

Neural Antecedents of the Endowment Effect

Brian Knutson,^{1,*} G. Elliott Wimmer,¹ Scott Rick,² Nick G. Hollon,¹ Drazen Prelec,³ and George Loewenstein⁴

¹Psychology and Neuroscience, Stanford University, Stanford, CA 94305, USA

²The Wharton School, University of Pennsylvania, Philadelphia, PA 19104, USA

³Sloan School of Management, Massachusetts Institute of Technology, Cambridge, MA 02139, USA

⁴Social and Decision Sciences, Carnegie Mellon University, Pittsburgh, PA 15213, USA

*Correspondence: knutson@psych.stanford.edu

DOI 10.1016/j.neuron.2008.05.018

SUMMARY

The “endowment effect” refers to the tendency to place greater value on items that one owns—an anomaly that violates the reference-independence assumption of rational choice theories. We investigated neural antecedents of the endowment effect in an event-related functional magnetic resonance imaging (fMRI) study. During scanning, 24 subjects considered six products paired with 18 different prices under buying, choosing, or selling conditions. Subjects showed greater nucleus accumbens (NAcc) activation for preferred products across buy and sell conditions combined, but greater mesial prefrontal cortex (MPFC) activation in response to low prices when buying versus selling. During selling, right insular activation for preferred products predicted individual differences in susceptibility to the endowment effect. These findings are consistent with a reference-dependent account in which ownership increases value by enhancing the salience of the possible loss of preferred products.

INTRODUCTION

Why do people find it hard to part with their possessions? According to rational choice theory, ownership should not influence preferences (Coase, 1960). Decades of behavioral research, however, suggest that even when allocation occurs by chance, people prefer items they own to similar items they do not own. This phenomenon has been called the “endowment effect” (Thaler, 1980). From a standard economic perspective, the endowment effect presents an anomaly, because it violates the reference-independence assumption of valuation in rational choice theories (Tversky and Kahneman, 1991).

While the endowment effect occurs regularly and robustly in both laboratory and natural settings (Camerer, 2001), the psychological and neural mechanisms underlying this effect remain unclear. Researchers initially proposed that the endowment effect results from loss aversion, or the tendency to weigh losses more heavily than gains of similar size (Kahneman et al., 1990, 1991). According to this account, while items to be bought are typically considered as potential gains, ownership resets the reference point so that items to be sold are instead considered

as potential losses. However, many alternative accounts have been advanced, some of which propose that ownership causes people to overestimate the positive features of an item, to underestimate the negative features of an item, or in a related vein, to personally identify with the item (Beggan, 1992; Nayakankuppam and Mishra, 2005; Peters et al., 2003). Event-related functional magnetic resonance imaging (fMRI) affords the possibility of distinguishing between at least two reference-dependent accounts of the endowment effect. People might find it difficult to part with their possessions either because of enhanced attraction to the item (possibly based on familiarity) or simply because of an aversion to potentially losing the item.

Prior event-related fMRI studies featuring second-to-second temporal resolution have implicated a limited number of brain regions in anticipation of gain and loss. Even in the absence of choice, nucleus accumbens (NAcc) activation has been associated with prediction of monetary gain (Knutson et al., 2001a), insula activation has been associated with prediction of monetary loss (Paulus and Stein, 2006), and mesial prefrontal cortex (MPFC) activation has been implicated in updating initial predictions of monetary gain (Knutson et al., 2003). Further, in choice scenarios such as buying, NAcc activation correlates with product preference and predicts purchasing, while increased insula activation and decreased MPFC activation occur in response to excessive prices and predict not purchasing (Knutson et al., 2007). These findings suggest a dynamic and componential process in which people weigh potential gains against potential losses to inform upcoming purchasing decisions (Prelec and Loewenstein, 1998). The findings also implicate distinct neuroanatomical circuits in the enhanced attraction versus the loss aversion accounts of the endowment effect. Specifically, if people have enhanced attraction to products when selling versus buying, they should show increased NAcc activation when viewing those products. On the other hand, if people have increased aversion to losing products when selling versus buying, they might show increased insula activation when viewing those products. Additionally, people should show decreased MPFC activation to low prices when selling (because they represent a net loss) but should show increased MPFC activation to low prices when buying (because they represent a net gain).

In the present study, we aimed to elicit the endowment effect by asking subjects to buy certain products, sell other products (given to them before the experiment), and choose between yet other products and cash (Figure 1). As subjects engaged in these three tasks, we scanned them with fMRI to determine whether

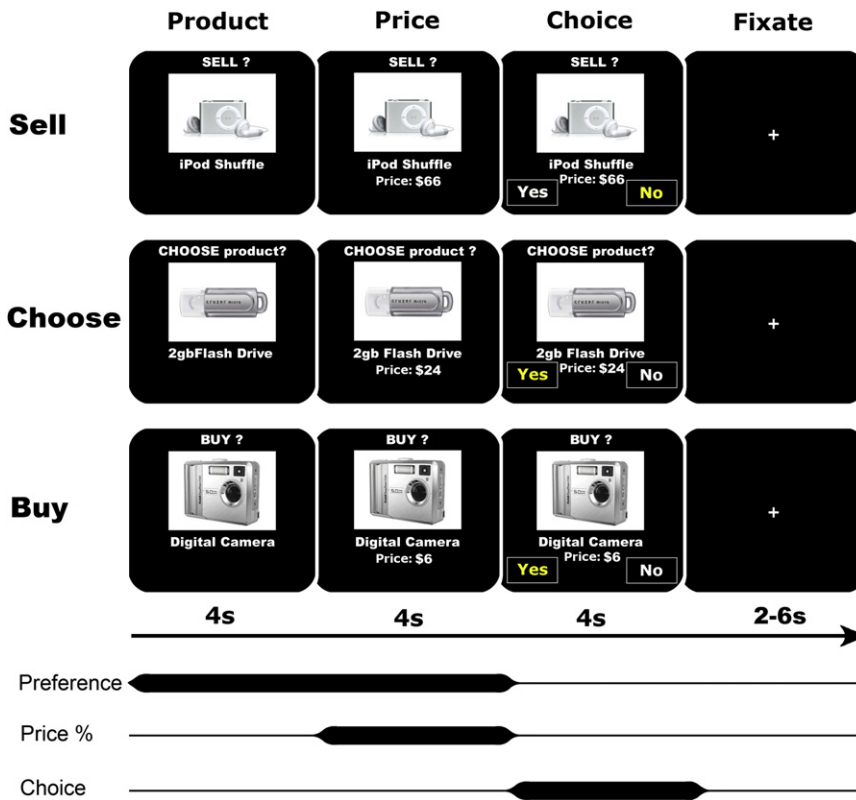


Figure 1. Task Trial Structure and Regressors

For trial structure (across Sell, Choose, and Buy conditions), subjects saw labeled products (product period; 4 s), saw an associated price (price period; 4 s), chose either the product or price (by selecting either “yes” or “no” presented randomly on the right or left side of the screen; choice period; 4 s), and then fixated on a crosshair (2–6 s) prior to the onset of the next trial. In regression models, preference was correlated with brain activation during the product and price periods, percentage retail price was correlated with brain activation during the price period, and choice of the product versus price was correlated with brain activation during the choice period.

RESULTS

Behavior

As in previous behavioral studies (Kahneman et al., 1990), subjects showed a robust endowment effect. The mean scanned indifference point for the Sell condition ($65\% \pm 4\%$; willingness to accept) was significantly greater than for the Buy condition ($32\% \pm 3\%$; willingness to pay), with the Choose condition falling in between ($45\% \pm 3\%$; $ps < 0.001$; Figure 2). Mean reaction

activation in regions of interest during buying versus selling would replicate and extend findings from a previous study of buying only (Knutson et al., 2007). We also examined whether activation in these regions could account for individual differences in susceptibility to the endowment effect. Consistent with a loss aversion account, we predicted that, during selling, insular activation in response to products might magnify the endowment effect. Based on behavioral evidence that the endowment effect reverses for undesirable items (Brenner et al., 2007) and is diminished for neutral versus desirable items (controlling for price) (Carmon and Ariely, 2000), we also predicted that this association might hold most powerfully for “high preference” (or desirable) products.

time did not differ for the Sell (1087.9 ± 45.87 ms) versus Buy (1089.0 ± 48.03) conditions but was greater for the Choose condition (1491.2 ± 74.18 ; $ps < 0.001$; Figure 2), consistent with increased response conflict in the Choose condition. Because anticipatory affect should have the most distinct influences in the Sell versus Buy conditions, and in order to control for potential reaction time confounds, primary analyses of neural data contrasted Sell and Buy conditions, and a parametric regressor modeling reaction time was also included in neural analyses during the choice period (Knutson et al., 2005).

Endowment effect estimates can be computed as the difference between the indifference point for selling (i.e., willingness

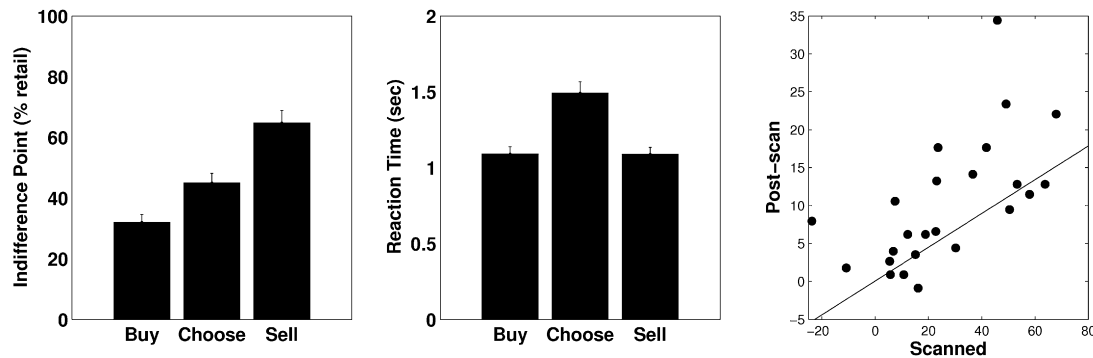


Figure 2. Choice Behavior

Mean indifference points (percent retail price \pm SEM), reaction times (averaged across both products in each condition \pm SEM), and correlation of scanned versus postscan endowment effect estimates (Sell – Buy indifference points; averaged across both products in each condition in units of percent retail price).

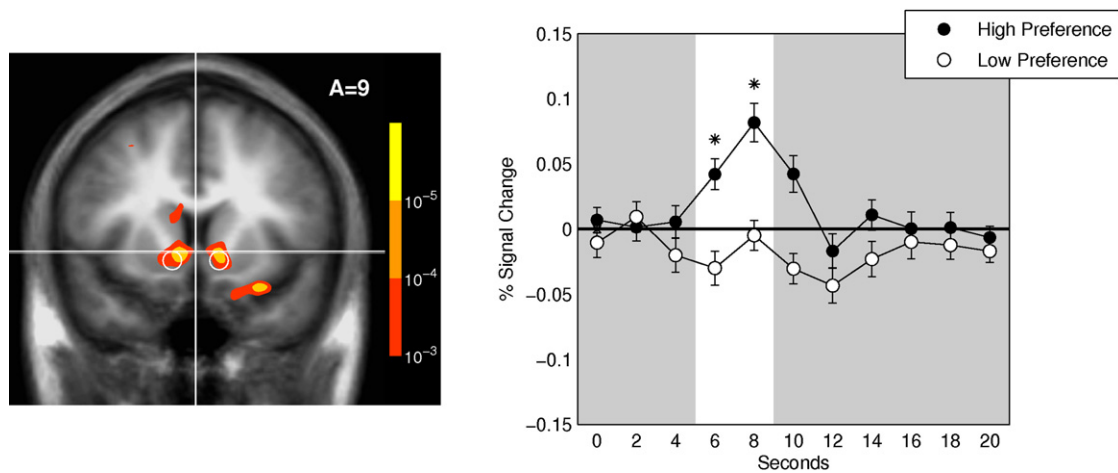


Figure 3. Association of NAcc Activation with Product Preference

NAcc activation correlated with product preference (across all conditions; anterior = 9) and VOI time courses (high versus low preference; mean \pm SEM; white = lagged product period; * $p < 0.05$).

to accept) versus buying (i.e., willingness to pay). Because subjects did not encounter the same products in different conditions in the scanner, both scanned and postscan estimates of the endowment effect were computed. The scanned estimate was computed as the difference between the indifference points for selling a particular product versus the mean indifference point for all other subjects who encountered that same product in the Buy and Choose conditions. The postscan estimate was simply computed as the difference between the self-reported postscan indifference point for selling versus buying the same product. Both the scanned estimate [$26.26\% \pm 4.84\%$; $t(23) = 5.42$, $p < 0.001$] and the postscan estimate [$10.15\% \pm 1.73\%$, $t(23) = 5.88$, $p < 0.001$] were significantly greater than zero. The scanned estimate was also significantly larger than the postscan estimate [$16.10\% \pm 4.00\%$; paired $t(23) = 4.03$, $p < 0.01$], consistent with previous behavioral evidence that people underestimate their susceptibility to the endowment effect in hypothetical scenarios (Loewenstein and Adler, 1995). The postscan estimate, however, did significantly correlate with the scanned estimate ($r = 0.62$, $p = 0.001$) and was reliable across six products (Cronbach's $\alpha = 0.66$), indicating that it provided a valid and reliable within-subject index of the scanned estimate. Both estimates were used in subsequent individual difference analyses. As expected, endowment effect estimates were greater for high-preference products than for low-preference products ($p < 0.05$, one-tailed; see Supplemental Data section 2 available online).

Brain Activation Localization

Parametric regressors tested for main effects across conditions, while interaction regressors tested for differences in main effects between Sell versus Buy conditions. Product preference correlated with NAcc activation across all conditions (Figure 3), but the interaction of product preference and Sell versus Buy condition did not correlate with activation in any of the volumes of interest (VOIs). In contrast, price percent did not significantly correlate with activation in any VOI across conditions, but the

interaction of price percent with Sell versus Buy condition correlated with activation in the MPFC (Figure 4). Choice of the product versus its associated price as well as the interaction of choice with Sell versus Buy condition did not correlate with activation in any of the VOIs (Supplemental Data section 3). The regressor modeling reaction time correlated positively with anterior cingulate, anterior insular, dorsolateral prefrontal, thalamic, and motor cortical activation and negatively with amygdalar and parahippocampal activation across conditions, but the interaction of reaction time with Sell versus Buy condition did not significantly correlate with brain activation (Supplemental Data section 5). Patterns of activation for nonspecific period regressors and their interactions are listed in Supplemental Data section 4.

Comparison of activation time course data extracted from NAcc and MPFC VOIs verified these localization findings (Figures 3 and 4). Pooled across all conditions, NAcc activation was higher for high (rating ≥ 5) versus low (rating < 5 ; based on a median split) preference products during product presentation ($p < 0.05$, two-tailed; Figure 3). On the other hand, MPFC activation for price percent during price presentation varied significantly as a function of condition. In the Buy condition, low price percent elicited significantly greater MPFC activation than high price percent ($p < 0.05$, two-tailed; Figure 4), while in the Sell condition, low price percent elicited significantly less MPFC activation than high price percent during price presentation ($p < 0.05$, two-tailed). Direct comparisons of Buy and Sell conditions revealed that MPFC activation during price presentation was significantly greater for low price percent in the Buy versus Sell condition ($p < 0.05$, two-tailed) and was significantly less for high price percent in the Buy versus Sell condition ($p < 0.05$, two-tailed; second acquisition only). While differences between Sell versus Buy conditions demonstrated that MPFC activation covaried with the subjective value rather than the objective magnitude of prices, only direct comparisons of Sell versus Choose conditions could establish a true framing effect, because these conditions featured identical incentives (i.e., subjects could choose either the product or its associated price in cash). Direct

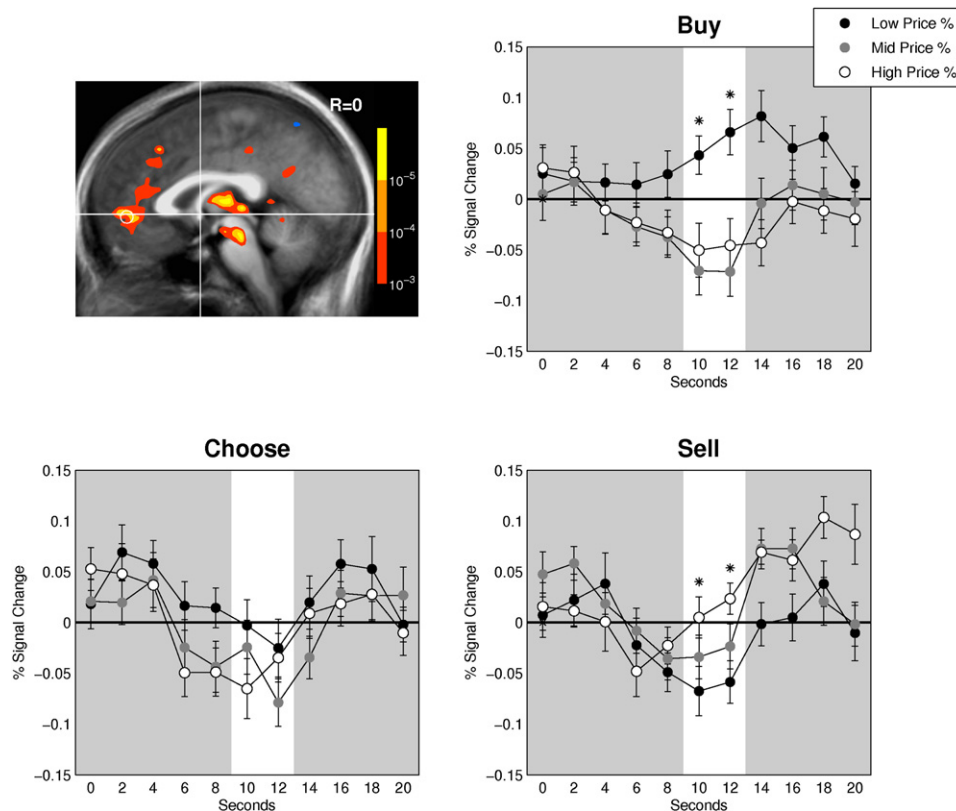


Figure 4. Association of MPFC Activation with Price Percent

MPFC activation correlated with the interaction of price percent and Sell versus Buy condition (right = 0) and VOI time courses by retail price percent (upper right = Buy; lower left = Choose; lower right = Sell; mean \pm SEM; white = lagged price period; * $p < 0.05$, paired t test of low versus high price).

comparisons of Sell versus Choose conditions revealed that MPFC activation during price presentation did not significantly differ for high price percent (i.e., differing at a trend level only) but was significantly greater for low price percent in the Choose versus Sell condition ($p < 0.05$, two-tailed; first acquisition only), demonstrating a true framing effect.

Individual Differences

Individual difference analyses correlated whole-brain parametric and interaction regressor coefficients from the localization model with estimates of susceptibility to the endowment effect (i.e., both scanned and postscan). The regressor for the interaction of product preference with Sell versus Buy condition correlated positively with both scanned and postscan estimates of endowment susceptibility only in the right insula. While the regressor for the interaction of product preference with Sell versus Buy condition correlated negatively with postscan estimates of endowment susceptibility in the NAcc, this was not true for the scanned estimate. Neither NAcc nor MPFC activation conjointly correlated with both scanned and postscan estimates of the endowment effect. Other regressors (i.e., product preference, percent price, and the interaction of percent price with Sell versus Buy condition) did not correlate with scanned and postscan estimates of endowment susceptibility in any of the VOIs.

To statistically decompose this finding, right insula activation (Talairach-defined, anterior to 0) during product presentation in

Sell and Buy conditions for high- versus low-preference products was extracted and correlated with both scanned and postscan estimates of endowment susceptibility. Because four subjects did not encounter high-preference products in the Sell condition, data from 20 subjects were included in analysis (i.e., 15 subjects encountered one high-preference product in the Sell condition, yielding 18 data points per individual estimate, and five subjects encountered two high-preference products in the Sell condition, yielding 36 data points per individual estimate). In the Sell condition, average right insula activation in response to high-preference products predicted both scanned and postscan estimates of susceptibility to the endowment effect (Figure 5), but this was not the case for activation in response to low-preference products. In the Buy condition, average right insula activation in response to high- and low-preference products did not significantly correlate with endowment susceptibility (Supplemental Data section 8). No significant correlations were observed with both scanned and postscan indices of the endowment effect when substituting activation from NAcc or MPFC VOIs.

DISCUSSION

We sought to determine whether neural activation associated with buying would extend to selling and to identify neural antecedents of the endowment effect. Localization analyses built

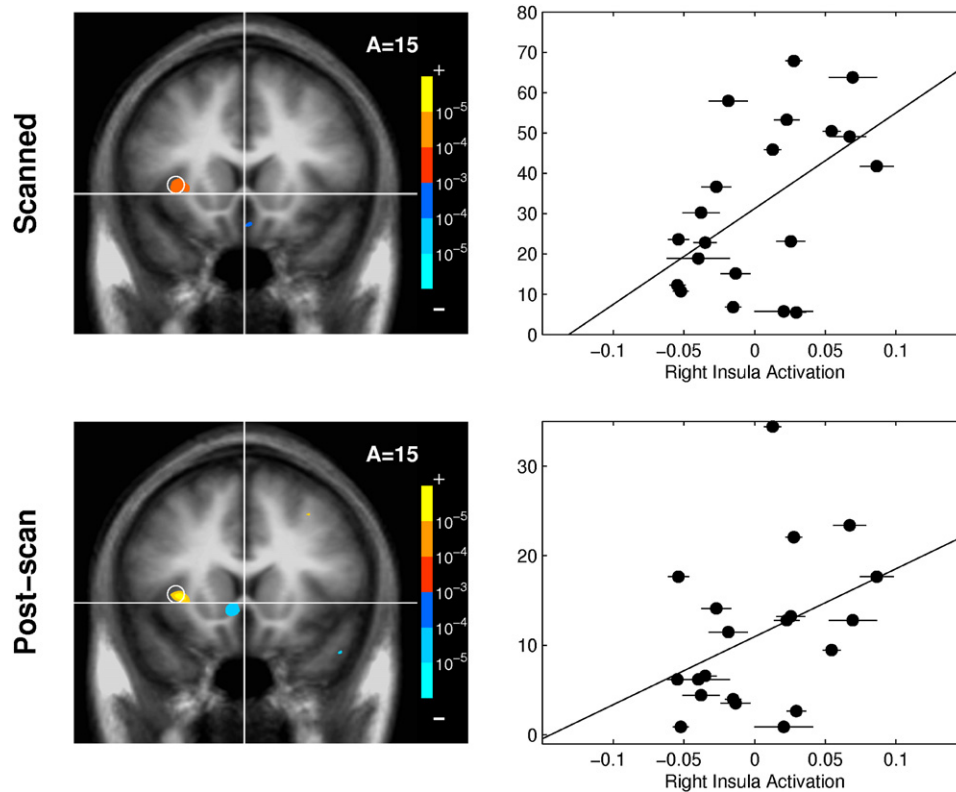


Figure 5. Association of Insula Activation with Susceptibility to the Endowment Effect

Right anterior insula activation correlated with the coefficient for the interaction of product preference by Sell versus Buy condition for both scanned (top left) and postscan (bottom left) estimates of individual differences in susceptibility to the endowment effect. Right insula VOI activation (Talairach-defined anterior > 0) for preferred products in the Sell condition (lag = 6 s; \pm SEM) also correlated with scanned (top right; Pearson $r = 0.52$; $p < 0.05$, two-tailed) and postscan (bottom right; Pearson $r = 0.39$, $p < 0.05$, one-tailed) estimates of individual differences in susceptibility to the endowment effect ($n = 20$).

upon and extended prior findings related to buying (Knutson et al., 2007), because NAcc activation correlated with product preference across both selling and buying conditions. MPFC activation, on the other hand, correlated negatively with price percent during buying but positively with price percent during selling. Finally, during selling, right insular activation in response to preferred products predicted individual differences in susceptibility to the endowment effect. These findings provide insights about neuropsychological mechanisms underlying the endowment effect.

Consistent with a gain anticipation account (Knutson et al., 2001a), NAcc activation correlated with product preference and did not significantly differ across conditions (even at a more liberal threshold; $p < 0.01$, uncorrected). Individual difference analyses did not reveal a significant association of NAcc activation by condition with endowment effect susceptibility. If anything, NAcc activation in response to preferred products during selling versus buying was negatively rather than positively correlated with susceptibility to the endowment effect. Together, these findings do not support the hypothesis that enhanced attraction to possessions promotes the endowment effect.

Consistent with a gain integration account (Knutson et al., 2003), MPFC activation appeared instead to track net gain with

respect to the initial product estimate. Specifically, MPFC activation increased in response to low price offers for Buy products but decreased in response to low price offers for Sell products and decreased overall in response to Sell versus Buy prices (Supplemental Data section 4). The dissociation in NAcc and MPFC patterns of activation provides further evidence that activation in different dopamine target regions reflects distinct gain-related computations at different steps of incentive processing (Knutson and Wimmer, 2007) rather than all representing the same unitary value (Tom et al., 2007). The dependence of MPFC activation on Sell versus Buy condition also suggests that this region tracks the subjective value rather than the objective magnitude of prices (Plassmann et al., 2007). MPFC activation also showed a true framing effect, because it was greater in response to low prices in the Choose than in the Sell condition, despite the fact that these conditions featured identical incentives (i.e., a choice of either a product or an associated price) (Loewenstein et al., 2008). This pattern of findings suggests that neural predictors of buying may only extend to selling after careful consideration of subjective valuation and framing effects.

Though predicted by a loss anticipation account (Buchel and Dolan, 2000; Kuhnen and Knutson, 2005; Sanfey et al., 2003), insular activation did not correlate with the interaction of product

preference by condition. However, individual differences in insular activation to preferred products in the Sell condition did predict susceptibility to the endowment effect (indexed by both scanned and postscan estimates). This finding provides some support for the hypothesis that insular activation in response to preferred products may induce loss aversion (Kahneman et al., 1991). The fact that this association is strongest for preferred products is consistent with behavioral findings in this experiment and previous behavioral findings suggesting that desirable items evoke stronger endowment effects (controlling for price) (Brenner et al., 2007; Carmon and Ariely, 2000). Unlike prior research on buying (Knutson et al., 2007), insular activation did not correlate with prices or choices. This difference may stem from distinct features of the present research design, because subjects saw the same product repeatedly at several different prices and could develop a sense of price range, potentially minimizing the negative impact of any single price offer (e.g., as often occurs in the case of bargaining).

Consistent with reference-dependent theories (Tversky and Kahneman, 1991), these findings support the notion that anticipated gains and losses are processed by distinct neural circuits that may exert different effects on subsequent choice (Knutson and Bossaerts, 2007; Kuhnen and Knutson, 2005). Additionally, output from these different circuits may sometimes come into conflict prior to choice, because anterior cingulate activation was greatest in response to prices close to the indifference point over all conditions (Supplemental Data section 5; Botvinick et al., 1999; Pochon et al., 2008). These findings support a loss aversion account of the endowment effect for several reasons. First, the association of NAcc activation with product preference did not vary significantly by condition. If anything, NAcc activation in the Sell condition was negatively correlated with susceptibility to the endowment effect, contrary to an enhanced attraction account. Second, the association of MPFC activation with price percent reversed as a function of Sell versus Buy condition (in addition to showing lower activation overall in the Sell versus Buy condition; Supplemental Data section 4). To the extent that decreased MPFC activation reflects correction of initial gain predictions, this pattern of results might indirectly support a loss aversion account. Third, right insular activation predicted two different estimates of individual differences in susceptibility to the endowment effect, consistent with a loss aversion account.

In a previous fMRI study of the endowment effect, subjects stated buying and selling prices for digitally recorded songs while being scanned (Weber et al., 2007). The investigators reported increased amygdala and caudate activation when subjects estimated selling versus buying prices, which they interpreted as evidence for increased sensitivity to both product loss and monetary gain (respectively) while selling. In the present study, direct contrasts of selling versus buying conditions overall did not reveal these patterns of activation (Supplemental Data section 3). Differences in findings between the present study and the Weber et al. study may have resulted from differences in experimental design and analysis. The Weber et al. study compared selling and buying price estimation, whereas the present study compared selling and buying decisions. The Weber et al. study's analysis simply contrasted sell and buy conditions, while

the present study's analysis included both regressors of interest that separately modeled different trial periods as well as additional regressors that controlled for periodic confounds. The Weber et al. study lacked a prediction component, whereas the present study used anticipatory brain activation to predict individual differences in susceptibility to the endowment effect. Unlike the Weber et al. study, the present study was designed to elicit anticipatory brain activation, which correlated more robustly with subsequent choice than did activation during choice, similar to an earlier fMRI study of buying but not selling (Knutson et al., 2007).

Other fMRI studies have not focused on the endowment effect, but several have elicited neural responses related to reference dependence. In fact, much of the fMRI literature involving monetary incentives bears relevance to reference dependence, beginning with initial demonstrations of distinct (rather than opposite) neural responses during anticipation of gains and losses of the same magnitude (Breiter et al., 2001; Knutson et al., 2001a) and of different neural responses to nongain versus neutral outcomes (Berns et al., 2001; Knutson et al., 2001b). Later studies examined neural responses to mixed gambles. For instance, one study's findings implicated orbitofrontal cortex (bordering the MPFC) activation in decreased susceptibility to framing effects (De Martino et al., 2006), while another implicated mesolimbic activation (in regions including the MPFC) in increased susceptibility to loss aversion (Tom et al., 2007). The designs of these mixed-gamble studies did not permit investigators to separate neural responses during anticipation of gambles from neural responses during choice execution or in response to possible outcomes. Yet both the present findings and a growing literature clearly indicate distinct patterns of neural activation during anticipation of gains versus in response to gain outcomes (Knutson and Cooper, 2005; O'Doherty, 2004). In the present study, framing effects were apparent in the MPFC but showed specific sensitivity to price information. MPFC activation increased when prices increased the net value of the associated product and decreased when prices decreased the net value of the associated product, consistent with gain integration accounts of MPFC function (Knutson et al., 2003). Further, neither of these mixed-gamble studies separately modeled choice or included an explicit feedback component. Yet the literature suggests a clear influence of outcome-related feedback on mesolimbic activation (Delgado et al., 2000; Poldrack et al., 1999). In the present study, choice might be considered an outcome, because it is incentive compatible and final for each trial. Finally, as in the study of the endowment effect described in the previous paragraph (Weber et al., 2007), these mixed-gamble studies did not control for potential trial phase or reaction time confounds, which might also influence activation in mesolimbic regions. In the present study, reaction time robustly correlated with activation of the anterior cingulate and deactivation of the amygdala across conditions (Supplemental Data section 5), a pattern of neural responses also observed when subjects chose gambles against the dominant frame (in the absence of statistical control for reaction time) (De Martino et al., 2006).

Strengths of the current study include use of highly desirable consumer products that command substantial retail prices

(e.g., iPods and digital cameras rather than less expensive but more commonly used items such as mugs or pens), incentive compatibility (i.e., one decision for each of six products counted “for real”), elicitation of a robust behavioral endowment effect, and the use of brain activation to predict susceptibility to the endowment effect. Additionally, the design elicited choices for the same products across a range of prices, obviating the need to employ a conceptually similar but less intuitive procedure commonly utilized in economics research (Becker et al., 1964). A necessary weakness includes the utilization of individual differences, because it was psychologically implausible to ask subjects to both sell and buy the same product in the same experiment. However, a postscan (i.e., strictly within-subject) estimate of the endowment effect correlated robustly with a scanned estimate of the endowment effect, and both implicated an overlapping right anterior insular region in susceptibility to the endowment effect. Indeed, future studies might profitably use similar methods to explore mechanisms underlying these individual differences (Harbaugh et al., 2001), because person variables such as emotional attachment to items have been reported to increase susceptibility to the endowment effect (Peters et al., 2003) while expertise decreases susceptibility (List, 2003).

These neuroscience findings have implications for both psychology and economics. Psychologically, the present findings are consistent with mechanistic accounts in which positive and negative affect flexibly guide decisions both to buy and sell (Peters et al., 2003), because product preference activated different brain regions than anticipated product loss. Economically, these findings provide evidence consistent with reference-dependent theories (e.g., prospect theory) rather than reference-independent theories (e.g., rational choice) and specifically support a loss aversion rather than an enhanced attraction account of the endowment effect (Novemsky and Kahneman, 2005). While products are viewed as gains when buying, they may additionally be viewed as losses when selling.

While many factors may contribute to the endowment effect (Bateman et al., 2005), these findings provide support for one mechanism involving increased aversion to loss of possessions during selling but not for another involving enhanced attraction to possessions during selling. In the future, methodological advances may enable investigators to examine potential contributions of other factors. Thus, neuroscience methods can advance economic theory not only by breaking down apparently unitary phenomena (e.g., choice) into constituent components (e.g., anticipation of gain and loss) but also by specifying which of these components matters when.

EXPERIMENTAL PROCEDURES

Subjects

Twenty-four healthy right-handed subjects (12 females) were scanned on a 1.5 T General Electric Signa Scanner. Subjects were excluded if they owned products similar to those in the experiment (listed below). Along with the typical magnetic resonance exclusions (e.g., metal in the body), subjects were screened for psychotropic drugs and ibuprofen, substance abuse in the past month, and history of psychiatric disorders (DSM IV Axis I), prior to collecting informed consent. Subjects were paid \$40.00 for participating, received \$20.00 in cash to potentially buy products, and received two products (randomly assigned) to potentially sell.

Task

Subjects participated in a modified version of the Savings Hold Or Purchase (SHOP) task (Knutson et al., 2007) while undergoing event-related fMRI scanning. In addition to “Buy” trials, the modified version of the task also included “Sell” and “Choose” trials. During Buy trials, subjects saw one of two products that they could buy (for 4 s), one of 18 prices (for 4 s), and spatially counterbalanced boxes (labeled “yes” and “no”) that they could press to indicate whether they wanted to buy the product at the displayed price or not (4 s). During Sell trials, subjects saw one of two products that they were given before the scan (4 s), one of 18 prices (4 s), and spatially counterbalanced boxes that they could press to indicate whether they wanted to sell the product at the displayed price or not (4 s). During Choose trials, subjects saw one of two products (4 s), one of 18 prices (4 s), and spatially counterbalanced boxes that they could press to indicate whether they preferred the product or the displayed price in cash. Because Choose and Sell conditions featured identical incentives (i.e., acquire money or the product), any difference in response to the two represents a true framing effect (Kahneman et al., 1990).

Two of six products (i.e., iPod shuffle, noise-cancelling headphones, iPod alarm clock base, 2 gigabyte USB flash drive, digital camera, and wireless mouse) were randomly assigned to each condition for each subject, counterbalanced across conditions. All products commanded substantial retail prices (mean retail price \$70.57, range \$35.00–\$95.00) and were rated as highly attractive on average to this sample (mean desirability from 1 to 7 = 4.55 ± 0.12). The 18 prices were pseudorandomly ordered and equally distributed from 5% to 95% of retail price for each product. Extreme high and low prices were always presented within the first four trials of each block to minimize anchoring effects (Ariely et al., 2003). Buy, Sell, and Choose trials occurred in pseudorandomly ordered blocks of six trials each, yielding 36 trials per condition, or 108 trials total (Figure 1). To ensure incentive compatibility and trial independence, subjects were informed that only one choice per product would be randomly selected at the end of the experiment to count “for real.” Thus, subjects received the outcome of six of their choices. Subjects were also informed that prices would appear in random order.

Subjects were first instructed in the task (Supplemental Data section 1) and played a short practice session with different products and hypothetical outcomes. Subjects were then tested for task comprehension and received \$60 in cash (\$20 for purchasing, as well as \$40 in compensation for the 2 hr experiment) to keep throughout the scan. Next, subjects saw all products (packaged) and received two randomly selected products to keep (for the Sell condition), which they then placed in their locker.

After scanning, subjects rated their preference for and familiarity with each of the six products (on 1–7 Likert scales). To obtain a measure of individual differences in susceptibility to the endowment effect and because different products were presented in different conditions, subjects then played a hypothetical but otherwise identical version of the task featuring all six products in both Buy and Sell conditions.

fMRI Acquisition and Analysis

Images were acquired with a 1.5 T General Electric MRI scanner using a standard birdcage quadrature head coil. Twenty-four 4 mm thick slices (in-plane resolution 3.75 × 3.75 mm, no gap) extended axially from the mid-pons to the top of the skull, providing whole-brain coverage and adequate spatial resolution of subcortical regions of interest (e.g., midbrain, NAcc, orbitofrontal cortex). Whole-brain functional scans were acquired with a T2*-sensitive spiral in-/out- pulse sequence (TR = 2 s, TE = 40 ms, flip = 90°) designed to minimize signal dropout at the base of the brain (Glover and Law, 2001). High-resolution structural scans were also acquired to facilitate localization and coregistration of functional data, using a T1-weighted spoiled grass sequence (TR = 100 ms, TE = 7 ms, flip = 90°).

Analyses were conducted using Analysis of Functional Neural Images (AFNI) software (Cox, 1996). For preprocessing, voxel time series were sinc interpolated to correct for nonsimultaneous slice acquisition within each volume, concatenated across runs, corrected for motion, slightly spatially smoothed to minimize effects of anatomical variability (FWHM = 4 mm), high-pass filtered (admitting frequencies with period <90 s), and normalized to percent signal change with respect to voxel means for the entire task. Visual inspection of motion correction estimates confirmed that no subject’s head moved more than 2.0 mm in any dimension from one volume acquisition to the next.

Data analysis proceeded through three sequential steps. The first step of localization analyses established associations between brain activation in volumes of interest and parametric variables with multiple regression. The regression model included 14 orthogonalized convolved regressors. Three unit-weighted period regressors contrasted product, price, and choice periods of each trial with all other time points in the experiment. Four regressors of interest modeled product preference for all trials during the product period (parametric), retail price percent for all trials during the price period (parametric), choice of the product versus the price for the choice period, and reaction time during the choice period (parametric). Finally, seven interaction regressors multiplied the contrast of sell versus buy trials by both period and parametric regressors. For product preference and price percent, interaction regressors facilitated detection of conditional effects. The regression model also included 12 additional regressors of noninterest that modeled baseline, linear, and quadratic trends for each of two blocks, as well as six degrees of displacement due to motion. To examine parametric and interaction effects in VOIs, a threshold of $p < 0.01$ (corrected for three comparisons) was applied to averaged bilateral NAcc, bilateral MPFC regions, and right insula VOIs, while a threshold of $p < 0.001$ uncorrected was adopted for all other brain regions (cluster criterion = three 4 mm cubic voxels).

The second step of time course analyses verified that brain activation in VOIs significantly differed at the predicted time points. Brain activation was averaged and extracted from 8 mm diameter spherical NAcc ($\pm 10, 12, -2$) and MPFC ($\pm 4, 46, -2$) VOIs, centered on coordinates identified in earlier research using a similar task (Knutson et al., 2007). Because the right insula VOI focus shows more variability across studies, we defined a larger VOI as the entire right insula in the Talairach atlas anterior to $A = 0$ (however, activation extracted from a smaller right insula 8 mm diameter spherical VOI centered on $+32, 10, 9$ yielded similar findings). Activation extracted from VOIs was compared across conditions with within-subject paired t tests at a threshold of $p < 0.05$, two-tailed.

The third step of individual difference analyses examined whether brain activation extracted from VOIs could predict individual differences in susceptibility to the endowment effect (i.e., both scanned and postscan estimates) with multiple regression. The scanned estimate was derived by subtracting the scanned indifference point for selling a product from all other subjects' average indifference points for buying and choosing the same product. The postscan estimate was derived by subtracting the average self-reported postscan indifference point for buying (i.e., willingness to pay) from selling the same products (i.e., willingness to accept) for each subject. In all cases, logistic regressions were used to estimate indifference points, which were computed in units of retail price percent (Ariely et al., 2003).

SUPPLEMENTAL DATA

The Supplemental Data for this article can be found online at <http://www.neuron.org/cgi/content/full/58/5/814/DC1/>.

ACKNOWLEDGMENTS

This research was supported in part by National Science Foundation Grant 0748915 to B.K., a National Science Foundation Graduate Research Fellowship to S.R., the John Simon Guggenheim Memorial Fellowship to D.P., and a MacArthur Foundation network grant to G.L. We thank Jeffrey C. Cooper, William T. Harbaugh, Ellen Peters, and three anonymous reviewers for comments on earlier drafts of the manuscript, as well as Stephanie Greer for extensive assistance with data analysis.

Received: October 24, 2007

Revised: February 21, 2008

Accepted: May 22, 2008

Published: June 11, 2008

REFERENCES

Ariely, D., Loewenstein, G., and Prelec, D. (2003). "Coherent arbitrariness": Stable demand curves without stable preferences. *Q. J. Econ.* 118, 73–105.

Bateman, I., Kahneman, D., Munro, A., Starmer, C., and Sugden, R. (2005). Testing competing models of loss aversion: An adversarial collaboration. *J. Public Econ.* 89, 1561–1580.

Becker, G.S., DeGroot, M.H., and Marschak, J. (1964). Measuring utility by a single-response sequential method. *Behav. Sci.* 9, 226–232.

Beggan, J.K. (1992). On the social nature of nonsocial perception: The mere ownership effect. *J. Pers. Soc. Psychol.* 62, 229–237.

Berns, G.S., McClure, S.M., Pagnoni, G., and Montague, P.R. (2001). Predictability modulates human brain response to reward. *J. Neurosci.* 21, 2793–2798.

Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S., and Cohen, J.D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* 402, 179–181.

Breiter, H.C., Aharon, I., Kahneman, D., Dale, A., and Shizgal, P. (2001). Functional imaging of neural responses to expectancy and experience of monetary gains and losses. *Neuron* 30, 619–639.

Brenner, L., Rottenstreich, Y., Sood, S., and Bilgin, B. (2007). On the psychology of loss aversion: Possession, valence, and reversals of the endowment effect. *J. Consum. Res.* 34, 369–376.

Buchel, C., and Dolan, R.J. (2000). Classical fear conditioning in functional neuroimaging. *Curr. Opin. Neurobiol.* 10, 219–223.

Camerer, C. (2001). Prospect theory in the wild: Evidence from the field. In *Choices, Values, and Frames*, D. Kahneman and A. Tversky, eds. (Cambridge, UK: Cambridge University Press), pp. 288–300.

Carmon, Z., and Ariely, D. (2000). Focusing on the foregone: How value can appear so different to buyers and sellers. *J. Consum. Res.* 27, 360–370.

Coase, R.H. (1960). The problem of social cost. *J. Law Econ.* 3, 1–44.

Cox, R.W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance images. *Comput. Biomed. Res.* 29, 162–173.

De Martino, B., Kumaran, D., Seymour, B., and Dolan, R.J. (2006). Frames, biases, and rational decision-making in the human brain. *Science* 313, 684–687.

Delgado, M.R., Nystrom, L.E., Fissell, C., Noll, D.C., and Fiez, J.A. (2000). Tracking the hemodynamic response to reward and punishment in the striatum. *J. Neurophysiol.* 84, 3072–3077.

Glover, G.H., and Law, C.S. (2001). Spiral-in/out BOLD fMRI for increased SNR and reduced susceptibility artifacts. *Magn. Reson. Med.* 46, 515–522.

Harbaugh, W.T., Krause, K., and Vesterlund, L. (2001). Are adults better behaved than children? Age, experience, and the endowment effect. *Econ. Lett.* 70, 175–181.

Kahneman, D., Knetsch, J.L., and Thaler, R.H. (1990). Experimental tests of the endowment effect and the Coase Theorem. *J. Polit. Econ.* 98, 1325–1348.

Kahneman, D., Knetsch, J.L., and Thaler, R.H. (1991). Anomalies: The endowment effect, loss aversion, and status quo bias. *J. Econ. Perspect.* 5, 193–206.

Knutson, B., and Cooper, J.C. (2005). Functional magnetic resonance imaging of reward prediction. *Curr. Opin. Neurol.* 18, 411–417.

Knutson, B., and Bossaerts, P. (2007). Neural antecedents of financial decisions. *J. Neurosci.* 27, 8174–8177.

Knutson, B., and Wimmer, G.E. (2007). Splitting the difference: How does the brain code reward episodes? *Ann. N Y Acad. Sci.* 104, 54–69.

Knutson, B., Adams, C.M., Fong, G.W., and Hommer, D. (2001a). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J. Neurosci.* 21, RC159.

Knutson, B., Fong, G.W., Adams, C.M., Varner, J.L., and Hommer, D. (2001b). Dissociation of reward anticipation and outcome with event-related fMRI. *Neuroreport* 12, 3683–3687.

Knutson, B., Fong, G.W., Bennett, S.M., Adams, C.M., and Hommer, D. (2003). A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: Characterization with rapid event-related fMRI. *Neuroimage* 18, 263–272.

Knutson, B., Taylor, J., Kaufman, M., Peterson, R., and Glover, G. (2005). Distributed neural representation of expected value. *J. Neurosci.* 25, 4806–4812.

- Knutson, B., Rick, S., Wimmer, G.E., Prelec, D., and Loewenstein, G. (2007). Neural predictors of purchases. *Neuron* 53, 147–156.
- Kuhnen, C.M., and Knutson, B. (2005). The neural basis of financial risk-taking. *Neuron* 47, 763–770.
- List, J.A. (2003). Does market experience eliminate market anomalies? *Q. J. Econ.* 118, 41–71.
- Loewenstein, G., and Adler, D. (1995). A bias in the prediction of tastes. *Econ. J.* 105, 929–937.
- Loewenstein, G., Rick, S., and Cohen, J.D. (2008). Neuroeconomics. *Annu. Rev. Psychol.* 59, 647–672.
- Nayakankuppam, D., and Mishra, H. (2005). The endowment effect: Rose-tinted and dark-tinted glasses. *J. Consum. Res.* 32, 390–395.
- Novemsky, N., and Kahneman, D. (2005). How do intentions affect loss aversion? *J. Mark. Res.* 17, 139–140.
- O'Doherty, J.P. (2004). Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Curr. Opin. Neurobiol.* 14, 769–776.
- Paulus, M.P., and Stein, M.B. (2006). An insular view of anxiety. *biological Psychiatry* 60, 383–387.
- Peters, E., Slovic, P., and Gregory, R. (2003). The role of affect in the WTA/WTP disparity. *J. Behav. Decis. Making* 16, 309–330.
- Plassmann, H., O'Doherty, J.P., and Rangel, A. (2007). Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *J. Neurosci.* 27, 9984–9988.
- Pochon, J.B., Riis, J., Sanfey, A.G., Nystrom, L.E., and Cohen, J.D. (2008). Functional imaging of decision conflict. *J. Neurosci.* 28, 3468–3473.
- Poldrack, R.A., Prabhakaran, V., Seger, C.A., and Gabrieli, J.D.E. (1999). Striatal activation during acquisition of a cognitive skill. *Neuropsychology* 13, 564–574.
- Prelec, D., and Loewenstein, G. (1998). The red and the black: Mental accounting of savings and debt. *Marketing Science* 17, 4–28.
- Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., and Cohen, J.D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science* 300, 1755–1758.
- Thaler, R. (1980). Toward a positive theory of consumer choice. *J. Econ. Behav. Organ.* 1, 39–60.
- Tom, S.M., Fox, C.R., Trepel, C., and Poldrack, R.A. (2007). The neural basis of loss aversion in decision-making under risk. *Science* 315, 515–518.
- Tversky, A., and Kahneman, D. (1991). Loss aversion in riskless choice: A reference-dependent model. *Q. J. Econ.* 106, 1039–1061.
- Weber, B., Aholt, A., Neuhaus, C., Trautner, P., Elger, C.E., and Teichert, T. (2007). Neural evidence for reference-dependence in real-market transactions. *Neuroimage* 35, 441–447.