Title

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Effects of Numeric Magnitude on the Cortical Valuation Network

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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. We hypothesized that involvement of intraparietal sulcus (IPS) in this network is specialized for processing numeric rather than monetary value. To test our hypothesis, we manipulated numeric magnitude and units to construct a range of economic rewards (e.g., +$1, +100¢) in response to simple decisions. Consistent with our hypothesis, BOLD activity in IPS was related to changes in numeric magnitude, independent of monetary value, whereas activity in OFC was associated with monetary value, independent of numeric magnitude. Finally, by using representation similarity analysis, we found that the information represented in IPS and OFC was more consistent with the patterns expected if representations of numeric magnitudes or monetary values, respectively, were in a compressive scale. Together, these findings show the importance of numerical cognition for understanding how the brain processes monetary rewards.

Keywords: monetary rewards; IPS; OFC; fMRI, representation similarity analysis, numerical cognition

Introduction

Humans are continuously faced with choices, often involving incommensurable options. When choosing among options for a romantic date, for example, it is not clear how to compare the esthetic pleasure of a movie with the gustatory pleasure of a nice dinner. Making decisions apparently requires computing the value of each option in some way that would register the difference in values (Montague, King-Casas & Cohen, 2006).

Economic models have long assumed that humans behave 'as if' they compute value for each option in a common mental currency (i.e., subjective value), and experiments on the distributed neural correlates of valuation (i.e., valuation network) suggest that this assumption may be correct (Kable & Glimcher, 2009; Padoa-Schioppa & Asad, 2006, 2008; but see Vlaev, et al., 2011; Tremblay & Schultz, 1999; Seymour et al., 2007; Nieuwenhuis et al., 2005).

One of the sources of information that comprise this common mental currency is the magnitude of the reward. Being rewarded two cookies feels better than being rewarded just one. A special case of using magnitude for valuation is the use of monetary rewards. By using money, dissimilar goods can be compared on the same scale (e.g., dollars or cents) and can be described with just one value, its numeric magnitude (e.g., +300 or -300).

Although translation of value into a numeric scale has many benefits, it may also come with a price. Numeric magnitude, like luminance and loudness, has a compressive psychophysical scale (Fechner, 1860/1966; Weber, 1846/1948; Dehaene, 1997). Thus, the difference between 10 and 15 appears larger than the difference between 120 and 125.

The compressive nature of numerical judgments is important because it may play a large role in how the brain tracks monetary value and makes economic decisions (Furlong & Opfer, 2009; Peters et al., 2008). Indeed, "unit effects" on decision-making have been known for many decades. For example, Kahneman and Tversky (1981) observed that participants were willing to trade 20 minutes of their time to save $5 on a $15 calculator, but not on a $125 jacket, even though in both cases they are trading 20 minutes of their time for the same amount of money (i.e. $5). Although, these effects can be explained by assuming that subjects pay more attention to the proportional gains, the compressive function of numeric representations might provide another explanation. Because larger numerals have smaller psychological distances between them, the difference between a $125 and $120 jacket is subjectively less than the difference between a $15 and $10 calculator.

In this paper, we were interested in why neural activation also appears to devalue marginal monetary gains. Specifically, we addressed whether the neural response to increasing quantities of money are caused by increases in objective monetary value (the value hypothesis), by increases in the numeric magnitude used to represent the magnitude of the monetary reward (the number hypothesis), both, or neither. This issue is important because neuroeconomists typically assume that the brain areas responsible for processing monetary rewards are not affected by the magnitudes of the numerals that represent the rewards, but this assumption has never been tested.

The Valuation Network: Neural Correlates of Monetary Value

Research in the field of neuroeconomics has suggested the existence of a neural valuation network. This network computes the subjective value of options under consideration and uses that valuation to make choices. The most critical brain areas associated with economic value are the orbitofrontal cortex (OFC)/ventromedial prefrontal cortex (VMPFC), striatum, anterior cingulate cortex (ACC), and posterior parietal cortex (PPC) (Glimcher, 2009; Kable & Glimcher, 2009). In theory, the function of this valuation network is to integrate the multiple value dimensions of an option to provide a one-dimensional scale of subjective value according to which choices can be ranked for future decisions.

Of critical importance for this paper are the roles of OFC and PPC. Both studies in monkeys and humans have consistently shown the importance of OFC in the valuation process. There are, however, different ways in which that value can be represented. Although some studies have found neurons in OFC that are associated with absolute value (Paddoa-Schioppa & Assad, 2006, 2008; Tom et al., 2007), other studies have found that other neurons in OFC are also associated with relative value with adaptive scaling (Kennerley, Behrens & Wallis, 2011; Tremblay & Schultz, 1999).

Parietal cortex activity related to valuation processes has been located in the lateral inferior parietal cortex (LIP) of monkeys and intraparietal sulcus (IPS) – its human homologue (Clithero, Carter, & Huettel, 2009; Kable & Glimcher, 2009; Platt & Glimcher, 1999). For instance, using pattern classification techniques, activity in IPS was related to the value of options, and it was even able to distinguish between intertemporal and probabilistic valuations (Clithero et al., 2009). Also, their data suggest that IPS is critical for the initial stages of valuation by representing and integrating the information necessary for computation of economic value in OFC and the striatum. Also, activation of IPS has recently been related to the outcome of monetary rewards, but not to the outcome of social rewards (Lin, Adolphs & Rangel, 2011). This result is important since it shows that the presence of (numeric) magnitude information in the reward presented may be a critical component of the value representation in IPS.

However, the meaning of magnitude in the studies reviewed is ambiguous. Because numeric magnitude and value magnitude typically go hand in hand, it is not possible to know if the increases in activation in IPS (or OFC) are related to an increase in the value of the reward or in the numbers used to represent that value. Moreover, there is strong evidence that suggests that IPS is a central area in the processing of numeric information (Arsalidou & Taylor, 2011 for a meta analysis). Therefore, we suggest – as an alternative hypothesis – that while OFC does process reward value, the role of IPS in these studies is to process the numeric magnitudes of the rewards being considered. If true, the activity of the valuation network would be susceptible to manipulations of numeric magnitude even when these manipulations do not change the objective monetary value of the rewards.

Present Study

Recently, Furlong and Opfer (2009) provided a method to discern between these two possibilities at the behavioral level. Although economic theories assume that the magnitude of the numbers should not affect economic behavior, Furlong and Opfer showed that in fact numeric magnitude and not economic value explained the degree of cooperation of participants in a prisoner's dilemma task. The device used to prove this point was exceedingly simple. By manipulating the unit of the rewards between dollars and cents, it was possible to achieve rewards with the same objective economic value while drastically changing the numeric magnitude associated with the same reward (e.g. \$1 = 100¢). This simple manipulation makes it possible to provide participants with a variety of rewards in such a way that allows to parametrically vary numeric magnitude and economic value independently.

To test whether IPS processes numeric magnitude or economic value, we conducted a functional magnetic resonance imaging (fMRI) study that was designed to introduce linear transformations to the magnitudes of rewards. In order to properly disambiguate the effects of numeric magnitude from those of monetary value on the valuation network, we developed a scratch-off lottery game in which we could manipulate the units (between dollars and cents) of the monetary rewards given to participants.

Method

Participants

Seventeen adults participated (mean age 22.2, range 18-41; 10 female). All were right-handed, had normal or corrected-to-normal vision and reported no neurological problems. One participant was excluded for failing to complete the task and complaints of headaches during scanning.

Design and Procedure

Participants were recruited to play a lottery game; \$15 was guaranteed for playing plus the chance to earn \$0 to \$20 more depending on the value of tickets uncovered during the experiment. To uncover 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 extra money earned (or lost) would be revealed. Participants had only one second to choose a ticket lest the choice be made for them; were 25 tickets missed during the session, all extra money would be forfeit.

Unbeknownst to participants, the lottery was rigged in several ways to optimize data for our experiment. First, the sequence of rewards and the jittered intertrial interval were presented in a pseudo-random order, determined by a custom MATLAB script (Poldrack, 2011) that optimizes contrast efficiencies of fMRI event-related designs. Jittered intertrial intervals varied from 2s to 8s and were derived from a pseudoexponential distribution (mean ITI = 4s). The optimization routine was created for each of the 5 individual runs, and order of runs varied randomly between subjects. Thus, participants had no actual control of the amount of money they received.

Critically, values of tickets came from all possible combinations of 5 numbers (i.e., 0, 1, 3, 100, 300), 2 units (i.e., dollars and cents) and 2 valences (i.e., win and loss). Combined, these components yielded a range of 17 possible tickets: (-1¢, -3¢, -100¢, -300¢, -\$1, -\$3, -\$100, -\$300, 0, +1¢, +3¢, +100¢, +300¢, +\$1, +\$3, +\$100, +\$300). To control for number of digits and position of units, rewards were presented such that valence signs always appeared in the leftmost position, units rightmost, and numbers between with three digits and one dot (e.g., "- 1.00 ¢").

The experiment consisted of 5 fMRI runs of 8 minutes each. Each run contained 57 trials, 51 trials corresponding to 3 repetitions of each of the 17 different tickets, and 6 extra tickets. Extra trials were added because equal repetitions of all tickets would yield no net gain thereby earning participants no extra money. Instead, the lottery was rigged so all participants earned an extra \$10.50 from the 30 extra tickets distributed randomly over the 5 runs.

fMRI Scanning Parameters

Imaging data was collected on a Siemens Tim MAGNETOM Trio 3T MRI scanner. For registration of images, we used a T1-weighted MPRAGE sequence (TR = 1900ms; TE = 4.68ms). In each run, we acquired 237 whole-brain T2* weighted echo planar images (TR = 2100ms; TE = 25ms; flip angle 90°). The first 4 volumes of images 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 (PFC).

Data Analysis

fMRI data were analyzed using FEAT 5.98 (FMRI Expert Analysis Tool) from FSL toolbox (www.fmrib.ox.ac.uk/fsl). Preprocessing of data consisted of brain extraction, motion correction, spatial smoothing with a 5mm (FWHM) Gaussian kernel, and registration to standard MNI space.

Statistical analyses were conducted with a whole-brain GLM parametric analysis in which parametric regressors were created to model wins and losses separately to account for the different subjective value functions predicted by prospect theory (Kahneman & Tversky, 1979). Specifically, activity for each trial was modeled using units (i.e. dollars = 1, cents = -1) and numbers (i.e. 1, 3, 100, 300) as regressors:

$$\text{BOLD(wins)} = \text{Units(wins)} + \text{Number(wins)} + (\text{Number(wins)} * \text{Units(wins)})$$

$$\text{BOLD(losses)} = \text{Units(losses)} + \text{Number(losses)} + (\text{Number(losses)} * \text{Units(losses)})$$

Where the Number*Units interaction corresponds to the objective monetary value of each ticket. In addition to these regressors of interest, motion correction parameters from MCFLIRT motion correction procedure were also included in the models as regressors of no interest. Whole brain statistical analyses were performed using a multi-stage approach to implement a mixed-effects model treating participants as random-effects. Regressors of interest 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 (HRF). All reported results in the following section were assessed for cluster-wise significance ($P < 0.05$, FWE-corrected) using a defining threshold of $Z > 2.3$.

Results

Behavioral Results

To ensure that participants were paying attention to the task, they were instructed to choose a lottery ticket within 1s of their onset on the screen. The typical participant was very attentive and only missed 3.88 tickets (range 0 – 11).

Imaging Results

The experimental design of this study allowed examining the effects of manipulating numeric magnitude, units and valence on neural activity. Wins and losses were modeled separately in agreement with prospect theory (Kahneman & Tversky, 1979). For space reasons, we will only describe results concerning winning trials.

Win Trials

As predicted by the number hypothesis, we found that bilateral activation of IPS was related to increases in numeric magnitude, but not to increases in monetary value. The activation clusters associated with the number parametric regressor extended to adjacent areas in lateral occipital cortex, inferior temporal gyrus, superior parietal lobule and angular gyrus. Also, we found significant clusters in middle frontal gyrus. (Fig. 1). Further, no clusters showed a negative relation between number and neural activation. These patterns are consistent with 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, 2009).

Conversely, activity in bilateral OFC, insula, inferior frontal gyrus, ACC, VMPFC, angular gyrus, and lateral occipital gyrus, (Fig. 2) was associated with increases in monetary value. These results are consistent with what is known about the neural correlates of absolute value (Kable & Glimcher, 2009; Padoa-Schioppa & Assad, 2008).

Activity associated with the units regressor (i.e. greater activity for dollars than for cents) was found in areas of bilateral OFC, insula, VMPFC, paracingulate cortex, ACC, and left striatum (Fig. 1). Here, areas that show significant relations with receiving rewards in dollars overlap with the areas associated with increases in monetary rewards. This overlap makes sense because – all else being equal –

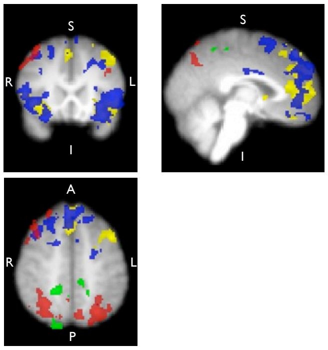

Figure 1: Regions for which activation was significantly modulated by numeric magnitude (red), monetary value (blue), dollars (yellow) and cents (green) of winning tickets.

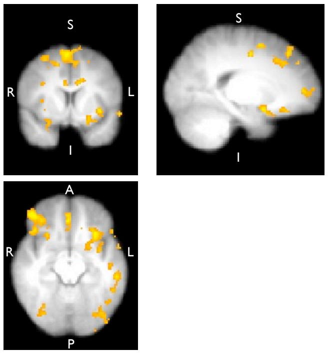

Figure 2: Regions of OFC, VMPFC and insula for which activation was significantly modulated by increases in monetary value for winning tickets.

changing the unit of the received lottery ticket from cents to dollars entailed a 100-fold increase in monetary value. Conversely, areas of left postcentral gyrus, anterior IPS, and right lateral occipital gyrus showed greater activity for cents than for dollars. Following a similar logic, a change from dollars to cents – holding the amount of money constant – entailed a 100-fold increase in numeric magnitude. However, as can be seen in Fig. 1 and unlike in the previous case, the areas in posterior parietal cortex that showed significant BOLD activity related to cents do not overlap with the areas associated with increases in numeric magnitude.

Evidence that PPC activation is associated with numeric magnitude adds to the current literature of the neural correlates of valuation by pointing out an important confound present in all studies of valuation that have used monetary rewards. Several of these studies have reported IPS activity and as a result have suggested that PPC is directly implicated in the network that computes economic value (Ballard & Knutson, 2009; Clithero et al., 2009; Hare, et al., 2011; Lin, et al., 2011; Louie, et al., 2011; Nieuwenhuis, et al., 2005; Platt & Glimcher, 1999). However, the present results suggest that the involvement of IPS in the valuation network is related to the processing of numeric magnitude information and not to economic value.

Conversely, signatures of absolute monetary values were obtained in OFC, VMPFC, striatum and ACC. In these areas, the magnitudes of the numbers used to represent the 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 suggested neural network charged with processing economic value. Combined, the findings from winning tickets are in agreement with the idea that there are in fact multiple valuation networks that may have different properties.

Representation Similarity Analysis

An important question underlying this study is whether brain regions like IPS or OFC treat 100¢ more like $1 (same economic value) or like $100 (same numeric value). One way to answer this question is to examine how the information of interest is represented in a particular brain area. Here, the main goal is not just to detect activation, but to characterize the information present in the particular area (Kriegeskorte & Bandettini, 2007). Representation similarity analysis (RSA; Kriegeskorte, Mur & Bandettini, 2008) is one kind of multivariate approach to fMRI data analysis that tries to accomplish this. RSA aims to find correspondences between the relations among stimuli, and the relations between the patterns of brain activation in a particular brain area in response to the same stimuli. Therefore, RSA can be applied to the present problem, since it can provide an answer to the question of whether a given brain area treats the full matrix of monetary rewards more like the numerical representation of those rewards or more like a sequence of distinct monetary values.

Furthermore, we were interested in comparing multiple theories of how the brain patterns of activity elicited by the full set of stimuli might be related. For the purposes of this study, RSA allowed us to compare the patterns of brain activity from anatomical regions of interest (ROI's) to the patterns expected if the given brain area processes numeric magnitude (both in linear and logarithmic scales), or monetary value (both in linear and logarithmic scales). Additionally, by using RSA we were able to check if positive and negative rewards were treated equally or not.

To conduct RSA, we computed dissimilarity matrices (DSMs) among all presented stimuli for the patterns of activity in each ROI, as well as for each theoretical model. Once these DSMs were obtained, Spearman correlations were computed between the ROIs and the model DSMs. This analysis allowed us to rank order the ROI-model similarities (Fig. 3).

As can be seen in Fig. 4, the DSM obtained from IPS activation was more similar to the DSM expected if the information represented were *numeric magnitude in a log scale*. Conversely, the DSM obtained from OFC activation was more similar to the DSM expected if the information represented were *monetary value in a log scale* (Fig. 4). These results not only are consistent with the GLM results presented in the previous section, but also provide important additional information regarding the details of the neural

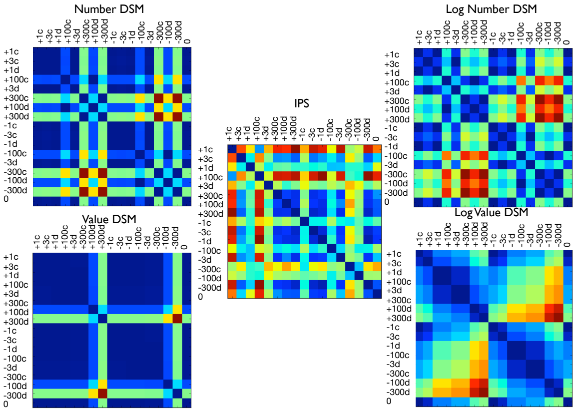

Figure 3: Middle: Single subject IPS dissimilarity matrix (DSM); Top Left: Absolute-magnitude Log Number DSM; Top Right: Log Number DSM; Bottom Left: Absolute-magnitude Log Monetary Value DSM; Bottom Right: Log Monetary Value DSM. In RSA the brain DSM is correlated with Spearman correlations to the model DSMs to provide a rank order of which model matches better the brain data.

representations. In particular, the results from RSA show that both numeric magnitude in IPS, and monetary value in OFC are represented in compressive scales.

Discussion

We proposed that the neural response to monetary rewards could be accurately predicted by the cognitive components of valuation. One such component, the processing of numeric magnitude, seemed likely to be especially important, though previous studies had not controlled it systematically. We thought this an important oversight: because the function relating objective numeric magnitudes to subjective magnitudes is compressive, a similar relation might exist in the neural response to monetary rewards.

The results presented in this paper generally confirm this hypothesis. In particular, when winning money of varying amounts, IPS activity was strongly associated with the numeric – and not monetary – value of the rewards. In contrast, activity of OFC, insula, ACC and VMPFC was strongly associated with the monetary – and not numeric – value of rewards. Further, RSA showed that numeric information in IPS and monetary value in OFC are represented in a compressive scale.

The fact the IPS was associated with increases in numeric magnitude and not to monetary value provides a new way to understand previous studies about the valuation network (Ballard & Knutson, 2009; Clithero et al., 2009; Hare, et al., 2011; Louie, et al., 2011; Nieuwenhuis, et al., 2005). In these studies IPS activity was interpreted as processing monetary value, but our results suggest that it is better understood as processing numeric information. Moreover, this conclusion is strengthened by the fact that IPS has been continuously associated with processing of numeric and mathematical information (Arsalidou & Taylor, 2011).

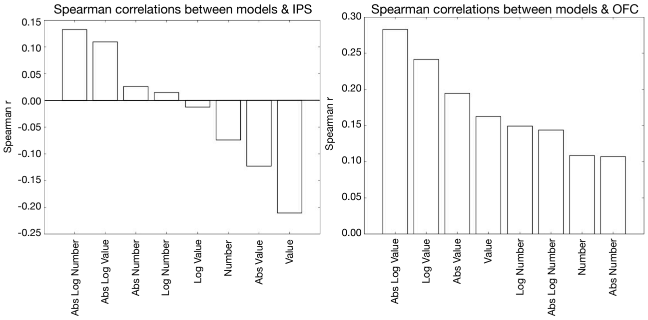

Figure 4: Spearman correlations between model DSMs and group-averaged DSM for IPS (left) and OFC (right).

On the other hand, the finding that activity in OFC, ACC, VMPFC, and insula was related to monetary value, is consistent with a wealth of studies that have established strong relations between these areas and the process of monetary value (Cunningham et al., 2009, Glimcher, 2009, O'Doherty, et al., 2003; Padoa-Schioppa & Assad, 2008). Thus, it seems that though the value hypothesis applies to OFC, the number hypothesis applies to the IPS.

Our results from RSA suggest that both numeric magnitude on IPS and monetary value in OFC are represented in compressive scales. An interesting question that should be explored further is whether the information is first compressed in one area (e.g., OFC uses the already compressed numerical information from IPS when processing monetary rewards) or whether information is compressed in both areas independently. Thus, performing effective connectivity analyses such as dynamic causal modeling (Friston et al., 2003) could provide useful information about the interactions between these brain areas.

Combined with the effects that numeric information have on economic behavior (Furlong & Opfer, 2009; Peters et al., 2008), the implications of these findings can be far reaching. The fact that simply changing the numerical magnitude of a reward (without altering at all the monetary value) can create these stark effects on the neural valuation network – and in particular in IPS – implies that individual differences in IPS should predict differences in decisions that involve monetary information. Therefore, people who suffer dyscalculia or neurological disorders that affect the functionality of parietal cortex (such as Williams or Turner Syndrome) may be at risk for deficits in economic decision-making.

For example, Peters and collaborators (2008) found that individual differences in both numeracy and number sense had an impact on the use of numeric information on economic decisions. Activity in IPS in response to monetary value can provide a neural link to this line of research.

Finally, the fact that both numeric magnitude and monetary value are represented in a compressive scale suggests that more attention has to be paid at the way we present monetary information when important decisions have to be made. For example, recent political discussions about deficit reduction deal with extremely large numeric magnitudes. The compressive scales that we use to represent money imply that it is very likely that decisions made with very large values would not be consistent with the decisions made in an equivalent situation with smaller numeric magnitudes. If monetary values are treated differently when only the numbers used to represent them are different, people might be easily deceived in supporting proposals that go against their own preferences.

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