Hippocampal damage reduces choice consistency:

Evidence for constructive preference from mediotemporal lobe epilepsy

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Abstract

Consistent decisions are intuitively desirable and theoretically important for utility maximization. Despite advances in neuroeconomics that describe the neurobiological bases of value representations, the question of which brain regions provide necessary input to the identified value-processing network is still open. The constructed preference tradition within behavioral decision making research emphasizes a critical role for cognitive processes relying on associations. This calls for an investigation of the role of the hippocampus in making consistent decisions. We investigated 31 patients with mediotemporal lobe (MTL) epilepsy and hippocampal lesions, 30 patients with extratemporal lobe epilepsy, and 30 healthy controls, in their binary choices between candy bars and in a number-comparison control task. MTL patients show more intransitive choices than the other two groups for the value-based but not number-comparison task, and their intransitive choices parametrically increase with their volume of compromised hippocampal tissue. These results suggest a critical involvement of the MTL in preference construction and value-based choices.

# Introduction

Imagine that you are slightly hungry late in the afternoon, and wander to a vending machine to select a snack. You are faced with an array of over 20 possibilities. How do you select among them? In the last decade, decision neuroscience has made significant progress in identifying neurobiological correlates of value representations using paradigms similar to this scenario (Hare, Camerer, & Rangel, 2009; Hare, Malmaud, & Rangel, 2011; Hare, O’Doherty, Camerer, Schultz, & Rangel, 2008; Hutcherson, Plassmann, Gross, & Rangel, 2012; Plassmann, O’Doherty, & Rangel, 2010, 2007). Specifically, a value network involving a fronto-striatal circuit including the ventral striatum (VS) and the ventromedial prefrontal cortex (vmPFC), as well as posterior cingulate cortex (PCC) has been proposed (Bartra, McGuire, & Kable, 2013; Haber & Knutson, 2010; Kable & Glimcher, 2009; Pessiglione & Lebreton, 2015; van den Bos & McClure, 2013). An unsolved question, however, is where the value signals processed by this network come from, particularly for more complex stimuli.

An independent tradition in the judgment and decision-making research suggests that preferences are often constructed as needed (Lichtenstein & Slovic, 2006). Opposing standard theories of rational choice that implicitly assume stable utility functions and choice options with preexisting values, a long stream of research explains many well-known inconsistencies in choice by suggesting that preferences are calculated on the fly and affected by factors such as the way options are posed and the content of the choice set. This construction can be thought of as involving multiple cognitive steps (Rangel, Camerer, & Montague, 2008): retrieval of relevant experiences with stimuli in the choice set, evaluation of current internal states, comparison of relevant attributes as facilitated by the decision mode, integrating the pros and cons of the options with the current state, imagining future consequences of potential choices to name just a few. Cognitive psychologists study some of these steps under memory processes. Psychological insights on memory processes and their accompanying opportunities and constraints have inspired several theories and frameworks to explain multiple decision phenomena that deviate from normative standards (Dougherty, Gettys, & Ogden, 1999; Reyna, Lloyd, & Brainerd, 2003; Schneider & Shanteau, 2003; Weber, Goldstein, & Barlas, 1995; Weber & Johnson, 2009).

A long line of work in cognitive neuroscience implicates the medial temporal lobe (MTL) in relation to these memory processes (Squire, Stark, & Clark, 2004). The involvement and interaction of the MTL (or more specifically one of its subcomponents, the hippocampus) with the value network, however, has only recently attracted attention. Several studies now provide evidence for the involvement of the hippocampus in value-related decisions, particularly when decisions involve novel options. Wimmer and Shohamy (2012), for example, show the involvement of the MTL in the transfer of value of rewarded stimuli by associative learning that biases later decisions on non-rewarded stimuli. Another recent study highlighted the involvement of the MTL in preference construction by showing activity in the hippocampus, in addition to medial prefrontal cortex, when subjects were asked to indicate preferences for novel food items based on two familiar, but previously uncombined tastes (Barron, Dolan, & Behrens, 2013). Other work motivated by the hippocampus’ involvement in imagining future experiences in addition to past ones (Hassabis, Kumaran, Vann, & Maguire, 2007; Klein & Loftus, 2002; Schacter & Addis, 2007) investigated its role in value-related decisions across time: When participants were asked to imagine future events, stronger activity in a set of brain regions including the hippocampus was associated with more patient choices (Benoit, Gilbert, & Burgess, 2011; Peters & Büchel, 2010). More recently, it has also been shown that hippocampal activity increases specifically for preference for future outcomes that require simulation of consequences, and degeneration of these pathways in patients with Alzheimers is associated with increased preference for options requiring less simulation (Lebreton et al., 2013).

Though these studies suggest the involvement of the hippocampus and memory processes in value-related decision-making, they do not provide conclusive evidence on the necessity of these regions and related cognitive processes. Such evidence requires comparing value-related decision-making abilities in the absence or impairment of relevant brain regions. Such differences in abilities would substantiate psychological models of decision-making involving memory processes and extend our understanding of the value network in the brain by providing hints on where the value signals for complex options originate. In fact, such evidence established the necessity of ventromedial frontal regions, now considered a key region in the value network, in representing value: Patients with damage in these areas performed poorly selectively in value-related decisions compared both to healthy controls, as well as patients with lesions elsewhere in the frontal cortex (Camille, Griffiths, Vo, Fellows, & Kable, 2011; Fellows & Farah, 2007).

In light of these findings we ask whether patients with hippocampal sclerosis are impaired in making consistent value-based decisions. We test this hypothesis with a simple paradigm, a series of binary choices among simple commonly consumed and familiar food products. Our measure of choice quality is transitivity, the degree to which choices between different option pairs are consistent. If a person chooses A over B, and B over C, transitivity requires that they pick A over C (Samuelson, 1938). Violations of transitivity have been investigated in early empirical work in decision-making (Tversky, 1969), recent decision neuroscience (Camille et al., 2011; Fellows & Farah, 2007; Fellows, 2006a; Kalenscher, Tobler, Huijbers, Daselaar, & Pennartz, 2010) and consumer choice (Lee, Amir, & Ariely, 2009). Transitivity of choices is embraced by most individuals as a desirable property of a choice process; that is, most people will change intransitive choice patterns to transitive ones when confronted with their intransitive choices (Birnbaum & Gutierrez, 2007). Our task examines binary choices among 20 common candy bars, a product familiar and interesting to participants. We also included a pairwise judgment control task, presenting respondents with pairs of numbers and asking them to judge which of the two is bigger. In both cases our dependent measure was the transitivity of (value-based or magnitude-based) choices. This is very similar to the protocols used to establish the necessary role of the vmPFC in value-related decisions (Fellows & Farah, 2007). Thus, selective differences in patients with MTL damage in value-based choices compared to numerical decisions should provide strong evidence for the involvement of the hippocampus, and thereby mnemonic processes in value-based decision-making as well.

Two conceptual clarifications are in order. Our central dependent measure, the frequency of intransitive preferences has been used before to examine the inability of decision makers to produce a stable representation of the value of choice options, with other patient groups (Camille et al., 2011; Fellows & Farah, 2007). Even earlier work, however, using choice intransitivity as a dependent measure did so to identify specific choice heuristics incompatible with utility maximization (Tversky, 1969). This resulted in a debate on the correct probabilistic model of transitivity that would account for errors in experimental data and whether that was evidence for a particular mechanism (Birnbaum & Gutierrez, 2007; Regenwetter, Dana, Davis-Stober, & Guo, 2011; Regenwetter & Davis-Stober, 2008). Our use of the term pairwise “transitivity” is not based on these frameworks and our design with two alternatives per choice not suited for such model comparison. Our use of intransitivity counts is instead a test of the error associated with the construction of value representations.

Second, our use of the term “transitivity” is only marginally related to the extensive literature measuring transitive inference, where a set of premises are learned in the experiment and participants are asked to generalize these learned rules to novel contexts and combinations of stimuli. Transitive inference tasks have been instrumental in establishing the role of the hippocampus in representing organizations of stimulus relations (Eichenbaum & Cohen, 2001). While animal lesion studies established the necessity of the hippocampus for transitive inference (Bunsey & Eichenbaum, 1996; Dusek & Eichenbaum, 1997), the involvement of this region in humans has also been confirmed with PET (Nagode & Pardo, 2002) and fMRI (Heckers, Zalesak, Weiss, Ditman, & Titone, 2004) studies. However transitive inference paradigms differ from ours critically in that the bases of the judgments in our design are preferences, not given premises. We do not present participants with transitive relations and ask them to reason following this rule. We simply ask for their preference between two candy bars. We do not hypothesize that if a participant chooses Snickers over Mars and Mars over Bounty they would also choose Snickers over Bounty because they are instructed that these choices must follow a given transitive relationship but because they anticipate that they will enjoy Snickers more. That is, while a transitive inference task implies a strict ordinal relationship between stimuli thereby recruiting working memory, transitivity of choice as measured by our design relies on values that have been learned over time and presumably relies on the recruitment of associative facilities (Halford, 2005).

# Methods

A total of 91 respondents participated. Thirty-one patients suffering from mesial temporal lobe epilepsy with clinically diagnosed uni- (left:n=14;right:n=8) or bilateral (n=9) hippocampal sclerosis from the presurgical program at the Department of Epileptology in Bonn were included in the study (MTL). Different from patients with lesions in the vmPFC (Fellows & Farrah, 2007), the lesion locations in MTL patients are very similar. This makes lesion volume a better individual difference marker, as further described below. Two control groups consisted of thirty patients with extratemporal lobe epilepsy (ETL) and thirty healthy control subjects (CON), respectively. The three groups did not differ with respect to age or gender (see Table S1 for details).



**Figure 1**. Three trials of the binary choice experiment. Subject indicated their preferred candy bar on each trial. Stimulus presentation and choice was self-paced, with a maximum length of 5 seconds.

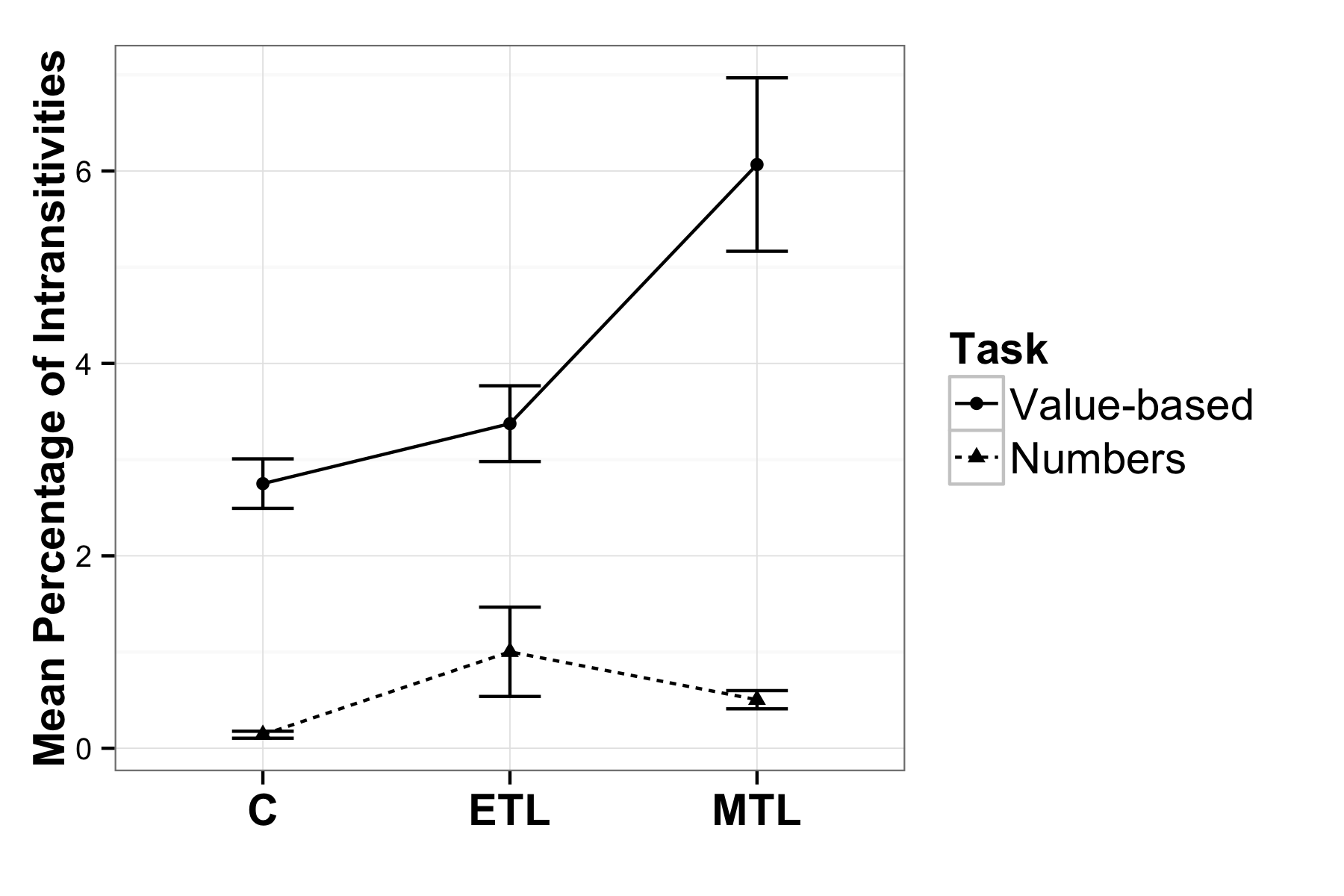
# Experiment

Each respondent made a series of choices between pairs of candy bars, presented pictorially on a computer as shown in Figure 1. Each pairwise combination was presented once, resulting in 190 choices, in a different random order for each participant. In a control task, subjects were presented with pairs of numbers, drawn from the range of one to twenty, and had to judge which number was larger. Judgment inconsistency across triplets of comparison was computed identically for the two tasks. Subjects knew that they would receive their candy bar of choice from one randomly selected choice trial, in addition to a participation fee of 10 €.

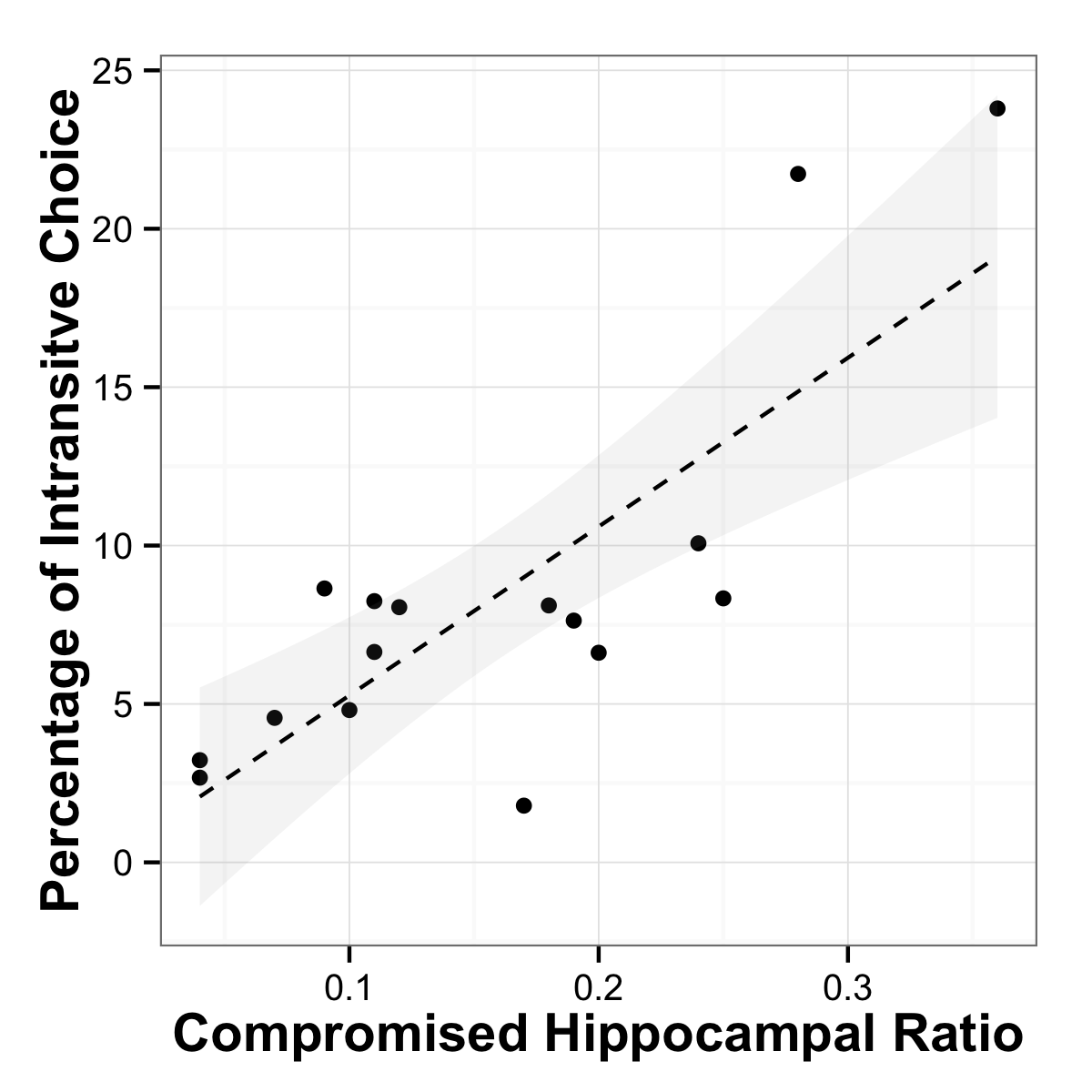
A triplet was marked as indicating intransitivity if (i) A was chosen over B and B was chosen over C, yet C was chosen over A or (ii) if B was chosen over A and C was chosen over B, yet A was chosen over C.

# Results

As shown in Figure 2, MTL patients showed a greater percentage of intransitive choices compared to the two control groups in the preference task compared to the control task (mean percentages for the preference task: MTL: 6.07%; ETL: 3.37%; CON: 2.75%; median percentages: MTL: 4.56%; ETL 2.72%; CON: 2.94%; mean percentages for the control task: MTL: 0.50 %; ETL: 1.00%; CON: 0.14%, median percentages: MTL: 0.36%; ETL: 0.00%; CON: 0.04% ; linear mixed model with orthogonal contrasts group task interaction b = – 0.06, t(91) = –2.98, p = 0.004). The difference between degree of intransitivity between the preference and control task did not differ significantly between the two control groups (linear mixed model with orthogonal contrasts group task interaction b = – 0.04, t(91) = 0.97, p = 0.333).



**Figure 2**. Mean percentage of intransitive choices per group in each task (nMTL = 31, nC = 30, nETL = 30). Error bars represent SEM.



**Figure 3**. Relationship between hippocampal lesion volume and intransitive choices. Scatterplot of compromised hippocampal volume (as a ratio of total volume) against percentage of intransitive choices, with a regression line with 95% CI for the observed correlation of rho=0.676, p=0.004.

Since an MRI was not available for all subjects, we performed the following analysis in a subset of participants (see SOM for details). We determined the ratio of compromised hippocampal volume to total volume and correlated this individual difference variable with the percentage of intransitive choices observed for these participants, using a non-parametric correlation coefficient that is insensitive to outliers. We found a strong and significant relationship between these two variables, as shown in Figure3 (Spearman-rho = 0.676; F(1, 14) = 11.78, p=0.004; n=16), such that the larger the lesion volume, the less consistent were the value-based choices.

To provide a context for interpreting the observed frequencies of intransitivity, we conducted a series of simulations that use a random utility model with a stochastic term added to the utility of the options, such that the probability of choosing option A () in a decision between A and B is:

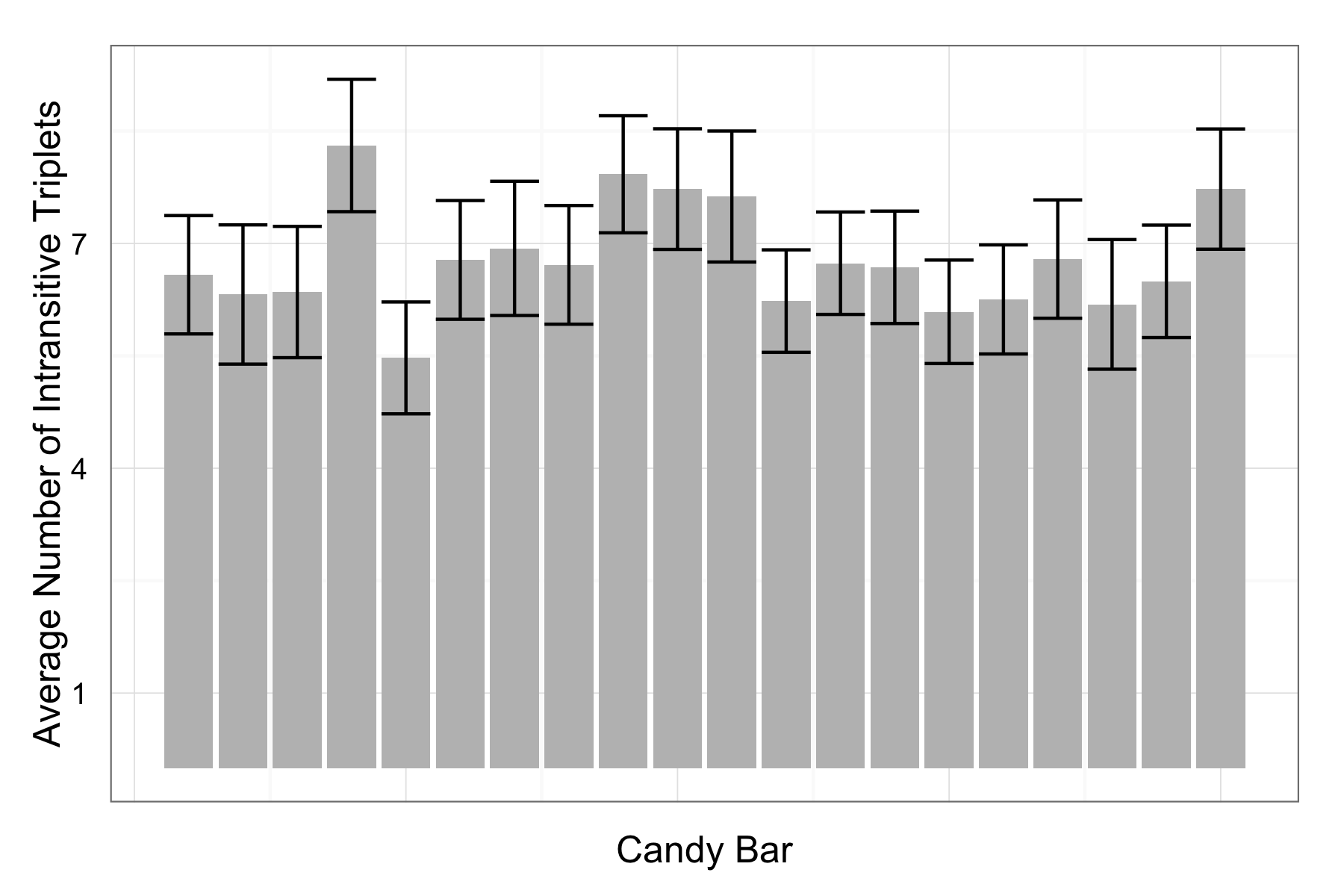
Equation 1

where and represent the utilities of option represents the proportion (between 0 and 1) of the observed utility due to random error, and is the random error. It can be shown analytically that the maximum proportion of intransitive triples is .25 (see SOM, also noted in the discussion section of Tversky, 1969). The question of interest to us, given our hypothesis that the degree of MTL patients’ hippocampal sclerosis increases , the proportion of random error in option value construction, is how the proportion of intransitive triples increases as error in utilities increases. The effect is non-linear (see SOM), and the observed intransitivities in the MTL group correspond to an of .3, i.e., the level expected if random error represented approximately 30 percent of the utility values in Equation 1.

Several explanations alternative to our account of random error in value construction can be tested with our data. One possible alternative explanation involves explicit episodic memory of previous value comparisons, rather than value construction for the two options of each pairwise choice. Under this account, non-MTL respondents may have better memory for their choices made earlier in the task, and this better episodic memory prevents intransitive choices. This account would suggest that the rate of intransitivities declines over time, as previous choices are remembered and used to avoid intransitive later choices, and this decline in intransitivities over choice trials would differ for the MTL and non-MTL groups. We tested this hypothesis and saw neither a significant decrease in intransitivities over choice trials (linear trend b = 7.155 × 10-3, t(17200) = 0.297, p = 0.766, quadratic trend b = 7.727 × 10-3, t(17200) = 0.458, p = 0.647), nor any difference in slopes for MTL vs. non-MTL groups (linear trend MTL group interaction b = - 0.003, t(88) = -0.955, p = 0.339).

Another alternative explanation involves group differences in speed-accuracy tradeoff. To test this, we examined response latencies of the choices, and the relationship between responses latencies and intransitivities for MTL and non-MTL groups. Contrary to a speed-accuracy tradeoff, we found that slower (rather than faster) trials were more likely to be involved in intransitive triplets (b = 0.275, t(17180) = 12.601, p < 0.001), and that the MTL group had a significantly slower average response time per trial (b = 0.301, t(88) = 2.11, p = 0.038). Together, these results suggest that intransitive triplets accompany more effortful, longer responding, eliminating the possibility of a speed-accuracy tradeoff.

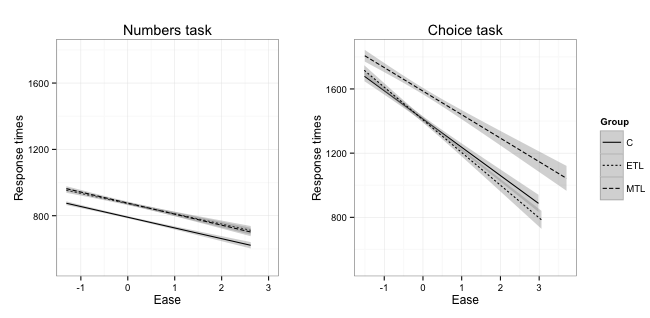
Lastly, we examined whether there were any idiosyncratic effects on preference intransitivity associated with specific stimuli (candy bars). We found no significant differences in the average number of intransitive triplets each bar was involved in (Figure 4, F(1, 18) = 0.003, p = 0.959). To further quantify the value of each candy bar we fit the Bradley-Terry-Luce (BTL) model (Bradley & Terry, 1951; Firth & Turner, 2012; Luce, 1959) to aggregate paired comparison data of each group. This confirmed poorer fits for the MTL group (AIC = 851.39) compared to the control (AIC = 840.42) and ETL group (AIC = 818.55).



**Figure 4**. Average umber of intransitive triplets each stimulus was involved in for the preference task. There were no idiosyncratic differences between the stimuli (F(1, 18) = 0.003, p = 0.959).

These aggregate level analyses mask, however, potential individual differences in preferences for the candy bars. To address this, we rank-ordered the candy bars depending on how often each bar was chosen out of the 19 potential times it could have been chosen. A candy bar that was chosen 16 times, for instance, would be assigned a rank-order value of 16. This also allowed us to ask whether decision difficulty might be processed differently between the groups. Decision difficulty was quantified as the difference between these rank-order values for the two candy bars in a given trial. As a result of higher intransitivity in the MTL group (and consistent with the group differences in the BTL model fits) the mean of the rank-order value differences was lower for the MTL group (b = -0.144, t(88) = -3.491, p<0.001). This can be explained by higher noise in value representations: Higher noise can lead to an underestimation of the value of most preferred candy bars and an overestimation of that of least preferred ones in pairwise counts of choices. Thus, in some sense all decisions are more difficult for the MTL group, consistent with their overall slower response times.

More interestingly, however, the three groups respond differently to decreasing difficulty. Expectedly, all groups were faster for easier trials in both tasks (numbers task: b = -0.19, t(1720) = -33.257, p <0.001, choice task: b = -0.24, t(1720) = -38.171, p < 0.001). Yet the MTL group was not only slower in general (b = 0.08, t(88) = 2.098, p = 0.039) but also slower to respond to decreasing difficulty in the choice task (b = 0.02, t(1720) = 4.461, p < 0.001). This pattern was not observed in the control task of number comparisons (b = -0.003, t(1720) = -0.865, p = 0.387). Although we cannot rule out alternative explanations for this response time pattern in the choice task due to other potential limitations posed by MTL lesions due to lack of additional neuropsychological data it still corroborates the necessary role for the MTL in stable value representations.



**Figure 5**. Response times as a function of decision difficulty. As decisions become easier in both tasks all groups respond faster. The MTL group is slower, however, to react to change in difficulty for the choice task, while this is not true for the control task.

# Discussion

In this paper we provide support for a critical role of brain regions associated with memory-related processes in value-based decision-making, by showing that hippocampal lesions are associated with an increase in intransitive value-based choices and that the degree of intransitivity is related to magnitude of the damage to the hippocampus. A control task not involving value-based choice does not show these effects, nor do respondents who have lesions outside of the medial temporal lobe. These dissociation results implicate a crucial role for the hippocampal areas in preference construction.

Though such data provide strong evidence for the involvement of a brain region in consistent value-based decisions, the delineation of specific cognitive and neural mechanisms provide multiple avenues for future research.

First, the hippocampus is just one part in a larger network of relevant brain areas involved in the retrieval and processing of choice values. A recent review by (Shohamy & Turk-Browne, 2013) suggests hippocampal involvement in a variety of cognitive functions outside of the domain of declarative memory. It provides two different hypotheses of hippocampal function. The memory modulation hypothesis proposes that representations within the hippocampus may transiently bias other cognitive functions such as value computations in our task. The adaptive function hypothesis, in contrast, highlights the hippocampus as a central processing unit with specific computations carried out in the hippocampal networks, depending on the task at hand.

Our hippocampal patients produce patterns of intransitivity of value-based choice that are similar to those observed in ventromedial prefrontal cortex (vmPFC) patients, suggesting that the associations and memories stored in the hippocampus may serve as inputs to value calculation occurring elsewhere (Barron et al., 2013), potentially in line with the memory modulation hypothesis. The hippocampus is one of the most highly interconnected brain areas (Cole, Pathak, & Schneider, 2010; Godsil, Kiss, Spedding, & Jay, 2013). In addition to being directly and monosynaptically connected to the prefrontal cortex, animal work suggests a topographically specific hippocampal projections map on functionally distinct prefrontal regions (Cole et al., 2010; Godsil et al., 2013; Ongür & Price, 2000).

This possibility calls for a nuanced investigation of the interactions between hippocampal and prefrontal regions in value-based decision-making. For example, Ranganath and Ritchey (2012) propose a division of the MTL into two systems for memory-guided behavior: the anterior (AT) and posterior-medial (PM) system. The AT, which is comprised of the perirhinal cortex and anterior parts of the hippocampus and amygdala has strong interconnections with the frontal cortex, has been argued to be involved in familiarity-based cognition, social behavior and saliency. This is also the part of the hippocampus which is most affected in patients with hippocampal sclerosis (Woermann, Barker, Birnie, Meencke, & Duncan, 1998). Ranganath & Ritchey (2012) suggest that the AT system could facilitate the use of past experiences to inform inferences about the personality and intentions of others. Our results suggest such inferential abilities specific to distinct regions in the MTL along with the connection to the ventromedial prefrontal cortex may also play a role in value-based decisions.

On the other hand, more in line with an adaptive function hypothesis, deficits in consistent choices might be due to hippocampus-specific computations. For example, Fellows, (2006b) showed that vmPFC lesioned patients differ from normal controls in their external information search, in ways that could be attributed to diminished planning capacity. Perhaps this planning capacity relies on hippocampus-specific computations. An interesting topic of research would be whether vmPFC patients exhibit deficits in different mnemonic processes.

A second future research topic are potential compensation mechanisms in patients with chronic hippocampal lesions. It is well-known that chronic brain lesions may lead to compensatory shifts in neural processes, e.g. in the domain of language processing (Kipervasser et al., 2008; Weber et al., 2006).The application of neuroimaging methods, like functional MRI, during a value-based decision task in these patients could provide answers to this question.

Third, although patients with temporal lobe epilepsy and hippocampal sclerosis do show neuropsychological deficits especially in the domain of declarative memory, the amount to which these deficits occur varies strongly between patients (Hoppe, Elger, & Helmstaedter, 2007). Future research combining in-depth neuropsychological testing together with value-based choice tasks may shed light on the specific cognitive components underlying the observed range of decision deficits.

Our results suggest a critical role for the hippocampus in the construction of the value of choice options. Most decisions require the construction of value based on past experience. Even a previously experienced option, like a favorite dish in a familiar restaurant, requires us to compare recollections of the value of that option to newly available options such as tonight’s specials. A better understanding of both internal and external inputs to preference construction processes and their aggregation and comparison will allow us to comprehend and model how the brain calculates value and makes wise and consistent choices.

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# Author contribution statements

BW, EJJ and EUW designed the experiment and wrote the manuscript, EJJ and AZE analyzed the behavioral data and wrote the manuscript, IZ performed experiments, JW analyzed the MRI data. CEE provided clinical data of the patients.

# References

Barron, H. C., Dolan, R. J., & Behrens, T. E. J. (2013). Online evaluation of novel choices by simultaneous representation of multiple memories. *Nature Neuroscience*, *16*(10), 1492–8. doi:10.1038/nn.3515

Bartra, O., McGuire, J. T., & Kable, J. W. (2013). The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage*, *76*, 412–427. doi:10.1016/j.neuroimage.2013.02.063

Benoit, R. G., Gilbert, S. J., & Burgess, P. W. (2011). A neural mechanism mediating the impact of episodic prospection on farsighted decisions. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(18), 6771–9. doi:10.1523/JNEUROSCI.6559-10.2011

Birnbaum, M. H., & Gutierrez, R. J. (2007). Testing for intransitivity of preferences predicted by a lexicographic semi-order. *Organizational Behavior and Human Decision Processes*, *104*(1), 96–112. doi:10.1016/j.obhdp.2007.02.001

Bradley, R. A., & Terry, M. E. (1951). Rank Analysis Of Incomplete Block Designs. The Method Of Paired Comparisons. *Biometrika*, *39*(3-4), 324–345.

Bunsey, M., & Eichenbaum, H. (1996). Conservation of hippocampal memory function in rats and humans. *Nature*.

Camille, N., Griffiths, C. a, Vo, K., Fellows, L. K., & Kable, J. W. (2011). Ventromedial frontal lobe damage disrupts value maximization in humans. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(20), 7527–32. doi:10.1523/JNEUROSCI.6527-10.2011

Cole, M. W., Pathak, S., & Schneider, W. (2010). Identifying the brain’s most globally connected regions. *NeuroImage*, *49*(4), 3132–48. doi:10.1016/j.neuroimage.2009.11.001

Dougherty, M. R. P., Gettys, C. F., & Ogden, E. E. (1999). MINERVA-DM : A Memory Processes Model for Judgments of Likelihood. *Psychological Review*, *106*(1), 180–209.

Dusek, J. A., & Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(13), 7109–7114. doi:10.1073/pnas.94.13.7109

Eichenbaum, H., & Cohen, N. J. (2001). *From Conditioning to Conscious Recollection: Memory Systems of the Brain*. *Group* (Vol. 4). doi:10.1093/acprof:oso/9780195178043.001.0001

Fellows, L. K. (2006a). Deciding how to decide: ventromedial frontal lobe damage affects information acquisition in multi-attribute decision making. *Brain : A Journal of Neurology*, *129*(Pt 4), 944–52. doi:10.1093/brain/awl017

Fellows, L. K. (2006b). Deciding how to decide: ventromedial frontal lobe damage affects information acquisition in multi-attribute decision making. *Brain : A Journal of Neurology*, *129*(Pt 4), 944–52. doi:10.1093/brain/awl017

Fellows, L. K., & Farah, M. J. (2007). The role of ventromedial prefrontal cortex in decision making: judgment under uncertainty or judgment per se? *Cerebral Cortex (New York, N.Y. : 1991)*, *17*(11), 2669–74. doi:10.1093/cercor/bhl176

Firth, D., & Turner, H. L. (2012). Bradley-Terry models in R : the BradleyTerry2 package. *Development*, (2002), 1–10. Retrieved from http://www.jstatsoft.org/search

Godsil, B. P., Kiss, J. P., Spedding, M., & Jay, T. M. (2013). The hippocampal-prefrontal pathway: the weak link in psychiatric disorders? *European Neuropsychopharmacology : The Journal of the European College of Neuropsychopharmacology*, *23*(10), 1165–81. doi:10.1016/j.euroneuro.2012.10.018

Haber, S. N., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology : Official Publication of the American College of Neuropsychopharmacology*, *35*(1), 4–26. doi:10.1038/npp.2009.129

Halford, G. S. (2005). Development of thinking. In K. J. Holyoak & R. G. Morrison (Eds.), *The Cambridge Handbook of Thinking and Reasoning* (pp. 529–558). New York: Cambridge University Press.

Hare, T. a, Camerer, C. F., & Rangel, A. (2009). Self-Control in Decision-Making Involves Modulation of the vmPFC Valuation System. *Science*, *324*(May), 646–648.

Hare, T. a, Malmaud, J., & Rangel, A. (2011). Focusing attention on the health aspects of foods changes value signals in vmPFC and improves dietary choice. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(30), 11077–11087. doi:10.1523/JNEUROSCI.6383-10.2011

Hare, T. a, O’Doherty, J., Camerer, C. F., Schultz, W., & Rangel, A. (2008). Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *28*(22), 5623–5630. doi:10.1523/JNEUROSCI.1309-08.2008

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. a. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(5), 1726–31. doi:10.1073/pnas.0610561104

Heckers, S., Zalesak, M., Weiss, A. P., Ditman, T., & Titone, D. (2004). Hippocampal activation during transitive inference in humans. *Hippocampus*, *14*(2), 153–62. doi:10.1002/hipo.10189

Hoppe, C., Elger, C. E., & Helmstaedter, C. (2007). Long-term memory impairment in patients with focal epilepsy. *Epilepsia*, *48 Suppl 9*, 26–9. doi:10.1111/j.1528-1167.2007.01397.x

Hutcherson, C. A., Plassmann, H., Gross, J. J., & Rangel, A. (2012). Cognitive regulation during decision making shifts behavioral control between ventromedial and dorsolateral prefrontal value systems. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(39), 13543–54. doi:10.1523/JNEUROSCI.6387-11.2012

Kable, J. W., & Glimcher, P. W. (2009). The neurobiology of decision: consensus and controversy. *Neuron*, *63*(6), 733–45. doi:10.1016/j.neuron.2009.09.003

Kalenscher, T., Tobler, P. N., Huijbers, W., Daselaar, S. M., & Pennartz, C. M. a. (2010). Neural signatures of intransitive preferences. *Frontiers in Human Neuroscience*, *4*(June), 1–14. doi:10.3389/fnhum.2010.00049

Kipervasser, S., Palti, D., Neufeld, M. Y., Ben Shachar, M., Andelman, F., Fried, I., … Hendler, T. (2008). Possible remote functional reorganization in left temporal lobe epilepsy. *Acta Neurologica Scandinavica*, *117*(5), 324–31. doi:10.1111/j.1600-0404.2007.00948.x

Klein, S. B., & Loftus, J. (2002). Memory and temporal experience : The effects of episodic memory loss on an amnesic patient’s ability to remember the past and imagine the future. *Social Cognition*, *20*(5), 353–379.

Lebreton, M., Bertoux, M., Boutet, C., Lehericy, S., Dubois, B., Fossati, P., & Pessiglione, M. (2013). A Critical Role for the Hippocampus in the Valuation of Imagined Outcomes. *PLoS Biology*, *11*(10). doi:10.1371/journal.pbio.1001684

Lee, L., Amir, O., & Ariely, D. (2009). In Search of Homo Economicus: Cognitive Noise and the Role of Emotion in Preference Consistency. *Journal of Consumer Research*, *36*(2), 173–187. doi:10.1086/597160

Lichtenstein, S., & Slovic, P. (Eds.). (2006). *The Construction of Preference*. New York: Cambridge University Press.

Luce, R. D. (1959). *Individual Choice Behavior: A Theoretical Analysis*. New York: John Wiley & Sons, Inc.

Nagode, J. C., & Pardo, J. V. (2002). Human hippocampal activation during transitive inference. *Neuroreport*, *13*(7), 939–44.

Ongür, D., & Price, J. L. (2000). The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cerebral Cortex (New York, N.Y. : 1991)*, *10*(3), 206–19. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10731217

Pessiglione, M., & Lebreton, M. (2015). From the Reward Circuit to the Valuation System: How the Brain Motivates Behavior. In G. H. . Gendolla (Ed.), *Handbook of Biobehavioral Approaches to Self-Regulation* (1st ed., pp. 157–173). New York: Springer Science+Business Media. doi:10.1007/978-1-4939-1236-0

Peters, J., & Büchel, C. (2010). Episodic future thinking reduces reward delay discounting through an enhancement of prefrontal-mediotemporal interactions. *Neuron*, *66*(1), 138–48. doi:10.1016/j.neuron.2010.03.026

Plassmann, H., O’Doherty, J. P., & Rangel, A. (2010). Appetitive and aversive goal values are encoded in the medial orbitofrontal cortex at the time of decision making. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *30*(32), 10799–10808. doi:10.1523/JNEUROSCI.0788-10.2010

Plassmann, H., O’Doherty, J., & Rangel, A. (2007). Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *27*(37), 9984–9988. doi:10.1523/JNEUROSCI.2131-07.2007

Ranganath, C., & Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nature Reviews. Neuroscience*, *13*(10), 713–26. doi:10.1038/nrn3338

Rangel, A., Camerer, C., & Montague, P. R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience*, *9*(7), 545–556. doi:10.1038/nrn2357

Regenwetter, M., Dana, J., Davis-Stober, C. P., & Guo, Y. (2011). Parsimonious testing of transitive or intransitive preferences: Reply to Birnbaum (2011). *Psychological Review*, *118*(4), 684–688. doi:10.1037/a0025291

Regenwetter, M., & Davis-Stober, C. P. (2008). There are many models of transitive preference: a tutorial review and current perspective. *Decision Modeling and Behavior in Complex and Uncertain Environments*, *21*, 99–124.

Reyna, V. F., Lloyd, F. J., & Brainerd, C. J. (2003). Memory, Development, and Rationality: An Integrative Theory of Judgement and Decision Making. In *Emerging Perspectives on Judgement and Decision Research* (pp. 201–245).

Samuelson, P. A. (1938). A Note on the Pure Theory of Behaviour Consumer ’s Behavior. *Economica*, *5*(17), 61–71.

Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*(1481), 773–86. doi:10.1098/rstb.2007.2087

Schneider, S. L., & Shanteau, J. (2003). *Emerging Perspectives on Judgment and Decision Research*. Cambridge University Press.

Shohamy, D., & Turk-Browne, N. B. (2013). Mechanisms for widespread hippocampal involvement in cognition. *Journal of Experimental Psychology. General*, *142*(4), 1159–70. doi:10.1037/a0034461

Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience*, *27*, 279–306. doi:10.1146/annurev.neuro.27.070203.144130

Tversky, A. (1969). Intransitivity of preferences. *Psychological Review*, *76*(1), 31–48. doi:10.1037/h0026750

Van den Bos, W., & McClure, S. M. (2013). Towards a general model of temporal discounting. *Journal of the Experimental Analysis of Behavior*, *99*(1), 58–73. doi:10.1002/jeab.6

Weber, B., Wellmer, J., Reuber, M., Mormann, F., Weis, S., Urbach, H., … Fernández, G. (2006). Left hippocampal pathology is associated with atypical language lateralization in patients with focal epilepsy. *Brain : A Journal of Neurology*, *129*(Pt 2), 346–51. doi:10.1093/brain/awh694

Weber, E. U., & Johnson, E. J. (2009). Mindful judgment and decision making. *Annual Review of Psychology*, *60*, 53–85. doi:10.1146/annurev.psych.60.110707.163633

Wimmer, G. E., & Shohamy, D. (2012). Preference by association: how memory mechanisms in the hippocampus bias decisions. *Science (New York, N.Y.)*, *338*(6104), 270–3. doi:10.1126/science.1223252

Woermann, F. G., Barker, G. J., Birnie, K. D., Meencke, H. J., & Duncan, J. S. (1998). Regional changes in hippocampal T2 relaxation and volume: a quantitative magnetic resonance imaging study of hippocampal sclerosis. *Journal of Neurology, Neurosurgery & Psychiatry*, *65*(5), 656–664. doi:10.1136/jnnp.65.5.656