC, bilateral OFC, insula, paracingulate cortex, ACC, striatum, superior frontal gyrus, and middle frontal gyrus

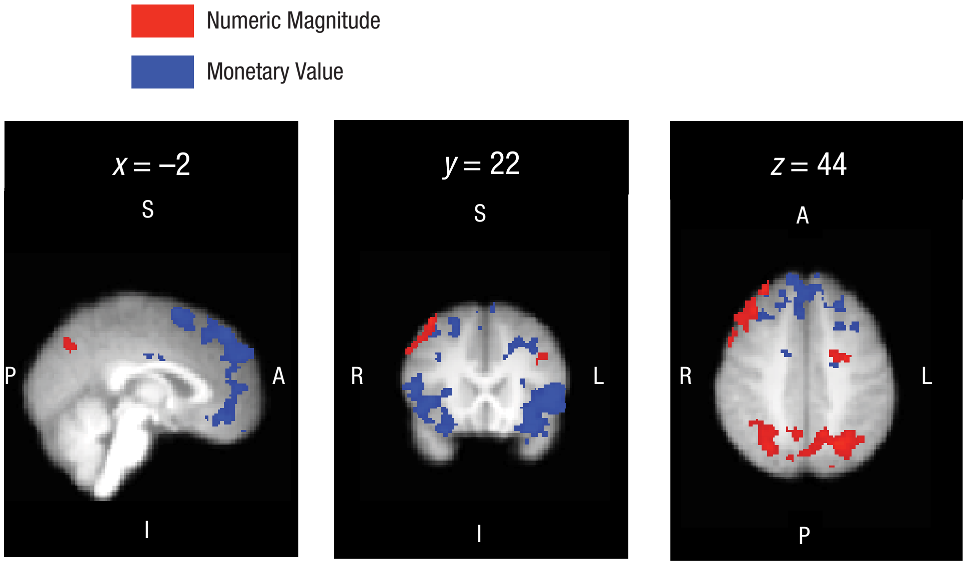

Fig. 2. Results of the parametric generalized-linear-model analysis: regions for which activation was significantly modulated by numeric magnitude and monetary value for trials on which participants won money. Coordinates are given in Montreal Neurological Institute space. A = anterior, I = inferior, L = left, P = posterior, R = right, S = superior.

(Table 1). Areas that showed significant relations with receiving rewards in dollars mostly overlapped with areas associated with increases in monetary rewards. This overlap makes sense because—all else being equal—changing the unit of the received ticket from cents to dollars entailed a 100-fold increase in monetary value. Conversely, areas of postcentral gyrus, superior parietal gyrus, supramarginal gyrus, and lateral occipital gyrus showed greater activity for cents than for dollars.

Could these results have arisen merely because numeric magnitude was coded as a main effect, whereas monetary value was coded as an interaction? To test this possibility, we ran a secondary analysis in which numeric magnitude and monetary value were coded solely as main effects:

$$\begin{aligned}\text{BOLD}_{\text{wins}} &= b_0 + \text{numeric magnitude}_{\text{wins}}\\ &\quad + \text{monetary value}_{\text{wins}}\end{aligned}$$

$$\begin{aligned}\text{BOLD}_{\text{losses}} &= b_0 + \text{numeric magnitude}_{\text{losses}}\\ &\quad + \text{monetary value}_{\text{losses}}\end{aligned}$$

In this analysis, both numeric magnitude and monetary value were normalized to account for differences in the range of possible values. Consistent with the previous analysis, results showed that activity in bilateral IPS increased with increases in numeric magnitude but not with increases in monetary rewards, whereas activity in mOFC, ACC, paracingulate gyrus, insula, OFC, superior frontal gyrus, inferior frontal gyrus, insula, and PCC increased with increases in monetary rewards and not with increases in numeric magnitude (Table 2). Thus, results do not appear to depend on arbitrary coding choices.

In summary, evidence that activation of posterior parietal cortex was associated with numeric magnitude adds to the current literature of neural correlates of valuation by pointing out an important confound present in all previous studies that have used monetary rewards. Several of these studies have reported IPS activity and, as a result, have suggested that posterior parietal cortex is directly implicated in the network that computes economic value (Ballard & Knutson, 2009; Clithero et al., 2009; Lin, Adolphs, & Rangel, 2011; Louie, Grattan, & Glimcher, 2011; Platt & Glimcher, 1999). However, the present results suggest that involvement of IPS in the valuation network is related to the processing of numeric magnitude and not economic value.

Conversely, signatures of monetary values were obtained in OFC, mOFC, striatum, and ACC. In these areas, the magnitudes of numbers used to represent economic values did not affect the representation of economic value. These results are consistent with the previous literature (Kable & Glimcher, 2009), since these are all major areas of the neural valuation network.

Comparison of win trials and loss trials. When looking at the effects of loss trials, we found no significant clusters associated with monetary value, and we found only one cluster associated with numeric magnitude in lingual gyrus—peak voxel: $x = 16$, $y = -74$, $z = -6$, $Z = 4.65$—such

Table 1. Brain Areas Significantly Associated With Monetary Units, Numeric Magnitude, and Monetary Value in Trials on Which Participants Won Money

			MNI coordinates		
Area	Maximum *Z*	Hemisphere	*x*	*y*	*z*
Areas with activation positively associated with monetary units					
Cluster 1 (2,861 voxels)					
Paracingulate gyrus	4.27	Mid	4	46	4
Superior frontal gyrus	4.20	Mid	4	28	52
Anterior cingulate cortex	3.97	Mid	–2	44	2
Medial orbitofrontal cortex	3.13	Mid	0	36	–20
Cluster 2 (1,230 voxels)					
Insula	4.70	Left	–36	16	–8
Caudate	4.04	Left	–6	6	4
Orbitofrontal cortex	3.53	Left	–26	18	–18
Nucleus accumbens	2.54	Left	–8	10	–4
Cluster 3 (720 voxels)					
Frontal operculum	4.25	Right	44	24	–4
Orbitofrontal cortex	4.23	Right	42	28	–6
Inferior frontal gyrus	3.83	Right	52	22	4
Insula	3.36	Right	36	16	–12
Cluster 4 (529 voxels)					
Middle frontal gyrus	3.89	Left	–44	14	50
Areas with activation negatively associated with monetary units					
Cluster 1 (1,114 voxels)					
Postcentral gyrus	3.90	Left	–18	–46	62
Superior parietal lobule	3.69	Right	26	–52	66
Precentral gyrus	3.50	Left	–10	–34	48
Cluster 2 (613 voxels)					
Lateral occipital cortex	4.23	Right	32	–84	36
Cluster 3 (411 voxels)					
Precuneus	2.42	Left	–8	–54	18
Cluster 4 (369 voxels)					
Supramarginal gyrus	3.76	Right	54	–22	28
Areas with activation positively associated with numeric magnitude					
Cluster 1 (3,144 voxels)					
Lateral occipital cortex	4.40	Left	–22	–72	56
Intraparietal sulcus	3.10	Left	–28	–52	48
Cluster 2 (1,613 voxels)					
Inferior temporal gyrus	4.49	Left	–46	–56	–16
Occipital pole	4.16	Left	–26	–94	–6
Temporal occipital fusiform cortex	4.00	Left	–40	–52	–14
Cluster 3 (912 voxels)					
Middle frontal gyrus	3.48	Right	44	6	58
Cluster 4 (511 voxels)					
Lateral occipital cortex	4.26	Right	44	–82	–2
Occipital pole	2.94	Right	30	–96	2
Intraparietal sulcus	2.91	Right	36	–46	50
Cluster 5 (476 voxels)					
Middle frontal gyrus	4.30	Left	–38	4	34
Inferior frontal gyrus	3.13	Left	–38	14	22

(continued)

Table 1. *(continued)*

Area	Maximum Z	Hemisphere	MNI coordinates x	y	z
Areas with activation positively associated with monetary value					
Cluster 1 (10,126 voxels)					
Inferior frontal gyrus	5.57	Left	–48	24	2
Orbitofrontal cortex	4.91	Left	–32	22	–12
Frontal pole	4.89	Right	46	46	–10
Superior frontal cortex	4.87	Right	6	40	48
Insula	4.00	Left	–32	20	–8
Medial orbitofrontal cortex	3.60	Left	2	42	–14
Anterior cingulate cortex	3.56	Left	12	40	16
Putamen	2.82	Left	–22	8	–12
Cluster 2 (1,308 voxels)					
Lateral occipital cortex	4.11	Left	–44	–68	24
Occipital fusiform gyrus	4.11	Left	–38	–70	–10
Cluster 3 (993 voxels)					
Supramarginal gyrus	4.39	Left	–46	–48	22
Angular gyrus	3.78	Left	–42	–50	24
Middle temporal gyrus	3.74	Left	–58	–28	–8
Cluster 4 (697 voxels)					
Lateral occipital cortex	4.08	Right	54	–60	22
Angular gyrus	3.20	Right	62	–48	30

Note: All areas listed were significant at $p < .05$, family-wise-error corrected. MNI = Montreal Neurological Institute.

that there were greater levels of activity in response to –1 than in response to –300 (see Table S1 and Fig. S1 in Additional Results in the Supplemental Material available online). Even after reducing the threshold to $p < .001$ (uncorrected), there were no other significant effects of numeric magnitude or monetary value. As in the analysis of win trials, we conducted a second analysis using numeric magnitude and monetary value as main regressors for loss trials. This analysis yielded similar results (see Table S2 in Additional Results). Comparing win trials with loss trials revealed overall greater activation for wins than for losses. There were significant clusters in bilateral striatum—peak voxel: $x = 14$, $y = 12$, $z = –6$, $Z = 5.41$. Additionally, we found greater activity in the following areas for numeric magnitude in win trials than in loss trials—bilateral IPS, peak voxel: $x = 48$, $y = –38$, $z = 46$, $Z = 3.96$; occipital pole, peak voxel: $x = 30$, $y = –98$, $z = 2$, $Z = 3.85$; striatum, peak voxel: $x = –12$, $y = 20$, $z = 2$, $Z = 3.65$; middle frontal gyrus, peak voxel: $x = 44$, $y = 28$, $z = 44$, $Z = 3.75$; and frontal pole, peak voxel: $x = –24$, $y = 64$, $z = –4$, $Z = 4.23$. For monetary value, no significant effects were found. Finally, there were no significant clusters showing greater activity for loss trials than for win trials, for overall activation, numeric magnitude, or monetary value (see Table S3 in Additional Results). This lack of reliable results for loss trials was not surprising: In a meta-analysis of valuation studies, reliable activity in IPS was observed for wins but not for losses (Liu et al., 2011). These and our own results caution against overreaching for interpretations to explain unreliable effects that are poorly understood.

ROI analyses. Although GLM analyses provided consistent results, we wanted to test whether these parametric results were driven by a systematic trend rather than extreme values (Poldrack, 2007). To do so, we created ROIs based on previous meta-analyses (Arsalidou & Taylor, 2011; Liu et al., 2011) of numeric and economic valuation tasks, respectively.

A stepwise regression with right IPS activity as the dependent variable and numeric magnitude, monetary value, log(numeric magnitude), and log(monetary value) as predictors (Fig. 3) settled on a model that included only log(numeric magnitude), model $R^2 = .421$, $F(1, 6) = 6.10$, $p = .024$, log(numeric magnitude) $\beta = 0.710$. Using left IPS as the dependent variable, the variable log(numeric magnitude) was marginally significant, model $R^2 = .275$, $F(1, 6) = 3.65$, $p = .052$, log(numeric magnitude) $\beta = 0.615$; and when mOFC was the dependent variable, the final model included monetary value and numeric magnitude as regressors, model $R^2 = .720$, $F(2, 5) = 10.00$, $p = .009$, monetary value $\beta = 0.134$, numeric magnitude $\beta = –0.786$. (See Additional Results for details on loss trials.)

Table 2. Brain Areas Significantly Associated With Monetary Value and Numeric Magnitude (Modeled as Main Effects) in Trials on Which Participants Won Money

			MNI coordinates		
Area	Maximum *Z*	Hemisphere	*x*	*y*	*z*
Areas with activation positively associated with monetary value					
Cluster 1 (4,409 voxels)					
Medial orbitofrontal cortex	4.45	Mid	0	36	–20
Superior frontal gyrus	4.34	Mid	4	40	48
Paracingulate gyrus	4.25	Mid	4	48	4
Anterior cingulate cortex	3.35	Mid	0	42	2
Cluster 2 (1,812 voxels)					
Insula	4.75	Left	–36	16	–8
Orbitofrontal cortex	4.17	Left	–30	20	–10
Inferior frontal gyrus	4.15	Left	–50	24	–4
Cluster 3 (1,480 voxels)					
Frontal operculum cortex	4.57	Right	44	24	–4
Inferior frontal gyrus	4.17	Right	52	24	10
Frontal pole	3.87	Right	48	46	–10
Orbitofrontal cortex	3.83	Right	28	14	–24
Insula	3.36	Right	30	16	–14
Cluster 4 (744 voxels)					
Superior frontal gyrus	4.28	Right	24	26	48
Middle frontal gyrus	3.46	Right	38	24	46
Cluster 5 (735 voxels)					
Superior frontal gyrus	4.02	Left	–24	20	44
Middle frontal gyrus	3.73	Left	–42	16	50
Cluster 6 (518 voxels)					
Middle temporal gyrus	4.50	Left	–56	–28	–8
Superior temporal gyrus	3.29	Left	–56	–10	0
Cluster 7 (394 voxels)					
Posterior cingulate cortex	4.08	Mid	2	–30	34
Anterior cingulate cortex	3.35	Mid	–4	6	28
Cluster 8 (369 voxels)					
Angular gyrus	3.30	Mid	38	–54	42
Lateral occipital cortex	3.25	Mid	48	–58	52
Areas with activation positively associated with numeric magnitude					
Cluster 1 (1,464 voxels)					
Lateral occipital cortex	4.42	Left	–22	–72	56
Intraparietal sulcus	3.00	Left	–34	–58	42
Cluster 2 (1,209 voxels)					
Inferior temporal gyrus	4.57	Left	–46	–56	–16
Temporal occipital fusiform gyrus	3.95	Left	–40	–52	–14
Occipital pole	3.67	Left	–26	–96	–6
Cluster 3 (1,101 voxels)					
Lateral occipital gyrus	4.17	Right	28	–70	64
Intraparietal sulcus	2.79	Right	36	–46	52
Cluster 4 (835 voxels)					
Middle frontal gyrus	3.44	Right	44	30	34

Note: All areas listed were significant at $p < .05$, family-wise-error corrected. No areas had activation negatively associated with monetary value. MNI = Montreal Neurological Institute.

Thus, results from GLM and ROI analyses consistently showed that activity in bilateral IPS is more consistent with coding numeric magnitude than monetary value, whereas activity in mOFC is more consistent with coding monetary value than numeric magnitude. Finally, consistent with previous literature (Merten & Nieder, 2009;

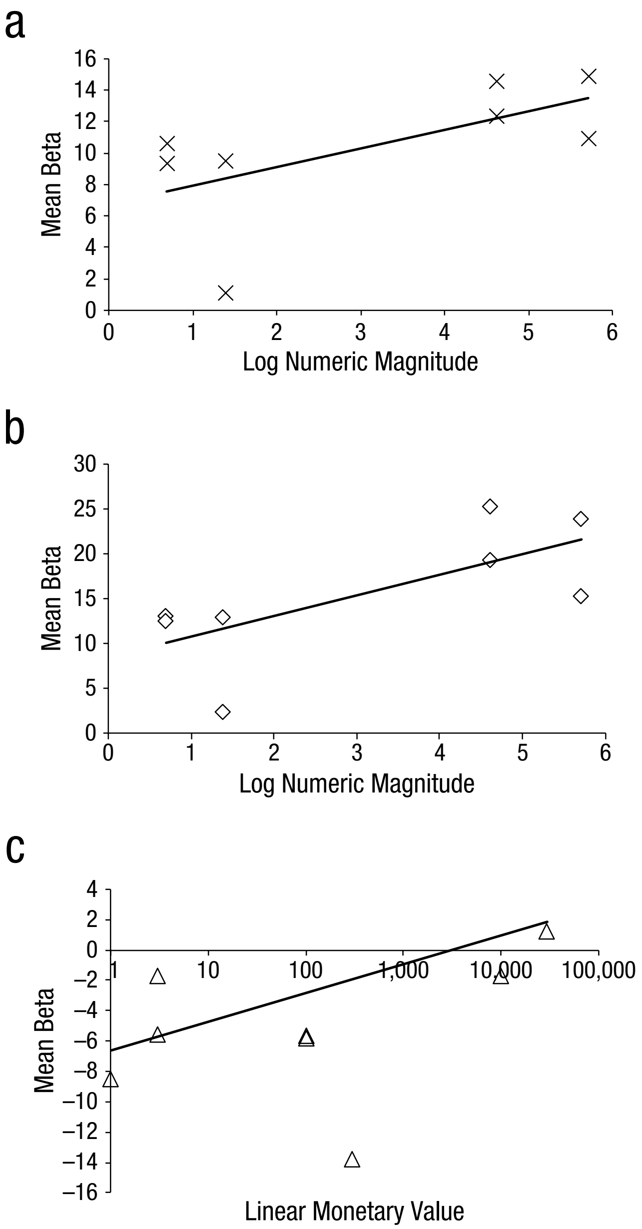

Fig. 3. Blood-oxygen-level-dependent activation levels. The graphs in (a) and (b) show extracted mean beta values in left intraparietal sulcus (IPS) and right IPS, respectively, as a function of the log of numeric magnitude. The graph in (c) shows extracted mean beta values in medial orbitofrontal cortex (mOFC) as a function of linear monetary value. Best-fitting regression lines are shown for each graph.

Piazza et al., 2004), these results suggested that numeric magnitudes were coded on a logarithmic scale.

Discussion

In previous research examining the neural response to monetary rewards, monetary and numeric value have been confounded, which has led to ambiguity about the functions of specific cortical regions within the valuation network. The results of our study partially confirm and partially disconfirm previous conclusions. Consistent with previous research (Cunningham, Kesek, & Mowrer, 2009; Glimcher et al., 2009; Hare et al., 2008; O'Doherty, Critchley, Deichmann, & Dolan, 2003; Padoa-Schioppa & Assad, 2008; Plassmann et al., 2007), our results showed that activity in anterior areas, such as mOFC, ACC, striatum, and insula, were best explained as a response to increases in monetary value and not as a response to increases in numeric magnitude. However, unlike previous research implicating IPS in the valuation network (e.g., Ballard & Knutson, 2009; Clithero et al., 2009; Louie et al., 2011; J. Peters & Bucher, 2009), the present study revealed that the response of IPS to reward was best explained as a response to increases in numeric magnitude and not as a response to increases in monetary reward.

Our results were quite robust and held under different coding schemes and analyses. The distinction between coding of numeric magnitudes in IPS and coding of monetary value in OFC and other anterior areas was found with parametric regressors and with ROI analyses that treated each reward as a different regressor. Combined, these different analyses give us confidence that these results are not driven by experimenter degrees of freedom (Simmons, Nelson, & Simonsohn, 2011). Additionally, the fact that there was no significant correlation between participants' choices and the subsequent rewards rules out the possibility that the effects found here were due to choice or response preparation.

For researchers examining numerical cognition, our findings will almost certainly seem like old news. After more than a decade of numeric-processing neuroimaging studies with a wide variety of tasks and imaging paradigms, a consensus has emerged about the importance of IPS in humans and its homologue in monkeys (LIP) for the representation of symbolic and nonsymbolic numeric information (Arsalidou & Taylor, 2011; Dehaene et al., 2003; Nieder & Miller, 2004). Some of the tasks that have yielded high activation of IPS are distance effects in comparisons of one-digit (Holloway & Ansari, 2010; Piazza et al., 2004) and two-digit numbers (Cantlon et al., 2009), and response to changes in numerosity in fMRI adaptation tasks (Cantlon, Brannon, Carter, & Pelphrey, 2006; Piazza et al., 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007). Although here we focused exclusively on numeric magnitude, IPS also processes magnitude more generally (Cohen Kadosh & Walsh, 2009). Therefore, results from this experiment seem likely to generalize to similar experiments that manipulate reward with other continuous magnitudes. For example, previous studies have found that LIP activity in monkeys increases with greater quantities of juice;

our results suggest this activity may reflect encoding of the quantity of juice rather than its value. On the other hand, rewards without continuous magnitudes should not be processed in IPS. Indeed, this prediction is consistent with experiments that find IPS activity for monetary rewards but not for social rewards, such as happy faces (Lin et al., 2011).

For researchers examining neural correlates of economic valuation, however, our findings will come as news. The way in which IPS responds to rewards, we found, does not depend critically on economic value, despite a correlation between value and IPS activity being reported in the literature (Ballard & Knutson, 2009; Clithero et al., 2009; Lin et al., 2011; Louie et al., 2011; Nieuwenhuis et al., 2005; Platt & Glimcher, 1999). If economic value caused an increase in IPS, then a change in reward from 1¢ to 100¢ would have yielded the same IPS response (and valuation) as the economically identical change in reward from 1¢ to $1. Contrary to this expectation, our results reflect that a change from 1¢ to $1 yields no change in IPS activity, whereas a change from 1¢ to 100¢ does. This pattern of activity will not mirror the values predicted by any economic theory that does not include numeric magnitude as a variable.

An alternative way to interpret the role of IPS in neuroeconomic tasks is that IPS codes economic value exclusively in relationship with the control of the process of selection (Hare, Schultz, Camerer, O'Doherty, & Rangel, 2011; Kable & Glimcher, 2009). Although we cannot rule out this possibility, the present results suggest that the evidence for this claim suffers from the same problem as the claim that IPS calculates economic value—namely, previous studies have confounded numeric and economic value, and the present results offer proof that controlling for this confound eliminates the correlation between economic value and IPS activity.

Looking beyond neuroeconomics, our findings also have implications for the interpretation of "unit effects" on decision making. For example, Tversky and Kahneman (1981) observed that participants were willing to trade 20 min of their time to save $5 on a $15 calculator, but not on a $125 jacket, even though they were trading 20 min of their time for the same amount of money (i.e., $5). Although these effects can be explained by assuming that subjects value proportional more than absolute gains in money, the compressive function of numeric representations can make the same prediction without the economic assumption. That is, because the subjective differences of large numerals (e.g., 120 and 125) are smaller than the differences of smaller numerals (e.g., 10 and 15), the value of the $5 savings is smaller for the jacket than for the calculator.

Our findings also imply that individual differences in IPS function may predict individual differences in economic decisions, and recent studies support this claim (E. Peters, Slovic, Västfjäll, & Mertz, 2008; Schley & Peters, 2014). In these studies, individual differences in numeracy and precision of mappings of numbers into mental magnitudes had an effect on the use of numeric information for economic decisions. The present results imply that this link is probably better mediated by IPS than by OFC.

In sum, this research provides the first direct evidence of the importance of the neurocognitive properties of numeric information for the neural network of valuation. Since one of the goals of neuroeconomics is to describe the actual way in which the brain processes economic variables—such as monetary value—to inform the theoretical models of economic decision making, the importance of this research lies in the fact that it reinterprets the role of IPS within the valuation network. As a result, studies of neural correlates of monetary value should always pay attention to the numeric magnitudes used to represent monetary rewards and should always keep in mind the distinctions between the numeric magnitude and the actual value of any reward.

Author Contributions

All authors developed the study concept and contributed to the study design. Testing and data collection were performed by F. J. Kanayet. F. J. Kanayet and W. A. Cunningham analyzed the data. F. J. Kanayet and J. E. Opfer drafted the manuscript, and W. A. Cunningham provided critical revisions. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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