Preference consistency relies on hippocampal function:

Evidence from mediotemporal lobe epilepsy

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Abstract

The General Axiom of Revealed Preferences states that one´s choices should be consistent and transitive. Recent studies showed that lesions in regions involved in value computation, i.e. the ventromedial prefrontal cortex, lead to an increase in intransitive choices. If preferences are constructed at the time of choice based on past experience, lesions in regions involved in associative memory, i.e. the medial temporal lobes, should also lead to increased intransitivity of value-based choices. 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 a number-comparison control task. Our results show an increase in intransitive choices in the MTL compared to the other groups for the preference but not number task, suggesting a critical involvement of the MTL in preference construction and value-based choices.

# Introduction

It seems obvious that our preferences draw on past experience and hence memory. Memory representation of past choices and their consequences allow us to learn what sources of food provide optimal nourishment and which predators and other dangers should be avoided, ensuring our survival and well-being. Confronted with a choice of snack food items at a vending machine, we use the packaging as memory cues to retrieve past experiences with the options to construct an estimate of their reward value.

In contrast, economics treats preferences as a primitive in axiomatic models of risky choice (Von Neumann & Morgenstern, 1944). As a result, the connection between properties of memory and those of preference and choice has historically been neglected, with only a few exceptions (Weber, Goldstein, & Barlas, 1995). More recently, memory processes and their accompanying opportunities and constraints have played a more prominent role in explanations of decision-making phenomena, in an attempt to leverage what we know about memory to explain well-known decision phenomena (Dougherty, Gettys, & Ogden, 1999; Reyna, Lloyd, & Brainerd, 2003; Schneider & Shanteau, 2003; Weber & Johnson, 2009).

If preferences are often constructed (see Lichtenstein & Slovic, 2006), an insight that might be psychology’s most successful export to economics, then memory processes must play a major role in this construction. Both memory encoding and retrieval processes influence judgment and choice in multiple ways (see Weber & Johnson, 2009 for a review). Query theory (Johnson, Häubl, & Keinan, 2007; Weber et al., 2007) suggests that decision-makers consult their memory (or external sources) with automatic and implicit queries about the choice alternatives, in particular arguments for choosing one or the other, i.e., their merits or liabilities. Past experiences and other associations provide the basis for such evaluation.

Similar lines of theory and investigation in neuroscience have focused on the Prospective Memory network. Here future-oriented episodic imagery, i.e. the mental construction of specific future events based on past experience, has been shown to influence decisions, including intertemporal choices. Stronger activity in this prospective memory network, including the hippocampus, is associated with decreased temporal discounting of monetary rewards (Benoit, Gilbert, & Burgess, 2011; Peters & Büchel, 2010). Wimmer and Shohamy (2012) showed involvement of the MTL in the transfer of value of rewarded stimuli by associative learning and the influence of these memory mechanisms on decisions. A recent study (Barron, Dolan, & Behrens, 2013) highlighted the involvement of the MTL in preference. When constructing preferences for novel food items based on two familiar, previously uncombined tastes, activation of the hippocampus as well as the medial prefrontal cortex were related to revealed preference.

The role of memory representations of past experience in choice can be demonstrated by showing that choice is impaired in individuals known to have memory encoding or retrieval deficiencies. Remembering past experiences and imagining future experiences activates a common set of brain regions that include the hippocampus (Schacter & Addis, 2007), and these functions are impaired in patients with hippocampal damage (Hassabis, Kumaran, Vann, & Maguire, 2007; Klein & Loftus, 2002). Thus we ask whether patients with hippocampal sclerosis are impaired in their preference construction.

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 preference transitivity, i.e., the degree to which preferences for different options are consistent across choices. For example, if a person chooses A over B, and B over C, transitivity requires that they pick A over C (Samuelson, 1938). Transitivity has been a central choice attribute in early empirical work in decision-making (Tversky, 1969), and recent preference research in neuroscience (Camille, Griffiths, Vo, Fellows, & Kable, 2011; Fellows & Farah, 2007; Fellows, 2006; Kalenscher, Tobler, Huijbers, Daselaar, & Pennartz, 2010) and consumer choice (Lee, Amir, & Ariely, 2009). One reason for focusing on transitivity is that it is central to the General Axiom of Revealed Preference and is a necessary and sufficient condition for value maximization (Houthakker, 1950). Transitivity of preferences 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).

Patients with lesions in the ventromedial frontal lobe in areas known to be involved in the expression of value have shown a greater frequency of intransitivity for choices between gambles (Camille et al., 2011) and for preferences for food, colors, and people (Fellows & Farah, 2007). The latter study included an important control: An increase in intransitivity was not observed for perceptual judgments, suggesting that preferential tasks were uniquely affected.

We adopt this paradigm but examine the effect of damage to the hippocampus, an area that has not been a focus of research on value determination, but that is, according to our hypothesis, an essential input to many kinds of value calculation. In particular, our task examines binary choices among 20 common candy bars, a product familiar and interesting to participants. We also included a control judgment, 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 (preference or magnitude) judgments.

# Methods

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). Two control groups consisted of thirty patients with extratemporal lobe epilepsy (ETL) and thirty healthy control subjects (CON), respectively (please see Supplemantary Material for data cleaning procedures). The study was approved by the local ethics committee of the University of Bonn and the Institutional Review Board at Columbia University (IRB-AAAB1301) and all subjects gave their written informed consent. The three groups did not differ with respect to age or gender (see Table S1 for details).

# Behavioral experiment

Each respondent made a series of binary choices on a computer between pairs of candy bars, presented pictorially as shown in Fig.1, drawn randomly out of a set of twenty. Each combination was presented once, resulting in 190 choices, with a different random order for each participant. This procedure was similar to that used to examine the effect of ventromedial frontal lobe damage on choice used by Camille et al. (2011), Fellows and Farah (2007) and Fellows (2006). In a control task, subjects were presented with pairs of numbers, randomly drawn from the range of one to twenty, and had to judge which number was larger. Judgment inconsistency in triplets of magnitude was computed identically for the two tasks. Subjects knew that they would receive their choice from one randomly selected candy bar choice trial, in addition to a participation fee of 10 €.

-------- Figure 1 --------

# MR sequence and analysis

For a random subgroup of the patients with unilateral hippocampal sclerosis (n=16), a 3D-T1 weighted high-resolution data set (MP-RAGE, voxel size 1x1x1mm, repetition time 1570ms, echo time 3.42ms, flip angle 15°, field of view 256mm x 256mm) was available for volumetric measurement of the hippocampus. This was done in a fully automated manner by means of the FreeSurfer image analysis suite (Version 5.1.0, Martinos Center, Harvard University, Boston, MA, U.S.A.) (Fischl et al., 2002, 2004). Because of the high variance in hippocampal volume between individuals, we used a lateral damage index of hippocampal volume to express the extent of unilateral hippocampal damage in our MTL group:

This lateral damage index can obviously be only assessed for subjects with unilateral hippocampal sclerosis.

# Statistical analysis

Statistical analyses were performed using SPSS Statistics 21.0 for Windows (IBM, Armonk, NY, U.S.A.) and R (Version 3.1.2) for Mac. We use a two-tailed p-value of 0.05 as our criterion for statistical significance and mark significant differences in the figures and tables with asterisks: \*p ≤ 0.05, \*\*p ≤ 0.01, and \*\*\*p ≤ 0.001.

## Tallying intransitivities

The binary choices made by each respondent were transformed into a matrix of choice-triplets, as the detection of intransitivity requires three choice pairs. Each matrix consisted of 1140 rows, representing all possible combinations of 3 choice pairs, out of the 190 paired comparisons of the 20 chocolate bars, that are relevant to determine transitivity. A triplet was marked as indicating intransitivity either if A was chosen over B and B was chosen over C yet C was chosen over A or if B was chosen over A and C was chosen over B yet A was chosen over C (Tversky, 1969):

or

The proportion of intransitive choices was obtained by dividing the number of intransitive triples by the total number of triples. This provided the central dependent measure. Intransitivity in revealed preferences can be expected if there is random error in the retrieval of the underlying subjective-value signals. Analytically, it can be shown that the maximum level of intransitivities (those produced by a random responder) is in 25% of all triplets. In the supplementary materials we report the result of simulations that demonstrate that the number of non-transitive choices varies non-linearly with the response error.

# Results

Patients with hippocampal sclerosis showed an increased percentage of intransitive choices compared to the two control groups in the preference task compared to the control task (Fig. 2; 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 -------

We hypothesized that hippocampal retrieval of associations acquired through past experiences with candy bars was used in preference construction and choice. Consistent with this the ratio of compromised hippocampal volume to total volume was significantly correlated with the percentage of intransitive choices (Fig.3; spearman-rho = 0.761; p<0.001; n=16).

------ Figure 3 -----

It might be the case that respondents explicitly remembered their previous choices and used this information to avoid intransitivities, and that it is such explicit declarative memory that is impaired in the MTL group. Although each pair of options is seen only once, prior choices involving one of the two candy bars might facilitate explicit recall and influence subsequent choices, and this facilitation might be impaired differentially across groups, particularly for the MTL group. We ruled out this possibility by examining whether the observed group differences in choice inconsistencies were stable across the course of the study session. The alternative explanation for the observed group differences in transitivity suggests that we should observe a general decrease in the number of intransitivities with time, but less so for the MTL group. We tested this hypothesis by looking for differences in the effects of trial on the frequency of intransitivities across groups. As detailed in the SOM, no such differences were found.

To examine the possibility of a speed-accuracy tradeoff, we examined response latencies of the choices, and the relationship between responses latencies and intransitivities. We found that slower trials were most likely to be involved in intransitive triplets, and that the MTL group had a significantly slower average response time per trial. Together, these results suggest that intransitive triplets accompany more effortful, longer responding, eliminating the possibility of a speed-accuracy tradeoff.

We also examined whether particular candy bars were more responsible for intransitivities. We regressed the number of times each candy bar was involved in an intransitive choice onto indicator variables representing the identity of each chocolate bar as well as on a factor representing group. None of these variables survived a post-hoc (Bonferroni) test of significance.

To ensure that the group differences in intransitives we observed are the result of greater random error in preference construction because of reduced access to stored associations with the candy bars (as opposed to more general computational impairments), we examined performance in the control task more closely. In the control task, respondents identified which of two numbers was larger. All groups did well, exhibiting a small percentage of intransitive judgments, though the ETL group did significantly worse than the control group (analysis of simple effects in linear mixed model, b = 0.12, t(168) = 2.05, p = 0.042) and ETL patients exhibited a much higher variance in this task. The absence of a difference in judgment intransitivity between the MTL and the control groups in this task (analysis of simple effects in linear mixed model, b = 0.04, t(168) = 1.18, p = 0.238) and the presence of a differences in choice intransitivity supports the involvement of hippocampal function in preferential choice, and not in a more general attentional or computational effect.

# Discussion

There is increasing interest in how value representations are constructed. In this paper we provide support for the role of memory in preference construction, by showing that hippocampal lesions are associated with an increase in intransitive preferences and that the degree of intransitivity is related to magnitude of the damage to the hippocampus. A control task not involving preferential choice does not show these effects, nor do respondents who have lesions outside of the medial temporal lobe. These results implicate the hippocampal areas in preference construction.

Our hippocampal patients produce patterns of intransitivity of preference that are strikingly 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). The hippocampus is one of the most highly interconnected brain areas, including a direct monosynaptic connection to the prefrontal cortex (Cole, Pathak, & Schneider, 2010; Godsil, Kiss, Spedding, & Jay, 2013; Ongür & Price, 2000). Ranganath and Ritchey (2012) proposed 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 peri-rhinal 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. Ranganath & Ritchey (2012) suggest that “the AT system could facilitate the construction of knowledge about people, so that past experiences can be used to inform inferences about the personality and intentions of others, irrespective of their behavior in a particular context.” Our results suggest that this connection to the ventromedial prefrontal cortex may also serve the construction of preferences. Fellows (2006) 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 retrieval of experiences from memory is also inhibited in vmPFC patients, and this is an interesting topic for future research.

Some early judgment and decision making research used the existence of specific forms of intransitive preferences as evidence for choice rules that differ from value maximization (Tversky, 1969), with some recent criticisms (Regenwetter, Dana, Davis-Stober, & Guo, 2011) that argue that deviations of choice patterns from value maximization may be due to simpler reasons, including changing preferences and indifference.  Our work uses intransitivities in a much simpler way, namely as evidence that preferences are less consistent in decision makers whose MTL regions have been impaired. We also show that the degree of preference instability is a function of the degree of hippocampal damage.

We do not take a specific stance on the mechanism producing these effects but speculate that they are consistent with retrieval in the MTL group that produces value representations with greater random error, either because of retrieval failures or because retrievals differ across occasions. Simulating the effect of random error or noise on the level of intransitivity shows that the observed inconsistency levels correspond to a value signal that contains approximately 25% error compared to a noiseless representation which would produce a completely transitive set of preferences (see SOM for details).

Our results suggest future research based on the following observations. 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 and 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. The role of either of these hippocampal functions in producing intransitive preferences awaits further investigation.

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 decision deficits.

Our results suggest a critical role for the hippocampus as the carrier of input into 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 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 better comprehend and model how the brain calculates value and makes wise choices.

# Acknowledgements

BW is funded by a Heisenberg-Grant of the German Research Council (WE 4427/3-1) and EUW and EJJ by NIA Grant 5R01AG027934.

# Author contribution statements

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

# Figure Legends

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

**Figure 2**. Mean percentage of intransitives per group (nMTL = 31, nC = 30, nETL = 30). Error bars represent SEM.

**Figure 3**. Relation of hippocampal ratio and intransitive choices. **a**) Example of a typical hippocampal sclerosis on a T2-weighted image highlighting both hippocampi which were used for the laterality index calculation. **b)** Scatterplot that maps hippocampal asymmetry (as a marker for unilateral atrophy) against percentage of intransitive choices, providing a regression line with 95% CI for the observed correlation of rho=0.761, p<0.001

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