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Cognitive mechanisms underlying memory-based choices

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Abstract

Most decisions we encounter in our daily life rely on past experiences. Before choosing where to go for dinner, we may think where we got delicious food last time. Suddenly, a restaurant comes to our mind that served only mediocre food. Then, instead of searching for other possibilities, we decide to go there again. We define this effect as *memory bias*: The tendency to prefer better-remembered options even if their value is below average. The aim of the present thesis is twofold. It first aims towards a better understanding of the neural mechanisms underlying memory-based choice (Manuscript 1) by reviewing the current findings of the relationship between a classical memory region (Hippocampus; HPC) and a classical valuation region (ventromedial Prefrontal Cortex; vmPFC). Second, the thesis focuses on two possible mediators explaining the influence of episodic memory on choice . The first mediator is uncertainty(Manuscript 2). Our hypothesis is that options that are remembered less are also more uncertain. As humans have a general tendency to avoid uncertain things, people prefer the better-remembered option. The second mediator is attention (Manuscript 3). We claim that visual attention mediates the memory bias as better-remembered items receive more attention and are thus chosen more often.

The review article in Manuscript 1 shows that the HPC and the vmPFC are communicating with each other during memory-based decisions. Several theoretical models try to explain this connectivity. The classical view states that HPC serves as a memory-encoding and retrieving instance while the vmPFC orchestrates what needs to be recalled for a specific choice as a central executive. Other views move away from this classical role differentiation to a common integration: both regions are involved for example in future thinking, and therefore both are relevant for memory-based decisions. Manuscript 2 shows that people have a memory bias with appetitive stimuli (monetary gains or positive images), but the effect reverses with aversive stimuli (monetary losses or negative images). This is analogous to the reflection effect in

decisions under uncertainty. Manuscript 3 shows that even though people do not pay more attention to better-remembered options, what they look at and for how long influences choices to a larger degree when they require memory retrieval during choice.

In sum, this thesis sheds light on the mechanisms underlying memory-based choice combining different techniques such as eye-tracking or computational modeling. Further directions are investigating the role of HPC in memory-based choice or the development of the memory bias over the life span.

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Chapter 1

General Introduction

> If you want to improve your memory, lend someone money.
>
> *African Proverb*

Many of our daily decisions rely on past experiences. For example, when one has to decide where to go for lunch, what hiking location to recommend to a friend, or whom to offer a job position. To choose an appropriate lunch location, one may think about the experience they last had in restaurant A: Was the food good? Where the waiters friendly? Were the prices reasonable? However, our memory is not perfect. Sometimes we cannot recall precisely how our last restaurant visit was. Previous findings (Gluth, Sommer, Rieskamp, & Büchel, 2015; Mechera-Ostrovsky & Gluth, 2018) suggest that in this case, one would prefer the better-remembered restaurant, simply because we can retrieve more details. Gluth et al. (2015) termed this effect the *memory bias* on choice. This thesis aims at a better understanding of the underlying mechanisms driving the influence of past experiences on current choices.

But why should we be interested in how memory shapes decisions? One important reason is that these findings may especially be relevant for studies focusing on memory decline in older adults. If memory declines with age, their ability to make memory-based choices should also decline. In a recent study, Levin, Fiedler, and Weber (2019) found that older adults with lower memory scores show choice inconsistencies as they prefer items with lower subjective value. One possible explanation is that their value retrieval process is noisier.

A crucial question is whether this increased noise is a direct consequence of the memory decline. Interestingly, older participants were not more inconsistent in value-based choices overall, as they did not show a higher number of intransitive choices. Moreover, some people can adapt better to the declining memory capacities than others, as implied by a study showing that the vmPFC might be crucial to do this (Lighthall, Huettel, & Cabeza, 2014). Additionally, memory states influence value-based decisions. Decisions made in the context of familiar images are more likely to be influenced by past events than decisions made in the context of novel images are (Duncan & Shohamy, 2016). Moreover, contextual novelty facilitates value learning, whereas familiarity facilitates the retrieval and use of previously learned values (Duncan & Shohamy, 2016). Another study study found that the influence might be bi-directional as deciding which information to encode enhances memory consolidation (Murty, DuBrow, & Davachi, 2015, 2019). In sum, there is already some evidence showing how memory and choice processes interact with each other. However, only recently scientists in both psychology and economics have been acknowledging the need for a simultaneous consideration of episodic memory and preferential decision-making as well as their connection to understand the choice process (Bordalo, Gennaioli, & Shleifer, 2020; Fechner et al., 2016; Gluth et al., 2015; Hoffmann, von Helversen, Weilbächer, & Rieskamp, 2018; Shadlen & Shohamy, 2016; Weilbächer & Gluth, 2017). Indeed, these two central aspects of psychology that have been studied separately for decades. This fact is also reflected in the classical view of separate brain regions exhibiting separate functions. Accordingly, episodic memory consolidation and retrieval has been attributed mainly to the Hippocampus (HPC) while the valuation of choice options to the ventromedial prefrontal cortex (vmPFC). At the same time these two regions also interact with each other during memory-based choice. Reviewing the literature on this neuronal processes is the scope of the first manuscript of my thesis (Chapter 2).

After having discussed the neuronal basis of memory-based choice, I move to investigate possible mechanisms mediating the memory bias on choice. Indeed, Gluth et al. (2015) identified the memory bias and discussed some possible mechanisms driving the effect. More specifically, they speculated if the belief

to recall better options, the uncertainty entailed in less-remembered options or visual attention towards better-remembered options would mediate the memory bias on choice. Because empirical evidence for possible mediators was still missing, further studies were needed to address these three open questions. One study already investigated and confirmed a first possible mediator: The subjective belief that options of higher value are recalled better (Mechera-Ostrovsky & Gluth, 2018). Accordingly, the next two manuscripts of my thesis will show empirical evidence on two possible mediators for the memory bias. The second manuscript (Chapter 3) focuses on uncertainty as possible mechanism mediating the memory bias on choice. Here, I aim at answering the question: is it possible, that people tend to prefer better-remembered options because they want to avoid the uncertainty entailed in the less-remembered option? The third and last manuscript of this thesis focuses on a third possible mediator for the memory bias: visual attention (Chapter 4). Here, the spotlight lies on the question whether increased attention towards better-remembered options mediates the preference for these options. In the concluding chapter (Chapter 5), I draw the conclusions of the present thesis and provide some input for future research addressing some open questions as well as new designs aiming to answer some of them. Analogous to the historical research development, I will start by giving an historical overview of the central concepts of episodic memory and preferential decision-making separately. Afterwards, I will present recent developments in studying the two concepts together.

1.1 Episodic Memory

Episodic memory is a form of long-term memory. It relates to the recall of past episodes and entails contextual details. One example is the following description of a past event: "When I think of my diploma ceremony, I clearly remember the dean giving his talk, then the diplomas were handed out to everyone after their name was said aloud. It was a sunny day in mid-October." The reader is referred to the work of Milner, Squire, and Kandel (1998) or Squire and Wixted (2011) for an overview of different memory systems and their neuroanatomy.

Importantly, to understand how we can reproduce the described episode,

we need to take into account the three stages entailed in memory: i) encoding, ii) consolidation (storage), and iii) retrieval. Moreover, during encoding and retrieval, short-term memory is essential, whereas the consolidation process is unique for long-term memory. Consolidation is an iterative process: every recall of a past event at the same time modifies this event. That selective retrieval influences recall performance has been reported in several instances (Anderson, 2003; Bäuml, 2019; Tulving & Arbuckle, 1966). For example, assume that someone asks you to define what differentiates the new Corona-virus from a normal flu: you may start thinking about what you heard and read in the media — you retrieve information from memory. Then, you give an answer. Next time you are asked the same question, other aspects might be more prominent because you retrieved them already last time, or while thinking again about it you see a more concise way to explain it to your interlocutor. Accordingly, we change our memories with every retrieval.

1.2 Value-Based or Preferential Choice

Classically, we distinguish between two types of decisions: perceptual and preferential. Perceptual decisions, such as indicating whether the traffic light is red or green, have an objective criterion defining what is correct or incorrect. Preferential or value-based decisions, such as choosing which car to buy, do not have an objective criterion. Instead, the option's value is subjective: Person A might like apples more than person B does. Therefore, in our studies, participants' preference assessment is crucial before starting the decision task as preferences change from individual to individual. The present thesis focuses on preferential or value-based decision-making.

According to rational choice theory, people always [1] select the choice option with a higher subjective value as they aim to maximize utility (von Neumann & Morgenstern, 1944) or expected value (see Fishburn, 1981 for a review on normative theories, for a more recent review see Rieskamp, Busemeyer, and Mellers, 2006). Consequently, also when making memory-based choices people should rely on utility maximisation.

[1] with exception of errors, which can occur for example in case of inattention

1.3 Memory-Based Choice

In the previous section, I have considered memory and decision-making as two distinct and independent processes. In this section, I present evidence showing how they are interdependent. In many cases, our previous experience influences our current choice behavior. Imagine, for example, a bored corona-locked-down person has to decide which way to go on their daily walking tour, escaping the permanent staying at home. They may think of their past experience: When turning left, they will come across a beautiful park while when turning right, hmm... what was there again? They cannot recall. What should they do in this situation? Should they go direction park or direction unknown?

Memory-based decision-making is currently experiencing a growing attention in research, however, already thirty years ago, researchers acknowledged that the two concepts of memory and choice might be related to each other. For example Dick, Chakravarti, and Biehal (1990) investigated how people decide when they do not have all information at hand. Assume, for example, that you are looking for a new smartphone. You might remember that there were some products you already saw and liked, but in the moment of recalling these options, not all information is readily accessible to you. Dick et al. (1990) found that in the case of low memory accessibility, participants inferred missing attributes based on the option's prior evaluation. However, when people could follow a diagnostic inference rule (for example a cheap camera has a low pixel resolution), they could infer missing attributes based on their previous experience. Accordingly, their inferences were not based on previous evaluations (*evaluative consistency*), but on a causal or ecological relationship between missing attributes and known attributes (*probabilistic consistency*).

The work presented in this thesis is mainly based on the finding from Gluth et al. (2015) who showed that people tend to prefer better-remembered items. To investigate the role of memory on preferential choice they introduced the *remember-and-decide task* (see details in Chapter 3.3). Assume, you remember one choice option while having forgotten the other one (like in the walking example above). How do people tend to deal with this situation? They tend to choose the better-remembered option, even though this option is (based on people's stated preferences before the choice task) lower in value than the for-

gotten option. This choice behavior is a deviation from rational choice theory. A rational decision-maker when they remember an option of average value, they would assume that the forgotten option is of average value too, and would choose it in 50% of the cases. However, it has been observed that this is not the case and thus this phenomenon has been categorized as a *bias*, more precisely the *memory bias*. However, people are not completely biased towards the remembered option: If it is a very lousy alternative, people would still reject it and go with the forgotten one. Gluth et al. (2015) discussed three possible mechanisms driving this effect: visual attention, uncertainty, and subjective belief. A first possible mediator for the memory-bias that has been confirmed is subjective belief (Mechera-Ostrovsky & Gluth, 2018) or the assumption that people form the belief that they recall more valuable options more often than bad options. The reason for this can be found in the tendency to search for logical explanations. When a building collapses, we investigate in detail the possible reasons for it, as we know buildings do not collapse just accidentally. Accordingly, when we stand in front of our office deciding to go towards restaurant A or B, we might think what is the reason that we recall all these details of restaurant A, but not B. Maybe restaurant A is simply better. From an evolutionary perspective it is useful to memorize things associated with positive emotions. Knowing where the best fruits grow can prevent us to die from starvation. Mechera-Ostrovsky and Gluth (2018) showed that there is a positive relationship between how well people think they recalled an option and the size of the memory bias. In other words, the stronger the belief in better memory for more desired options is, the larger the memory bias on choice is. However, this might be only a part of the picture: Even though this belief represents an adaptive behavior, the memory bias persists after correcting for the value of the forgotten option, indicating that there are more underlying cognitive mechanisms that may play a role for memory-based choices. During my PhD, I investigated other two possible mechanisms more in detail: uncertainty (Chapter 3) and visual attention (Chapter 4).

1.4 Describing Choices using Sequential Sampling Models

In the study presented in Chapter 4 the intent is to better understand the underlying cognitive mechanisms of memory- and value-based choice as well as their interaction with visual attention. Computational models are tools helping us researchers to do so. These models translate assumptions on cognitive processes underlying behavior into mathematical equations. We can estimate the model's parameters and check if its predictions match the observed data. Sequential Sampling Models (SSM) do exactly this including two important determinants of decision-making and predict them reliably: choice accuracy (in preferential choice determined by the subjective value of items [2]) and the response time (how long did it take until the decision-maker pressed a key indicating its choice, starting from stimulus onset). SSM can be divided into two classes (Ratcliff, Smith, Brown, & McKoon, 2016): diffusion models and accumulator models. All models have one central aspect in common: over time, evidence in favor of one or the other option is being accumulated (assuming a binary choice: a decision between two options). Once a pre-defined threshold is reached, a choice is made. A widely used model in the decision-making literature is the Ratcliff Diffusion Decision Model (DDM; Ratcliff, 1978, for an illustration see Figure 1 upper panel) [3]. The simplest version of the standard DDM includes four parameters (see Figure 1): non-decision time (ndt), starting point bias (z), the drift rate (v), and the boundary separation (a). The non-decision time is the time allocated to components such as stimulus encoding and response execution (Ratcliff & Tuerlinckx, 2002). The starting point bias z determines if the decision maker has an initial preference towards one or the other option. Assume, for example, the choice between two snack items: If we learned that the chips we like so much will probably appear on the left screen size, we might be biased towards preferring items on this side of the screen. The boundary separation a determines at which time point the evidence accu-

[2] As introduced earlier, preferential choice does not have an objective criterion for which option is better. However, this can be inferred from participants subjective stated preferences. If a person rated the apple with a 5, and a banana with a 7, they should prefer the banana over the apple.

[3] Interestingly, the original DDM was used as "A theory of memory retrieval" as the 1978 article was entitled. The use as a model of decision-making came only later.

mulation ends. When the boundaries are low, less evidence is needed to make a choice. This also depends crucially on the fourth parameter in the model: the drift rate v. This parameter determines the slope of the accumulation process: The steeper, the faster the boundary is reached and the shorter the response time. This class of models can account for central findings in speeded-choice experiments: the speed-accuracy trade-off (people need to trade-off whether to make few errors at the cost of a slower response time, or in contrast, to make more errors but being faster), higher accuracy and faster response times for easy choices, as well as RT distributions for correct and incorrect choices.

The attentional Drift Diffusion Model (aDDM; Krajbich, Armel, and Rangel, 2010; see Figure 1 lower panel) is an extension of the classical DDM. The key idea of the aDDM is that fixations toward an item introduce a temporary bias in favor of this option. This is realized including a gaze bias parameter θ. The central difference to the classical DDM is that the slope of the drift rate depends on the fixation location. The aDDM is able to explain choice biases that arise from the amount of visual fixation. First, the model predicts a last-fixation bias: The option fixated as last is more likely to be chosen. Second, it predicts a bias in favor of the option that was fixated longer. Third, it correctly predicts left-biases: If the left option is being fixated first, its choice probability increases. Here, the model accommodates for cultural norms, like reading left to to right. In chapter 4 I present a recent adaptation of the aDDM more in detail: the Gaze-Weighted Linear Accumulator Model (GLAM; Thomas, Molter, Krajbich, Heekeren, and Mohr, 2019). We implemented that model to better understand the interplay of memory and attention in preferential choice.

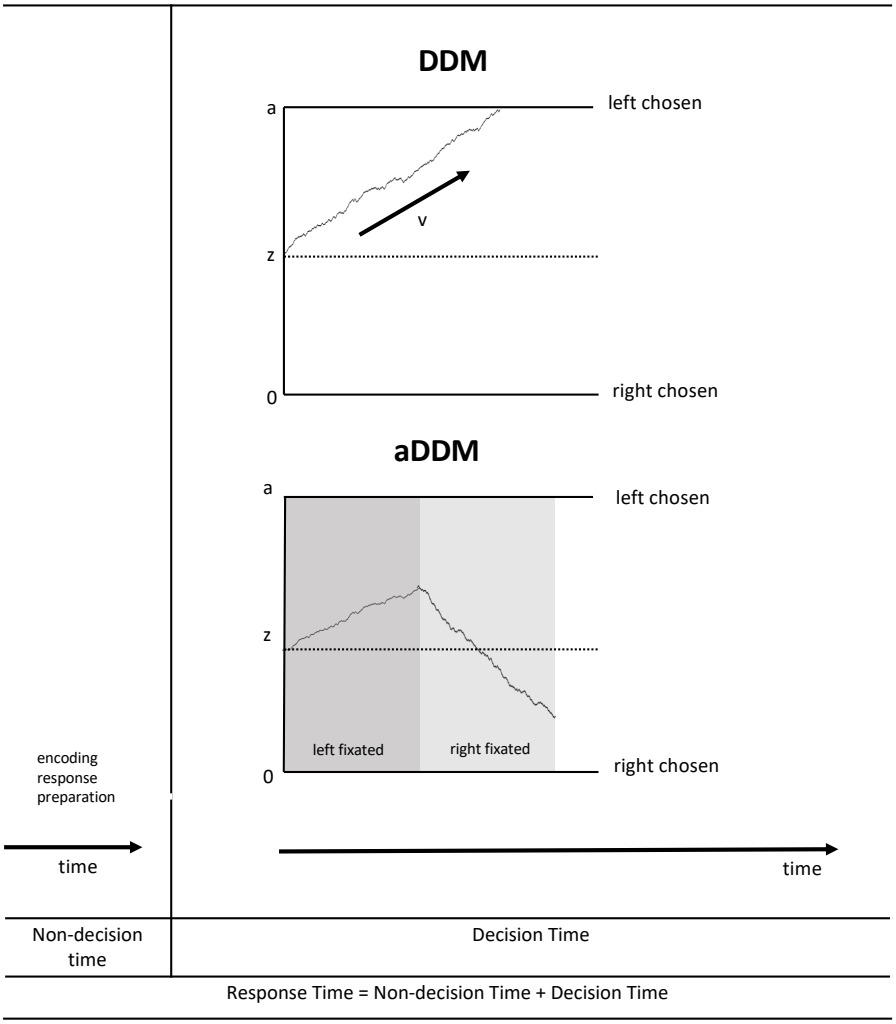

Figure 1: Overview of the diffusion model. On the left, is indicated the non-decision time, including time for encoding the stimuli and preparation for the response. On the upper right, is depicted the DDM, with the drift rate v, the boundary separation a, and the starting point z. On the lower right is the aDDM with a changing drift rate according to the fixation location. The figure has been inspired by Wagenmakers, Van Der Maas, and Grasman (2007).

Chapter 2

The Neuronal Evidence of the Interplay of vmPFC and HPC

As I have shown in the introduction of this thesis (Chapter 1), memory and choice processes have mainly been studied separately. Recent work, however, focuses on the interplay of these two fundamental aspects of cognitive psychology (Bakkour et al., 2019; Biderman, Bakkour, & Shohamy, 2020; Gluth et al., 2015; Wimmer & Büchel, 2016). The review article I am going to present here aims at giving an overview over this new development from a neuronal perspective, focusing on the interplay of a classical *choice* region — the ventromedial prefrontal cortex (vmPFC) — and a classical *memory* region — the Hippocampus (HPC). For an overview of the results reported in this chapter see Table 1. The article sheds light on the mechanisms underlying the interplay of these regions and on their theoretical meaning. Moreover, it develops some new research question for future directions. Importantly, neuroeconomics is a fast evolving field, therefore, since the publication of the following review article several advances have been made in the attempt to fill this gap. In the General Discussion in Chapter 5, I will also discuss them in relation to the open questions and future directions stated in the review article. Before presenting the evidence on the interplay of HPC and vmPFC, I present each area and the classically attributed functions separately.

2.1 Manuscript 1: The Interplay of Hippocampus and ventromedial Prefrontal Cortex in Memory-Based Decision Making

Weilbächer, R.A., & Gluth, S. (2017). The interplay of hippocampus and ventromedial prefrontal cortex in memory-based decision making. *Brain sciences*, 7(1), 4. https://doi.org/10.3390/brainsci7010004

2.2 Memory and the HPC

One method to find regions that are essential for memory recall are lesion studies. The patient H.M. (1926 - 2008) is probably one of the most studied cases related to the loss of consolidating memories, also referred to as anterograde amnesia. H.M. suffered from severe epilepsy, therefore in a surgery, large parts of the Medial Temporal lobe, including about 2/3 of the HPC, were removed bilaterally. As a consequence, H.M. did not suffer from epileptic seizures but was also unable to store long-term memories. However, associative memory was not affected; for example, he was able to learn to play golf. His lesion and the consequent memory impairment contributed crucially to the development of the Hippocampus structure model (Knierim, 2015; Milner et al., 1998; Squire, Genzel, Wisted, & Morris, 2015; Squire & Wixted, 2011). Accordingly, the HPC is essential when it comes to long-term memory consolidation and retrieval. With the development of neuroscientific methods[1] like functional magnetic resonance imaging (fMRI), it became possible to observe the neuronal activity of specific brain regions directly without the need to wait for a person suffering from a lesion in a specific brain region . Consequently, the functionality of the HPC could be examined in healthy participants. There is converging evidence, that episodic memory depends on HPC and the surrounding medial temporal lobe cortices (Kensinger & Corkin, 2004; Paller & Wagner, 2002; Squire & Bayley, 2007). Episodic memory is a quite large term, research has found the HPC to be relevant for all processing steps, such as encoding (Raynal, Schnider, & Manuel, 2020), (re-)consolidation (Girardeau

[1] For an overview of different neuroscientific methods with a focus on financial decision-making see Kraemer, Weilbächer, Fontanesi, and Gluth, 2020.

& Zugaro, 2011; Nadel & Moscovitch, 1997; Takehara-Nishiuchi, 2020)), and retrieval (Carr, Jadhav, & Frank, 2011).

2.3 Decision-Making and the vmPFC

The vmPFC has been recognized as a crucial area evaluating the value of choice options (Bartra, McGuire, & Kable, 2013; Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994; Grueschow, Polania, Hare, & Ruff, 2015). But an important issue is that in contrast to the HPC, which is also a clearly distinguishable anatomical structure [2], the vmPFC is a purely functional area in the brain. Accordingly, when reading about vmPFC readers must be careful, as the choice of what is vmPFC and what not might be (more or less) arbitrarily chosen by the authors and is not determined by Brodman Areas or MNI coordinates.

On the one hand, there is evidence from lesion studies, showing an impairment in making transitive choices (Fellows & Farah, 2007) and making future-oriented decisions (Peters & D'Esposito, 2016). Also more recent lesion studies, published after the review article corroborate these findings. For example a study has found an impairment in integrating counterfactual value signals in a risky choices lottery task (Bault et al., 2019). The authors of another more recent study conclude that "The vmPFC may provide an important neural mechanism for aligning behavioral choices with expressed preference" (Bowren, Croft, Reber, and Tranel, 2018, p.280) as they report that following a vmPFC damage, patients showed less consistency between their stated preferences and later choices (Bowren et al., 2018). Importantly, this decreased consistency between choices and preferences was only observable in a social context (spouse choice) but not in a non-social context (house choice).

On the other hand, the advances and increased use of fMRI have contributed crucially in the understanding of this region of interest. Most notably and largely accepted is the finding that vmPFC processes subjective value (Chib, Rangel, Shimojo, and O'Doherty, 2009; Lebreton, Jorge, Michel, Thirion, and Pessiglione, 2009; for review articles see Clithero and Rangel, 2014; Vaidya

[2] the name indeed describes his form - and derives from the mythological sea-horse or Hippocampus

and Fellows, 2020). Based on these findings the theory of *common currency* has been developed, stating that the vmPFC integrates value signals into one common value, which allows comparing apples and oranges (Gross et al., 2014; D. J. Levy & Glimcher, 2011; Dino J Levy & Glimcher, 2012) and thus confirming a *valuation system* in the brain including vmPFC and the ventral striatum (for details see this meta-analysis: Bartra et al., 2013).

2.4 Other Directions: HPC is Important for Choices

Even though the vmPFC appears to be a crucial area involved in value-based choice, also the HPC appears to play a non-neglectable role. A recent study found that a higher hippocampal activity for longer deliberations on choice (Bakkour et al., 2019). This result was confirmed using both fMRI results of an empirical study as well as comparing lesion patients to healthy participants. Moreover, another study (Palombo, Keane, & Verfaellie, 2015) investigates how the HPC shapes decisions. The authors argue that the HPC is potentially involved in three processes: updating, generalization, and construction. A recent review (Biderman et al., 2020) moreover points out the crucial role of the HPC in guiding future behavior (see also Schacter, Benoit, De Brigard, and Szpunar (2015). We know that the hippocampal place cells are also related to future planning from animal studies (Ambrose, Pfeiffer, & Foster, 2016). The HPC seems to be involved in several processes crucial for decision-making: memory integration, generating value, and recombining value (Palombo et al., 2015). Importantly, value guides what we remember as we remember highly arousing things better (Kensinger & Corkin, 2004), leading to anticipation and retroactive consolidation. Moreover, a recent study focusing specifically on memory retrieval of past episodes experienced once (Wimmer, Liu, Vehar, Behrens, & Dolan, 2020) showed with Magneto-Encephalo-Graphy (MEG) that retrieval one day later was supported by the sequential replay of episode elements. Similarly, a recent preprint (Wimmer & Büchel, 2020) shows that the HPC is involved in the retrieval of aversive experiences and this affects later choices (stimuli avoidance). Taken together, these results indicate that the HPC appears to be more than a simple episodic memory retrieval location, especially when it comes to the anticipation of future events, what choices often are.

Interestingly, a similar role has been found to execute the vmPFC (Benoit, Szpunar, & Schacter, 2014).

2.5 Interactions between vmPFC and HPC

Despite the technical advances in the last decades the neural mechanisms underlying the connection between vmPFC and HPC are mostly unclear. Mainly two methods have been used to investigate the interplay of these two regions: theta/gamma band phase coherence of oscillations and Dynamic Causal Modeling (DCM). DCM allows to measure the extent and direction of effective connectivity between different brain regions (for a review of functional and effective connectivity see Friston, 2011). Coherence in theta-band (approx. 5-10 Hz) or gamma-band (low: 35-55 Hz, high: 65:90 Hz) can be measured with MEG or Local Field Potentials (LFP) in humans and animals. Results from studies in rodents showed a higher theta-band synchrony in memory (for a review see Colgin, 2011) or in human decision-making (Guitart-Masip et al., 2013). An increased gamma-band oscillation synchrony has been related to spatial learning and memory (Spellman et al., 2015).

The study of Gluth et al. (2015) already presented earlier in relation to memory-based choices and the remember-and-decide task also collected fMRI data and used DCM investigating the coupling between vmPFC and HPC. They found this coupling not only important for processing memory-based decisions but also for mediating the memory bias specifically.

On a theoretical note we can draw some conclusions from this coupling: Shin and Jadhav (2016) relate it explicitly to memory-based decisions, among memory consolidation and contextual memory retrieval. From a classical role differentiation perspective one could conclude that HPC is merely involved in memory encoding, while the vmPFC in memory retrieval, this retrieval is crucial for memory-based choice. Many results described above, when it comes to the separate roles of these two regions, as well as some presented connectivity analyses would come to a similar conclusion. However, a classical role differentiation model might be insufficient to explain the entire picture. The PFC is more than a simple executive control and the HPC more than a memory-encoding region. Another theory put forward is the one that this

coupling refers mainly to schema formation and retrieval (Preston & Eichenbaum, 2013). A more recent study reports an increased connectivity between our two regions of interest during the construction of episodic future events (Campbell, Madore, Benoit, Thakral, & Schacter, 2018). Another study reports effective connectivity within the vmPFC-HPC-amygdala network during the elaboration of emotional autobiographical memories (Nawa & Ando, 2019), indicating that the vmPFC drives hippocampal activity during memory elaboration. These results have been confirmed by a recently published preprint (McCormick, Barry, Jafarian, Barnes, & Maguire, 2020). This study confirms moreover the theory of systems-consolidation. Accordingly, the vmPFC may communicate with the hippocampus early in the consolidation process (Bonnici & Maguire, 2018; Kitamura et al., 2017) to start integrating autobiographical memories with existing schemata. Once memories are consolidated, vmPFC acts like a conductor orchestrating the memory recall, selecting what ends up in the HPC and can be then used to re-construct past events that are already consolidated (McCormick, Ciaramelli, De Luca, & Maguire, 2018). Additionally findings from developmental research show that an increased vmPFC-HPC coupling from adolescence to adulthood is related to better problem solving and future planning skills (Calabro, Murty, Jalbrzikowski, Tervo-Clemmens, & Luna, 2020).

Taken together, recent research seems to focus more and more on memory-based choices leading to a more differential picture away from the classical role attributions (HPC=memory, vmPFC=value) to a more interactive picture. Both, HPC and vmPFC are crucially involved when it comes to future planning, and this planning is important when selecting which past experiences are relevant in the current situation (Biderman et al., 2020).

Table 1: Overview findings reported in Chapter 2

Area of interest	Role
vmPFC	
	• Impairment in making transitive choices after lesion (Fellows & Farah, 2007) or future-oriented decisions (Peters & D'Esposito, 2016)
	• Impairment in integrating counterfactual value signals (Bault et al., 2019)
	• Alignment choices with stated preferences (Bowren, Croft, Reber, & Tranel, 2018)
	• Processing and integrating subjective value as part of valuation system (for example, Vaidya and Fellows, 2020) in accordance to the common currency theory (D. J. Levy & Glimcher, 2011)
HPC	
	• Long-term memory storage impairment after lesion (for example, Milner, Squire, and Kandel, 1998)
	• Importance in all phases of episodic memory (encoding, consolidation, retrieval; for example, Squire and Bayley, 2007)
	• Choice deliberation (Bakkour et al., 2019)
	• Anticipation of future events (for a review see Biderman, Bakkour, and Shohamy, 2020)
	• Generating and recombining value (Palombo, Keane, & Verfaellie, 2015)
Interaction vmPFC - HPC	
	• Theta-band synchrony in animal memory (Colgin, 2011) and human decision-making (Guitart-Masip et al., 2013)
	• Gamma-band synchrony in spatial learning and memory (Spellman et al., 2015)
	• Effective connectivity: processing memory-based choice and mediating the memory bias (Gluth, Sommer, Rieskamp, & Büchel, 2015)
	• Schema formation and retrieval (Preston & Eichenbaum, 2013)
	• Memory consolidation (Bonnici & Maguire, 2018; Kitamura et al., 2017) and reconstruction (McCormick, Barry, Jafarian, Barnes, & Maguire, 2020; McCormick, Ciaramelli, De Luca, & Maguire, 2018; Nawa & Ando, 2019)
	• Problem solving and future planning (Calabro, Murty, Jalbrzikowski, Tervo-Clemmens, & Luna, 2020; Campbell, Madore, Benoit, Thakral, & Schacter, 2018)

Chapter 3

Uncertainty is Driving the Memory Bias

Uncertainty is a multi-faceted term with various definitions depending on the context. Classically, with uncertainty we indicate a situation where the outcome is uncertain. In the case of lotteries we distinguish between uncertainty with known probabilities (risk) and uncertainty with unknown probabilities (ambiguity[1]; Ellsberg, 1961). To make the distinction between risk and ambiguity clearer let us first consider the case of a risky choice as it is entailed in the lottery. Many people play it, but the chance to win is extremely low. However, the motivation to play it is that if one wins, they get a multiple of the amount they invested by playing it. Therefore, the decision if one should play the lottery having a low chance to win or keeping the money for a coffee, depends on what expectations the gambler has to win. The described situation entails decisions under risk, here the extent of uncertainty is known, as the probabilities of winning are known (for the Swiss lottery, the chance to get six numbers correct from 42 possible numbers is 1 in 5'245'786). However, one could also face the situation where the probabilities on an event to occur are (partially) unknown. For example, how probable is it that there will be a new global pandemic caused by a new virus in 2030? A scientist might come up with some estimations based on data of past pandemics, but these estimates might be imprecise as pandemics are rare events. However, the scientist will not

[1] However, often the term ambiguity and uncertainty are used interchangeably, what leads to additional imprecision in the use of the term *uncertainty*.

be able to say chances are 1:1milion. They might say something like chances are between 1:1bilion and 1:1milion (depending on how different factors are included, for example, a region's preparedness). This information is ambiguous. Importantly, a central finding is that people's behavior differs when they play to win a monetary reward or when they want to avoid a monetary loss. On the one hand, in the gain domain, people tend to be uncertainty averse, preferring the save alternative. For example, most people would prefer receiving 5 CHF for sure, instead of 10 CHF with a probability of 50%). On the other hand, people tend to be more uncertainty seeking in the loss domain thus preferring to gamble. This effect has been termed the *reflection effect* (Kahneman & Tversky, 1979). In the following manuscript I present how I used the reflection effect to explain how uncertainty is driving the memory bias on choice.

3.1 Manuscript 2: The Reflection Effect in Memory-Based Decisions

Weilbächer, R. A., Kraemer, P. M., & Gluth, S. (in press). The reflection effect in memory-based decisions. *Psychological Science*.
Preprint: https://doi.org/10.31234/osf.io/jsqp4

3.2 Theoretical Background and Hypotheses

In this manuscript, we investigated if uncertainty mediates the memory bias. We hypothesized that memory-based choices are comparable to decisions under uncertainty. Deciding between a well-recalled and a poorly-recalled choice option might be analogous of choosing between a safe and an ambiguous lottery. Research on decision-making under risk (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981) and ambiguity (Kahn & Sarin, 1988; Viscusi & Magat, 1992) have demonstrated a *reflection effect*. The reflection effect states that people tend to be uncertainty averse in the gain domain but become uncertainty seeking in the loss domain. As stated in the introduction of this chapter, we define uncertainty as outcome variance: an uncertain option entails more variable consequences. We assumed that with our *remember-and-decide* task, we would elicit a similar kind of uncertainty, or more specifically ambiguity

when people recall one option better and one less. In this case, participants might think: "Well, I forgot the right option, but I know what is hiding behind the left option. Therefore, it is better to go with that option to avoid picking a lousy option". As people differ in their risk/ambiguity attitude, they also differ in the strength of the memory bias. Therefore we additionally assumed to find a relationship between these two measures.

3.3 Methods

The Remember-and-Decide Task

The *remember-and-decide task* is a paradigm to investigate the memory bias in preferential choices (Gluth et al., 2015). It is comparable to a memory game (also known as the pairs game) and it consists of four phases that repeat over several rounds: encoding, distraction, decision, and recall. For an overview of the task used in M2 and M3 see Figure 2. In the encoding phase, participants learn the association of a location on the screen (a square) and a stimulus (snack item, monetary reward, or image). In the memory game, this would correspond to the player turning around a card to see its content. The distraction phase is crucial to investigate long-term declarative episodic memory and not short-term memory. Therefore, participants perform a two-back working memory task for 30 seconds. In this task, participants have to indicate if the current stimulus is equal to the one two stimuli before. We used either numbers or letters. For example, in the series 1-5-1-8, the participant would need to press the space bar as soon as the second "1" appears. In the memory game, this would correspond to the players talking about the weather before playing the next round. In the decision phase, the participant sees highlighted two positions. Their task is to indicate the preferred option. The arrangement allows one option to be more left and one more right. As the participant does not see the stimulus on each location, they need to retrieve them from memory. Here, three things can happen: they recall both stimuli, they recall none or they recall one. If they recall both, they should be able to indicate the better-preferred item easily. If they recall none, they can only guess, therefore their choice accuracy should be at 50%. Crucial for us is what we observe when participants recall

only one option. Here, participants should prefer the remembered option if its subjective value is average or higher than the average of all seen options. However, we observe a shift: participants still prefer remembered items that are below average until a specific cut-off while still rejecting nasty alternatives. We call this shift the memory-bias of choice as it represents a deviation from the utility maximisation theory introduced earlier. Last, we need to asses if participants recalled a particular item or not. Therefore, in the recall phase we show each location again, asking the participants either to indicate the name of the product associated with that location (free recall) or to select the correct item among a set of possibilities (multi-alternative forced-recall).

Assessing the Memory Bias

To asses the memory bias on choice I used a logistic regression. The aim is to predict the choice probability for the remembered item based on the stated value of the remembered item using a sigmoid function. Accordingly, the probability p_i to choose the remembered option i over the forgotten option is given by:

$$p_i = logit(\beta_0 + \beta_1 * x_i), \tag{3.1}$$

where x_i refers to the standardized subjective value of option i, and β_0 and β_1 refer to intercept and slope coefficients, respectively. The probability that the remembered option will be chosen is estimated by drawing from a Bernoulli distribution with success probability p_i:

$$y \sim \text{Bern}(p_i), \tag{3.2}$$

A memory bias in the sense of preferring remembered over forgotten options is present if the intercept coefficient of this regression is positive (Gluth et al., 2015). Note, we always used a corrected value as predictor, meaning we subtracted the average value of participant's forgotten options from the value of the remembered item before performing the regression analysis. This correction ensured that the memory bias was not solely driven by the possibility that forgotten options were less valuable than remembered options [for more details, see Mechera-Ostrovsky and Gluth (2018)].

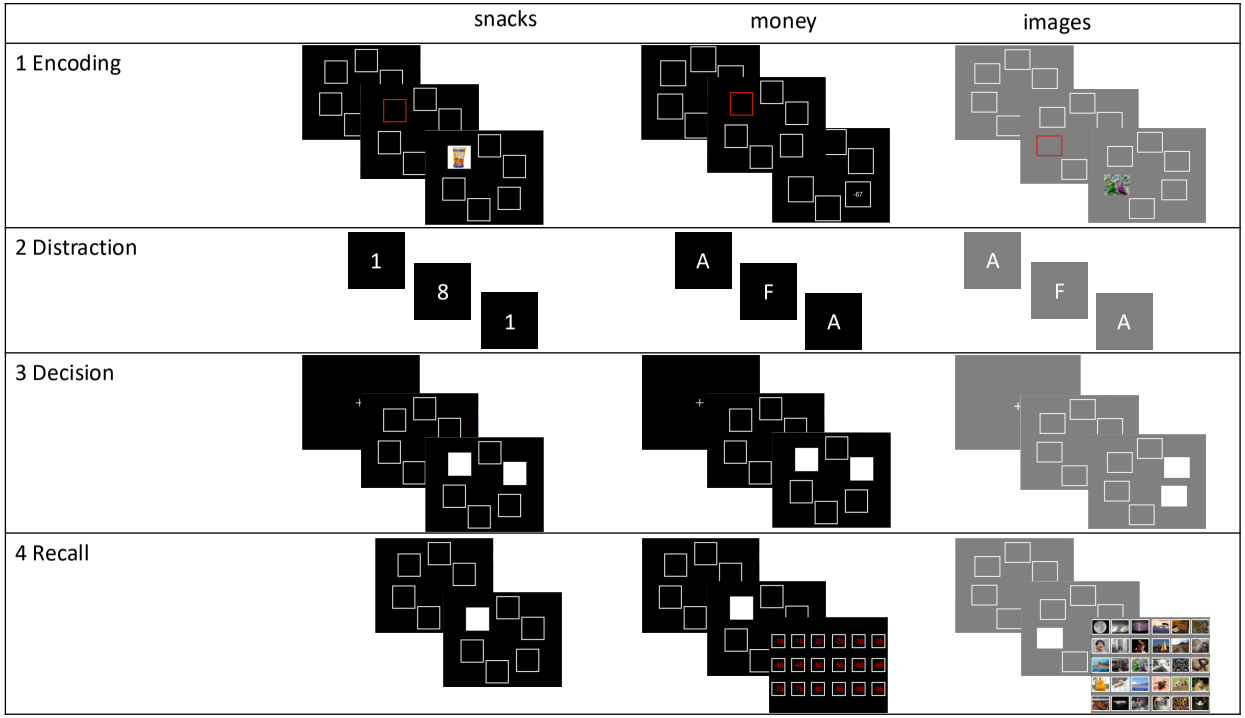

Figure 2: Experimental paradigm (*remember-and-decide task*). An example round of the task is shown for three different stimuli (snacks, money, and images). Each round consists of four phases. In the first phase participants encode the association of items and screen locations. The second phase is a 2-back task to overwrite working memory. Third, participants perform binary preferential choices. Critically, only locations but not items are shown, so that the items need to be recalled from memory. Fourth, participants are asked to recall each item and to rate their memory strength by answering to the question "How well do you remember the product?". The answer ranges from "very poorly" to "very well".

In M2 the logistic regression was estimated in the hierarchical Bayesian framework while in M3 in the frequentist framework via maximum likelihood. The results are similar. In M2 we reverted to a hierarchical Bayesian framework because we were interested in comparing two conditions against each other: the memory bias in the gain domain and in the loss domain on the group level (not the individual participant level). Is the difference credible we observe a reflection effect. While in M3 our aim was simply to replicate the memory bias, therefore we used the individual frequentist version, thus estimating the size of the memory bias for each participant individually.

In Figure 3 the raw data from the three empirical studies are shown (only for the gain domain) including snacks (M3), money (M2), and images (M2). For all three stimuli types the memory bias could be replicated.

3.4 Results

Replicating the Memory Bias and Confirming its Reflection in the Loss Domain

In both experiments, with monetary rewards and images, we could replicate the memory bias in the gain domain (Figure 3). The central finding of this paper is that the memory bias seems indeed to be analogous to the reflection effect, indicating uncertainty aversion in the gain domain and the opposite behavior in the loss domain (Figure 2 Appendix B). In other words, in the gain domain people are more uncertainty averse, and show a memory bias. While in the loss domain they show the inverted effect: they become more uncertainty-loving and prefer less-remembered options. In short, the memory bias is present in the gain domain only, while the effect inverts in the loss domain when it comes to the loss of money or the presence of aversive images.

The Memory Bias is not related to the Uncertainty Attitude in an independent Gambling Task

With our remember-and-decide task we measured the size of the memory bias in the gain compared to the loss domain. As reported previously, we found a reflection of the memory bias in the loss domain. This confirms our main

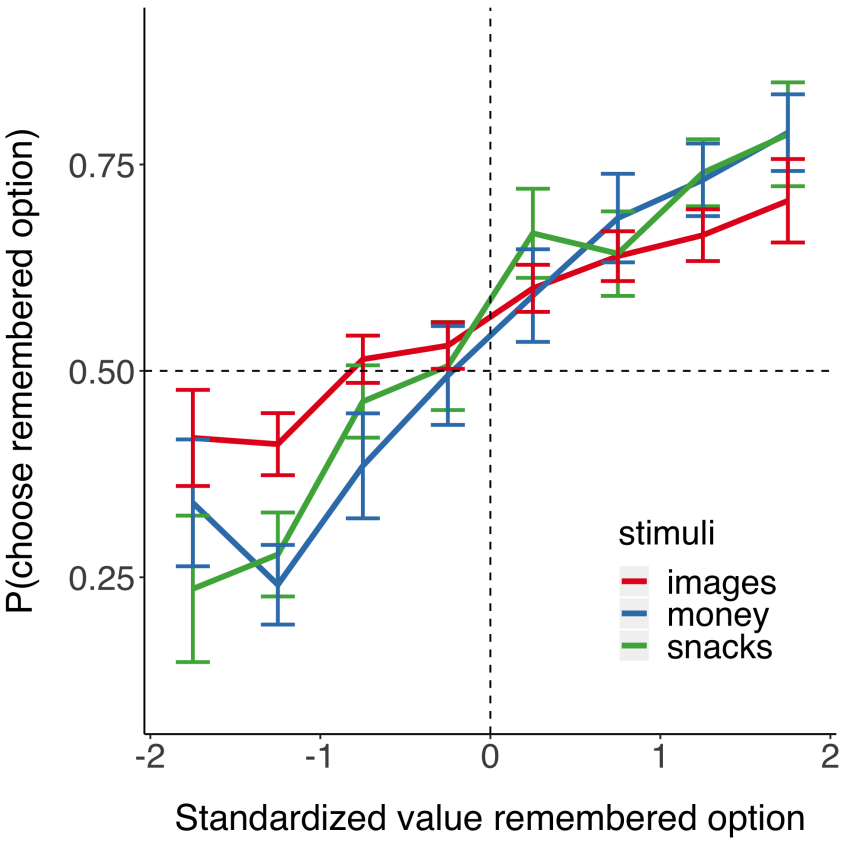

Figure 3: The raw data (gain domain only) for the three stimuli types including: snacks (M3), money (M2), and images (M2). The probability to choose the remembered option (x-axis) increases with the value of the remembered option (y-axis). Importantly, when the standardized value of the remembered option equals 0, or in other words is of average value, people choose the remembered option in more than 50% of cases. This is the memory bias of choice.

hypothesis on the analogy between memory-based choices and choices under uncertainty. To further strengthen this notion, we also measured participants risk and ambiguity attitudes in a separate gambling task in a second experimental session. We expected the difference of the memory bias in the gains vs. losses to be correlated with the difference in risk or ambiguity attitudes in gains vs. losses. Moreover, we assumed to find an association specially with ambiguity attitudes. As not remembering well an option is similar as not knowing the probability to win a lottery. However, we did not observe any relation between the memory bias and the separate uncertainty measures, nor with risk neither with ambiguity. The only significant effect was the experiment: the size of the memory bias is larger with images than with monetary rewards. Crucially, in our study we did not find a relation between the extent of the memory bias and people's uncertainty attitudes as measured in a separate gambling task (Figure 3 Appendix B).

3.5 Discussion

In M2 I tested whether the memory bias on preferential choice shares characteristics of the well-known reflection effect in choices from uncertainty (Kahn & Sarin, 1988; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981; Viscusi & Magat, 1992). Using two different stimuli, images and monetary rewards, I showed that in the gain domain people prefer better-remembered options as in previous studies (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018). But in the loss domain the effect inverts: here less-remembered options are preferred. This finding suggests that the uncertainty entailed in weak memories influences choice behavior.

A future direction would be to investigate how strongly recall certainty (for example a person remembers an option in all its details) influences choices. Analogous to the probability weighting function of prospect theory (Amos Tversky & Kahneman, 1992). Secondly, episodic memory capacity declines over the life span (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012). Further investigations may uncover how the relationship between uncertainty attitudes and the memory bias evolve over time. Thirdly, neuroscientific results may backup our behavioral results. For ambiguous choices a brain circuitry

including amygdala, orbitofrontal cortex, and dorsomedial prefrontal cortex (dmPFC) has been established (Hsu, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006). Or the dmPFC as well as the anterior Insula for risky choices (Mohr, Biele, & Heekeren, 2010; Morriss, Gell, & van Reekum, 2019). One could speculate the role of these regions to be similarly involved when people perform our memory-based choices in the gain and the loss domain.

Next, I discuss some possible reasons why we did not find an association between the memory bias and people's uncertainty attitudes. First, there are several ways how risk (and ambiguity) attitudes can be assessed. As we were interested to discriminate between both measures, we relied on the behavioral task proposed by (FeldmanHall, Glimcher, Baker, & Phelps, 2016; I. Levy, Snell, Nelson, Rustichini, & Glimcher, 2010). However, there is evidence showing that these measures of risk are only weakly correlated with self report measures of risk (Frey, Richter, Schupp, Hertwig, & Mata, 2020; Mata, Frey, Richter, Schupp, & Hertwig, 2018). Moreover, even behavioral risk elicitation methods correlate only to a small degree (risk elicitation puzzle; Pedroni et al. (2017)). A proposed recently risk propensity scale, the General Risk Propensity Scale GRiPS (Zhang, Highhouse, & Nye, 2019), tries to overcome this issue. Alternatively, Schildberg-Hörisch (2018) proposed the use of different measures, and average them to get an overall risk attitude measure. This measure would be more stable than a single measure and reduce measurement error. In this light, however, a single correlation between two measures as we did would not be useful, as these two measures might be uncorrelated because focusing on different sub-aspects. Another possibility is the proposal to use a representative design (Steiner & Frey, 2020) to create a task design, where the stimuli represent the environment the construct aims to generalize. Moreover, the question was raised recently (Schildberg-Hörisch, 2018) about the stability of risk preferences. It has been shown that risk aversion decreases over the life span (Josef et al., 2016; Mamerow, Frey, & Mata, 2016; Schildberg-Hörisch, 2018) or that specific negative life events (like the loss of a child) have a persistent effect on risk attitude (Bucciol & Zarri, 2015). Analogously, we could assume that with increasing age people show a smaller memory bias, even though they would forget more options due to age-related memory capacity de-

cline (Burke & Magkay, 1997; Salthouse, 2003). Moreover, we could investigate individuals who experienced important life events and ask how their "shadow of the past" (Bucciol & Zarri, 2015) influences memory-based choices. Results would provide additional evidence on the similarity between uncertainty and memory.

Chapter 4

Attention plays a Crucial Role for Memory-Based Choices but is not driving the Memory Bias

After having shown the analogy between the memory bias and uncertainty resulting in a reflection effect, here I focus on another possible component explaining why people rely on past experiences when deciding between two options: visual attention. Researchers assume that people tend to look at options they are also processing, meaning there is an overlap between overt and covert attention. These finding are coming mainly from findings on reading and visual search (for a review and discussion see Rayner, 2009). Accordingly, I recorded participants eye movements while they made choices in our remember-and-decide task. Moreover, this manuscript also implements a sequential sampling model that has been adapted from the aDDM and aims to explain how visual attention influences choice processes. For our purpose, we also had to include a memory mechanism, as with the memory bias we have an example on how memory also influences choices remarkably.

4.1 Manuscript 3: The role of attention on preferential memory-based choice

Weilbächer, R. A., Krajbich, I., Rieskamp J., & Gluth, S. (2020). The role of visual attention on memory-based choice. Manuscript submitted for publication.

4.2 Theoretical Background and Hypotheses

In this study, we investigated if attention mediates the memory bias on choice. We speculated that people tend to look more often and longer to better-remembered options compared to less-remembered options or if the attentional influence on choice is overall enhanced in memory-based choices because the value needs to be retrieved from memory. Therefore, we repeated the classical version of the remember-and-decide task by simultaneously recording participants' gaze with an eye-tracker. Attention is known to play a crucial role in decision processes and in memory. From the decision-making literature the *gaze cascade effect* (Shimojo, Simion, Shimojo, & Scheier, 2003) shows that over a trial, people tend to look more and more towards the later chosen option. This effect, also referred to as *attention bias* describing in more general terms that people tend to look more and longer towards the option they later choose, has been replicated many times (Cavanagh, Wiecki, Kochar, & Frank, 2014; Fiedler & Glöckner, 2012; Gluth, Kern, Kortmann, & Vitali, 2020; Krajbich et al., 2010; Orquin & Mueller Loose, 2013; Stewart, Gächter, Noguchi, & Mullett, 2016). From the memory-based judgment literature the *looking-at-nothing effect* shows that people tend to look at locations, where items have been presented during encoding (Richardson & Spivey, 2000; Scholz, Mehlhorn, & Krems, 2016; Scholz, von Helversen, & Rieskamp, 2015). In line with these finding one hypothesis would be that attention mediates the memory bias. We would expect people to look more and longer to better-remembered items, and this would lead to a higher choice proportion of theses options.

However, we could also speculate that memory per se could play a differential role in memory-based choice. When options are not present on the screen but their identity needs to be recalled from memory, people need to also

retrieve the value information. In this case, the influence of value would be independent of the retrieval success. Accordingly, it has been found that looking at an option more amplifies its subjective value (Smith & Krajbich, 2019). By additionally adopting a computational modelling approach, I aimed to getting insights into the interplay of visual attention and memory-based choice. Therefore, I adapted an already proposed model (for an overview on the model mechanics see Figure 4): the Gaze-weighted Linear Accumulator Model or GLAM (Thomas et al., 2019). The model has been inspired by the attentional Drift Diffusion Model or aDDM (Krajbich et al., 2010). It is a sequential sampling linear stochastic race model (Tillman & Logan, 2017; Usher, Olami, & McClelland, 2002). Like any other sequential sampling model (see Chapter 1) it assumes that during the choice process people accumulate evidence. Like in a race, this evidence is being accumulated separately for each option, and once one option's accumulator reaches a previously specified boundary, a choice in favor of this option is being made. The model incorporates the information from the response times, the choices (in our binary case left or right), the gaze proportion, the option's value and newly the memory recall success (dummy variable, was the item recalled or not). In the following method section I describe the model mechanics with the according mathematical equations and how I adapted the original GLAM to include a memory mechanism.

4.3 Methods

Eye-tracking

Eye-tracking is a widely used method to investigate peoples' gaze behavior. With the so-called *eye-mind assumption* (Just & Carpenter, 1976) researchers assume that there is no lag between what is being fixated and what is being processed. An alternative *signal detection assumption* (Orquin & Holmqvist, 2018) states that fixations to an object implies that the object has been processed. Even though we need to be careful, as false positives (fixated but not processed) and false negatives (not fixated but processed) can occur. False negatives can occur due to peripheral processing. In other words, a person can identify an object without fixating it. Nevertheless, I implemented this method

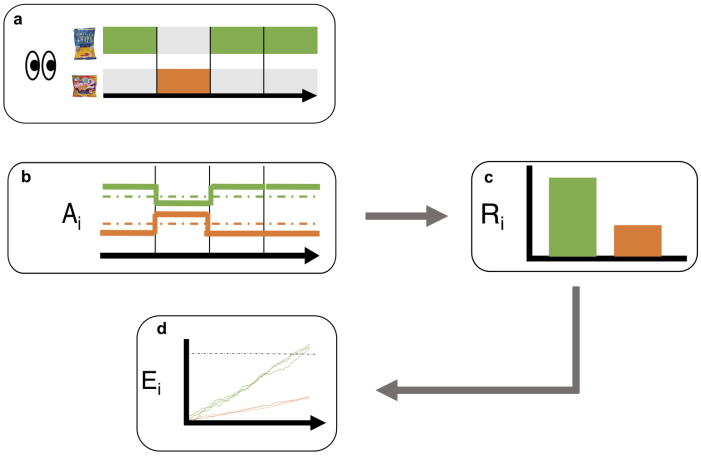

Figure 4: Depiction of the GLAM adapted from Thomas, Molter, Krajbich, Heekeren, and Mohr (2019). a) Gaze allocation towards two snack options (depicted as orange and green options). b) Absolute evidence signal depending on the gaze allocation (and memory success in our adapted model version). c) Relative decision signals after the logistic transformation. d) An option is chosen (here the green one) as soon as the accumulated evidence reaches the choice boundary.

in this project to investigate how long and how often people were looking at each location highlighted on the screen during the decision phase. The collected raw data consists of samples (x and y coordinates) recorded at a specific sampling rate, in our case 500Hz, equivalent to 1 sample every 2ms. This raw data is then re-coded into events, these are fixations (a small area on the screen was fixated for a minimal amount of time), saccades (the eyes moved from one location to another), and blinks (no samples available for a small period). To further investigate our hypothesis we only analyzed the duration and number of fixations to specific locations on the screen, i.e. the squares where the choice options appeared.

However, eye-tracking also poses some methodological challenges that threat internal and external validity (Orquin & Holmqvist, 2018). One important factor is the selection of areas of interest (in our case the six squares). By changing their size, a researcher can manipulate the fit of a model (Orquin, Ashby, & Clarke, 2016). This is one issue that comes from the large number of researchers degrees of freedom. Another issue is data quality, we included a fixation crite-

rion between each decision trial, to assure that our eye-tracker was still reliably calibrated. However, we did not use a chin rest, which could have prevented unnecessary head movements from our participants. Eye-trackers differ in the sensitivity to such movements (Niehorster, Cornelissen, Holmqvist, Hooge, & Hessels, 2018).

Adapting an Existing Computational Model

In this work we were also interested to investigate the underlying cognitive mechanisms of memory-based choice. To this aim, we adapted an existing computational model that takes into account to what extend gaze influences choice. This model is the gaze-weighted linear accumulator model (GLAM; Thomas et al., 2019). This model is a race model, meaning it assumes that evidence for each choice option is being accumulated independently and once a threshold is reached, a choice is being made. In our case we needed to introduce an additional parameter that estimates the value of the less-remembered option. This parameter allows to replicate the memory bias on choice. Overall, this model performs similarly well as the original GLAM, indicating that further investigations are needed to test the predictive power of our model. The final aim is to predict new unseen data accurately after having trained the model on empirical data. Due to a small number of data we could not do this in our data. A future study might need many more trials in which one item has been forgotten while the other remembered.

The extended GLAM works as follows. First, for each option i relative evidence is being accumulated at each time point t (see Figure 4d):

$$E_i(t) = E_i(t-1) + v * Ri + N(0, \sigma^2), \text{with } Ei(0) = 0 \tag{4.1}$$

Here the two parameters v and σ are being estimated. The parameter v is the velocity corresponding to the overall speed of accumulation. The parameter σ is the zero-centered normally distributed noise of the drift term R_i. The drift term R_i* is the average amount of relative evidence for option i accumulated at each time point t or in other words the difference between the absolute evidence signal A_i of the left option minus the right option:

$$R_i* = A_i - A_j \tag{4.2}$$

The absolute evidence signal A_i can be seen as the core equation of the model. It incorporates the option's value $value_i$, the gaze proportion $gaze_i$ and the recall success $remembered_i$. From its equation we derive two crucial parameters: the gaze bias parameter γ and the memory bias parameter ρ (see Figure 4b):

$$\begin{aligned} A_i = gaze_i * value_i * remembered_i + \\ gaze_i * \rho * (1 - remembered_i) + \\ (1 - gaze_i) * \gamma * value_i * remembered_i + \\ (1 - gaze_i) * \gamma * \rho * (1 - remembered_i) \end{aligned} \tag{4.3}$$

The gaze bias parameter γ determines the amount of down-weighting during the biased state. If $\gamma = 1$ there is no gaze bias. The memory bias parameter ρ determines the reference value of the forgotten option. If this value is smaller than the true average of all forgotten options, a memory bias is likely to occur, because the remembered option is more often considered to be better.

Lastly, the scaling parameter tau is being estimated taking into account participants' different use of the rating scale and it determines the sensitivity to differences in relative evidence R_i. Therefore, a logistic transformation is being implemented as follows:

$$s(x) = \frac{1}{1 + e^{-\tau * x}} \tag{4.4}$$

Accordingly, the final relative evidence R_i is determined as (see Figure 4c):

$$R_i = s(R_i *) \tag{4.5}$$

4.4 Results

Attention is central for Memory-Based Choices but is not Mediating the Memory-bias

First, we could replicate the memory bias on choice (see Figure 3) meaning people tend to prefer better-remembered options over less-remembered ones. Second, the effect of gaze influence is greater in memory-based choices than non-memory-based choices. An attention bias is present in independently of the fact that choice options needed to be recalled from memory (memory trials)

or not [1] (control trials; Figure 3 Appendix C). Importantly, this gaze influence is similar between trials where both options were recalled and trials where only one option had been recalled. Third, people do not fixate more or longer to remembered compared to forgotten options. They both receive a similar amount of visual attention (Figure 4 Appendix C).

What can we learn from our adapted GLAM?

The results show that our adapted GLAM predicts the memory bias on choice, whereas model alternatives without the memory bias parameter ρ cannot (Figure 5 Appendix C). However, quantitatively, comparing the model fits with the Widely Applicable Information Criterion (WAIC; Vehtari, Gelman, and Gabry, 2017), our new model is not a clear winner. Out of 33 participants, 19 participants (57.6%) are better described by the original GLAM, 9 by our modified GLAM (27.3%), and 5 by a restricted GLAM model without a gaze bias (15.1%). Notably, the differences between the models' WAIC is small. Additionally, we also compared our modified GLAM qualitatively with the original GLAM. First, only our model is able to predict the memory bias on choice. Second, both models can account for our result that memory-based choices are more influences by gaze behavior (Figure 6 Appendix C). Importantly, the original GLAM predicts a difference in the gaze influence between memory trials with one option remembered and memory trials with both options remembered. Whereas, according to the empirical data, our modified GLAM does not make this prediction.

4.5 Discussion

The present study aimed to better understand the role of attention in memory-based choice by combining several methods such as eye-tracking and computational modeling. Concerning the crucial role of attention in decision-making there is already a large body of evidence (Fiedler & Glöckner, 2012; Gluth, Spektor, & Rieskamp, 2018; Krajbich, 2019; Orquin & Mueller Loose, 2013; Stewart et al., 2016; Tavares, Perona, & Rangel, 2017). The most impor-

[1] In this experiment we included rounds with trials where the choice options were presented during the decision phase of the remember-and-decide task.

tant finding in the literature is the *attention bias* stating that people tend to choose options they fixated longer. We could replicate this influence of gaze on choice. Its strength in our non-memory-based choices is similar to previous studies (Folke, Jacobsen, Fleming, & De Martino, 2017; Krajbich et al., 2010; Krajbich & Rangel, 2011; Tavares et al., 2017; Thomas et al., 2019). Importantly, the gaze influence is larger in memory-based choices independent of recall success (both or only one option being recalled). This finding could also be replicated with our adapted GLAM.

Further investigations could focus on clinical populations, such as people suffering from both mnemonic and attentional deficits like people affected by Alzheimer's Disease (Baddeley, 2001; Calderon et al., 2001; Perry, Watson, & Hodges, 2000). A recent study investigating the choice behavior of older adults found that people despite not showing more intransitive choices, were less accurate according to their stated preferences (Levin et al., 2019). Other evidence shows that older adults are not more inaccurate, but they need more time for their choices (Lighthall et al., 2014). The combined study of how memory deficits affect memory-based decisions and attention could be a direction for further studies. To further strengthen our computational results, these future studies would need more participants and crucially more trials with one option being better-remembered while the other is less-remembered or even forgotten. Additionally, in our study memory performance was relatively high, because some items where encoded twice. Therefore, the recall task was relatively easy for some participants with high memory capacities. A future study could adapt the number of items needed to be recalled per round to these individual memory abilities. This would mean to invest more time participants need to be in the lab, but it could be easily assessed in a separate session. However, a more precise, individually adapted design could lead to more stable and reliable results. The study of Thomas et al. (2019), where the GLAM was introduced, crucially showed how important it is to take into account individual differences when it comes to the *attention bias* on choice as some people did not show the effect at all. The same holds true when it comes to the *memory bias*: people differ not only in their memory capacities but also to what degree they rely on them. To what degree they rely on their memory cannot easily be manipulated,

but their memory capacities could be accounted for as described above.

Additionally, we used a Bayesian estimation method for estimating the GLAM but fitted the model separately for each individual. A hierarchical application had convergence issues. Further efforts in this direction could improve the GLAM in general, and our adapted version of it specifically. In a hierarchical framework it would be possible to compare conditions (e.g. memory- vs. non-memory-based choices) directly via the group posteriors.

Moreover, we could replicate the memory bias further showing that it represents a robust and strong effect. However, our hypothesis that better-remembered options are not only chosen more often, but also receive more attention, was not confirmed. We relied here on the *looking-at-nothing* phenomenon (Richardson & Spivey, 2000), stating that people tend to look at locations where options were previously presented. Accordingly, we assumed people would look more at the better-remembered option, as this re-fixation may support the memory retrieval. However, a parallel process could take place for the less-remembered option. Here, a person might try to re-fixate its location in the attempt to be able to recall it even though they fail. Interestingly, the looking-at-nothing effect has been shown to become weaker when memory certainty is stronger (Scholz, Mehlhorn, Bocklisch, & Krems, 2011). During the recall phase of the remember-and-decide task we also asked participants to indicate their certainty. In case they recalled an option, they tended to be very certain about it. As a consequence, they might not have needed to fixate at their location for long. This point might also be related to the discussion above concerning the validity of eye-tracking research: people do not always need to fixate an option they are paying attention to.

Chapter 5

General Discussion

To conclude, the current thesis aimed at a better understanding of memory-based, preferential choice. The first manuscript (Chapter 2) is a review article shedding light on the neuronal basis, specifically on the interaction of vmPFC and HPC. Recent developments focus on the role of HPC in preferential choice, whereas less focus has been put on the interaction of vmPFC and HPC in memory-based choice. The second manuscript (Chapter 3) focuses on the analogy between decisions from memory and decisions under uncertainty showing that people might prefer better-remembered options because they represent a safer alternative compared to the less-remembered option. We find evidence for this hypothesis by showing a reflection effect in memory-based choice: People show a memory bias in the gain domain, and its reflection in the loss domain. However, this could be independent of the risk behavior shown in other domains, such as monetary rewards, sexual behavior, or alcohol consumption. Further investigations would need to look more closely at the role of memory in risky choices across domains and over the life span. The third manuscript (Chapter 4) focuses on the role of visual attention in memory-based choice. We showed that where people look at is influencing choices to a larger degree in memory-based choices overall. However, it does not seem to be relevant if an option has been recalled or not. The simple fact that an option is hidden enhances attention to it. It would be interesting to observe the choice behavior in mixed trials: assume one option is being presented while the other needs to be retrieved from memory. Such a mixed trials design is also relevant in our daily

life. Assume, for example, a person is in a grocery shop and stands in front of a product deliberating whether to buy it or not. However, the person also knows that another shop offers a similar product. The person might now deliberate whether to buy the product in the current shop or go to the other shop. A study on attention in risky choice showed that risky gambles attract more attention than safe ones (Brandstätter & Körner, 2014). Accordingly, I would predict that the presented option receives less attention because the decision-maker knows its identity. In other words, they are certain about the option presented to them but uncertain about the other option. This study would combine the findings from M2 on the role of uncertainty in memory-based choice with the findings from M3 on the role of attention on memory-based choice. In the next section, I discuss some further possible directions for future investigations.

5.1 Future Directions

In M1 (Chapter 2) I reviewed some of the current evidence on the interplay of HPC and vmPFC in memory-based choice. In the last section of the review article we raised four questions for future directions. The first question asks for the neural code that underlies memory-based decisions. One idea to address this question would be to compare choices that involve memory retrieval to choices that don't (or to a smaller degree). We are currently testing a design in which we compare choices across and within domains. Choices within domains are simple value-based choices as we know them from previous studies, for example choose which snack do you prefer. Choices across domains are choices between an option from domain A (e.g., smartphones) and one option from domain B (e.g., hotel stays). Here the main hypothesis is that decisions across domains involve memory retrieval, while choices within domains do not. In choices across domains, the options cannot be compared directly, a person cannot say Smartphone A is better than Hotel Stay B. However, after having retrieved the subjective values of each option, the decision-maker can do this inference, as they recall that Smartphone A was more valuable to them than Hotel Stay B. Whereas in the traditional within domain design, choice options can be compared directly, values could even be constructed in the moment of choice. Here, memory should play a minor role. In an fMRI study this would

be made evident by a higher hippocampal activation and a stronger functional connectivity between our regions of interest vmPFC and HPC in choices across domains compared to within domains. Importantly, this assumption that value is either *constructed* (Simonson, 2008; Slovic, 1995) directly or retrieved from memory, or in other words *revealed* (Samuelson, 1938), contrasts the common currency theory, the standard approach in neuroeconomics (for a meta-analysis see Dino J Levy and Glimcher, 2012). Here, the idea is that all value is computed in the vmPFC, and then a choice is made accordingly. Therefore, a comparison between "apples and oranges" becomes possible as everything is transformed to the same "currency", for example money. Moreover, how does the brain calculate value is a highly debated question in neuroscience, the field appears to move from a *value-first* approach, where the brain evaluates each option separately to a *comparison* approach, where the option's value is determined relatively to other options presented (for a review see Vlaev, Chater, Stewart, and Brown, 2011).

A second question asks what is the precise type of HPC-vmPFC interactions. On the one hand, these interactions have been identified in complex inferential memory associations (Zeithamova, Dominick, & Preston, 2012). On the other hand, they have been identified as mediating value-based decision from memory (Gluth et al., 2015). However, these findings are not necessarily contradictory. If memory integration of past events informs new behavior as shown in Zeithamova et al. (2012) this process could also underlie memory-based choices (Gluth et al., 2015): The more decisions rely on past experiences, the more important it becomes to infer how this relates to future events. Another interesting point is that a decision between two restaurants is also the projection into the future on how much value I will gain from each option. Based on the past, I infer how the future might be. This brings us back to the recent review article of (Biderman et al., 2020), making exactly this claim on the role of the HPC in (memory-based) choice, yet the role of vmPFC remains unclear.

The third question asks for the directionality of these interactions. Indeed the study presented above addressing the first open question could also address this question by adapting the Dynamic Causal Modeling (Friston, 2011).

Importantly, this method can also be used with other neuroimaging methods, such as MEG. It would be interesting to see whether study designs reporting a crucial involvement of HPC in memory-based choice (for example a recent preprint on the relation between the reactivation of pain-related patterns and successful memory-based choice also reported previously Wimmer and Büchel, 2020) would also find a higher HPC-vmPFC connectivity and, importantly, its directionality, when using DCM methods.

The fourth question asks whether the HPC represents subjective value. Some answers were given in a recent study (see Chapter 2.4), showing that the HPC is also crucial for deliberation in choice (Bakkour et al., 2019). Taken together, HPC appears to be crucially involved in choice processes, however, its role on computing value has only begun to be investigated.

In M2 (Chapter 3) I showed evidence that uncertainty might be related to the memory bias. In the previous section I discussed four open questions raised by the review article in M1, taking the finding in M2 into account, could raise an important fifth question: If uncertainty is related to the memory bias, could this also be observed on a neuronal basis? Importantly, risk and ambiguity are dissociable also at a neuronal level. Risk has been associated with the anterior insula, the dorsomedial prefrontal cortex, and the striatum (Mohr et al., 2010; Preuschoff, Bossaerts, & Quartz, 2006), whereas ambiguity has been linked to the amygdala, the orbitofrontal cortex, and the inferior frontal sulcus (Hsu, 2005; Huettel et al., 2006). A question for further research is how these brain regions relate to the interaction of vmPFC and HPC during memory-based choice. However, future studies would moreover need to address specifically what kind of certainty is entailed when people prefer the save and remembered option. Is this more related to risk aversion or ambiguity aversion? In our case, we found no association between peoples' memory bias and ambiguity attitude, even though they show a reflection of the memory bias in the loss domain, analogous to decisions under uncertainty. A first possible conclusion is that there is no relationship between ambiguity attitude and the memory bias. However, another possible explanation for our null finding, is that we were measuring an unrelated construct. One possible solution to solve this issue, would be to create a representative study design (Araújo, Davids, & Passos, 2007; Ham-

mond & Stewart, 2001) for the used lottery task. A representative design uses stimuli that represent the environments to which measured constructs should generalize. In our case, we would need to test if the used lottery task is representative for risky/ambiguous choices. However, a recent study showed that for one measure of risky choices, the Balloon Analogue Risk Task, an improved representative design does not solve issues like low test-retest reliability or low convergent validity (Steiner & Frey, 2020). Instead of developing valid tasks we might test their ecological validity, or how well real-life behaviors correspond to the tasks used in the lab. As a consequence, to test if, for example, a person behaving risk averse in the lottery task is also risk averse in their financial decisions, more experiments are required that administer multiple tasks in different settings (e.g., lab vs. field) to the same people, contributing in bridging the gap between economic and naturalistic risk-taking (Schonberg, Fox, & Poldrack, 2011).

In M3 (Chapter 4) I showed that attention plays a differential role in memory-based choice but is not mediating the memory bias. Interestingly, we did not observe an effect of choice presentation length neither: People did not choose the option that was presented longer, but had a general preference for the second choice option. There might be two possible reason for our null-finding: either there is no effect of presentation length (higher amount of attention) on memory-based choice, contrasting our main finding in the first experiment, or our design was inappropriate. To dissociate between these possibilities, a further study could use an alternative paradigm: *attentional cueing* (Posner & Cohen, 1984). In an attentional cueing paradigm a specific aspect is being highlighted during the experiment, for example one choice option is made more salient by being written in a larger font. As an experimental proposal, during the choice phase, I would always highlight one of the two choice options for a short time period (e.g. 2 seconds), then I would present both choice options simultaneously. In this potential experiment, only at this time point people could indicate their choice. I predict that participants tend to choose the cued item more often, since that would be the item they would look at for a longer time period (Krajbich et al., 2010; Shimojo et al., 2003). Moreover, I also expect participants' choice behavior to be mediated by memory

retrieval success: in case the cued option is extremely bad, participants would not choose it despite the longer fixation time.

To further investigate the memory bias and test its malleability, I would develop a design that allows the effect to disappear under certain conditions. Therefore, I would use a gaze contingent design, i.e., a design where choice options are uncovered only after they have been fixated on (for a recent example in risky choices see Sui, Liu, and Rao, 2020). In such a design, participants would be able to decide what options they want to encode and how often they want to look at such items in a first learning phase before continuing to the choice phase. In this way, they would get the possibility to better encode certain items, and remember them better in the later choice phase. As a consequence, I would expect the memory bias to disappear completely, as the least memorable choice options have been trained extensively.

Moreover, to investigate memory-based choice, so far we were relying on the remember-and-decide task. I have showed in this thesis that the task is generalizable to different stimuli (snacks, images, monetary rewards). However, another task measuring the same underlying process, would allow to make our claim even more generalizable. One first possible approach could be to develop a game app, that can be easily played on a smartphone, thus also allowing to get multiple data from single participants (and more data overall). A similar approach has been adopted by the Great Brain Experiment (Brown et al., 2014; McNab & Dolan, 2014). A second approach would be to ask to order the six choice options according to their preference instead of letting them make binary decisions. Here, I would get a ranking from 1 to 6. Then I could test whether this ranking corresponds to the stated preferences or whether better-remembered items get a higher ranking. Crucially, more arousing facts or events are memorized better. This has been shown in many instances, for example with emotional words (Kensinger & Corkin, 2003), pictures (Canli, Zhao, Desmond, Glover, & Gabrieli, 1999), or specifically focusing on memory of the location of different pictures (Mather & Nesmith, 2008). Moreover, I need controlling for the fact that extreme value options are more memorable by excluding them from the choice set, as done in all the studies described in the present dissertation that used the remember-and-decide task.

5.2 Conclusion

In this dissertation, I first reviewed the empirical evidence for the neuronal mechanism underlying memory-based choice, showing that the connectivity between vmPFC and HPC might be crucial, even though further evidence is missing. Then, I focused on two possible mechanisms explaining why people tend to prefer better-remembered options: uncertainty and attention. Based on the evidence laid out in the manuscript, I conclude that that recalling better an item is similar to being certain about that item, whereas forgetting corresponds to a higher level of uncertainty. Moreover, even though better-remembered options do not receive more attention, attention appears to be more critical in memory-based decisions compared to non-memory-based ones. A third possible mediator for the memory bias has been shown in Mechera-Ostrovsky and Gluth (2018): subjective belief. Here, participants were asked to indicate how well they think they remembered the items. Results indicate a strong relation between the strength of the memory bias and this subjective belief.

This thesis also shows that there are many open questions. In my view, two central open issues are first to investigate further the neuronal processes underlying memory-based choices with the design described above comparing choices that require more memory retrieval to one who require less memory retrieval. Second, it would be important to investigate the development of the memory bias over the life span. In particular, understanding how the memory bias changes over time, would have important implications for policy makers. Our hypothesis is that the memory bias increases with age, because people rely more on their previous experiences. Additionally, evidence shows that elderly people recall less due to age-related decline. Having this in mind, how can we support elderly people in making better choices? These two aspects would bring us a step closer to the understanding human choice behavior and allow to bring fundamental research to the field, in the long way to make it relevant for daily applications.

To conclude with the quote of the beginning of this thesis, "If you want to improve your memory, lend someone money": The decision to lend someone money today is a decision related to the future, but depending crucially on your memory about past experiences. In case you cannot recall if you got

your money back last time you lent money to your friend, you are more likely not to lend money in the future. Alternatively, if you recall the last lending experience, for example, the friend you lent money also gave it back to you, you are more likely to do this again, even though you did not get back the entire amount you gave. You are biased by your memory. But there is hope: You can improve your memory.

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Appendix A. Weilbächer & Gluth, 2017

brain sciences

MDPI

Review

The Interplay of Hippocampus and Ventromedial Prefrontal Cortex in Memory-Based Decision Making

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Abstract: Episodic memory and value-based decision making are two central and intensively studied research domains in cognitive neuroscience, but we are just beginning to understand how they interact to enable memory-based decisions. The two brain regions that have been associated with episodic memory and value-based decision making are the hippocampus and the ventromedial prefrontal cortex, respectively. In this review article, we first give an overview of these brain–behavior associations and then focus on the mechanisms of potential interactions between the hippocampus and ventromedial prefrontal cortex that have been proposed and tested in recent neuroimaging studies. Based on those possible interactions, we discuss several directions for future research on the neural and cognitive foundations of memory-based decision making.

Keywords: hippocampus; prefrontal cortex; episodic memory; value-based decision making

1. Introduction

Without a doubt, episodic memory and value-based decision making are amongst the most widely studied psychological constructs. Thus, when entering either of them as search terms in the research database PubMed [1], one obtains over 8000 results each. On the contrary, the combined term "memory-based decision making" produces only 77 results, with the great majority of them (i.e., 90%) dating not further back than the year 2000. This just reflects the novelty and relative under-appreciation of this specific research topic. In fact, the two research fields of episodic memory and value-based decision making have often adopted different research methods and developed separate conceptual definitions.

In our every-day life, memory- and choice-processes are often intertwined such as when choosing between chocolate bars in the supermarket and recalling past experiences [2]. Accordingly, in this review, we argue that even though memory and decision making can be understood as distinct processes, studying their interactions is a promising agenda for current and future research. We highlight recent advances in this regard and discuss how the existing knowledge about the neural mechanisms of memory, decision making, and their combination lead to novel predictions and research hypotheses. In particular, we will focus on two brain regions, the ventromedial prefrontal cortex (vmPFC) and the hippocampus (HPC), that appear to play crucial roles in memory encoding, consolidation and retrieval processes as well as in value-based decision making.

In order to have a common definitional ground and to avoid misunderstandings, let us define the central terms used in this article: episodic memory, value-based decision making, and memory-based decision making. *Episodic memory* is part of the declarative memory system (i.e., memory that can be stated) together with semantic memory (or memory for facts). Episodic memory is the memory for episodes, which means that when we recall a specific episode from the past, e.g., our first lecture at university, we recall not only what happened but also the specific context (in time and space) in which the event took place. *Value-based decisions* are decisions about what we like, want, or prefer, that is,

choices based on the subjective value that the decision maker attributes to the available choice options. Value-based decisions are often distinguished from perceptual decisions, as the latter but not the former can be identified as being objectively correct or incorrect. Finally, *memory-based decision making* refers to the process of making decisions that require memory retrieval. For instance, when your friend is ordering Italian food and asks you to make your choice immediately (without presenting you the menu), you have to retrieve potential options from your memory and choose among those memory items. Importantly, not every value-based decision is a memory-based decision (at least according to our definition): when you have the menu at hand, there is no need to retrieve potential options from memory (although identifying your favorite Italian dish might still require episodic memory; cf. [2]).

This review article is structured as follows: first, we will summarize the literature of research on the role of HPC in episodic memory; second, we will give a similar overview with respect to vmPFC and value-based decision making; third, we will present recent work on the interplay of these two brain regions in both memory and decision making; fourth and last, we will propose research questions and hypotheses for future research in the field(s) that derive from our current knowledge.

2. The Central Role of the Hippocampus in Episodic Memory

The HPC comprises distinct sub-regions (i.e., CA1 to CA3, dentate gyrus and subiculum) and is part of the hippocampal formation, which also includes the parahippocampal, perirhinal and entorhinal cortices [3]. Figure 1 gives an overview of the input and output pathways of the hippocampal formation as described in [4]. The role of HPC in encoding, consolidation and retrieval of declarative long-term memory, especially episodic memory, is well established. Important contributions to our understanding of the HPC have been made by case studies such as patient H.M., who suffered from severe anterograde amnesia for facts and events (declarative memory) after bilateral removal of large parts of the medial temporal lobe, including HPC [5] (implicit long-term memory was not affected, as H.M. was able to learn procedural skills). Another relevant case study is patient R.B. who suffered from anterograde amnesia after a lesion of hippocampal CA1 region [6]. Additional evidence of the hippocampal role in episodic memory provide case studies of three children who suffered brain injuries at several ages (birth, four years old, and nine years old) in which HPC was affected [7]. These case studies showed that hippocampal lesion affected episodic but not semantic memory significantly.

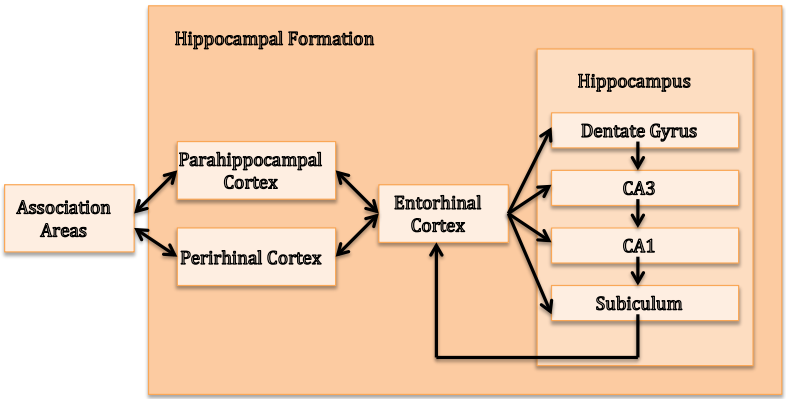

Figure 1. Input and output pathways of the hippocampal formation (adapted from [4]).

More recent investigations suggest distinct roles of the different parts of the hippocampal formation for recognition memory [8,9]. Recognition memory is a form of episodic memory and is typically assessed by a task in which participants see different options and have to indicate

which of them they encountered previously (old–new distinction). According to the role distinction view of different parts of the hippocampal formation, HPC appears to be mainly involved in creating associations between objects and places (source-based associative memory, a process termed recollection), the Parahippocampal cortex in place memory and the Perirhinal cortex in object familiarity (item-based non-associative memory) [8]. However, other results show a less clear localization of the two processes of familiarity and recollection, and a simple dichotomy of them may be too simplistic [10]. In fact, some researchers argue that the methods used to distinguish between recollection and familiarity instead separate between strong and weak memories, and higher HPC activity is associated with strong memories. This account is supported by the nonlinear relationship between hippocampal functional magnetic resonance imaging (fMRI) activation and memory strength [11]. Memory strength is defined as the rate of responses where participants clearly state that they remembered an item or indicate the source of the information. Therefore, a high response rate is associated with high memory strength. The nonlinear relationship mentioned above has been reported to be typical for the fMRI activation pattern (see Figure 2) and can be described as follows: during encoding as well as retrieval of weak memories, fMRI activation is constantly low, while during the linear increase of memory strength (leading to strong memories), the fMRI activation increases steeply [11].

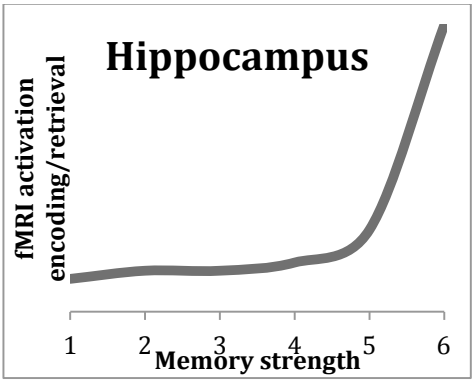

Figure 2. Nonlinear relationship between functional magnetic resonance imaging (fMRI) activation (ordinate) and memory strength (abscissa) in the hippocampus (HPC). The pattern is equal during encoding as well as during retrieval. The memory strength in this example ranges from 1 (weak) to 6 (strong). The figure shows that weak to middle strong (1–5) memories show a constant fMRI activation, where very strong (6) memories are associated with an extremely high fMRI activation in the HPC (according to [11]).

During encoding [12] and retrieval [13] of long-term memories, we rely on working memory. Therefore, consolidation is the only "purely" long-term memory process. Concerning declarative memory consolidation and the role of HPC in it, the Multiple Trace Theory (MTT) [14,15] has been put forward and subsequently updated as transformation hypothesis [16]. MTT states that HPC is always required for encoding as well as recall of episodic memories. During retrieval, a new trace element is added and the memory is strengthened. According to MTT, contextual information will always stay in the HPC. Over time, however, this contextual information can be lost and the memory may be transformed into more generic (semantic) memory stored in the neocortex so that it is not affected by HPC lesions anymore [15,16]. MTT seems to account better for the process of declarative memory consolidation than previous theories such as cognitive map (CM) or the system consolidation model (SC) [15]: the CM theory [17] sees the HPC involved in the creation of an allocentric spatial

representation of the environment that is independent from the position of the observer. Contextual information is based upon this representation and as the context is a constituent part of episodes, HPC is important for the encoding, consolidation and retrieval of episodic memory. The central difference to MTT is that the CM theory does not differentiate between remote and recent memories. The SC model [18] assumes a process of prolonged consolidation, which is only temporally HPC dependent. Over time, however, neocortical regions store long-term memories and also mediate their retrieval. Contrary to MTT, also contextual information, like any other declarative long-term memory, becomes HPC independent over time. Additionally, SC does not differentiate between episodic and semantic memory.

The work we have outlined above focused on human studies. However, episodic-like memory in animals has also been investigated in recent years. Compared to human studies, animal models allow a first and simplified understanding of functionally complex cognitive processes as well as neuropsychiatric and neurodegenerative diseases in simpler models. Animals cannot tell us what events they remember, but we can derive their knowledge of past events from their behavior [19]. An example of an episodic-like memory task is the WWWhen [20,21] (what, where and when; for an overview see [19]). In the WWWhen task, animals perform a three-trial object exploration task. During this task, long-term memory for different objects (what), their spatial location (where) and their order of presentation (when) is assessed [20]. In other animal studies, hippocampal place cells, in most cases pyramidal CA1 cells, have been suggested to underlie spatial navigation in rats [22–24]. Spatial knowledge is consolidated via spontaneous recurrence of HPC place cell activity during slow-wave sleep (SWS) [25] in animals [26] and humans [27]. Such neural replay has also been reported in awake states, for instance, when rodents pause in exploring a maze [28,29]. Neural replay can be either forward or reverse [22]. Reverse replay has been suggested to be a learning mechanism while forward replay could be crucial for memory retrieval and future paths planning [22,30].

In summary, the HPC is central to guiding self-referenced navigation as well as to supporting the encoding, consolidation and retrieval of declarative episodic memory [31].

3. The Ventromedial Prefrontal Cortex Is Essential for Value-Based Decisions

Before we review the extent of the literature on the critical role of the vmPFC for decision making, we provide a brief overview of the anatomy and connectivity of this cortical region. The vmPFC is not an anatomically distinct area, as it is not restricted to specific Brodmann areas (BA) or standard MRI coordinates. The vmPFC can be subdivided into caudal (posterior) and rostral (anterior) parts. The caudal vmPFC includes BA 25 and 32 (primarily subgenual cingulate bundle) and caudal BA 14 [32]. The rostral vmPFC, although not explicitly described according to BA in [32], could include BA 10, 11 and 32 (in humans), as described in [33]. However, researchers have also delineated this area on the basis of anatomical and functional connectivity analyses performed with (f)MRI data. Thus, vmPFC could also be seen as a cluster resulting from parcellation, where the fMRI signal changes for a specific construct, such as rewards [34]. Figure 3 gives an overview of the principal connections from and to the vmPFC (as suggested by [32]). The vmPFC has connections to and receives input from the dorsal, anterior and ventrolateral prefrontal cortex, the dorsal anterior cingulate cortex, as well as the insula. Unidirectional connections to the vmPFC come from the hypothalamus and HPC, while output regions are mainly the shell of the nucleus accumbens and the amygdala. Additionally, vmPFC is bidirectionally connected to the entorhinal and perirhinal cortices [35–38], which are part of the hippocampal formation and are, in turn, connected to the HPC (cf. Figure 1).

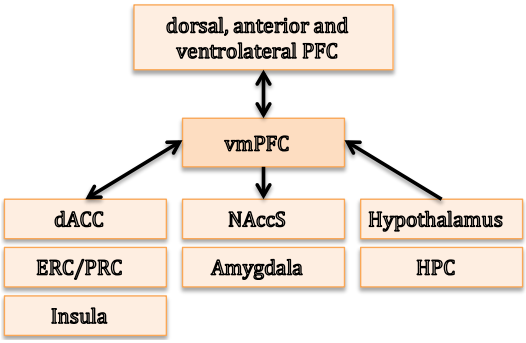

Figure 3. Principal connections from and to the ventromedial prefrontal cortex (vmPFC) adapted from [32]. dACC = dorsal anterior cingulate cortex; ERC = entorhinal cortex; PRC = perirhinal cortex; NAccS = nucleus accumbens shell; HPC = hippocampus.

A wealth of research in cognitive neuroscience over the last three decades has established the vmPFC as a core brain structure for value-based decision making [39–41]. First of all, lesions to the vmPFC lead to various decrements in decision making abilities, including learning from reward and punishment [42], making transitive choices [43], making future-oriented decisions [44], or directing attention towards reward-predicting information [45]. Neuroimaging studies have established a remarkably strong coupling between activity in vmPFC (and ventral striatum) and the subjective value of available choice options or any presented stimuli in general [46–49] (for reviews/meta-analyses, see [41,50]). This has led to the neuroeconomic proposal of a common currency for the vmPFC: in order to allow value-based comparisons between any form of putatively incommensurable choice options (e.g., a choice between buying a car or having a trip around the world), the subjective value of each option is translated into the common currency of vmPFC activation, so that the option with the highest subjective value can be identified by means of the neural vmPFC signal [51]. Interestingly, a recent review article suggests that the vmPFC may receive memory-related information from the HPC in order to estimate the subjective value of options that have been experienced in the past [2]. Importantly, the authors of this review article argue that this HPC-vmPFC communication should underlie value-based decision making, even when choice options are directly visible and do not have to be (explicitly) retrieved from memory.

In contrast to the widely accepted view of the vmPFC as representing subjective value, it is still a matter of debate whether the vmPFC also processes the decision itself. In other words, does the vmPFC represent the value of options and transfers this information to downstream areas that select the best option via a dynamic comparison process, or does this dynamic comparison process take place in the vmPFC itself? Some studies, including single-unit recording studies in non-human primates, have identified activation patterns in vmPFC that are best accounted for by assuming comparison-like mechanisms such as evidence accumulation or mutual inhibition [52–54]. Other work points to the dorsomedial PFC, including the anterior cingulate cortex and the pre-supplementary motor area (pre-SMA), as a potential downstream area that receives information from the vmPFC in order to select among the available choice options [55–57]. The diversity of choice-related impairments that are caused by lesions to the vmPFC (see above) seems to favor the former account. On the other hand, it is well established that decision making is not processed in a strictly serial manner by the brain (i.e., identification of choice options → representation of values → comparison of values → execution of an action), and that even purportedly motor-related areas such as pre-SMA or the primary motor cortex play an active role during the choice process [56,58–60].

On a related note, a large number of behavioral studies [61–63] and a few neuroimaging experiments [64–67] have shown converging evidence that valuation and choice processes cannot be separated from each other. This is because the relative choice probabilities of two options depend on the presence of other options in the choice set, a phenomenon denoted as context effect. Such effects imply that the brain does not assess option values independently from each other before starting the choice process, but that valuation and choice mechanisms must be intertwined. With respect to the vmPFC's role in value-based decision making, it remains open whether context effects lend further evidence for a common valuation and choice mechanism within vmPFC, or whether bi-directional interactions between vmPFC and downstream areas could also account for them. Figure 4 provides a schematic overview of the core features of value-based decision making and the associated brain regions.

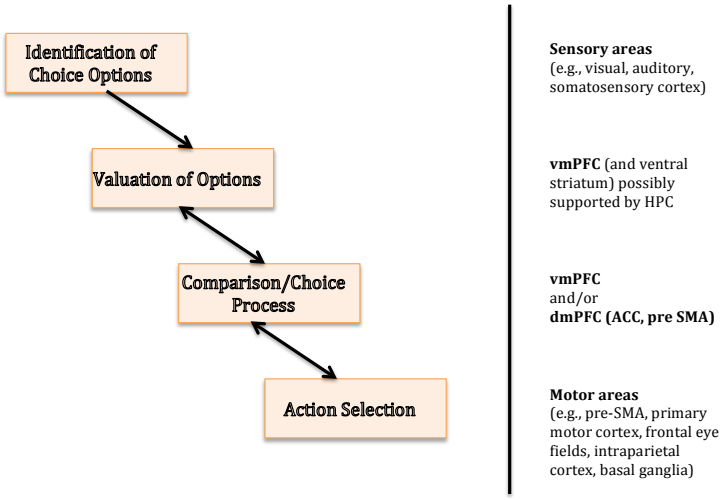

Figure 4. Value-based decision making in the human brain. The central features of a value-based decision are outlined on the **left**; associated brain regions are listed on the **right**. The bidirectional arrows between valuation and choice as well as choice and action selection indicate that these mechanisms are not processed in a strictly serial and independent manner and may even be computed within a single brain region. vmPFC = ventromedial prefrontal cortex, dmPFC = dorsomedial prefrontal cortex, ACC = anterior cingulate cortex, HPC = hippocampus, pre-SMA = pre-supplementary motor area.

4. Hippocampal-Prefrontal Interactions in Episodic Memory and Decision Making

In recent years, researchers have started to investigate the interplay of HPC and vmPFC in several related contexts, such as retrieval-mediated learning [68], learning and choosing based on conceptual (episodic) knowledge [69], deliberative decision-making [70] or memory-based preferential choices [71]. Although more and more research focuses on the connections between these two regions, the neural mechanism underlying the coordinated action of HPC and PFC are still unclear [72]. In this chapter, we present two methods used to measure the neural mechanisms underlying the coupling between HPC and PFC. The first method employs coherence of theta- and gamma band oscillations, and the second method performs dynamic causal modeling of fMRI data. We then present theories and frameworks that were inspired by the results obtained from these connectivity studies. They include the differentiation between HPC and PFC concerning their roles as well as memory as a process of schema creation vs. integration.

The first method used to investigate the coupling between HPC and PFC is the phase coherence of oscillations across specific frequency ranges. Those oscillations are usually measured with magneto encephalography (MEG) and local field potentials (LFP) in humans and non-human animals, respectively. Hippocampal theta-band (5–10 Hz in [73] or 4–8 Hz in [74]) oscillations [75] have been reported to be associated with (spatial) learning and memory consolidation in rats [73,76]. Theta-band synchrony with prefrontal regions has been investigated in several rodent studies concerning memory (for a review, see [77]) as well as in human decision making [74]. Hippocampal–prefrontal gamma-band (low: 35–55 Hz, high: 65–90 Hz) oscillations synchrony has been also linked to spatial learning and memory [78]. Recent research indicates that gamma and theta oscillations might not be independent from each other. In fact, gamma oscillations recorded in neocortical areas appear to be biased by hippocampal theta oscillations via cross-frequency coupling [79]. The authors explain this biasing effect by the "reciprocal information transfer" [79]: The recipient brain structure temporally biases activity in the source structure, and, as a consequence, the recipient structure can receive information more effectively. However, a demonstration of causality between oscillations coherence and cognitive processes (e.g., memory or decision making) is still missing [72]. Consequently, the measurement of oscillation coherence is a promising method but needs further specifications in order to provide evidence for a causal role of those oscillations in mediating cognitive processes.

The second method investigating HPF-PFC coupling has been used in a recent fMRI study [71], where Gluth and colleagues studied how people make decisions about options that are not directly visible but have to be retrieved from memory. Participants learned associations between choice options (food snacks) and locations on the screen and then decided between two options based on their locations. The authors found that memory exerts a bias on value-based decisions, that is, options that were better remembered were preferred even if their subjective value was comparatively low. Dynamic Causal Modeling (DCM) [80] of the fMRI data, a technique that allows measuring the extent and direction of effective connectivity between distant brain regions, revealed that the coupling from HPC to vmPFC was not only important for processing memory-based decisions in general but also for mediating the memory bias. Figure 5 shows the most likely DCM network of effective connectivity between HPC and vmPFC. The strength of HPC-vmPFC coupling was dependent on whether participants chose the better remembered snack or not.

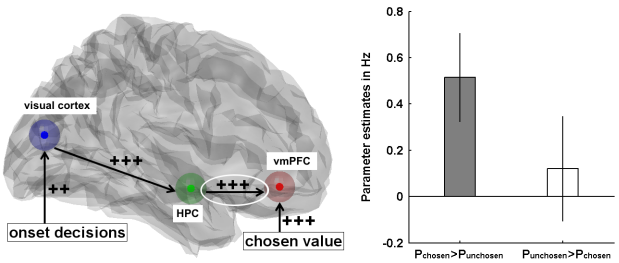

Figure 5. Effective connectivity in preferential choices from memory. **Left**: the most likely Dynamic Causal Model with connection strengths ("++" = positive at $p < 0.01$; "+++" = positive at $p < 0.001$); **right**: the connection from hippocampus to ventromedial prefrontal cortex (circled) was only significantly positive when participants chose the better remembered snack. Error bars represent 95% confidence intervals (adapted with permission from [71]).

Based on the findings from these studies on the functional neural coupling between HPC and PFC, different theories and frameworks have been put forward. First of all, Shin and Jadhav [72] conclude that the bidirectional flow of memory-related information between HPC and PFC supports memory formation (consolidation), contextual memory retrieval and memory-guided decisions. Specifically,

the insights from neural connectivity analyses seem to strengthen the hypothesis of a role differentiation between PFC and HPC, where HPC is mainly involved in memory encoding while the PFC is more engaged during memory retrieval [81,82]. Accordingly, during the consolidation process, the vmPFC is supposed to take over the role of HPC making the stored events more accessible to the PFC [83,84]. This view clearly opposes the previously presented MTT, stating that contextual information will always be kept in the HPC [16] but supports more the account of SC [15]. Moreover, a recent review [85] suggests that vmPFC is similar to a control instance, as it selects the appropriate memory for a specific context, and then controls the retrieval of the detailed memories in the HPC (context-guided retrieval). This explanation is reminiscent of the classical view of PFC as "central executive". In addition, vmPFC may not be crucial only at the end of consolidation but already during earlier stages of learning, e.g., in the development of schemata. According to Piaget [86], a schema is a structured mental representation of related associations. Preston and Eichenbaum [85] reviewed the interplay of HPC and PFC in memory concluding that vmPFC and HPC interact during schema formation (encoding), consolidation and expression (retrieval). Furthermore, it has been suggested that only new events overlapping with previous experiences need the interplay of HPC and vmPFC. This is the case for items learned according to the association inference paradigm: in this paradigm, a first association between two items is learned (A-B, e.g., the pair ball-hat), and then a second association is learned that includes a known and a new item (B-C, e.g., the pair hat-fork). The schema A-B-C refers to the fact that the three items ball-hat-fork belong to the same group. During the stage of schema formation, the strategic roles of vmPFC and of the vmPFC-PC coupling come into play. After having learned the schema, subjects can infer that A-C (i.e., ball-fork) also belongs to the same group although they were never shown together. In contrast, if events do not overlap, HPC may integrate the memories predominantly alone (resulting in a lower vmPFC-HPC coupling). This would be the case when, for example, we learn two completely new and independent associations like A-B and C-D, for which we have no previous knowledge. The previously described processes can be linked to the classical concepts of assimilation and accommodation [85] introduced by Piaget, who also shaped the definition of a schema [86].

Finally, also derived from findings showing evidence for a neural mechanism underlying the connectivity between HPC and PFC, Wang and colleagues proposed a framework for understanding cognitive and/or behavioral choices [87]. The framework is called Covert Rapid Action-Memory Simulation (CRAMS) [87] and states that covert memory processing of HPC interacts with action-generation processing of PFC in order to arrive at memory-guided choices with little effort. The term "covert" indicates that this process can take place without conscious awareness (implicitly and automatically) and this is consequently the reason why the process is also "rapid". This framework aims to explain the mechanism underlying difficult decisions, that is, decisions where the options appear to have the same outcome value. In those situations where a response conflict arises, PFC provides the HPC with possible plans for action via CRAMS. In other words, first the possible actions are simulated (lateral PFC), and then covert memory is retrieved (HPC) and finally evaluated (medial PFC). This process is repeated until a goal threshold is reached. Afterwards, the action can be performed, and a choice is made (motor systems). Interestingly, the CRAMS model is in accordance with the above mentioned notion that HPC-dependent memory retrieval should be relevant even in value-based decisions that do not require an explicit recall of information from the past [2]. However, it is widely acknowledged that not only PFC but also HPC contributes to imaging future events [88–91]. As far as we know, the CRAMS framework does not account for those findings. Indeed, the fact that HPC may simulate the past and/or the future could represent an important extension to this framework. Additionally, the CRAMS model is currently only a theoretical framework and needs specific empirical testing in order to be able to relate a specific region to a distinct function.

5. Open Questions and Tentative Predictions for Future Studies on the Interplay of Value-Based Decisions Making and Episodic Memory

Even though the findings of HPC-vmPFC interactions outlined in the previous chapter are remarkable and promising, we are still far away from having a clear picture of how exactly they work together in enabling memory-based decision making. So far, the studies differ greatly with respect to their research questions, methodologies, and interpretations of the data. In fact, researchers even refer to different things when they speak of "memory-based decisions". In contrast to our definition (see Section 1), this term is sometimes used to refer to decisions about memory, that is, whether a currently presented stimulus has been encountered before or not (old vs. new) [92]. In the following, however, we will focus on value-based decisions that require the retrieval of information from memory [71], that is, decisions about (memory-based) preferences and not about memory itself (for a definition of the different concepts see the Section 1). The goal of the present chapter is to identify relevant open questions and to make some tentative predictions of how HPC and vmPFC interact with respect to memory-based decision making by a critical appraisal of what we already know and what we do not know in this regard.

5.1. Question 1: What Is the Neural Code That Underlies Memory-Based Decisions?

As outlined in the previous chapter, there is ample evidence that HPC-vmPFC interactions rely on the coherence of low-frequency (i.e., theta-band) long-range neural oscillations. The study by Guitart-Masip and colleagues [74] indicates that such a synchronization of neural signals in the theta-band may also underlie memory-based decisions. However, the task paradigm employed in this study is not a pure episodic memory task but has typical reinforcement learning features. Hence, it remains open whether theta-band oscillations between HPC and vmPFC are critical in decisions that are based on retrieving episodic memory content, and also whether these oscillations are generally beneficial for making accurate decisions [69,74] or whether they might bias decisions toward better memorized choice options [71]. The use of the MEG technique together with source reconstruction methods will be crucial for answering these questions.

Additionally, Guitart-Masip and colleagues [74] reported no significant effects of reward, punishment or their interaction on the low-frequency coupling between HPC and vmPFC. This result is not in line with the DCM results of Gluth et al. [71] and is also difficult to reconcile with accumulating evidence for value-based signals in HPC (see Question 4 below). Again, such discrepancies might be due to the fact that different tasks do or do not contain reinforcement learning elements. Hence, it will be important to employ similar experimental paradigms with different neuroimaging techniques such as fMRI and MEG in the future.

5.2. Question 2: How Can We Bring Schema-Related and Choice-Related HPC–vmPFC Interactions Together?

Hippocampal-vmPFC interactions seem to lie at the heart of both enabling complex inferential memory associations [68] as well as mediating value-based decisions from memory [71], but how can we bring these two findings together? A possible answer could be that an increased HPC–vmPFC coupling enables a richer representation of (choice-relevant) past events so that decision making is altered on a qualitative level. For example, if a currently visible cue A (e.g., a deck of cards) triggers only a direct association with another event B (e.g., gambling in a casino) that has been linked to A in the past, the decision to engage in an action might differ as compared to when an (HPC–vmPFC coupling dependent) indirect association from A via B to C (e.g., the loss of money) is also triggered.

Importantly, the associations created in the example above are of personal value to the participants. In the study of Zeithamova and colleagues [68], however, the association task included different images with assumed neutral valence, such as common objects and outdoor scenes. An additional valence-rating task could provide information about whether the images are really perceived as neutral. Alternatively, pictures from the International Affective Picture System (IAPS) [93], for which arousal and valence information is available, could be used in such memory- and schema-based task.

The general point that we want to make here is that "memory researchers" should be aware of the fact that the vmPFC, one of the brain regions they are (currently) interested in, is very sensitive to value-related information (which might also be true for the HPC; see Question 4 below). This has to be taken into account to avoid confounding effects and misinterpretations. On the other hand, "decision-making researchers" should be aware of the fact that different choice options might easier or harder to store into and retrieve from memory (e.g., [71]).

5.3. Question 3: What Is the Direction of HPC–vmPFC Connectivity?

For the connectivity analysis in [71], DCM was applied which (in contrast to methods such as psycho-physiological interactions) allows identifying the direction of the information flow from one brain region to another. The authors tested different potential circuits with connections from HPC to vmPFC, from vmPFC to HPC, and bidirectional connections, and found the first circuit (i.e., from HPC to vmPFC) to provide the best account of the data. Interestingly, context-guided retrieval of memory as in the processing of mental schemata has been hypothesized to instead rely on the vmPFC impacting on activation in the HPC [85]. Therefore, it is tempting to speculate that the direction of HPC-vmPFC coupling can dissociate between the processes of retrieving information from memory to guide decision making and the process of constructing complex memory representations. Accordingly, it will be important for future studies to apply methods such as DCM (which is not only applicable to fMRI but also to MEG) that allow identifying in which way HPC and vmPFC communicate with each other.

5.4. Question 4: Does the HPC Represent Subjective Value?

The common view is that the vmPFC (perhaps together with the ventral striatum) represents subjective value, while HPC is crucial for episodic memory. Some studies, however, found an activation in HPC during the encoding of subjective value [47,71,94–96]. A question that arises here is how the HPC can access value information. Two possibilities have been proposed [94]: on the one hand, the HPC may receive these information via its connections with vmPFC/ventral striatum and is thus only indirectly linked to value computation; alternatively, the HPC might play a direct role in value processing. Importantly, most studies that reported strong correlates of subjective value in HPC employed an experimental paradigm that requires people or animals to rely on spatial memory for making good decisions [71,95,97,98]. Hence, we speculate that a putative direct value-coding function of HPC may be restricted to spatial memory demands. This hypothesis could be tested by modulating spatial vs. non-spatial episodic memory demands within the same task.

On a more general note, we want to repeat our appeal to researchers in the two fields of episodic memory and value-based decision making that they should be aware of the fact that they are studying interrelated constructs that rely on interrelated brain regions. We hope that reviews such as the present article will help to sensitize researchers of both fields that their findings may sometimes be easier and better explained by referring to these relationships of memory and decision making rather than by strictly staying within the theories of a single domain of research.

6. Conclusions

In the present review article, we have reviewed the classical views concerning the roles of HPC and vmPFC in episodic memory and value-based decision making, respectively, and we highlighted various methods and theories concerning the interplay of HPC and vmPFC. Based on our emerging knowledge about the cross-talk of these brain areas, we proposed several directions for future research. In our opinion, designing studies that address those questions will lead to a clearer picture of the reasons why and the circumstances in which HPC and vmPFC interact in processing memory and decision making. Methods that allow joint measurements of HPC and vmPFC activity as well as their connectivity profile, such as MEG and fMRI, will be of extraordinary importance for this endeavor.

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Conflicts of Interest: The authors declare no conflict of interest.

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Appendix B. Weilbächer, Kraemer, & Gluth, in press

The reflection effect in memory-based decisions

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Abstract

Previous research indicated a bias in memory-based decision making, with people preferring options that they remember better. However, the cognitive mechanisms underlying this memory bias remain elusive. Here, we propose that choosing poorly remembered options is conceptually similar to choosing options with uncertain outcomes. We predicted that the memory bias is reduced when options have negative subjective value, analogous to the reflection effect, according to which uncertainty aversion is stronger in gains than in losses. In two preregistered experiments (n = 36 each), participants made memory-based decisions between appetitive or aversive stimuli. People preferred better-remembered options in the gain domain, but this behavioral pattern reversed in the loss domain. This effect was not related to participants' ambiguity or risk attitudes, as measured in a separate task. Our results increase the understanding of memory-based decision making and connect this emerging field to well-established research on decisions under uncertainty.

Keywords: decision-making, episodic memory, uncertainty

Statement of Relevance

Many decisions in our everyday life, such as choosing whether to have the same lunch meal as yesterday, are shaped by our memories. However, we are just beginning to understand how memories and decisions interact. Based on the proposal that choosing a poorly remembered option is conceptually similar to choosing an option with uncertain outcomes, the present study draws an analogy between decisions from memory and decisions under uncertainty. In line with this rationale, we find that decisions from memory elicit a preference reversal between gains and losses that mirrors the well-known reflection effect in decisions under uncertainty: People prefer better-remembered over less-remembered options in the gain domain, but exhibit the opposite preference in the loss domain. Our findings connect two hitherto separate branches of decision-making research and have potentially broad implications for understanding the impact of aging- or disease-related changes in memory abilities on behavior.

Introduction

Many of our daily choices require us to retrieve relevant information from memory, and the role of memory in shaping such value-based decisions is receiving growing interest (Shadlen & Shohamy, 2016; Weilbächer & Gluth, 2017; Wimmer & Büchel, 2016; Weber & Johnson, 2006; Murty, Feldmanhall, Hunter, Phelps, & Davachi, 2016; Gershman & Daw, 2017). Episodic memory and decision making were studied separately for decades, but more recent studies have started to investigate how these two psychological constructs interact (Murty et al., 2016; Gershman & Daw, 2017; Wimmer & Büchel, 2016). In our previous work, we have shown that memory-based decisions can give rise to a bias in choice behavior (Gluth, Sommer, Rieskamp, & Büchel, 2015; Mechera-Ostrovsky & Gluth, 2018). More precisely, the *memory bias* in preferential choice states that people tend to prefer options they remember better to an extent that is not compatible with standard notions of optimality and utility maximization. To illustrate this, assume a decision between two hiking locations, A and B, of equal subjective value. Remembering past experiences of hiking location A more vividly than B will induce a preference for A over B. In fact, our findings suggest that even if A has somewhat lower subjective value than B, the memory bias still induces a preference for A.

An open question is why people exhibit this memory bias, or stated differently, what the cognitive mechanisms are that drive this effect. Here, we argue that uncertainty plays a critical role in decisions from memory and can explain why people show a memory bias. We assume that choosing between a vividly remembered and a poorly remembered option is conceptually similar to choosing between a certain and an uncertain option. Our argumentation follows a recent proposal that people retrieve past instances from their memory when deliberating on the likely consequences of choosing an option(Shadlen & Shohamy, 2016; Bakkour et al., 2019). Accordingly, a more vivid memory of previous encounters with an option (e.g., previous hiking trips to location A) provides higher confidence about its subjective value. In contrast, a poorly remembered option entails

greater ambiguity about its potential consequences given that previous encounters of it cannot be remembered so well anymore (e.g., whether hiking location B might have included some dangerous parts). This renders the poorly remembered option an uncertain choice candidate. Importantly, research on decision making under risk (Tversky & Kahneman, 1981; Kahneman & Tversky, 1979) and ambiguity (Kahn & Sarin, 1988; Viscusi & Magat, 1992) have demonstrated a *reflection effect*, meaning that uncertainty aversion is less pronounced and sometimes even reverses in the loss as compared to the gain domain. Thus, we derive the analogous hypothesis that the memory bias is stronger in the gain domain than in the loss domain. Stated differently, when choosing between two appetitive options, we predict people to exhibit a preference for the option they remember better and whose consequences are more certain to them. But when having to choose from aversive options, this tendency should be decreased and possibly reversed, implying that people go with the less-remembered and uncertain option in hope that its consequences might not turn out to be so bad.

To investigate this hypothesis, we leveraged our *remember-and-decide* task (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018), in which participants first learn to associate different choice options with different locations and then make a series of value-based decisions between two highlighted locations (Fig. 1). Since only the locations but not the choice options themselves are presented, participants need to recall the options from their memory when making decisions. Following these decisions, participants are then asked to recall the option-location associations, which allows us to identify remembered and forgotten options (i.e., the label *forgotten* refers to options which could not be recalled correctly). Ultimately, the memory bias is quantified by the strength of preference for remembered over forgotten options. So far, this task has only been used with appetitive (food snack) items. As we aimed to investigate decisions in the gain as well as in the loss domain in the current study, we used appetitive and aversive images in one experiment and positive and negative monetary amounts in a second independent experiment. Beyond

testing our main hypothesis, these two experiments with their different sets of stimuli also allowed us to assess to what extent the memory bias (and its putative reversal in the loss domain) generalizes to different domains of decision making.

In essence, we found that participants indeed preferred remembered over forgotten options in the gain domain, but showed the opposite pattern in the loss domain. This confirms our hypothesis of an analogy between decisions from memory and decisions under uncertainty. Thus, concerning options of positive subjective value, people stick to better remembered options and avoid the risk of choosing what they do not recall well. But when it comes to options of negative subjective value, people take the risk of choosing the unknown.

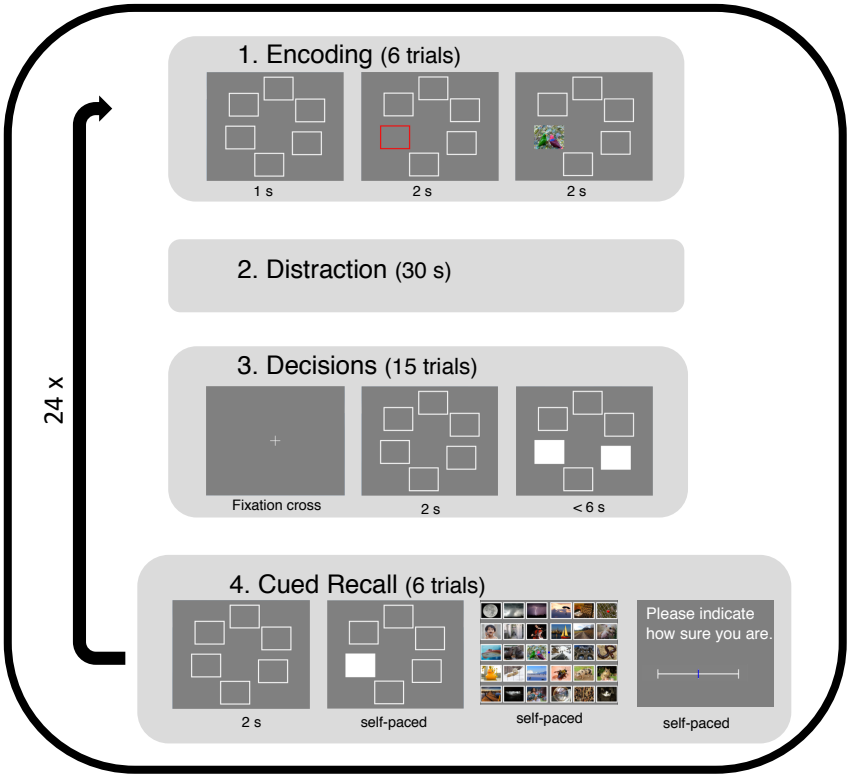

Fig. 1. The remember-and-decide task for the Images Experiment. Participants first encode the association of images with locations on the screen. After a distracting working-memory task, they make binary decisions between the images from memory. Finally, they are asked to recall each image. This procedure is repeated in 24 rounds, 12 rounds with options of positive subjective value and 12 rounds with options of negative subjective value. The figure displays one example round. The procedure was analogous for the Money Experiment but with positive and negative monetary values as choice options (the analogous figure for the Money Experiment can be found in the Supplementary Online Material [SOM]).

Method

We preregistered our two experiments (including hypotheses, experimental design, and analysis plan) on the Open Science Framework website (https://osf.io/eumj5). The complete project (including the processed data and data analysis files in the programming languages R and Python) can be found here https://osf.io/x935r/.

Sample size rationale

In the preregistration protocol, we proposed to perform a two-step analysis approach (i.e., first hierarchical Bayesian parameter estimation, second frequentist t-tests on the mean parameter estimates; see below) and performed a power analysis to estimate the required sample size.

The central hypothesis of our experiments was the difference of the memory bias in gains and losses. While the memory bias itself appears to be a strong effect (effect sizes Cohen's d in previous studies (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018) were between 0.7 and 1.0), the effect size of the difference between gains and losses is unknown. Therefore, we assumed a medium effect size of $d = 0.5$. We used the software program G*Power (version 3.1.9.4) to conduct a power analysis (paired-sample t-test, one-tailed, effect size $d = 0.5$, alpha error probability = .05, power = .9), which suggested a sample size of n = 36 participants. Note that we selected a power of .9 for each experiment, because we sought to achieve a power of greater than .8 across both experiments combined (i.e., $.9^2 \sim .8$).

Participants

Participants were recruited at the University of Basel (convenience sampling). In the Images Experiment a total of 53 participants started the experiment. In the Money Experiment a total of 47 participants started the experiment. Participants were between 18 and 35 years old, did not suffer from mental disorders, and were allowed to participate in

only one of the two experiments.

Based on our preregistered exclusion criteria, we did not analyze the data of 17 participants from the Images Experiment for the following reasons: The participant aborted the study (n=2), did not perform all tasks (n=1), were not in the targeted age range (n=1), did not yield the minimal number of trials for the logistic regression analysis (see below; n=8), rated less than 30 images as positive or less than 30 images as negative (n=5). For the Money experiment, we did not analyze the data of 11 participants for the following reasons: Participant aborted the study (n=5), did not perform all tasks (n=2), were not in the targeted age range (n=1), did not yield the minimal number of trials for the logistic regression analysis (n=2), did not understand the n-back task (n=1). We thus included n=36 participants for the analysis of the Images Experiment (25 women, age: range 18-34, M = 23.94, SD = 4.45), and n=36 participants for the Money Experiment (26 women, age: range 18-35, M = 24.42, SD = 4.32).

Participants could only take part in the study after reading and signing the informed consent form, which had been approved by the ethics committee of north-west and central Switzerland (EKNZ). Participants were reimbursed 5 CHF for every started 15 minutes (resulting in 20 CHF per hour). Psychology students of the University of Basel had the opportunity to receive course credits instead of the monetary reimbursement. Additionally, in the Images Experiment participants received a bonus in the sense of looking at the image that they selected in a randomly selected choice trial (details provided below). In the Money Experiment participants could earn a monetary bonus between 0 and 9.50 CHF based on their decision in a randomly selected choice trial. In the additional gambles task that participants in both experiments performed on a separate day (details provided below), participants also had the opportunity to receive a monetary bonus between 0 and 60 CHF.

Apparatus and Stimuli

Participants were seated in front of a 24-in. computer screen (resolution 1680 x 1050 pixel, refresh rate 60Hz). Stimulus presentation and creation of choice sets were realized using MATLAB Version R2016a and its toolbox Cogent 2000 (version 1.33). The screen resolution was set to 1280 x 1024 pixel.

The images for the Images Experiment were selected from the OASIS database (Kurdi, Lozano, & Banaji, 2017). The OASIS database includes a total of 900 images. To reduce the amount of images for our preference rating task, we first excluded all images with arousal and/or valence ratings <2 and >5 (ratings were on a scale from 1 to 7, rated by a large sample of n=822 participants; details provided in Kurdi et al. (2017)). Thereby, we excluded too arousing images (e.g., mutilations) and not arousing images, to avoid that some images were much more memorable than others. Second, we excluded all images from the category "Nudes". Third, we renamed redundant categories (e.g. "Graveyard" and "Cemetery"). Fourth, we selected one image per category (e.g., if 5 images displayed a dog, one of them which was judged to be most representative was selected). This procedure resulted in a final set of 103 images.

Experimental Procedures

We conducted two independent experiments, and each participant was allowed to take part in only one of them. Each experiment consisted of two sessions, performed with a delay of one week ± three days. The two experiments differed only in the used stimulus material: images or money. In the first session, after participants gave their informed consent, they read the instructions for the remember-and-decide task (as in Gluth et al., 2015; Mechera-Ostrovsky and Gluth, 2018). The task consists of multiple blocks of 4 phases each: 1) encoding of the association of six locations and the choice options (money or images), 2) 2-back working memory task, 3) binary choice task (in which the options need to be recalled from memory, as only the locations are presented), and 4) cued recall of

the six stimuli (Fig. 1). Participants were familiarized with the task by performing two training rounds. Afterwards, they conducted 24 rounds in total – 12 times with negative stimuli and 12 times with positive stimuli. The order (positive or negative first) was counterbalanced across participants. In the Images Experiment participants made one break between the two blocks (12 rounds). In the Money Experiment participants made a break after each quarter of the rounds (6 rounds).

In the Images Experiment, participants' subjective value of the images was assessed with an incentivized rating task prior to the remember-and-decide task. Participants rated the images on a discrete rating scale ranging from -10 to 10 in steps of 1. They were asked to use the entire range of the rating scale and rated every image twice. To incentivize the rating task, participants were informed that at the end of the experiment two images were drawn randomly, and that the higher-rated image was presented to them for 3 minutes. The 103 rated images were divided into positive and negative images, based on the mean rating value. For the *remember-and-decide* task, at least 30 positively and 30 negatively rated images were needed to generate enough trials. Based on previous experience (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018), the two images with the most extreme negative and positive ratings were excluded, because people tend to have exceptionally good memory for these items. In case a participant had rated less than 30 images as positive on average or less than 30 images as negative on average (for example when the participant used only the negative part of the rating scale), the participant was informed that it was not possible to generate enough trials and the experiment was aborted. In this case, the data being collected so far was not used for data analysis. In the Money Experiment, the positive (appetitive) stimuli were monetary values ranging from 10 to 95 in experimental currency unit (ECU) which were translated into Swiss Francs (CHF) by being divided by 20 (e.g. 95 ECU = 4.75 CHF). Similarly, the negative (aversive) stimuli were monetary values ranging from -95 to -10 in steps of 5, resulting in 18 stimuli each. Participants could win up to 4.75 CHF from the gains trials and the loss trials,

respectively, resulting in a possible bonus of 9.5 CHF. In the gains lottery, participants earned the monetary amount they chose in the randomly selected choice trial, whereas in the losses the amount of the choice was subtracted from and initial endowment of 4.75 CHF (e.g., if a trial was selected, where the participant choose -50 ECU, she received the following bonus: 4.75 - [50 ECU / 20] = 2.25).

This first session lasted approximately 75 to 90 minutes. On average the Images Experiment lasted approximately 15 to 20 minutes longer than the Money Experiment, because of the additional rating task. At the end of session 1, participants could indicate in an answer box which strategy they used to memorize the stimuli.

In the second session (approx. 30 min), participants first reported demographic information about their age, country, education, gender, handiness, income, current job and mother tongue. Afterwards, they completed two tasks. First, they performed the *estimate-your-memory* task, in which they indicated how well they remembered each possible item from the *remember-and-decide* task of session 1 (similar to Mechera-Ostrovsky and Gluth, 2018). Second, they performed a gambling task (see Fig. 3) including risky and ambiguous gambles in the gain and the loss domain. We included this task to test whether participants who exhibit a stronger reduction of the memory bias in the loss compared to the gain domain would also show a stronger reflection effect in decision under risk or ambiguity. We adapted a task from previous studies (Levy, Snell, Nelson, Rustichini, & Glimcher, 2010; Tymula, Rosenberg Belmaker, Ruderman, Glimcher, & Levy, 2013), in which participants made binary decisions between a sure gain/loss of a small amount of money (in our case ±5 CHF) and a risky or ambiguous gamble of a larger gain/loss amount. More specifically, participants could either choose ±5 CHF for sure or an amount between ±6 and ±30 CHF with a given probability. During a trial, participants first saw a fixation cross for 1s, followed by the depiction of the safe amount and the lottery. They had 10s to indicate their choice by pressing either the Q (left choice) or P (right choice) button on a keyboard. Finally, a green feedback rectangle appeared around

their chosen option for 1s. The gambles included six gain/loss amounts (±6 , 12, 16, 22, 26, 30 CHF). The risky trials had five winning probability levels (0.2, 0.35, 0.5, 0.65, 0.8). In the ambiguous trials, the five levels of ambiguity (0.2, 0.35, 0.5, 0.65, 0.8) were indicated by the area of a grey bar which prevented a glimpse on the underlying probabilities. Following previous work (Levy et al., 2010; Tymula et al., 2013), the grey bar covered the red (lottery probability) and the blue (safe option probability) parts to the same extent. Therefore, if an ambiguous trial was played at the end of the experiment, a random number between the lowest winning probability and the highest (area covered by the grey bar) was drawn. Then an outcome was drawn based on this randomly selected probability. We repeated each amount twice, thus resulting in a total of 240 trials [12 unique amounts x (5 probability levels + 5 ambiguity levels) x 2 repetitions]. Seven participants in the Money Experiment did 280 trials, because an older version of the experiment was used, in which 40 catch trials with one option stochastically dominating the other option (e.g., choice between 5 CHF for sure and 5 CHF with a probability of 80%) were included. These trials were excluded for analysis.

Data exclusion

To ensure high data quality, we specified and preregistered a number of exclusion criteria. The following criteria were assessed separately for positive and negative trials: First, to reliably assess the memory bias with a hierarchical Bayesian logistic regression model, we determined a minimum number of 20 trials per participant, in which one option has been remembered, while the other has been forgotten. Moreover, we required a minimum number of 5 per observed choice (i.e., remembered option chosen; forgotten option chosen). These numbers were based on analyzes of pilot data. Additionally, we adopted a hierarchical Bayesian approach with mildly informed priors that is more robust compared to frequentist approaches (Gordóvil-Merino, Guàrdia-Olmos, & Peró-Cebollero, 2012; McNeish, 2016; Kruschke, 2010). Furthermore, participants who responded too fast

(i.e., RT <200 ms) in $\geq$ 30% of trials of the decision task or in $\geq$ 30% of the gambles task were excluded (however, none of the participants had to be excluded for being too fast).

Data analysis

Memory bias estimation. The memory bias was assessed in a similar way as in our previous work (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018), but instead of maximum likelihood estimation we employed hierarchical Bayesian logistic regression analyses. Note that the hierarchical Bayesian framework allowed us to compare the group posterior distributions directly and provided us with an estimate of certainty (Wagenmakers et al., 2018). Moreover, it is especially recommended when the number of observations varies across participants, which is the case for our remembered-forgotten trials (McNeish, 2016). The memory bias analyses are based on trials (t) with one remembered and one forgotten option. The probability p_t to choose the remembered option over the forgotten option is given by

$$p_t = \frac{1}{1 + \exp^{-(\beta_0 + \beta_1 * x_t)}}, \tag{1}$$

where x_t refers to the standardized subjective value of the remembered option in trial t, and β_0 and β_1 refer to intercept and slope coefficients, respectively. The probability that the remembered item will be chosen is estimated by drawing from a Bernoulli distribution with success probability p_t:

$$y \sim \text{Bern}(p_t), \tag{2}$$

Hierarchical priors for the two regression coefficients in the model (β_0 and β_1) and hyper priors are specified as follows:

$$\begin{aligned} \mu_\beta &\sim N(0, 1) \\ \sigma_\beta &\sim \text{HalfCauchy}(5) \\ \beta &\sim N(\mu_\beta, \sigma_\beta) \end{aligned} \tag{3}$$

For each coefficient (intercept and slope) the mean μ_β was drawn from a normal distribution, and the standard deviation σ_β was drawn from a Half-Cauchy distribution.

We specified the prior distributions based on the developers' recommendations of the used estimation package.

The slope of the logistic function β_1 specifies to what extent decisions depend on the value of the remembered option, the intercept β_0 quantifies the overall tendency to prefer remembered or forgotten options, and thus the memory bias. Notably, in our previous work we introduced a corrected version of the memory bias which controls for the possibility that participants remember high-value options better than low-value options (Mechera-Ostrovsky & Gluth, 2018). This correction consists of subtracting the average value of all forgotten options from the value of the remembered option x_i. In the present study, we also implemented this correction when quantifying the memory bias.

The statistical test for an influence of memory on choice was based on the group posterior samples of the intercept parameter β_0. If the 90% HDI of the distribution did not overlap with 0, we inferred a significant memory bias (a positive memory bias if the distribution lies to the right of 0, a negative memory bias if the distribution lies to the left of 0)[1]. Moreover, to test for the difference between gains and losses, we tested for an overlap with 0 as before for the estimated difference parameter. As a sanity check that participants take the value of remembered options into account when choosing between a remembered and a forgotten option, we also checked that the posterior distribution of the mean slope parameter β_1 was larger than 0 in all conditions (gains and losses, Images and Money Experiments) by testing whether the 90% HDI (highest density interval) did not overlap with 0.

[1] At this point, we deviated from our preregistration protocol, in which we announced to fit the logistic regression model and perform frequentist tests on the means of the individual posterior distributions. Such a two-step procedure can lead to inflated results in favor of the alternative hypothesis (Boehm, Marsman, Matzke, & Wagenmakers, 2018). Therefore, here we report the fully Bayesian tests only. For completeness the SOM includes the (invalid) two-step approach as well as a (purely frequentist) random-effects regression analysis [as in Gluth et al. (2015), Mechera-Ostrovsky and Gluth (2018)].

Risk and ambiguity attitudes assessment. To assess participants' risk and ambiguity parameters we used an adapted version of a previously proposed model (Levy et al., 2010; FeldmanHall, Glimcher, Baker, & Phelps, 2016). According to this model, the subjective value of an option is given by:

$$SV = (p - \beta * \frac{A}{2}) * v^{\alpha} \tag{4}$$

where p is the probability of the gain/loss amount of the lottery, A indicates the level of ambiguity, v is the gain/loss amount, α the individual risk attitude and β the individual ambiguity attitude. Note that a loss aversion parameter is not included, because the task does not contain mixed lotteries, and risk and ambiguity attitudes are estimated separately for gains and losses. The probability of choosing the lottery is given by a logit function (as in Equation 1) with the intercept being fixed at 0.

Notably, we adopted a "bug fix" (Stewart, Scheibehenne, & Pachur, 2018) that ensures commensurability of the sensitivity parameter γ across different risk preferences. Without this bug fix the risk parameter α trades off with the sensitivity parameter, because the risk parameter determines the range of possible values (e.g., the range is much larger if α=2 compared to α=1/2). This problem is solved by transforming the subjective value SV as follows:

$$\begin{aligned} SV &= SV^{1/\alpha} \text{ for } SV \geq 0 \\ SV &= -(\mid SV \mid)^{1/\alpha} \text{ for } SV < 0 \end{aligned} \tag{5}$$

Similar to the logistic regression described above, the model prior and hyper-priors were specified as follows:

$$\begin{aligned} \mu_{\beta} &\sim N(0, 1) \\ \sigma_{\beta} &\sim \text{Inv-Gamma}(3, 0.5) \\ \beta &\sim N(\mu_{\beta}, \sigma_{\beta}) \end{aligned} \tag{6}$$

Risk and Ambiguity attitudes were estimated separately for gains and losses, and for the two experiments (Images and Money).

To test our predictions that the memory bias is related to ambiguity (more so than risk) attitudes, we estimated a Bayesian linear regression predicting the difference of the memory bias between gains and losses with the following three predictors: i) the experiment (Images and Money), ii) the difference in risk attitudes (gains - losses), and iii) the ambiguity attitudes (gains - losses). The priors of the glm module were defined as follows: intercept and regressors $\sim$ Normal(mu=0, sd=1), standard deviation $\sim$ Half-Cauchy(10). As exploratory analyses, we also correlated the mean estimates for the memory bias with the mean estimates of the risk and ambiguity attitudes (separately for gains and losses). Thereto, we used an uniform prior between -1 and 1 for the correlation coefficient r. To calculate the Bayes Factors (BF) we compared our posterior samples to samples from the prior distribution. BFs indicate the evidence provided by the data in favor of an hypothesis. We were interested in the evidence in favor of the Null hypothesis denoted as BF_{01}. A BF of 1 indicates that both hypotheses (Null and Alternative) predict the data equally well(van Doorn et al., 2019).Generally, a $BF \geq 10$ indicates strong evidence.

Bayesian parameter estimation details. Bayesian models for estimating the memory bias were implemented using the pymc3 Python library. We sampled four chains, with 10000 samples each (5000 tuning samples), using the no-U-turn sampler (NUTS). Bayesian models estimating the risk/ambiguity attitudes were implemented using the rstan R library. We sampled two chains, with 5000 samples each (2000 tuning samples), using NUTS. Convergence was diagnosed using the Gelman–Rubin criterion ($|\hat{R} - 1| < 0.05$) for all analyses. Effects were declared as statistically meaningful either when the 90% HDI excluded zero or when 90% of the posterior density was above (below) zero. In the latter case, we also reported the proportion of the posterior mass above (below) zero, directly indicating the posterior probability of the effect being larger (smaller) than zero. (Kruschke, 2014).Bayesian model estimation for the assessment of the memory bias, the Bayesian linear regressions and Bayesian correlations for the relationship of the memory bias and the risk/ambiguity attitudes were performed in Python v3.6.9, using the NumPy

v1.17.2, Pandas v0.25.1, Theano v1.0.4 and PyMC3 v3.7 libraries. All other analyses (frequenstist tests in the SOM, descriptives, figures and data-preprocessing, Bayesian risk/ambiguity attitude estimation) were performed in R v3.6.1, using additionally the libraries psych v1.8.12, ggplot2 v3.2.1, rstan v2.19.2 and bayestestR v0.4.0.

Results

The memory bias in preferential choice in gains and losses. Our central hypothesis was that the memory bias, that is, the tendency to prefer remembered over forgotten options, is more positive in the gain as compared to the loss domain. To test this hypothesis we performed hierarchical Bayesian logistic regression analyses for trials with one remembered and one forgotten option, and predicted the choice of the remembered option based on its value. Before testing for the memory bias, however, we checked whether participants were more likely to choose remembered options of higher subjective value. In line with this, we found that the HDI of the group-level posterior distributions of the logistic slope coefficient was positive and did not overlap with 0 in all conditions (Images Experiment, gains: $M = 0.47$, $SD = 0.10$, 90% HDI = [0.30,0.64], losses: $M = 0.33$, $SD = 0.09$, 90% HDI:[0.17,0.47, difference gains - losses: $M = 0.14$, $SD = 0.14$, 90% HDI = [-0.07,0.38]; Money Experiment, gains: $M = 0.88$, $SD = 0.13$, 90% HDI = [0.62,1.10], losses: $M = 0.76$, $SD = 0.15$, 90% HDI = [0.53,1.01], difference gains - losses: $M = 0.12$, $SD = 0.20$, 90% HDI = [-0.16,0.44]).

More importantly, to test for a more positive memory bias in gains compared to losses we contrasted the group-level posterior distributions of the logistic intercept coefficient between gains and losses. In both experiments, we found that the memory bias was more positive in the gain than in the loss domain, and that the overlap of the two posterior distributions was less than 5% (i.e., 0.47% in the Images Experiment and 4.96% in the Money Experiment; Images Experiment difference gains - losses: $M = 0.34$, $SD = 0.13$, 90% HDI = [0.13,0.56]), Money Experiment difference gains - losses: $M = 0.15$, $SD =$

0.09, 90% HDI = [0.01,0.31], which confirmed our hypothesis (Fig. 2). In addition, we tested whether the memory bias was positive in the gain domain and negative in the loss domain (in absolute terms). Descriptively, this was the case in both experiments, but only in the gain condition of the Images Experiment the 90% HDI did not overlap with 0 (Images Experiment, gains: M = 0.24, SD = 0.09, 90% HDI = [0.10,0.39], losses: M =-0.10, SD = 0.09, 90% HDI:[-0.25,0.06], ; Money Experiment, gains: M = 0.09, SD = 0.07, 90% HDI = [-0.03,0.20], losses: M = -0.06, SD = 0.06, 90% HDI = [-0.16,0.03]).

Taken together, participants in both experiments indeed preferred remembered over forgotten options in the gain domain but forgotten over remembered options in the loss domain, with the difference between gains and losses being credible.

Testing an association of the memory bias with risk and ambiguity aversion. In addition to our main hypothesis, we tested whether the difference of the memory bias in gains vs. losses is correlated with the difference in risk or ambiguity aversion in gains vs. losses. We predicted to find an association with ambiguity but not risk, because choosing a less-remembered option whose consequences are uncertain should be conceptually similar to choosing a lottery option whose probabilities are not even known. To test this hypothesis, participants in both experiments performed an additional task, in which they made binary decisions between a sure gain or loss and either a risky or ambiguous lottery (Fig. 2a and b). We modeled their decisions to derive individual risk and ambiguity attitudes separately for gains and losses in a hierarchical Bayesian framework. Then, we linked the individual risk and ambiguity attitude parameters (individuals' mean estimates) with the memory bias parameter using a combined Bayesian multiple linear regression analysis for both experiments. We found that neither the ambiguity nor the risk attitudes as measured by the gambles task were related to the memory bias, as the 90% HDI included 0. However, we observed an effect of experiment, as the size of the memory bias differed if monetary rewards are used or images (intercept: M = 0.34, SD = 0.07, 90% HDI = [0.23,0.47], Experiment (money as reference): M = -0.19,

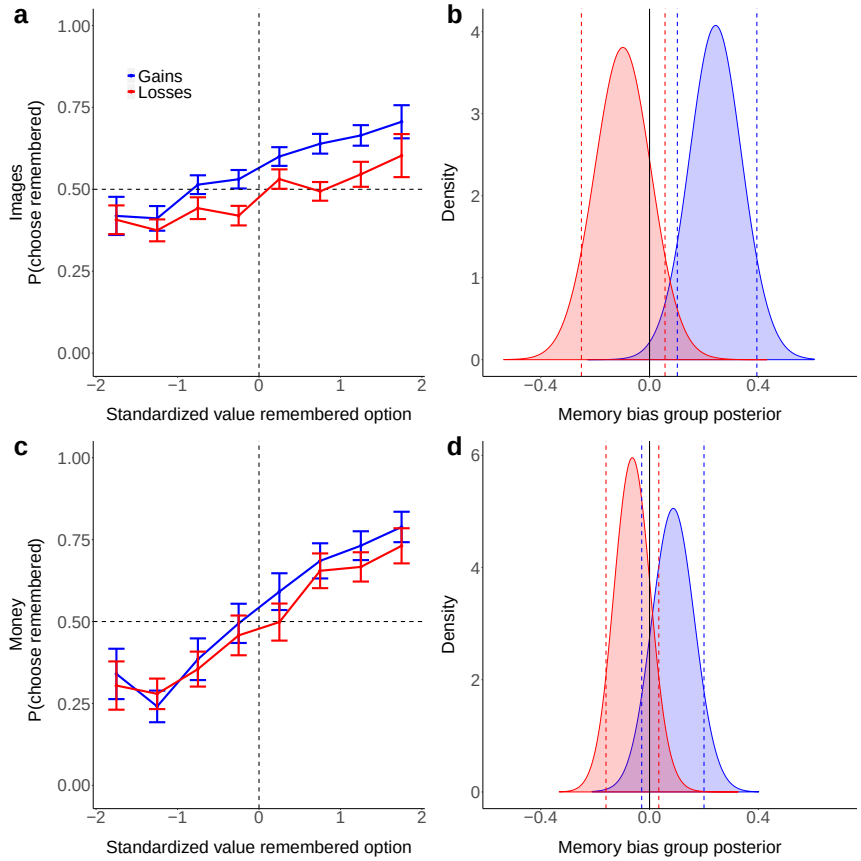

Fig. 2. Memory bias for gains and losses in both experiments. The upper panels refer to the Images Experiment, the lower panels refer to the Money Experiment. The left panels depict the probability to choose remembered over forgotten options as a function of the remembered option's subjective value. The right panels depict the posterior samples of the group-level intercept coefficient of the logistic regression, that is, the memory bias parameter. Error bars in the left panels indicate 95% CI. In the right panels, the dashed lines indicate the 90% HDI of the posterior distribution.

SD = 0.10, 90% HDI = [-0.36,-0.04], effect of risk: M = 0.00, SD = 0.09, 90% HDI = [-0.16,1.15], effect of ambiguity: M = 0.01, SD = 0.08, 90% HDI = [-0.11,0.14]). To quantify the evidence in favor of the Null, we also computed Bayes Factors, which suggest that there is strong evidence in favor of the Null for an effect of ambiguity (BF_{01} = 13.01) and strong evidence in favor of the Null for an effect of risk (BF_{01} = 10.86).

As additional exploratory analyses, we correlated the gain-loss difference in the memory bias with the gain-loss difference in risk and ambiguity attitudes. Results indicate that neither the risk attitude nor the ambiguity attitude as measured by the gambles task were related to the memory bias (Fig. 3c and d). More specifically, we calculated the correlations separate per experiment (money or images), finding no credible correlation ($r_{\text{images,risk}}$: M = -0.05, SD = 0.17, 90% HDI = [-0.32,0.23], BF_{01} = 4.18; $r_{\text{money,risk}}$: M = 0.14, SD = 0.16, 90% HDI = [-0.13,0.41], BF_{01} = 4.21; $r_{\text{images,ambiguity}}$: M = -0.04, SD = 0.17, 90% HDI = [-0.31,0.24], BF_{01} = 3.00; $r_{\text{money,ambiguity}}$: M = 0.22, SD = 0.16, 90% HDI = [-0.04,0.48], BF_{01} = 1.87).

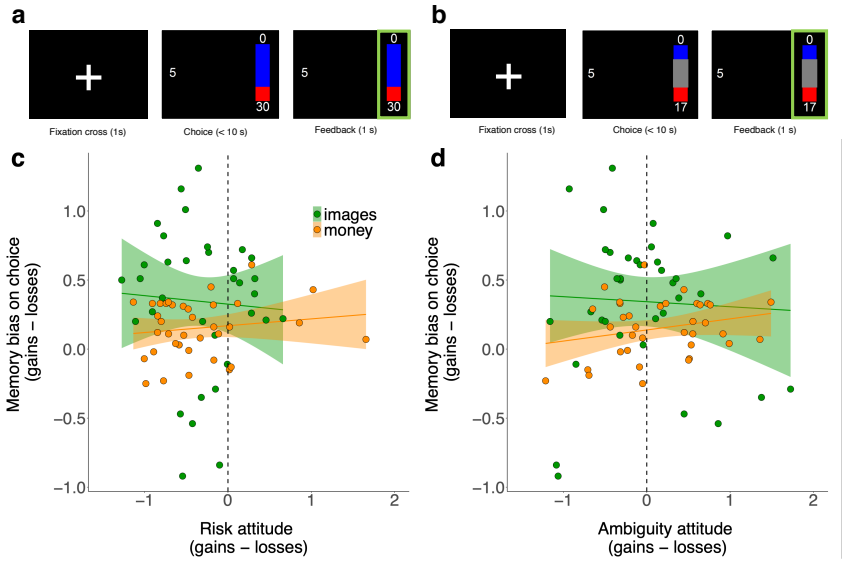

Fig. 3. Ambiguity and risk attitudes. In an additional lottery task, participants made binary decisions between a sure gain or loss and a risky (a) or ambiguous (b) lottery. The colored areas indicate the probability of the upper and lower amounts of the lottery. In case of ambiguous options, parts of the probability information are occluded. The gain-loss difference in the memory bias was not related to the gain-loss difference in risk (c) or ambiguity (d). Regression lines are added separately per experiment with their 95% CI.

Discussion

In the current preregistered study, we investigated an analogy between decisions from memory and decisions under uncertainty. More specifically, we tested whether the memory bias on preferential choice underlies characteristics of the well-known reflection effect (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981; Kahn & Sarin, 1988; Viscusi & Magat, 1992). If so, it should be reduced and possibly even reversed in the loss domain, meaning that people should prefer less-remembered over better-remembered options of

negative subjective value. We conducted two experiments in which participants made preferential choices from memory between images and money amounts. Both experiments were carried out within the gain and loss domain. In both experiments, we observed that participants preferred better-remembered options in the gain domain but less-remembered options in the loss domain, with the gain-loss difference being credible. These results confirm our hypothesis that the memory bias shares characteristics with decisions under uncertainty.

By drawing a link between memory and uncertainty, our work connects two hitherto separate branches of decision-making research. It suggests that the uncertainty entailed in weak memories influence our choice behavior. Importantly, this connection offers several new avenues for future research. First, it will be important to further specify the nature of memory-induced uncertainty in more detail. Along this line, we speculate that the strength of memory for an option could be conceptualized as the probability weight assigned to it. Thus, a parametric effect of memory strength could exhibit a similar profile as the probability weighting function of prospect theory (Tversky & Kahneman, 1992) and lead to similar effects on behavior. Among such effects are the certainty and the possibility effect, according to which the subjective weighting of sure (i.e., 100%) and impossible (i.e., 0%) events are exceptionally larger/smaller than those of almost sure (e.g., 99%) and almost impossible (e.g., 1%) events. If memory strength exhibits a similar weighting profile, then remembering an option "for sure" (i.e., in all its episodic details) and not remembering an option at all should have exceptionally strong influences on our decisions. Second, the link between memory and uncertainty could stimulate research on the impact of inter-individual differences in memory abilities on decision making. For example, the fact that episodic memory shows a considerable decline over the lifespan (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012) should have important implications for older adults' attitudes toward uncertainty, at least with respect to those decisions that rely heavily on memory retrieval. Third, it will be critical to test whether our notion of a

memory-uncertainty link can be supported by neuroscientific data. More specifically, neuroimaging research on decision under risk and uncertainty suggest a brain circuitry comprising the amygdala, the orbitofrontal cortex, and the dorsomedial prefrontal cortex (dmPFC) being involved in ambiguous choices (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006), as well as the dmPFC and the anterior insula (aIns) being critical to risky choices (Morriss, Gell, & van Reekum, 2019; Mohr, Biele, & Heekeren, 2010). The aIns is also central to the processing of aversive stimuli (Nitschke, Sarinopoulos, Mackiewicz, Schaefer, & Davidson, 2006). Therefore, we assert that these areas should also be involved in memory-based decisions, possibly as a (negative) function of the vividness with which the chosen option is remembered.

Contrary to our prediction, the gain-loss difference in the memory bias was not related to the corresponding difference in participants' ambiguity (or risk) attitudes. We discuss three possible explanations for this null finding. First, it could be due to a lack of statistical power. This notion is partially supported by the comparatively low Bayes Factors in favor of the Null hypothesis (which were all below 10 when computing the correlations, thus never suggesting strong evidence). Second, the null result may relate to the finding that behavioral risk measures appear to have a low test-retest reliability (Frey, Pedroni, Mata, Rieskamp, & Hertwig, 2017), rendering them less suitable for studying inter-individual differences. Hence, it might be that an actual relationship between the reflection effect in memory-based decisions and the reflection effect in lottery decisions was concealed by the poor reliability of the later (and possibly of the former as well, since we have not assessed the test-retest reliability of the memory bias, yet). In this light, future studies may consider adding self-report measures of risk and ambiguity, as these measures appear to have higher reliability. Third, it is conceivable that uncertainty induced by poor memories of choice options and uncertainty induced by risk and ambiguity (i.e., known and unknown probabilities of outcomes) are only weakly related to each other. Notably, previous research has shown that risk attitudes are indeed highly domain-specific (Weber,

Blais, & Betz, 2002; Blais & Weber, 2006), and behavioral measures do not only suffer from low reliability but also appear to exhibit low convergent validity (Frey et al., 2017). Therefore, even though the finding of a reflected memory bias supports our notion that weak memories induce a feeling of uncertainty, this form of uncertainty may be distinct from the uncertainty induced by not knowing whether a potential monetary amount will be paid out. Along all these lines, it is interesting to note that we found positive (albeit not significant) correlations between the memory bias and participants' risk and ambiguity attitudes in the Money Experiment but not in the Images Experiment. We speculate that this may reflect the similarity of choosing between monetary amounts retrieved from memory and of choosing between (uncertain) monetary rewards in the gambles task - a similarity not given in the Images Experiment. Certainly, a comprehensive understanding of the exact nature of memory-induced uncertainty in decision making requires more research efforts in the future, and possibly testing a larger sample.

Importantly, we do not consider uncertainty to be the sole driver of the memory bias on preferential choice. Our previous work showed that, in the gain domain, people believe to remember high-value options better than low-value options, and that the strength of this subjective belief was associated with the strength of the memory bias (Mechera-Ostrovsky & Gluth, 2018). Remarkably, in the current study, we found that not only participants' preferences but also their beliefs were inverted in the loss domain. That is, participants believed to remember strongly negative items better than weakly negative items (see SOM). Yet, after taking these value- and domain-dependent beliefs into account, the gain-loss difference of the memory bias remained significant (see SOM). Thus, the influence of memory on decisions appears to be multifaceted and to depend on both, what we infer about poorly remembered choice options (belief) and how we feel about choosing such options (uncertainty).

In sum, our two experiments showed that the influence of memory on preferential decisions generalizes to different types of choice options and exhibits a striking parallel to

decisions from uncertainty: In the gain domain, people prefer better-remembered items, but in the loss domain they tend to prefer less-remembered options. We take this finding as evidence for a conceptual similarity between choosing poorly remembered options and choosing options with uncertain outcomes, thus connecting two different branches of decision-making research. Further research that should include neuroimaging and computational modeling approaches will be required to develop a comprehensive theory of the interplay between memory, uncertainty and preferential choice.

Supplemental Material

Additional supporting information can be found in the Supporting Online Material that accompany this manuscript.

Open Practices

All data and data analysis files have been made publicly available via the Open Science Framework (OSF) and can be accessed at https://osf.io/x935r/. The experiments were preregistered at the OSF (https://osf.io/eumj5/).

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Appendix C. Weilbächer, Krajbich, Rieskamp, & Gluth, submitted

The influence of visual attention on memory-based preferential choice

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Abstract

Many decisions rely on past experiences. Recent research indicates that people's choices are biased toward choosing better-remembered options, even if these options are comparatively unattractive. In the current study, we used eye tracking to compare the influence of visual attention on preferential choice between memory-based and non-memory-based decisions. Participants completed the remember-and-decide task. In this task, they first learned associations between screen locations and snack items. Then, they made binary choices between snack items. These snacks were either hidden and required recall (memory-based decisions), or they were visible (non-memory-based decisions). Remarkably, we found that choices were more strongly influenced by attention in memory-based compared to non-memory-based decisions. However, we did not find evidence that visual attention mediates the memory bias on preferential choices. Finally, we adopt and expand a recently proposed computational model to provide a comprehensive description of the role of attention in memory-based decisions. Our work elucidates how visual attention interacts with episodic memory and preference formation in memory-based decisions.

Keywords: preferential choice, visual attention, episodic memory, neuroeconomics, eye tracking

Highlights

- Memory and attention influence value-based choices
- Increased gaze influence in memory-based choices
- People prefer the better-remembered options, but do not fixate them longer
- A computational model predicts memory and non-memory-based choices accurately

1 Introduction

Imagine you are planning to go to the supermarket during a short break from work to buy a snack. The supermarket is vast and you do not have the time to go through all the shelves. To save time, you recall potential snack options (e.g., chocolate bars, pretzels), together with their locations, from your memory, and choose which one to buy before you even leave the office. As in this example, many of people's every-day decisions rely critically on episodic memory.

Accordingly, there is a growing body of research on decisions from memory (Fechner et al., 2016; Shadlen & Shohamy, 2016; Wimmer & Büchel, 2016; Sali, Anderson, & Courtney, 2016; Gluth, Sommer, Rieskamp, & Büchel, 2015; Weilbächer & Gluth, 2017; Hoffmann, von Helversen, & Rieskamp, 2014; Bordalo, Gennaioli, & Shleifer, 2020). In previous studies (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018; Weilbächer, Kraemer, & Gluth, 2020), we have investigated the role of memory in preferential choice by asking participants to recall pairs of options and to choose between these memorized options (subsequently referred to as *remember-and-decide* task). The critical decisions in this task are those between a successfully remembered and a forgotten option. In all our studies, we found that people prefer remembered options even when their subjective value is below average. Neuroimaging analyses (Gluth et al., 2015) further indicate that this *memory bias* is mediated by increased effective connectivity between the hippocampus and the ventromedial prefrontal cortex. Yet, it remains an open question what cognitive mechanisms give rise to this memory bias and why people tend to prefer better-remembered options.

In the current study, we investigated whether the memory bias can be attributed to interactions between memory and attention. Attention has been shown to play a crucial role in preferential (and perceptual) choice, as people tend to choose items that they have looked at longer (Krajbich, Armel, & Rangel, 2010; Orquin & Mueller Loose, 2013; Fiedler & Glöckner, 2012; Stewart, Gächter, Noguchi, & Mullett, 2016; Gluth, Kern, Kortmann, &

Vitali, 2020; Cavanagh, Wiecki, Kochar, & Frank, 2014) leading to an *attention bias*. Furthermore, research on the interplay of attention and memory has shown that when people are asked to recall information, they tend to fixate on the location where that information was previously presented, a phenomenon known as *looking-at-nothing* (Scholz, von Helversen, & Rieskamp, 2015; Scholz, Mehlhorn, & Krems, 2016; Richardson & Spivey, 2000). This finding suggests that the memory bias in choice may be mediated by attention. More specifically, better-remembered items might be looked at more than forgotten items, leading to an advantage for those items in the choice process.

On the other hand, in memory-based choices, attention might overall play a more prominent role because participants can rely less on the options' subjective values, as they do not see them directly, but have to retrieve them from memory. In this case, the necessity to retrieve options might enhance the influence of visual attention, independent of the recall success. Recent work suggests that looking more at an option amplifies its subjective value (Smith & Krajbich, 2019). In our remember-and-decide task, people are presented with two equally salient white squares and they try to recall the identities and their value to find the better option. We hypothesize that the choice process is mediated by attention: looking longer at a particular area makes that option more attractive and more likely to be chosen in memory-based compared to non-memory based choice.

To test these predictions, we conducted an eye-tracking experiment in which participants completed an adapted version of the remember-and-decide task (Figure 1). In this task, participants first learned the association between choice options (i.e., snack items) and locations. Then, they were asked to indicate their preferred option in binary decisions. In two-thirds of trials (subsequently referred to as *memory trials*), participants had to recall the choice options from memory. The remaining third of trials served as *control trials*, in which the options were displayed on the screen. After the decision phase, the memory for each option was probed via cued recall. During the learning and decision phases we used eye-tracking to record participants' eye movements.

To better understand the cognitive process underlying the role of attention in memory-based decisions, we applied and adapted a recently proposed computational model that integrates eye-movement data into the choice process. The Gaze-weighted Linear Accumulator Model [GLAM; Thomas, Molter, Krajbich, Heekeren, and Mohr (2019)] is based on the attentional Drift Diffusion Model [aDDM; Krajbich et al. (2010), Krajbich and Rangel (2011)] and describes how the value of the presented choice options and the gaze proportion of each option determine decisions. It is a multi-alternative sequential sampling model (Busemeyer, Gluth, Rieskamp, & Turner, 2019), and thus makes joint predictions of response times and decisions for two or more choice options.

Our results provide evidence for an even stronger influence of attention on preference formation in memory-based decisions, as participants' tendency to prefer the option they looked at longer was enhanced in memory trials as compared to control trials. Computationally, this difference mapped onto different estimates of the parameter that quantifies the influence of attention on preference formation in memory and control trials. However, we did not observe longer dwell time on remembered (compared to forgotten) items, so that attention does not appear to mediate the memory bias on choice.

2 Method

We uploaded all processed data and data analysis files on the Open Science Framework website (https://osf.io/fvqhu/).

2.1 Participants

We performed a power analysis with G*Power [version 3.1.9.2; (Faul, Erdfelder, Lang, & Buchner, 2007)] indicating that a sample size of n = 32 is required to identify the memory bias in preferential choice (one sample t-test, one-tailed, power = 0.95, effect size = 0.6). A total of 51 participants started the experiment and we continued data collection until complete data was obtained from 40 participants (data from 11 participants had to be excluded; 5 participants did not show up for the second session, 3 were excluded due to technical problems, 2 could not be eye-tracked, 1 aborted the study). In addition, the data of one participant was excluded from the analyses because there were too few critical trials with one remembered and one forgotten option (see section data exclusion). In our behavioral analysis we thus included n=39 participants (women=29, age: range 18-46, M = 24.08, SD = 5.34, BMI: range 16.92-35.08, M = 22.16, SD = 3.27). Participants performed two sessions differing only in the decision phase on the *remember-and-decide task* (more details see section experimental procedures). From the 39 included participants, 20 participants completed first a parallel presentation session and one week later a sequential presentation session [1], and vice versa for the other 19 participants. In the parallel session, choice options were presented simultaneously on the screen (see details in section 2.3). All participants had normal or corrected-to normal vision with glasses. The study was approved by the Institutional Review Board of the Faculty of Psychology, University of Basel, and all participants gave written informed consent. For their participation, they received either course credit or 5 Swiss Francs (CHF) per each 15 minutes. In addition,

[1] Here we report findings from the former only. Details concerning the sequential session can be found in Appendix D.

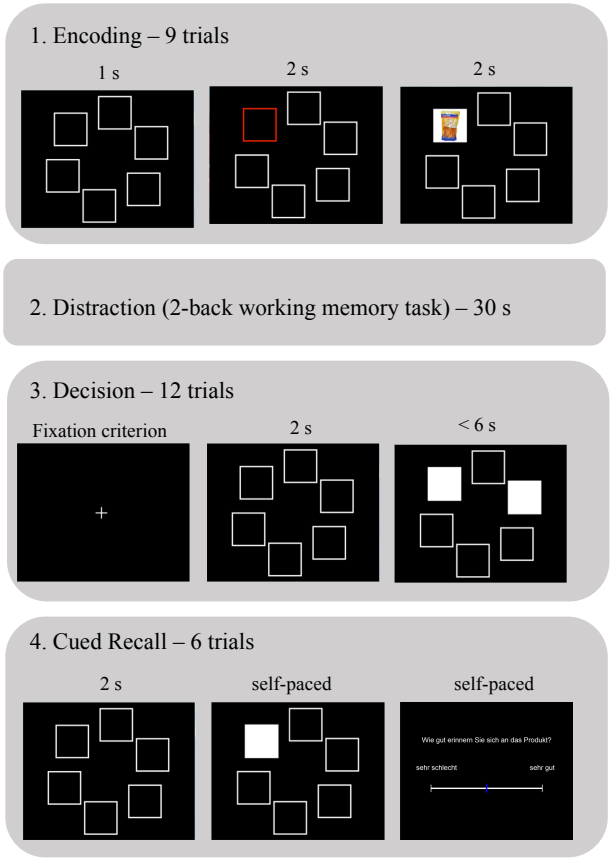

Fig. 1. Experimental paradigm (*remember-and-decide task*). An example round of the task is shown. Each round consists of four phases. In the first phase participants encode the association of snack items and screen locations. The second phase is a 2-back task to overwrite working memory. Third, participants perform binary preferential choices. Critically, only locations but not items are shown, so that the items need to be recalled from memory. Fourth, participants are asked to recall the name of each item and to rate their memory strength (English translation of the text on the slide: "How well do you remember the product?" The answer ranges from "very poorly" to "very well".

they had the opportunity to get two snack bonuses per session (see the section 2.3.2).

2.2 Apparatus

Participants were seated in front of a 24-in. computer screen (resolution 1680 x 1050 pixel), instructed to move as little as possible during the main experiment and to sit comfortably. If necessary the chair or the screen were moved to optimize eye tracking (with an ideal distance between participant and screen of 60 to 80 cm). Stimulus presentation and creation of choice sets were realized using MATLAB Version R2016a and its toolbox Cogent 2000 (version 1.33). The screen resolution was set to 1280 x 1024 pixel. An SMI RED 500 eye-tracking device was used to record participants' gaze positions at a sampling rate of 500 Hz.

For the main *remember-and-decide* task participants performed 24 rounds in four blocks of approx. 20 minutes each with a mandatory break after every sixth round. We included the breaks to avoid participants getting tired and unfocused, therefore we asked participants to either leave the room or to stand up and move around during that time. The eye-tracking recording software (iView X™ SDK version 3.6) was controlled via MATLAB using remote commands. The eye tracker sampled data of both eyes at 500 Hz during the encoding and the decision phases. The calibration procedure consisted of a five-point calibration followed by a four-point validation. The calibration procedure was repeated after each break or in case a fixation criterion was not reached while participants had to fixate on a fixation cross centered on the screen. The fixation criterion tested whether the collected eye-tracking data sample deviated > 200 pixels left/right/top/down from the screen's centroid within ten independent data samples (a data sample contains 100 data points collected every millisecond, consisting in the x and y coordinates of the left eye's gaze).

2.3 Experimental Procedures

After participants gave their written informed consent and confirmed not having eaten in the previous 4 hours, they were familiarized with the snacks. Then participants were given the written instructions. Afterwards they sat down in front of the computer and typed in demographic information (age, gender, education, job, height, weight). Next, they were asked to indicate how hungry they felt at that moment using a continuous rating scale from 0 (not hungry) to 10 (very hungry). Subsequently participants were shown all 48 food snacks together with their names on the screen. Participants were asked to memorize the names for the recognition phase of the remember-and-decide task. Participants were then asked to indicate for all food snacks how much they would like to eat them at the end of the study on a continuous scale ranging from 0 (not at all) to 10 (very much). They rated each snack twice, the first time with the slider bar starting in the middle (i.e., at a rating of 5), the second time with the slider bar starting at their first rating (such that they were given the opportunity to adjust their initial rating).

Based on participants' ratings, choice trials were generated using the following algorithm. As in previous studies (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018), we excluded the 6 highest-rated snacks to minimize the influence of value on memory (since best options are remembered much better than other options). From the remaining 42 snacks, we created 24 sets of six snacks, one set for each of the 24 rounds of the main task. Snacks were split into 3 value levels (low, medium, and high) for each participant and each set contained 2 snacks from each level. Some snacks were repeated during the experiment. However, we minimized the number of repetitions of snacks across runs to avoid intrusions. After the choice trials had been generated, participants performed the main task with two training rounds.

2.3.1 Remember-and-decide task. The remember-and-decide task (Figure 1) had 24 rounds, each consisting of four phases: encoding (9 trials), distraction (30 seconds) , decision (12 trials) and cued recall (6 trials). Out of the 24 rounds, 16 (i.e. 192 decision

trials) were memory rounds (with items being covered during the decision phase), while the remaining 8 rounds (i.e. 96 decision trials) were control rounds (with items being depicted during the decision phase). Therefore, memory and control rounds differed with respect to the decision phase only.

During the encoding phase participants learned the association between 6 food snacks and their location on the screen. Encoding consisted of 9 trials, with the first 6 trials showing each snack once in its location, and the last 3 trials showing 3 randomly chosen snacks a second time. After an option appeared on the screen, participants had to indicate whether the snack was salty (key Q) or sweet (key P).

The n-back phase was a 2-back task used to overwrite participants' working memory before the decision phase. Participants saw a number for 1 second and had to press the space bar if the current number was identical to the second-last seen number. Numbers ranged from 0-9. A total of 30 numbers were presented each round, such that each distraction phase lasted for 30 seconds.

In the decision phase participants chose their preferred snack items. Participants selected the left option by pressing the "Q" key and the right option by pressing the "P" key on the keyboard (options were arranged in a way that one square was always more left and one more right). Participants had to make their choice within 6 seconds. We restricted the decision time to prevent participants from using the first trial to recall all 6 items before making a choice. The decision phase consisted of 12 trials per round. In the memory rounds, snacks were "hidden" behind a white square, while in the control rounds option were directly visible.

Lastly, participants' memory performance was assessed in the cued recall phase. Thereto, participants saw one highlighted position per trial and said the name of the associated snack item aloud. If they could not remember the item, they said aloud "next". The experimenter confirmed the participant's response by saying "yes". Participants were not informed about the correctness of their response. After the experimenter confirmed the

response, participants pressed the space bar and indicated how well they remembered the specific item (recall certainty) on a continuous visual analogue scale (ranging from very poorly to very good).

2.3.2 Incentives. After completing the remember-and-decide task, a lottery was performed, in which participants could win up to two snacks. The first snack was drawn from participants' preference ratings, the second from their decisions during the remember-and-decide task. For the preference ratings, two items were randomly selected, and the participant received the higher-rated item. For the decision phase, the lottery algorithm first assessed participants' accuracy in pressing the key "Q" (salty) or "P" (sweet) during encoding and their performance in the 2-back task. If their accuracy was below .7 in either task, the chance to get a snack was set to 70%, otherwise it stayed at 100 %. If the algorithm determined the participant to receive a reward, then a decision trial was randomly selected. If the participant made a choice in this trial they received the chosen snack from that trial. If no choice was made, the participant received no snack. These incentive rules were explained to participants prior to performing the task and aimed to motivate participants to perform well.

2.3.3 Familiarity and Distinctiveness Questions. After completing the remember-and-decide task and receiving their rewards, participants were asked to rate their familiarity with each snack and to judge each snack's distinctiveness. The ratings were entered on a continuous visual analogue scale ranging from -3 to 3 (with the two extremes and the midpoint being highlighted).

2.3.4 Final questions about hunger and strategies. At the end of the experiment, participants rated their current hunger feeling and were asked to report what strategy they used to remember the locations of the snacks. Participants could enter text in an answer box. After completing the second session, participants could provide any comments regarding the entire experiment in an answer box.

2.4 Data exclusion

The following exclusion criteria were applied either to all trial types (memory and control) or only to a subset of trials. Memory trials were further divided into two categories depending on the cued recall: in *remrem* trials both options were recalled (i.e. two *rem*embered options), in *remfor* trials only one option was recalled (i.e. one *rem*embered and one *for*gotten option; these trials are used to assess the memory bias on choice).

2.4.1 Behavioral data exclusion. From the 40 participants that completed both experimental sessions and had complete data sets, we checked the following behavioral exclusion criteria: not more than 30% of misses (no response given) during the decision phase; at least 20 remfor trials of the decision phase; from these 20 trials at least 5 trials with the remembered item being chosen at least 5 trials with the forgotten item being chosen (these criteria assured that the logistic regression analysis of the memory bias could be performed accurately). Due to this minimal number of trials criterion we had to exclude one participant, resulting in n = 39 participants.

2.4.2 Eye-tracking data exclusion. For the eye tracking data (fixations only) we focused on data quality first at the fixation level by i) excluding all fixations with a tracking ratio $\leq$ 60% and ii) by excluding all fixations not to the chosen or unchosen option. Tracking ratio is defined by the used analysis software BeGaze as the number of non-zero gaze positions divided by sampling frequency multiplied by run duration, expressed in percent. Accordingly, a low tracking ratio might be unreliable. On the participant level we excluded participants with $\leq$ 15 trials in any trial type (control, remrem and remfor). Due to this exclusion procedure the number of trials was reduced, remaining with a total of 8189 trials and n = 37 participants for the analysis on gaze influence and the GLAM model fitting. For the included 37 participants we could analyze eye-tracking data for a mean of 88.38 (SD = $\pm$ 9.01; range 61-96) control trials and a mean of 132.95 (SD = $\pm$ 32.15; range 50-180) memory trials. Trials in which both options were forgotten were excluded from data analysis due to their small number (M = 18.24, SD = 14.48, range 2-57).

2.5 Data analysis

2.5.1 Assessment of the (corrected) memory bias. We were interested in replicating the memory bias on preferential choice (Gluth et al., 2015). Thereto, we performed a logistic regression via maximum likelihood on *remfor* trials (the number of remfor trials varies from participant to participant, $M = 66.19$, $SD = 19.83$, range 29-102). The probability p_i to choose the remembered option i over the forgotten option is given by:

$$p_i = logit(\beta_0 + \beta_1 * x_i), \tag{1}$$

where x_i refers to the standardized subjective value of option i, and β_0 and β_1 refer to intercept and slope coefficients, respectively. The probability that the remembered option will be chosen is estimated by drawing from a Bernoulli distribution with success probability p_i:

$$y \sim \text{Bern}(p_i), \tag{2}$$

This logistic regression analysis was performed on an individual level. A memory bias in the sense of preferring remembered over forgotten options is present if the intercept coefficient of this regression is positive (Gluth et al., 2015). We calculated a *corrected memory bias* by subtracting each participant's average value of their forgotten options from the value of the remembered option before performing the regression analysis. This correction ensured that the memory bias was not solely driven by the possibility that forgotten options were less valuable than remembered options [for more details, see Mechera-Ostrovsky and Gluth (2018)].

2.5.2 Pre-processing of eye-tracking data. Raw eye-tracking data (in idf file format) from the decision phase were preprocessed using the software BeGaze Version 3.6.40. Preprocessing included recoding of gaze positions into events (fixations, saccades, and blinks) using the high-speed detection algorithm and default values (i.e., peak velocity threshold 40°/s, minimal fixation duration 50ms, peak velocity start at 20 % of saccade length and end at 80%). AOIs (area of interest) were defined as the six squares where

snacks were shown. Fixations outside of the pre-defined AOIs were counted as empty gazes.

Next, we aggregated all fixations at the trial level. Importantly, we computed the gaze proportion (relative dwell time on an option) for option i as follows:

$$\text{gaze proportion}_i = \frac{(0.5 * \text{non-fixation time} + \text{total fixation time}_i)}{\text{response time}} \tag{3}$$

Note that the gaze proportions to the left and right option sum up to 1. We chose this specification of gaze proportion, as we had many trials with a large discrepancy between the total fixation time (left and right option) and the response time due to our experimental design. Assume, for example, a response time of 4000 ms with the left option being fixated for only 300 ms and the right option for only 700 ms. Thus the total fixation time is 1000ms. The simple ratio between left and right dwell times would mean that the left (right) option was fixated in 30% (70%) of the trial, disregarding the fact that neither option was fixated for 3000 ms. With Equation 3, the numbers are 55% (45%) for left (right) and thus less extreme. Thereby, we avoided an over-weighting of small differences in trials with poor recording quality.

2.5.3 Assessment of gaze influence on choice. We sought to replicate previous findings on the influence of attention on decision making (Armel, Beaumel, & Rangel, 2008; Krajbich & Rangel, 2011; Krajbich et al., 2010; Folke, Jacobsen, Fleming, & De Martino, 2017; Gluth et al., 2020), to extend these findings to memory-based decisions, and to test whether the influence of attention is present in memory-based decisions. Thereto, we tested whether the allocation of gaze influences choice probability over and above the influence of value (Thomas et al., 2019). Following previous approaches (Krajbich et al., 2010; Thomas et al., 2019), we first estimated the probability that an option is chosen based on its value (logistic regression). Then, we subtracted this estimated probability from the observed choice (binary variable, 1=option chosen, 0=option not chosen). Finally, we averaged the resulting choice probability for trials in which the option had a positive vs. negative final gaze advantage (i.e., difference between the total fixation duration to one option and the total fixation duration to the other option). We estimated

this gaze influence separately for each participant and each of the three different conditions: control, remrem, and remfor.

To test for an increased influence of visual attention (gaze) in decisions from memory, we performed a linear mixed effects analysis of the relationship between gaze influence and condition (control, remrem and remfor). As fixed effect, we entered the condition into the model. As random effects, we entered intercepts for the participants. As effect size measure we used R^2. In sum, the model equation was:

$$gaze\,influence \sim condition + (1|participant) + \epsilon \tag{4}$$

We additionally performed two post-hoc contrasts, testing whether the control condition differs from the two memory conditions (control - (remrem + remfor)/2), and whether the two memory conditions differ from each other (contrast remrem - remfor).

2.6 Computational Modeling Procedure

We aimed to investigate how the influence of attention maps onto cognitive processes of memory-based preferential choice. In particular, we were interested in explaining the increased impact of attention in memory-based compared to "regular" non-memory-based decisions.

We applied the Gaze-weighted Linear Accumulator Model (GLAM) proposed by Thomas et al. (2019), who made their code publicly available on GitHub at http://ww.github.com/glamlab/glam. Note that we re-scaled all participants' item rating values to range from 1 to 10 (original values ranged from 0 to 10), so that model parameter values were comparable to the original publication.

2.6.1 GLAM details. The GLAM (Thomas et al., 2019) describes the influence of gaze allocation on the decision process as a linear stochastic race (Usher, Olami, & McClelland, 2002; Tillman & Logan, 2017) and is inspired by the multialternative attentional Drift Diffusion Model (Krajbich & Rangel, 2011)). This model represents each choice option with a separate evidence accumulation process, and the option whose

accumulator reaches a decision boundary first wins the race and is chosen. One advantage of linear stochastic race models is that they are easy to generalize to tasks with more than two choice options. More relevant for the current study are the additional advantages of GLAM that it can fit parameters robustly, and that it comes as a toolbox with a Bayesian implementation and efficient code leading to fast fitting (Theano implementation).

Detailed specifications of the GLAM are provided in Thomas et al. (2019). Here, we we summarize the model mechanics briefly, with an emphasis on how we adapted it to the present case of memory-based decisions. Each option i is represented by a separate noisy accumulator of evidence. As soon as the first accumulator reaches a decision boundary, the corresponding option is chosen. The boundary is set to 1. First, for each item i relative evidence is being accumulated at each time point t:

$$E_i(t) = E_i(t-1) + v * Ri + N(0, \sigma^2), \text{with } Ei(0) = 0 \tag{5}$$

Next, the relative evidence R_i* is defined as the difference in the absolute evidence signal A_i:

$$R_i* = A_i - max_J(A_J) \tag{6}$$

Where A_i is a constant and depends on the option's $value_i$ and on how long an option is fixated ($gaze_i$):

$$A_i = gaze_i * value_i + (1 - gaze_i * \gamma * value_i) \tag{7}$$

γ is the gaze bias parameter, determining the amount of down-weighting during the biased state. If $\gamma = 1$ there is no gaze bias. In other words, the absolute evidence signal A_i implements the gaze bias mechanism. Importantly, to estimate the GLAM for our data, which included memory-based and non-memory-based trials, we expanded the original

equation for A_i as follows:

$$\begin{aligned} A_i = gaze_i * value_i * remembered_i + \\ gaze_i * \rho * (1 - remembered_i) + \\ (1 - gaze_i) * \gamma * value_i * remembered_i + \\ (1 - gaze_i) * \gamma * \rho * (1 - remembered_i) \end{aligned} \tag{8}$$

where the dummy variable *remembered* indicates whether an option had been recalled (1) or not (0; relevant only to memory trials). Most importantly, we introduce a new parameter ρ, determining the reference value of the forgotten option. If this value is smaller than the true average of all forgotten options, a memory bias is likely to occur, because the remembered option is more often considered to be better.

As in the original GLAM, to take into account participants' different use of the rating scale, we also adopt a logistic transformation of the relative evidence R_i estimating the scaling parameter τ as follows:

$$s(x) = \frac{1}{1 + e^{-\tau * x}} \tag{9}$$

$$R_i = s(R_i*) \tag{10}$$

The model has an analytical solution for the first passage time density.

2.6.2 GLAM variants. We estimated three model variants. The first variant (GLAM_orig) is the original full GLAM (with gaze bias) including four free parameters (v, γ, σ, and τ). As the value of forgotten items in remfor trials, we took the average value of all forgotten options per participant. The second model variant (GLAM_ρ) takes the memory bias on choice into account. Therefore, we added parameter ρ to the model, which represents the value that a participant assigns to forgotten options (and which may differ from the average of those options). Consequently the model includes five free parameters (v,γ, σ, τ and ρ). The third variant (GLAM_nobias) assumes that gaze does not play a role in the choice process. It is a restricted version of GLAM_ρ with four free parameters (v, σ, τ and ρ) and the gaze bias parameter γ being fixed to 1. We included this model

variant, as not all participants may show a gaze influence on choice [see detailed discussion in Thomas et al. (2019)].

We first compared the model fits of three model variants quantitatively on the basis of the Widely Applicable Information Criterion [WAIC; Vehtari, Gelman, and Gabry (2017)]. The WAIC measure takes model complexity into account. Lower values indicate a better model fit. We also compared the models qualitatively, by testing the models' ability to reproduce choice and RT patterns accurately as well as to predict a (potential) influence of gaze on choice and a (potential) memory bias on choice in remfor trials.

2.6.3 Estimation, simulation and recovery of GLAM. To estimate the model, we sampled four chains with 1000 tuning samples (being discarded) and 2000 posterior samples. Convergence was checked with the following two criteria: Gelman-Rubin statistic ($\widehat{R} < 1.05$) and number of effective samples larger than 100. As parameter estimates we report the maximum a posteriori (MAP) estimates. We fitted the model for all trials per participant. To take different trial types into account, we included a dummy variable coding whether a trial is a control or a memory trial and another dummy variable coding whether the options were remembered or not (relevant to memory trials only). Gaze influence (γ) scaling (τ) parameters were estimated separately per condition (control and memory). Preliminary model fits indicated that the other two parameters (velocity v and noise σ) did not differ significantly per condition (see supplementary material).

The full GLAM (denoted in the following as *GLAM_rho*) has five parameters $(v, \gamma, \sigma, \tau, \rho)$. We used uninformative, uniform priors:

$$v \sim Uniform(10^{-6}, 0.0003)$$

$$\gamma \sim Uniform(-10, 1)$$

$$\sigma \sim Uniform(10^{-6}, 0.02)$$

$$\tau \sim Uniform(0, 5)$$

$$\rho \sim Uniform(-10, 10)$$

We estimated the GLAM separately to each participant (n=37). The model did not converge for four participants, even when increasing the number of samples to an extremely large amount. Therefore, we report the model fits of n=33 participants.

Choices and RT for all trials that were included in the parameter estimation were simulated with 50 repetitions each. For every trial, the model used the option values, the gaze distributions and the information, whether options have been recalled or not. The simulation produced a random choice and RT between participants' minimum and maximum observed RT with a fixed rate of 5% to account for a small proportion of "trembling-hand" errors. Choices and RTs were simulated from the GLAM with a rate of 95%. We additionally performed a parameter recovery to ensure our estimates were reliable. All generating and recovered parameter estimates showed sufficiently high correlations ($r > 0.7$). The recovery results are reported in the Appendix E..

3 Results

3.1 Replication of the memory bias in preferential choice

Our first aim was to replicate the memory bias in preferential choice. Thereto, we regressed the choice of the remembered option in remfor trials on its standardized subjective value. In line with a (corrected) memory bias, the average intercept coefficient was significantly greater than 0 ($t(38) = 3.01$, $p = .002$, $d = 0.49$, see Figure 2). Thus, people tend to prefer remembered options over forgotten options, controlling for their subjective value.

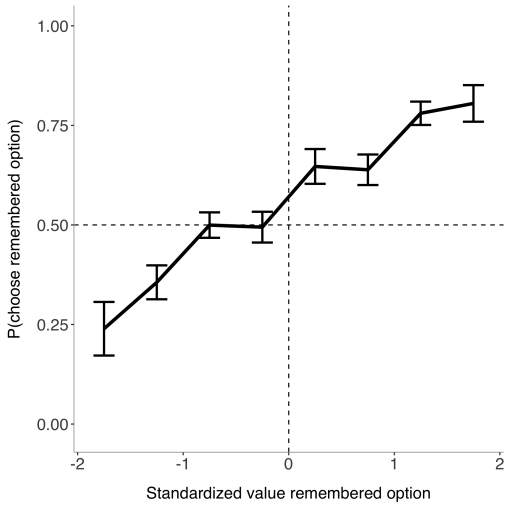

Fig. 2. Corrected memory bias in preferential choice. Probability to choose the remembered option over the forgotten option depending on its standardized subjective value (corrected for the value of all forgotten options). The memory bias is evident by the fact that the point of indifference (50% choice probability) is not at 0 but shifted towards negative (standardized) values. Error bars represent the 95% confidence interval.

3.2 Visual attention influences preferential choices from memory

The effect of gaze influence on choice is significantly greater than zero in all three conditions (control $t(36) = 6.62$, $p < .001$, $d = 1.09$; remrem $t(36) = 8.42$, $p < .001$, $d = 1.38$; remfor $t(36) = 8.14$, $p < .001$, $d = 1.34$) . Therefore, we replicate the presence of an *attention bias* in the control condition.

Moreover, results from a linear mixed effects model show that the fixed effect of condition affected the amount of gaze influence($t(88.95)$=5.35, p< .001, $R^2 = 0.53$) suggesting a differential role of the condition.

A further investigation of this difference with a post-hoc contrast analysis confirms the gaze influence to be significantly lower in the control condition compared to the two memory conditions ($t(76.1)$=-3.74, p< .001). Moreover, the two memory conditions do not differ from each other ($t(76.1)$=-1.16, p= 0.25, see Figure 3). These findings indicate that the influence of attention on the formation of preferences is stronger in memory- compared to non-memory-based decisions. Note that the result is independent from the definition of gaze proportion (see appendix G).

3.3 Visual attention does not differ between remembered and forgotten options

We predicted that remembered options would receive more attention compared to forgotten options. To test this hypothesis we performed a paired t-test to compare the average number and duration of fixations towards remembered and forgotten options in remfor trials. Contrary to our prediction, the eye-tracking data do not provide evidence for a statistically significant difference, neither in terms of the average number of fixations per trial (remembered: $M = 1.98$, $SD = 0.43$, forgotten: $M = 2.00$, $SD = 0.43$;$t(38)$ = -0.44, $p = 0.33$, $d = 0.07$) nor in terms of the average duration of fixations (remembered: $M = 432.71$, $SD = 139.03$ ms, forgotten options: $M = 443.32$, $SD = 155.00$ ms; $t(38)$ = -0.72, $p = 0.24$, $d = 0.12$, see Figure 4).

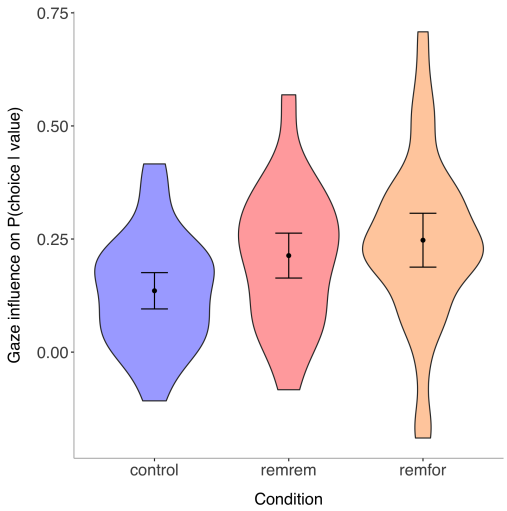

Fig. 3. The influence of attention on choice separately per condition (control, remrem and remfor). The gaze influence quantifies to what degree decisions depend on the gaze difference (left - right) after correcting for the influence of value (estimated with a logistic regression). In other words, if one option is being fixated longer, that option has an increased probability of being chosen. The gaze influence is stronger in memory-based decisions compared to control decisions. Black dots represent the mean value and the error bars the 95% confidence interval.

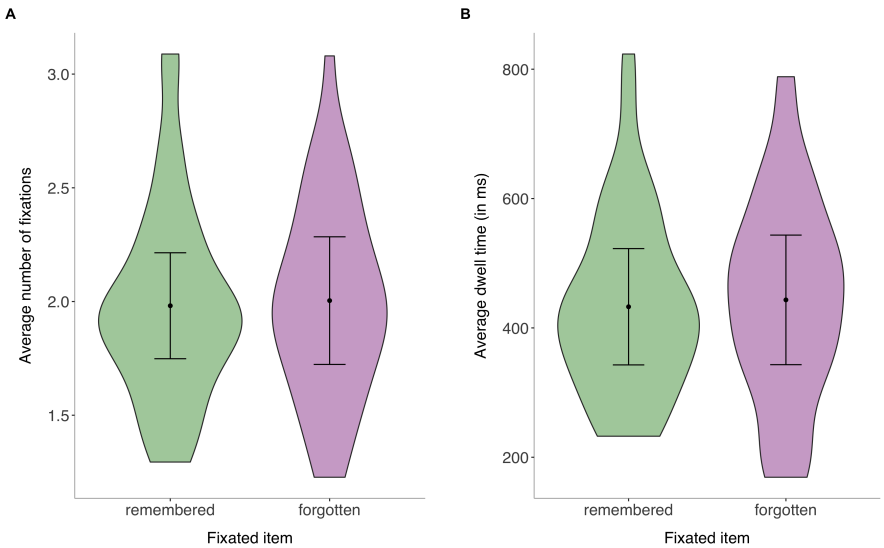

Fig. 4. Mean number of fixations (A) and mean duration of fixations (B) in remfor trials. On average, participants looked similarly often and long to the two options. Black dots represent the mean value and the error bars the 95% confidence interval.

3.4 Modelling gaze and memory influences on choice

To elucidate the computational processes underlying the interaction between visual attention and memory-based decision making (and in particular the increased influence of gaze on choice in memory-based decisions), we applied the recently proposed GLAM (Thomas et al., 2019), a sequential sampling model that takes eye-movement data into account.

3.4.1 Quantitative and qualitative model comparison. We first compared the three model variants quantitatively via the WAIC. We found that 19 participants were best described by the original GLAM model (GLAM_orig), 9 by the new 5 parameter GLAM model (GLAM_ρ), and 5 by the restricted GLAM model (GLAM_nobias).

Notably, the difference in WAIC was small between GLAM_orig and GLAM_ρ models (difference: M = 0.41, SD = 3.66), but large between GLAM_orig and GLAM_nobias (difference: M -15.92 SD = 15.81) as well as between GLAM_ρ and GLAM_nobias (difference: M = -16.33, SD = 14.13). One reason why the more complex GLAM_ρ did not outperform the simpler GLAM_nobias could have been the limited number of trials (i.e., the remfor trials) in which the former model can actually make more accurate predictions than the latter.

In addition to assessing the quantitative model fit, we also checked whether the model variants predicted individuals' behavior qualitatively. Thereto, we compared the simulated RT and choices for each participant with the empirical data.

Despite its good quantitative fit, the GLAM_orig model could not account for a presence of the memory bias (for the remfor subset of trials) on choice, in contrast to GLAM_ρ (Figure 5). This pattern was also confirmed by testing for the memory bias in simulated data. The simulated data of GLAM_ρ exhibited a significant memory bias ($t(31)$ = 3.60, p < .001, d = 0.63), but not the simulated data of GLAM_orig ($t(32)$ = -0.14, p = 0.56, d = 0.03).

Second, both the GLAM_orig model and the GLAM_ρ model could account for the stronger influence of gaze on choice in memory-based decisions (results linear mixed effects models contrast control vs. memory: GLAM_orig $t(64)$=-5.79, p< .001; GLAM_ρ $t(64)$=-3.79, p< .001). However, the GLAM_orig further predicted a difference between the remrem and remfor trials, which was not in line with the empirical data. The GLAM_ρ did not predict such a difference (results linear mixed effects models contrast remrem vs. remfor: GLAM_orig $t(64)$=2.10, p= .04; GLAM_ρ $t(64)$=0.46, p= .65) (Figure 6).

3.4.2 Interpreting the GLAM_ρ model. Taking both quantitative and qualitative criteria into account (Palminteri, Wyart, & Koechlin, 2017), GLAM_ρ best described our data as it provided a sufficient quantitative model fit and was able to predict both the memory bias on choice and the enhanced influence of attention on choice in

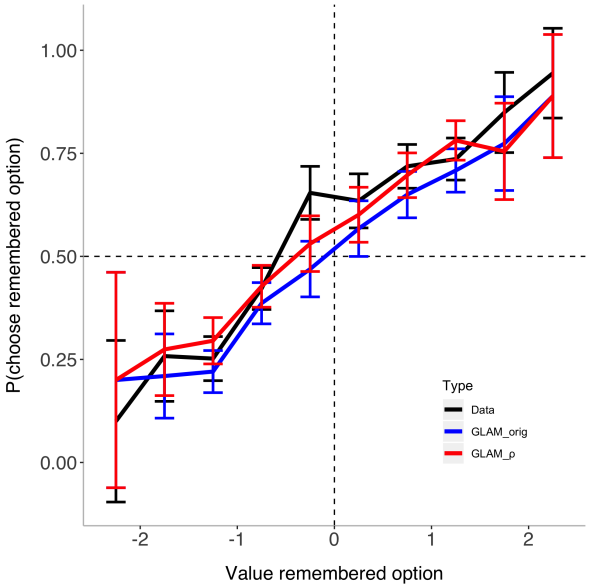

Fig. 5. Comparison of qualitative choice predictions of the GLAM variants without (i.e., GLAM_orig; blue line) and with the memory bias parameter (i.e., GLAM_ρ; red line). Only GLAM_ρ allows to capture the shift in the choice curve as seen in the empirical data (black line).

memory-based decisions. In the following we report the parameter estimates and discuss their impact (for an overview of the GLAM_ρ model estimates, see Table 1).

The attention parameter γ determines the extent to which the accumulation of evidence for a non-fixated item is reduced. If $\gamma = 1$, there is no influence of gaze on decisions. Our individual gamma estimates ranged from -1.1 to 0.99. Importantly, the parameter estimates of γ were significantly higher for control trials compared to memory trials (γ_{memory}: $M = 0.12$, $SD = 0.46$; γ_{control}: $M = 0.42$, $SD = 0.45$, two-sided t-test: $t(32)$ = -3.83, $p < .001$, $d = 0.67$), suggesting that the increased influence of gaze in

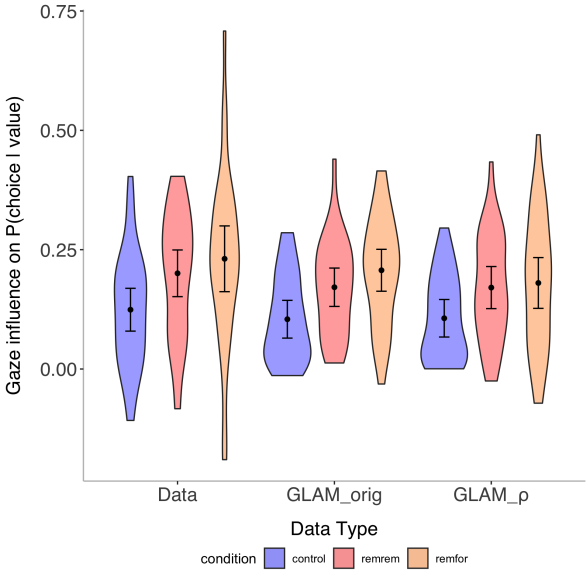

Fig. 6. The influence of gaze on choice according to simulated data from GLAM_orig and GLAM_ρ, compared to the data used for modeling. Black dots represent the mean value and the error bars the 95% confidence interval.

memory-based decisions mapped onto a lower γ parameter.

In addition, decisions in memory trials were more stochastic, meaning that decisions were less consistent with preference ratings (control: M = 83.19 %, SD = 9.54 %; remrem: M = 76.32 %, SD = 10.59 %; remfor: M = 68.58 %, SD = 9.27 %). In the GLAM, this increased stochasticity is reflected in the scaling parameter τ (which scales the difference of the relative evidence) being reduced in memory trials (τ_{memory}: M = 0.35, SD = 0.24; τ_{control}: M = 0.96, SD = 1.14; two-sided t-test: $t(32)$ = -0.98, p = .002, d = 0.59).

Last, we looked at the newly added ρ parameter (M = 3.53, SD = 3.42), which replaces the value of the forgotten option in remfor trials and thus models the memory bias

on choice. Although this parameter was required to reproduce the qualitative finding of a memory bias on choice (see Figure 5), it was neither significantly lower than the average value of all forgotten items (M = 3.59, SD = 1.35; one-sided t-test: $t(32)$ = -0.10, p = .54, d = 0.02), nor than the average value of all used snacks (M = 3.76, SD = 1.27; one-sided t-test: $t(32)$ = -0.42, p = .66, d = 0.07).

Table 1

Summary of the parameter estimates from the GLAM_ρ model.

	mean	sd	median	min	max
γ_{memory}	0.1239	0.4602	0.1300	-1.1100	0.9500
γ_{control}	0.4179	0.4532	0.4800	-0.4700	0.9900
τ_{memory}	0.3482	0.2447	0.2700	0.0300	1.0900
τ_{control}	0.9591	1.1416	0.4600	0.0900	4.7800
v	0.0001	0.0000	0.0001	0.0000	0.0002
σ	0.0097	0.0011	0.0096	0.0074	0.0126
ρ	3.5285	3.4193	3.7800	-7.9600	11.1400

4 Discussion

This study investigated the role of attention on memory-based choice and aimed to contribute to a better understanding of the cognitive mechanisms driving memory-based choices. A growing body of research shows that attention plays a crucial role in decision processes (Orquin & Mueller Loose, 2013; Krajbich, 2019; Fiedler & Glöckner, 2012; Stewart et al., 2016; Tavares, Perona, & Rangel, 2017; Gluth, Spektor, & Rieskamp, 2018). Most importantly, there is strong evidence that people choose options that they have spent more time looking at. Our results indicate that the influence of gaze on preference formation is increased in memory-based as compared to non-memory-based choices, independently of whether only one option (remfor trials) or both options (remrem trials) were remembered. Note that the strength of the gaze influence on choice in our control trials, in which the snacks could be seen and thereby representing a task similar to previous paradigms, was comparable to previous findings (Thomas et al., 2019; Krajbich et al., 2010, 2011; Tavares et al., 2017; Folke et al., 2017). Hence, it appears that attention indeed plays an particularly influential role in decisions that require options to be retrieved from memory. The cognitive modeling results further strengthen this notion: The GLAM parameter γ, which quantifies the influence that attention exerts on valuation and choice, was significantly different between memory-based and non-memory-based decisions. Importantly, this result rules out that the increased influence of gaze on memory-based choice is solely driven by the increased stochasticity of these decisions as compared to non-memory-based decisions (or, in other words, by the fact that memory-based decisions are less determined by subjective values).

Notably, an increased impact of attention on preference formation in memory-based decisions could be potentially relevant for studying these type of decisions in clinical populations that are known to be affected by both mnemonic and attentional deficits, such as Alzheimer's Disease (Baddeley, 2001; Perry, Watson, & Hodges, 2000; Calderon et al., 2001). A recent study investigated the impact of memory decline on choice focusing on

choice inconsistencies. Older adults were less consistent according to their stated preferences but did not show more intransitive choices (Levin, Fiedler, & Weber, 2019). Interestingly, a related study, that used a task consisting of a learning and a decision phase (similar to our *remember-and-decide task*) found no evidence of older adults being more inaccurate (Lighthall, Huettel, & Cabeza, 2014), but they needed more time for their choices (speed-accuracy trade-off). Future studies could further address the question of how memory deficits in clinical or elderly populations affect memory-based preferential choice by including eye-tracking measures. Based on our results and previous findings, we would expect an even more substantial gaze influence for older adults in memory-based choice compared to younger people.

In our study, we replicated the presence of a memory bias on choice, according to which people prefer better-remembered items, even if their value is comparatively low (Gluth et al., 2015). This result confirmed our previous work (Gluth et al., 2015; Mechera-Ostrovsky & Gluth, 2018; Weilbächer et al., 2020), showing that the tendency to prefer better-remembered options is a robust and comparatively strong effect. Contrary to our prediction, however, our results suggest that attention does not mediate the memory bias. Based on previous work on the role of memory on gaze allocation [i.e., the looking-at-nothing phenomenon, Richardson and Spivey (2000)], we hypothesized that participants would pay more attention to better-remembered options during the decision phase. This increased attention could then lead to a higher choice probability, thus mediating the memory bias. Yet, remembered options did not receive more attention. This may be because participants' tendency to look at the location of remembered options could trade off against those fixations that are made to recall the (eventually) forgotten options. Interestingly, research investigating the stability of the looking-at-nothing effect (Scholz, Mehlhorn, Bocklisch, & Krems, 2011), suggests that the effect decreases as memory uncertainty decreases, meaning that if an item is easier to recall then the effect is weaker. In our case, the recall certainty for remembered options was quite strong (i.e., people were

sure about the remembered item; see additional analyses in the Appendix F), so participants might not have needed to look at their locations for long.

In previous studies, we tested two other potential mediators for the memory bias on choice. First, we showed that the memory bias is related to a person's belief that they tend to remember good options more than bad options (Mechera-Ostrovsky & Gluth, 2018). Second, we reported evidence that the uncertainty entailed in choosing forgotten options leads people to reject these options in the gain domain but to choose them in the loss domain (Weilbächer et al., 2020). Given the fact that uncertainty appears to be a critical factor, we speculate that increased gaze time could reduce this uncertainty, thereby further boosting the attractiveness of the longer fixated option, and thus causing the main finding of the current work: that the influence of gaze on choice is increased in memory-based decisions.

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CRediT author statement

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All authors approved the final version of the manuscript for submission.

Appendix A. Selection of stimulus material

Prior to running the study, we conducted a pilot experiment to select a suitable set of food snack items. A separate group of participants (n = 21, women = 15, age: range 18-29, M = 21.86, SD = 2.5) rated 60 snacks on the dimensions familiarity, distinctiveness, representativeness (of their snack category), and preference on a discrete scale from 0 to 10. Snacks were grouped into six categories (bars, bonbons, chocolate, wine gums, nuts, salty snacks). The study took around 15 minutes. From these 60 snacks, 48 were then selected for the current study, mainly on the basis of familiarity and preference (e.g., snack items that were unfamiliar to many participants were excluded).

The mean ratings for the 48 remaining snacks for the four dimensions were: familiarity (M = 7.01, SD = 2.02), preference (M = 6.17, SD = 1.23), distinctiveness (M = 6.11, SD = 1.42) and representativeness (M = 8.43, SD = 1.09).

Appendix B. Arrangement of squares for the *remember-and-decide* task

The six squares (i.e., option locations) were arranged on a circle with their centroid being equidistant from the screen center. The squares had a side length of 280 pixels. To allow a choice between left and right squares, the squares were arranged so that there was always one option more on the right and the other more on the left. This was achieved by rotating the squares on a circle (with a radius of 360 pixels) by 35 degrees.

Appendix C. Software

For the linear mixed effects model estimating the gaze influence we used the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) (version 1.1-21) as implemented in R (version version 3.6.1). P-values were obtained with the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017) version 3.1-0, using Satterwaite approximation. For post-hoc contrasts we used the R package lsmeans (Lenth, 2016) version 2.30.0.

The GLAM model versions were implemented in the Python library PyMC3 version

3.6 (Salvatier, Wiecki, & Fonnesbeck, 2016) and fitted using the NUTS [No-U-turn sampler, Hoffman and Gelman (2011)] sampling method for all model variants. In addition, the following python packages were required: NumPy, SciPy, Pandas, Statsmodels, and Theano.

Appendix D. Sequential Presentation Session

As stated in the main article, we included a second experimental session, where the options were presented sequentially during the decision phase (n=40 participants). Presentation durations were either long (1500 ms) or short (500ms). We varied all possible combinations, resulting in four types of presentation length trials: long/long, short/short, long/short, short/long.

We hypothesized that a longer presentation of an option would increase its choice proportion, whereas a shorter presentation time would decrease its choice proportion. However, our behavioral results indicated that the presentation duration had no influence on the choice proportion. Instead, across all possible four types of presentation length trials, the choice proportion was stable. In the control trials, participants chose the first and the second option equally often (around 50% of the time), while in the memory trials there was a small preference for the last presented option. Accordingly, a repeated-measures 2x4 ANOVA with the factors Trial Type (memory vs. control) and Presentation Length (long/long, short/long, long/short, short/short) and the probability to choose the last presented option as dependent variable showed a significant effect of Trial Type ($F(1, 301) = 27.87$, $p < .001$), but no main effect of presentation length ($F(3, 301) = 1.99$, $p = 0.116$) nor an interaction effect ($F(3, 301) = 0.72$, $p = 0.542$, see Fig.D 1).

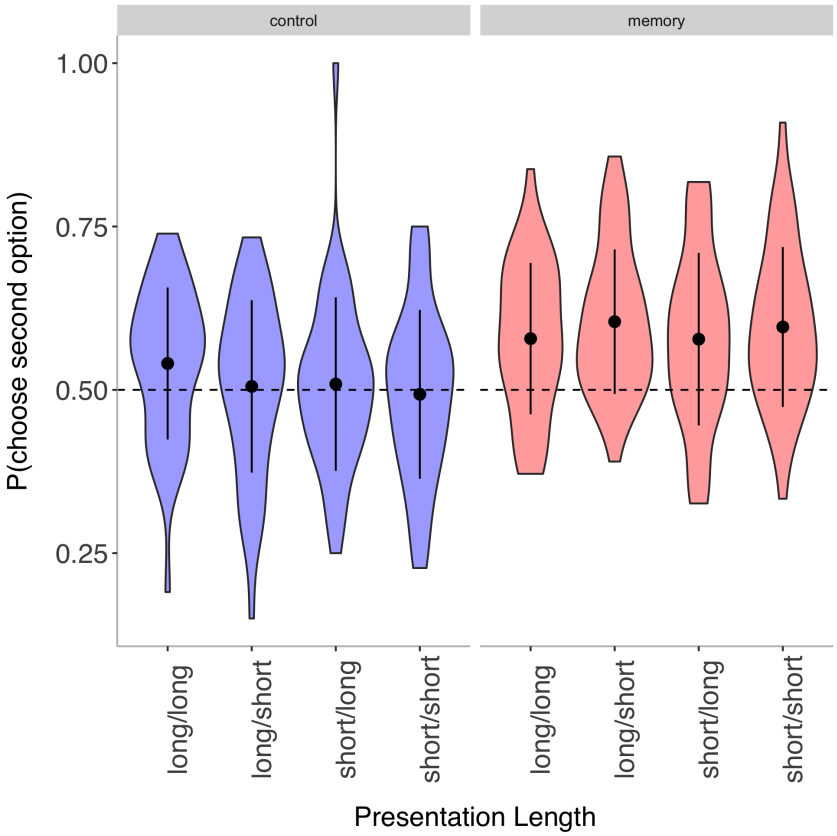

Fig.D 1. Choice proportion of the item presented last in the sequential presentation session. Left the control trials are depicted, right the memory trials. Across the presentation length conditions there was no difference in the choice proportion, even though, participants tend to choose the item presented last more often in the memory trials.

Appendix E. Computational Modeling: GLAM

GLAM_ρ Parameter Recovery

We performed a parameter recovery analysis for our adapted GLAM_ρ model in the context of our study design. Parameter estimates from the individual fits were used to generate one predicted data set. This data set was then used to fit the model again. We checked whether the generating and recovered parameter estimates showed sufficiently high correlations. We only included the 33 subjects, for which the model converged (see main text). We found very high correlations for all parameters. All correlations are significant: ($r[v](31)$=0.99, p<.001, $r[\gamma_{control}](31)$=0.88, p<.001,$r[\gamma_{memory}](31)$=0.89, p<.001,$r[s](31)$=0.91, p<.001,$r[\tau_{control}](31)$=0.71, p<.001, $r[\tau_{memory}](31)$=0.92, p<.001, $r[\rho](31)$=0.75, p<.001). Even though the correlations are lowest for the newly added ρ parameter and the scaling parameter τ_{control}, they are still sufficiently high (see Fig.E 1).

Correlations between empirical data and model predictions

Finally, we assessed the correlations between the empirical data and the models' qualitative predictions concerning four measures: mean RTs, choice accuracy, gaze influence and memory bias (see Fig. E 2).

GLAM Parameter Correlations

We looked to what extent the parameters correlated with each other, as potential trade-offs between parameters can limit the informative value of computational models. As expected, the same parameters across different conditions such as (γ_{memory} and $\gamma_{control}$ as well as τ_{memory} and $\tau_{control}$) were correlated to a substantial degree ($r_\gamma = 0.53$; $r_\tau = 0.52$). Moreover, both τ parameters correlated substantially with the velocity parameter v (r=-0.43 and r=-0.6 respectively). All other correlation were smaller than ± 0.35 (see Fig.E 3).

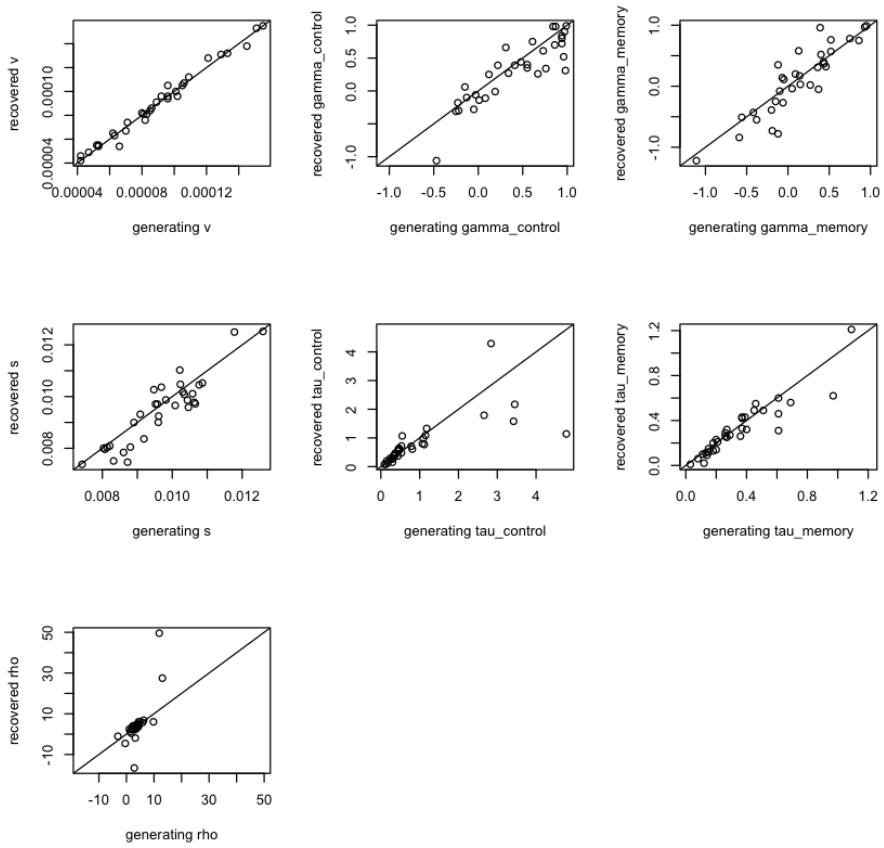

Fig.E 1. Parameter correlations between the generating and the recovered estimates.

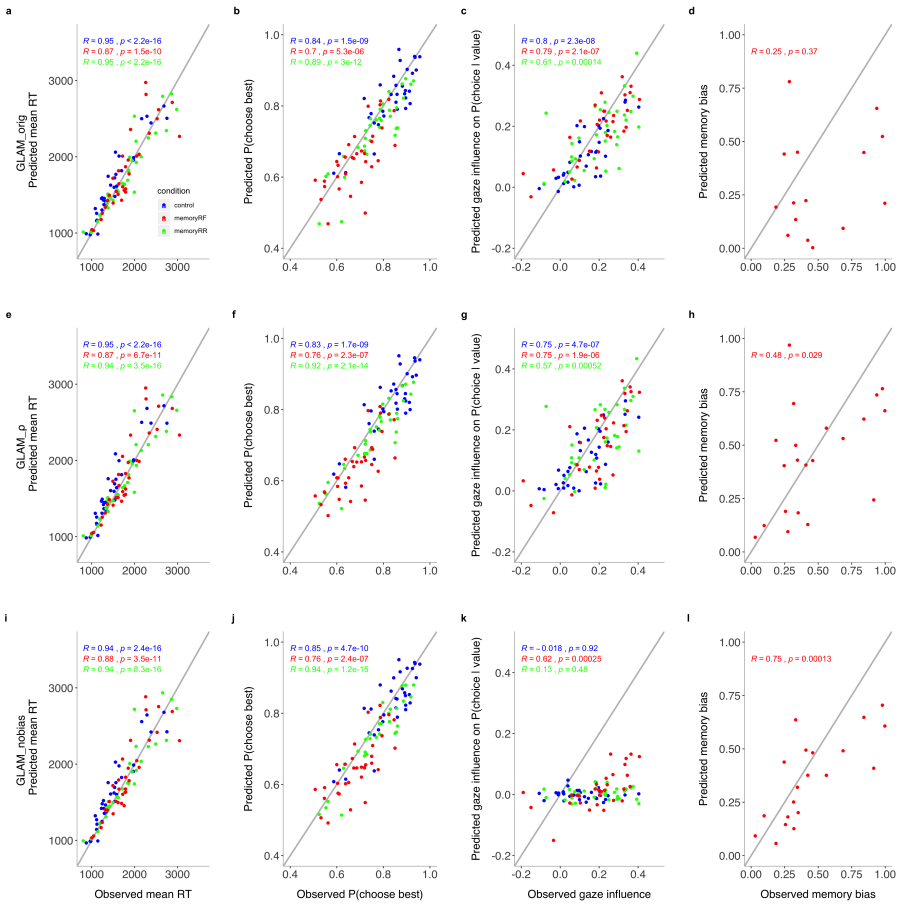

Fig.E 2. Correlations between the observed data and model predictions. Each of the three rows depict a model variant (upper row = GLAM_orig, middle row = GLAM_ρ, lower row = GLAM_nobias). All model variants predict the mean RT and choice proportions similarly well. However, GLAM_nobias fails to predict the gaze influence on choice, and GLAM_orig does not predict the presence of a memory bias.

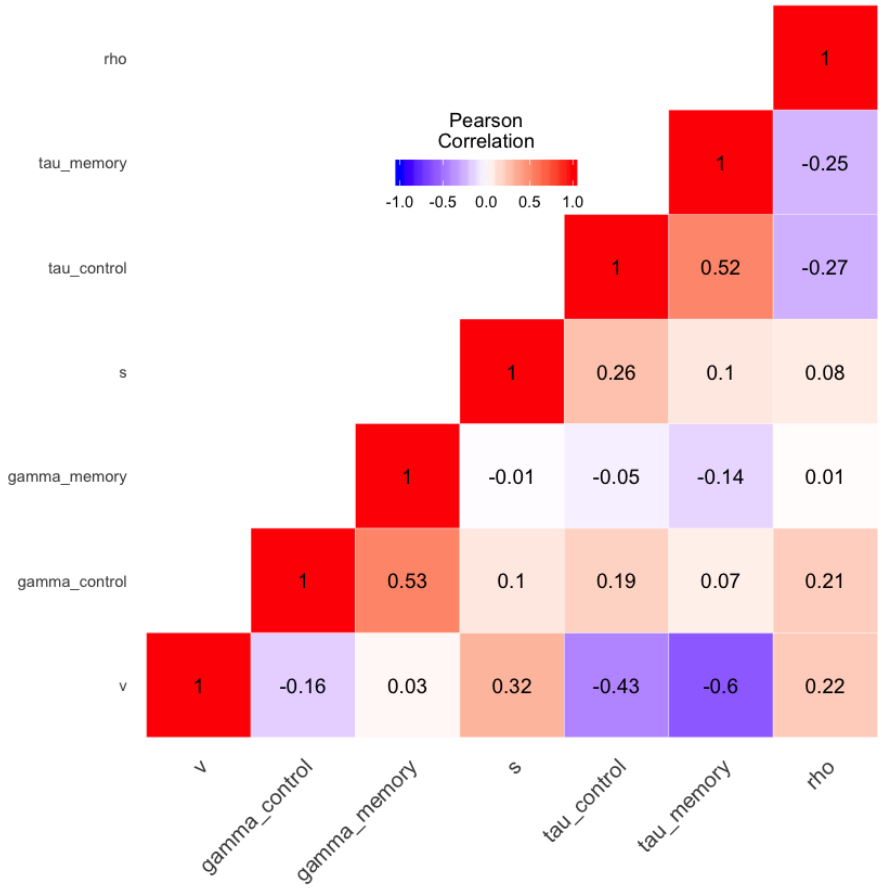

Fig.E 3. Parameter correlations across all parameters in the GLAM_ρ, including the newly added ρ parameter.

GLAM qualitative model fit

Here, we use Bayesian mixed-effects models to test whether the different GLAM variants reproduce the gaze influence on choice, the memory bias, and overall choice accuracy (defined as the consistency of decisions with preference ratings) and RT effects on a qualitative level. The models were implemented and estimated using the code made available from Thomas et al. (2019). Accordingly, we used the Python library bambi, sampled two chains with 20000 samples each and used the NUTS sampler. As for the GLAM estimation, the convergence was tested with the Gelman-Rubin statistic ($\widehat{R} < 1.05$). Fixed effects were statistically meaningful when the 95% HDI excludes zero. The predictor was a binary variable, indicating whether the dataset represents empirical data (predicted=0) or simulated data based on model estimates (predicted=1). We performed a mixed-effects regression for each behavioral measure: mean response times (RTs), choice accuracy, gaze influence and memory bias. As random effect we included the condition (control, remrem, remfor).

Overall, the predicted data accurately replicated the empirical choice and RT patterns for all three model variants. However, the GLAM_nobias model version (γ parameter fixed to 1), could not predict the influence of gaze on the choice probability (depending on value). In addition, the GLAM_orig model could not predict the memory bias on choice (see details in Table E 1).

Relationship between the ρ parameter and the behavioral data

In addition to our qualitative predictions reported in the main text, we checked if the estimated memory bias parameter ρ is also associated with the behaviorally estimated memory bias as well as its relation to the mean of all forgotten values (the reference value used in the GLAM_orig model for the forgotten item in remfor trials). In general, there is a significant negative association between the estimated ρ parameter and the memory bias as well as between the mean of all forgotten items and the memory bias (see Fig.E 4).

Table E 1

Fixed effects estimates and credible intervals for the Bayesian mixed-effects models comparing the empirical and the simulated data.

	$GLAM\_orig$		$GLAM\_nobias$		$GLAM\_\rho$	
	β	$95\%HDI$	β	$95\%HDI$	β	$95\%HDI$
RTs (ms)	40.28	[-242.51,319.71]	36.93	[-235.64,333.55]	28.05	[-297.30,409.31]
CA (%)	-3.02	[-10.90,6.32]	-2.85	[-11.37,6.33]	-3.27	[-11.82,6.13]
GI (%)	-2.42	[-9.64,4.41]	-16.08	[-25.34,-3.24]	-3.20	[-10.65,4.22]
MB	-0.22	[-0.41,-0.03]	-0.05	[-0.27,0.18]	-0.08	[-0.28,0.11]

Note. RTs= reaction times; CA = choice accuracy; GI = gaze influence; MB = memory bias. Estimate β is the mean estimated difference between the empirical and the simulated data.

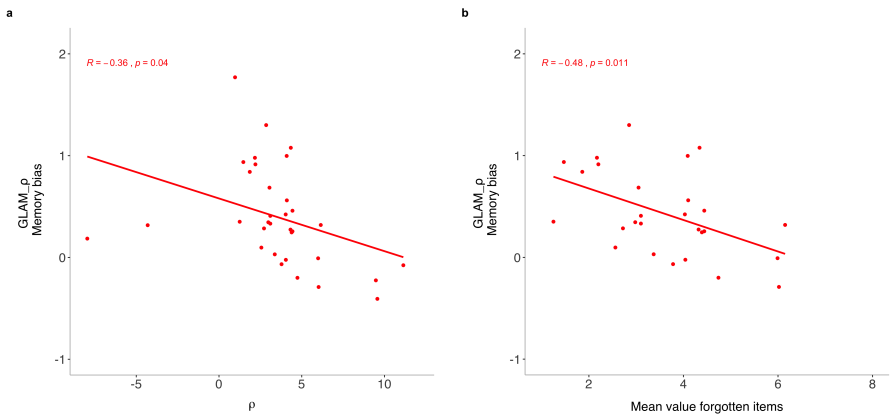

Fig.E 4. Correlations between the behaviorally estimated memory bias and the model estimates of the ρ parameter (a) or the mean value of all forgotten items (a).

Appendix F. Relationship between memory uncertainty and recall success

During the recall phase of the *remember-and-decide task*, participants did not only recalled items but also indicated how certain they were about their answer. We tested whether participants' recall certainty depended on whether they recalled an item correctly or not. Overall, participants were quite confident that they did not recall an item correctly (M = -1.21, SD = 0.64; one-sided t-test if smaller than 0: $t(38)$ = -11.82, $p < .001$, d = 1.89). Similarly, they were also quite confident of having indicated the correct item when they did so (M = 1.54, SD = 0.59; one-sided t-test is greater than 0: $t(32)$ = 16.37, $p < .001$, d = 2.62). Consequently we can conclude that participants knew whether they indicated the correct snack item or not during the recall phase (see Fig.F 1).

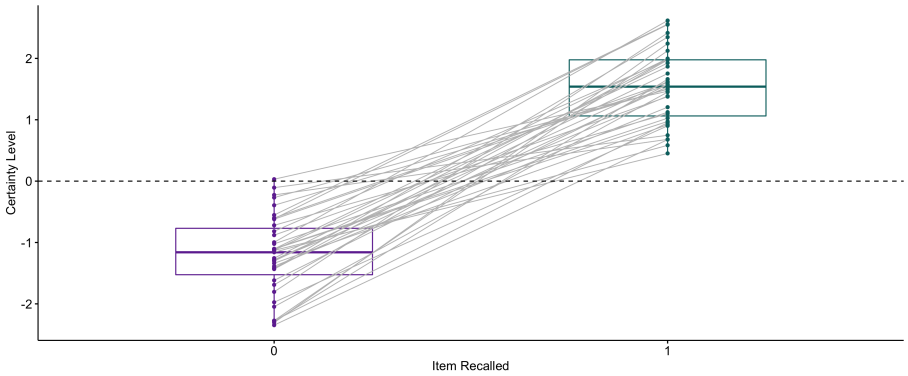

Fig.F 1. Association between the indicated recall certainty level (ranging from -3 to 3) and the actual recall (0 = item not recalled correctly, 1 = item recalled correctly). Participants appear to be relatively confident whether they recalled an item correctly or not.

Appendix G. Impact of gaze proportion calculation

We tested if the gaze influence reported in the main text persists when using the classical definition of gaze proportion (i.e. fixation duration to one option divided by the

total fixation duration), instead of the definition used in equation 3. Indeed, the gaze influences do not change, because the sign of the final gaze advantage (difference between the total fixation time to the left option minus the right option) remains unchanged.

Therefore, our gaze proportion calculation only impacts the model fitting. Fig.G1 shows, that in our data we would often have a gaze proportion difference of either -1 or 1. With the calculation used we reduce these cases to a minimum, allowing the GLAM being estimated more reliably.

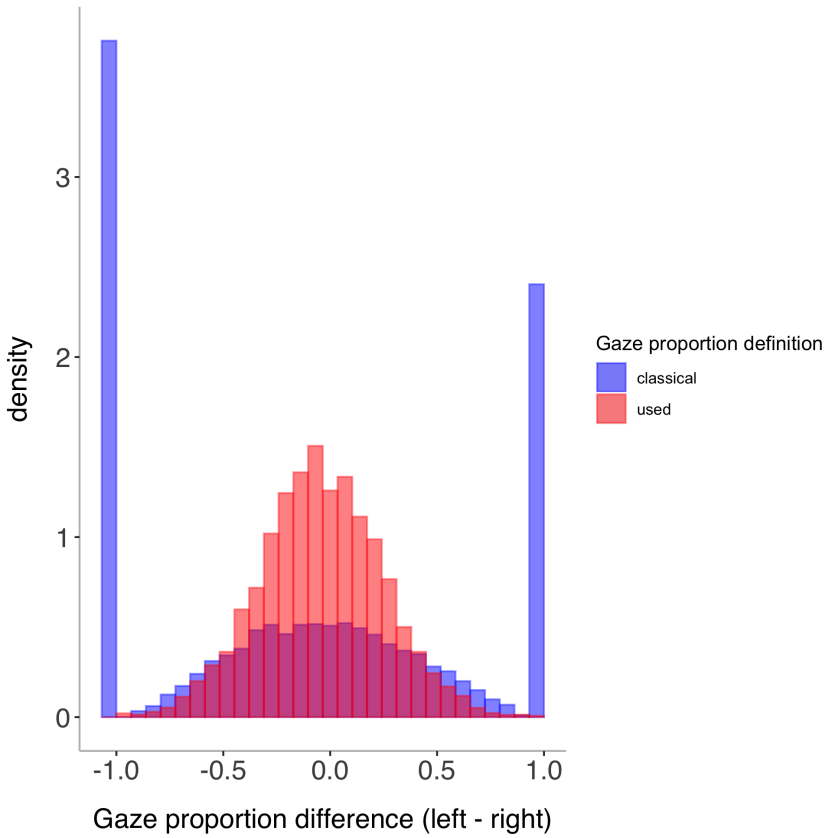

Fig. G 1. Histograms of gaze proportion difference (left - right) in case the classical definition of gaze proportion is being used (blue), or our adapted version (red).

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Appendix D. Academic Curriculum Vitae

CURRICULUM VITAE

September, 2020

REGINA AGNES **WEILBÄCHER**

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EDUCATION

07/2016 – present **Ph.D. in Decision Neuroscience in the Social, Economic and Decision Psychology Doctoral Program,** University of Basel
(Advisors: Prof. Sebastian Gluth and Prof. Jörg Rieskamp)
Ph.D. thesis title: *The role of episodic memory on value-based choice*
Due for submission September 2020

07/2014 – 06/2016 **MSc in Psychology, Major Neuroscience and Clinical Psychology,** University of Basel (Advisors: Dr. Leo Gschwind and Dr. Christian Vogler)
Master thesis title: *Hierarchical clustering of IAPS pictures based on fMRI activation patterns and the relation to semantic categories and heritability*

09/2011 – 06/2014 **BSc in Cognitive Psychology,** University of Basel (Advisor: Dr. Gilles Dutilh)
Bachelor thesis title: *Website appraisal and first impression*

ACADEMIC EXPERIENCE

07/2016 – present **Ph.D. student**, University of Basel, Faculty of Psychology, Center for Decision Neuroscience 100%
(Advisors: Prof. Sebastian Gluth and Prof. Jörg Rieskamp)
Duties: Data Science: Performing behavioral and neuroscientific (eye-tracking, fMRI, EEG) data analysis of complex data (Python, R, MATLAB), programming experiments, using mathematical and computational modeling (Bayesian/frequentist). Other: Presenting at international conferences, writing research articles, teaching, supervising research assistants, preparing, conducting, and managing research projects

02/2013 – 06/2016 **Student Research Assistant**, University of Basel, Faculty of Psychology, Center for Economic Psychology 15-25% (Advisor: Dr. Janina Hoffmann)
Duties: Coordinating studies, programming experiments (Python and MATLAB), writing literature reviews, performing data analysis (SPSS, MATLAB, R, PLINK)

01/2015 – 03/2015 **Clinical Internship**, UPK University Psychiatric Clinic, Ambulant Service for Addiction 80% (Advisor: Dr. Kenneth Dürsteler)
Duties: Administering psychological diagnostic tests and questionnaires, clinical data (including genetic data) management and data analysis (SPSS, R)

06/2013 – 10/2013 **Research Internship**, University of Zurich, Faculty of Psychology Division of Neuropsychology 50% (Advisor: Dr. Jürg Kühnis)
Duties: Performing data collection and analysis for an EEG experiment

AWARDS

2017 **Travel Award** Swiss Academy of Humanities and Social Sciences, 1000 CHF

2018 **Travel Award** Society of Neuroeconomics, 500 USD

2019 **Antelope Career Program** for female researchers including coaching sessions (financial, personal, career), and a travel award for an expert exchange (Prof. Daphna Shohamy, Columbia University, New York, USA)

PUBLICATIONS

Weilbächer, R. A., & Gluth, S. (2017). The interplay of hippocampus and ventromedial prefrontal cortex in memory-based decision making. *Brain sciences*, *7*(1), 4.

Hoffmann, J. A., von Helversen, B., **Weilbächer, R. A**., & Rieskamp, J. (2018). Tracing the path of forgetting in rule abstraction and exemplar retrieval. *Quarterly Journal of Experimental Psychology*, *71*(11), 2261-2281.

Kraemer, P. M., **Weilbächer, R. A.**, Fontanesi, L., & Gluth, S. (2020). Neural Bases of Financial Decision Making: From Spikes to Large-Scale Brain Connectivity. In Psychological Perspectives on Financial Decision Making (pp. 3-19). Springer, Cham.

Weilbächer, R. A., Kraemer, P. M., & Gluth, S. (in press). The reflection effect in memory-based decisions. *Psychological Science*.

Weilbächer, R. A., Krajbich, I., Rieskamp J., & Gluth, S. (2020). The role of visual attention on memory-based choice. Manuscript submitted for publication.

CONFERENCES

2017 **Weilbächer, R.A.,** Krajbich, I., Rieskamp J., & Gluth, S., The influence of visual attention on memory-based decisions, 10th JDMx meeting for Early Career Researchers, Bonn, May 31 – June 6, *talk*

2017 **Weilbächer, R.A.,** Krajbich, I., Rieskamp J., & Gluth, S., The influence of visual attention on memory-based decisions, SPUDM26, August 20 – 24, Haifa, *talk*

2017 **Weilbächer, R.A.,** Krajbich, I., Rieskamp J., & Gluth, S., The influence of visual attention on memory-based decisions, Neuroeconomics 2017, October 6 – 8, Toronto, *poster*

2018 **Weilbächer, R.A.,** Krajbich, I., Rieskamp J., & Gluth, S., Is visual attention mediating the memory bias in preferential choice? 11th JDMx meeting for Early Career Researchers, Konstanz, June 6 – 8, *talk*

2018 **Weilbächer, R.A.,** Krajbich, I., Rieskamp J., & Gluth, S., Do we choose what we remember because we pay more attention to it? 60th TeaP, Marburg, March 11 – 14, *talk*

2018 **Weilbächer, R.A.,** Krajbich, I., Rieskamp J., & Gluth, S., Is attention mediating the memory bias in preferential choice? Neuroeconomics 2018, Philadelphia, October 5 – 7, poster & poster spotlight

2019 **Weilbächer, R.A.,** Kraemer, P. M., & Gluth, S., Memory as uncertainty: a reflection effect in memory-based decisions? 12th JDMx meeting for Early Career Researchers, Trento, June 27 – 29, *talk*

2019 **Weilbächer, R.A.,** Kraemer, P. M., & Gluth, S., Memory as uncertainty: the reflection effect in memory-based decisions SPUDM27, August 18 – 22, Amsterdam, *talk*

2019 **Weilbächer, R.A.,** Kraemer, P. M., & Gluth, S., A reversed memory bias on value-based decisions in the loss domain, Neuroeconomics 2019, Dublin, *poster*

2020 **Weilbächer, R.A.,** Gluth, S., Comparing choices across and within domains, NeuroPsychoEconomics 2020, Online conference, June 11 – 12, *talk*

WORKSHOPS AND SUMMER SCHOOLS

2017 Summer School on Decisions, Law, and the Big Data Revolution, August 20 – 28, Haifa, *summer school*

2018 Models in Judgment and Decision Making, June 21 – 23, Hamburg, *workshop*

2018 5th Summer School on Computational Modeling, July 7 – 21, Couches, France, *summer school*

TEACHING EXPERIENCE

BSc. course, "Introduction to neuroscientific methods in the psychology of learning and decision-making" held three times (2017, 2018 and 2019)

SERVICE TO PROFESSION

Reviewing

for Brain Sciences, Psychological Bulletin, eLife

ACADEMIC SKILLSET

Programming/Software

R / Python / Jupyter Notebook	●●●●●
MATLAB / MS Office / Github	●●●●○
Stan / JAGS / Pymc3 / Bash / Shell	●●●○○
Google Suite / Slack	
Latex	●●○○○

OTHER SKILLS

Languages

(Swiss) German / Italian	●●●●●
English / French	●●●●○
Modern Hebrew	●●○○○