Final report of grant n° 384/20

SCHEMA-BASED TEMPORAL MEMORY IN PARIETAL CORTEX (SCHETEMP)

The present project lasted from the 2021.10.01 to the 2023.09.30.

This project has branched out over time and produced a set of behavioral, electrophysiological and neurostimulation experiments. More specifically, it aimed to investigate the role of schematic knowledge in biasing temporal memory judgments of movie scenes (behavioral group; section 1); to identify an EEG signature of the precision of temporal memory (EEG study; section 2), and to test the hypothesis of a causal role of the angular gyrus in temporal memory precision (TMS study; section 3).

Each of these objectives has produced successful results. We have already published two behavioural studies (on *Psychological Research* and *Memory*), one behavioural study is under review and two (EEG and TMS studies) are in preparation. The results of each work are described below.

1. Behavioral studies: The role of schematic knowledge in biasing temporal memory judgments

These studies have shown that temporal memory is influenced by schematic knowledge in several ways. More specifically, incomplete material is 'filled in' with the missing parts in relation to the memory schema, and this effect occurs immediately upon retrieval, regardless of consolidation or a long delay between encoding and retrieval (section 1.1., below). In addition, material that is complete but presented in a scrambled order is retrieved in a linear fashion that is more consistent with the schema (section 1.2.). Finally, using another type of paradigm, we studied the decay of temporal information (forgetting process) and found that it seems to persist within a week after encoding along with a group of other dimensions (WWW elements of episodic memory), unlike the verbal elements of memory (i.e., dialogues or what is said between two people), which are much more labile over time (section 1.3.). Overall, we replicated and extended our findings on the role of schematic knowledge in biasing temporal judgments of movie scenes.

1.1.

Background. The ability to organize our memories by order of occurrence is a hallmark of episodic memory. However, relatively little is known about the cognitive and neural mechanisms underlying temporal memory. In our previous studies, we found that schematic prior knowledge can play a scaffolding role for temporal memory judgments.

Aims. We used popular movies (i.e., complex audiovisual material) to investigate whether the effect of schema-based temporal memory is modulated by whether the material is presented completely or incompletely at encoding (i.e., does watching a movie without the last half hour have an effect on temporal memory judgments?), by the material that is cut (e.g., the last or middle part of a movie), and by the passage of time (i.e., making the temporal memory judgment immediately or after 24 h).

Method. In a timeline positioning task, participants were asked to indicate when short video clips extracted from a previously encoded film occurred on a horizontal timeline representing the duration of the video.

Results. Consistent with our previous findings, removing the last part of the film led to a systematic underestimation of the position of clips as a function of their proximity to the missing part ($N = 18$). Further experiments show that the direction of this automatic effect depends on which part of the film is removed from the encoding session ($N = 19$), consistent with the inferential structure of the schema, and does not depend on consolidation or reconsolidation processes ($N = 18$), at least under the present experimental conditions.

Conclusions. We propose that the observed bias depends on the automatic influence of reconstructive processes on judgments about the time of occurrence based on prior schematic knowledge.

Publications The results of these experiments are published in the journal *Psychological Research*:

Frisoni, M., Di Ghionno, M., Guidotti, R., Tosoni, A., & Sestieri, C. (2022). Effects of a narrative template on memory for the time of movie scenes: Automatic reshaping is independent of consolidation. *Psychological Research*, 7, 1 – 15.

1.2.

Background. Our previous studies have shown that people add the missing parts to complete the temporal representation according to their schematic knowledge. What happens if the parts are all there, but in no particular order?

Aims. The purpose of this study was to test the role of schematic knowledge on temporal judgments for disordered or scrambled material. We aimed to investigate whether and what kind of temporal bias could be found when the presented material differed greatly from schematic knowledge. Specifically, we investigated the effect of manipulating the temporal linearity of a narrative on subsequent temporal memory performance.

Method. To this end, adult participants were asked to report, using a visual analogue scale (timeline positioning task), the time of occurrence of short video clips extracted from a movie that had previously been encoded in either a linear (story time = viewing time) or a temporally scrambled (story time ≠ viewing time) presentation. Different scrambling versions were administered to different groups of subjects to systematically manipulate the temporal relationship between story and viewing time.

Results. While the scrambled presentation produced a mild and general impairment of recognition memory, it biased temporal judgments as a function of the direction and magnitude of the discrepancy between story and viewing time. This effect is consistent with an automatic reshaping of temporal memory by schema-based knowledge. This effect could be distinguished from a more general tendency to shift judgments towards the centre of the timeline, independent of the specific scrambling arrangement, consistent with the idea that the non-linearity of the story also generally increased the degree of temporal uncertainty.

Conclusions. Taken together, our results provide further evidence that temporal memory is automatically biased according to schematic prior knowledge.

Publications. The results of this study are currently under review:

Frisoni, M., Bufagna, A., Tosoni, A., & Sestieri, C. (under review). Seek for linearity: reconstructive processes reverse temporal scrambling in temporal memory for movie scenes.

1.3.

Background. Our studies have shown that temporal memory is influenced by schematic knowledge. But we know little about how long this of information can remain in memory in its exact form. That is, after how long does temporal information begin to decay? For example, is it still possible to correctly remember the temporal order of two events that happened a few days ago?

Aims. In the present study we investigated how memory for temporal information decays over time. More specifically, we wondered how accurately the temporal order of two events was remembered one week after encoding. Moreover, how long does this aspect of memory last? And is it stronger or weaker than other memory dimensions that make up a complex scene?

Method. To answer these questions, we used a paradigm other than the visual analogue scale. Specifically, participants watched a movie and had to answer questions about scenes from the movie at different delays.

We conceptualized the temporal dimension as part of the WWW triad of episodic memory: information about object/characters (“what”), spatial layout (“where”) and temporal relations (“when”). We investigated how these elements, as well as verbal information (i.e., dialogues), are forgotten over the course of a week. Moreover, we tested whether the amount of dimension-specific forgetting differed as a function of the participant’s age.

In a mixed design, younger and middle-aged participants (*N* = 60; control experiment: *N* = 22) were asked to watch a ~ 90 min movie and provide yes/no answers to detailed questions about different dimensions of the presented material after 1, 3 days, and 1 week.

Results. The results indicate that memory decay mainly affects the verbal dimension, both in terms of response accuracy and confidence. Instead, detailed information about temporal relations, as well as objects/characters’ features and spatial layout, seems to be relatively preserved, despite a general decrease in response confidence. Furthermore, younger adults were in general more accurate and confident than middle-aged participants, although, again, the verbal dimension exhibited a significant age-related difference.

Conclusions. We propose that this selective forgetting depends on the progressive advantage of visual compared to auditory/verbal information in memory for complex events. Future studies should investigate how schematic knowledge can modulate forgetting of temporal information.

Publications. The results of these experiments are published in the journal *Memory*:

Frisoni, M., Selvaggio, A., Tosoni, A., & Sestieri, C. (2023). Long-term memory for movie details: selective decay for verbal information at one week. *Memory*. 2023 Oct;31(9):1232-1243.

2. EEG study: Temporal memory for complex events is supported by oscillatory gamma activity

Background. Recent fMRI studies suggest that the hippocampal-entorhinal network is involved in judging precisely the time of occurrence of episodic memories (Montchal, 2019) and in representing the temporal structure of the event (Bellmund, 2022).

Aims. We asked whether these two processes (temporal precision and temporal structure), which have been studied separately, are in fact related in some way; whether they overlap in time, and when they occur (e.g., during or after stimulus presentation), and whether the temporal representation is associated with a spatial distribution of signals beyond the hippocampal-entorhinal circuitry.

Method. We ran an EEG study (*N* = 20) consisting of the encoding of a movie and a timeline task at retrieval. The EEG activity was recorded only during retrieval using a 128-channel system (Electrical Geodesic).

Data Analysis. Time–frequency representation (TFR) was computed for each EEG channel by means of a continuous Complex Morlet transformation in the range 3–40 Hz, at 1 Hz of frequency resolution.

Classification analysis. A multivariate pattern analysis (MVPA) of the time-frequency data was used to classify trials associated with low, medium and high temporal memory precision. The "input/feature" of the classifier was the calculated power (ERD/ERS) for each frequency and time point in each channel. The training of the classifier was made with a leave-one-subject-out approach. Specifically, a three-classes Linear Discriminant Analysis (LDA) classifier was trained for each time-frequency point of the EEG data using a time-frequency generalization analysis. Considering 122 EEG channels, N time instant and N frequency bins, the total number of LDA classifier input features was N.

ERD/ERS source reconstruction. To determine the underlying cortical sources of the TFR maps, we applied eLORETA to the TFR representation in the time-frequency window corresponding to significant accuracy values. The volume conductor model was given by a boundary element method (BEM) of a template brain and the source space was modeled by a Cartesian 3D grid bounded by the template anatomy with 5113 voxels. Visualization of cerebral sources was performed using the connectome workbench (https://www.humanconnectome.org/software/connectomeworkbench).

Representational similarity analysis (RSA). An RSA was used to investigate the similarity between behavioral and neural distance associated with pairs of movie parts, independently from temporal precision. We asked whether the mnemonic representation of the temporal structure is associated with a particular oscillatory activity in time. To answer this question, we created a behavioral matrix and a neural matrix, and we looked for a possible correlation between the two across all frequency bands and time points. The "behavioral matrix" represented the "subjective distance" between pairs of movie parts. In other words, we used the "estimated position" on the timeline for each movie part, averaged across subjects and independent of the correct answer. And then we calculated the distance (or difference) between each movie part. The "neural matrix" represented the "neural distance" between movie parts, calculated using the representational similarity analysis. In other words, we used the activity distributed across all channels and we calculated how similar it was between each pair of movie parts.

Results. At the neural level, using MVPA, we observed a significant pre-stimulus multiband activity, which we believe reflects a preparation effect. Importantly, we found an electrophysiological signature of temporal precision in the high beta/low gamma band (28-40 Hz) during presentation of the timeline, extending outside the entorhinal-hippocampal network.

We also performed a source analysis to localize the effect. The results of the whole-brain ANOVA contrasting the three groups of precision indicates that the precision effect is particularly evident in a network of right-lateralized regions.

The independent RSA of spatially distributed activity revealed a strong coupling between behavioral and neural distance related to pairs of movie parts at the same time and frequency band compared to the precision effect. This effect survived a permutation test. The correlation was also significant in 18 out of 20 subjects.

Finally, although we used two independent analyses, we found that temporal precision and temporal structure are both associated with the same frequency band and time point. We asked what the relationship was between these two effects. We conducted a Spearman Correlation Test between individual subject measures of memory precision (behavioral) and temporal structure (behavioral-neural). We found that subjects showing higher temporal precision were those who also exhibited a stronger correlation between behavioral and neural distance ($rs = - 0.50$, $p < 0.05$).

Conclusions. We found that oscillatory activity in the high beta/low gamma frequency codes for both temporal memory precision and the representation of event structure. These effects occur simultaneously after stimulus presentation but before the manual response and extend beyond the MTL, suggesting that temporal memory is supported by a distributed cortical network. These results help to link different phenomena reported in the literature on temporal memory and shed new light on how complex events in our life become “infused with time”.

Publications & Congress. The results of this study were presented as a Regular Talk at a major cognitive science congress, and are in preparation for submission to a high-impact journal:

ESCOP 2023, 23rd Conference of the European Society for Cognitive Psychology, 6-9 September, 2023. Regular Talk: “Temporal memory for complex events is supported by gamma oscillatory activity. Speaker: M. Frisoni.

Frisoni, M., Croce, P., Zappasodi, F., Sestieri, C. (in preparation). Temporal memory for complex events is supported by gamma oscillatory activity.

3. TMS study: Beta stimulation of the right parietal cortex facilitates temporal memory for complex events

Background. Causal evidence for the role of the lateral parietal cortex, and in particular the left angular gyrus (i.e., one of the core regions of the default-mode network, DMN), in episodic memory retrieval comes from recent studies using interference approaches that can mimic the effects of brain lesions ('virtual lesion' approach). However, it is unclear whether the same network subserves temporal memory.

Aims. We tested the role of the left angular gyrus in human temporal memory. Meanwhile, the results of the EEG experiment (see section 2) - conducted in parallel with the TMS experiment during the present project - showed a clear right-lateralized activation. We therefore decided to stimulate the right angular gyrus, using the same task as for the left angular gyrus. However, we used a different number of trials and a different sampling of stimuli from the video, so the two experiments are not comparable. In addition, still based on our EEG study, we decided to use beta stimulation. Indeed, there is evidence that beta oscillations (~20 Hz) play a role in the production and perception of temporal intervals (Fujioka et al., 2012; Kononowicz & van Rijn, 2015; Merchant & Bartolo, 2018; Wiener et al., 2018), and that beta parietal tACS (transcranial alternating current stimulation) can influence Mental Time Travel tasks, or tasks in which a person mentally project himself forward or backward in time (D’Angelo et al., 2023).

Method. We conducted a TMS study (N = 48) consisting of the encoding of a movie, a timeline task at retrieval (separated by a 24-hour interval from encoding), and a Number Line task (i.e., a single session performed on the same day as the timeline task, in counterbalanced order, in which participants had to place numbers on a VAS from 0 to 1000). In both tasks, participants had to position the clips by left-clicking the mouse when they were most confident and by right-clicking when they were least confident about the position of the clip (or number).

The first group (N = 24) of participants was stimulated over the left AG (vs vertex), whereas the second group (N = 24) was stimulated over the right AG (vs vertex).

Repetitive TMS was delivered during the timeline and the number line tasks. An rTMS train of 150 ms duration, 20 Hz frequency, and intensity set at 100% of the individual motor threshold was delivered at the onset of stimulus presentation. Based on the results of our EEG study (which showed an effect relate to temporal memory in the high beta/low gamma band), we expected a facilitatory effect of rTMS for the timeline task and no effect for the number line task.

The experimental design included two rTMS conditions, counterbalanced across subjects. The coordinates of the two cortical regions were based on previous fMRI studies (Vilberg & Rugg, 2008; Bonnici et al., 2016) assessing task-evoked activity during episodic retrieval and TMS studies (Yazar et al., 2017; Wynn et al., 2018) finding an effect on episodic memory, and were as follows: left AG: −43, −66, 38 (x, y, z in millimetres); vertex: 0, −15, 74 (x, y, z in millimetres). The right angular gyrus site (MNI coordinate: 42, - 72, 38) was based on an fMRI study of Mental Time Travel (Gauthier & van Wassenhove, 2016).

Results

Left AG

Timeline Task. The level of absolute error across trials was 643±143 s for the left AG and 640±137 s for the vertex. A paired sample t-test revealed that TMS to the left angular gyrus relative to TMS to the vertex had no effect on the level of absolute error ($t(23) = 0.13$, $p = 0.90$). These results suggest that the left angular gyrus does not play a causal role in the precision of temporal memory. For the confidence level, we performed a 2-way repeated measures ANOVA with Site (AG, V) and Confidence (High, Low) as within-factors, and the level of absolute distance as the dependent variable. We found only the main effect of Confidence [$F(1,23) = 43.90$, $p < 0.0001$], but no effect of Site [$F(1,23) = 0.00$, $p = 0.99$], nor the interaction of Confidence x Site [$F(1,23) = 0.09$, $p = 0.77$]. The main effect of Confidence was explained by higher absolute error for Low Confidence (972 ± 264) responses compared to High Confidence (559 ± 138) responses. This means that subjects were able to modulate their response appropriately, with low confidence responses actually associated with greater error than high confidence responses.

Number Line Task. A paired sample t-test found no difference between AG (44±15; mean ± SD) and vertex (46±19) stimulation ($t(23) = -1.17$, $p = 0.25$). We performed a 2-way ANOVA with Confidence and Site as within-factors, and the level of absolute error as the dependent variable. We did not find an effect of Confidence [$F(1,9) = 4.74$, $p = 0.06$], nor of Site [$F(1,9) = 0.09$, $p = 0.76$], nor of Confidence x Site interaction [$F(1,9) = 0.04$, $p = 0.86$]. These results suggest that the stimulation of the left AG had no effect on the number Line performance.

Right AG

Timeline Task. The level of absolute error across trials was 671±169 for the right AG and 715±178 s for the vertex. A paired sample t-test revealed that TMS to the right angular gyrus relative to TMS to the vertex significantly reduced the level of absolute error ($t(23) = -2.26$, $p < 0.05$). Overall, these results suggest that stimulation of the right AG reduces the amount of error, so that participants are more accurate in the temporal positioning of memories. For the confidence level, we performed a 2-way repeated measures ANOVA with Site and Confidence as within-factors, and the level of absolute distance as the dependent variable. We found the main effect of Confidence [$F(1,23) = 30.375$, $p < 0.0001$], the main effect of Site [$F(1,23) = 7.17$, $p < 0.05$] and the Confidence x Site interaction [$F(1,23) = 7.17$, $p < 0.05$]. The main effect of Confidence was explained by higher absolute error for Low Confidence (983 ± 256) responses compared to High

Confidence (573 ± 200) responses. This means that subjects were able to modulate their response appropriately, with low confidence responses actually associated with greater error than high confidence responses. When examining the interaction between Confidence and Site, Post-hoc analyses showed that participants made significantly more errors for low (vs high) confidence for both AG ($p < 0.0005$) and vertex ($p < 0.0005$) stimulation. Importantly, there was no significant difference between AG (569 ± 208) and vertex (566 ± 220) for High Confidence responses (p = n.s.), but a significant difference between AG (903 ± 282) and vertex (1120 ± 499) for Low Confidence responses ($p < 0.01$). Thus, with right AG stimulation, participants were still able to estimate their major error with low confidence, but their ability was weakened compared to vertex stimulation, and thus they rated their own objective performance worse than it was.

Number Line Task. A paired sample t-test found no difference between AG (41±18) and vertex (40±17) stimulation (t(23) = 0.78, $p = 0.44$). We performed a 2-way ANOVA with Confidence (High vs Low) and Site (AG, V) as within-factors. We found the main effect of Confidence [F(1,12) = 4.93, $p <0.05$], but no effect of Site [F(1,12) = 1.24, $p = 0.29$], nor Confidence x Site interaction [F(1,12) = 2.51, $p = 0.14$]. These results suggest that stimulation of the right AG had no effect on the number line performance, and so the difference found between AG and V for temporal memory cannot be attributed to a participant's difficulty in placing stimuli on the line.

Comparison between Timeline and Number Line Tasks. We used the absolute distance between points on the timeline (without converting them into seconds or numbers) as a common measure (“VAS distance”) to compare the two tasks. We performed a 2-way repeated measures ANOVA with Task (Timeline, Number Line) and Site (AG, V), and the VAS distance as the dependent variable. We found the main effect of Task [F(1,23) = 179.3, $p < 0.0001$], with the Timeline being more difficult that the Number Line Task. Crucially, we found the Task x Site interaction [F(1,23) = 5.53, $p <0.05$], with post-hoc analyses indicating no difference between AG (41 ± 18 VAS points) and V (40 ± 17 VAS points) for the Number Line Task (p = n.s.), and a higher precise performance for AG (128 ± 32 VAS points) compared to vertex (136 ± 34 VAS points) stimulation for the Timeline Task ($p < 0.05$).

For the confidence level, we performed a 3-way ANOVA with Confidence (High, Low), Task (Timeline, Number Line) and Site (AG, V) as within-factors, and the VAS distance as the dependent variable. The ANOVA only revealed the main effect of Confidence [F(1,12) = 10.31, $p < 0.01$], Task [F(1,12) = 56.99, $p < 0.0001$] and the Confidence x Task interaction [F(1,12) = 7.83, $p < 0.05$]. The main effect of Confidence was explained by a higher error for Low Confidence Responses. The main effect of Task was explained by a higher error for the Timeline (vs Number

Line) Task. When examining the Confidence x Task interaction, post-hoc analyses revealed no difference between High and Low Confidence for the Number Line Task (p = 0.86), but a significant difference between High and Low Confidence for the Timeline Task (p < 0.005), suggesting that participants were only able to modulate their confidence judgement according to the level of error in the temporal memory task. However, we did not find a Confidence x Task x Site interaction [F(1,12) = 4.64, p = 0.52], suggesting that AG stimulation had no clear effect on the level of temporal memory confidence.

Conclusions. Our findings suggest that stimulation of the right angular gyrus reduces the amount of error, so that participants are more accurate in the temporal positioning of memories. However, we found no effect on temporal memory confidence (apart from a small effect on low confidence responses, which we did not confirm in the analysis comparing the two tasks directly). Taken together, our results suggest that the right angular gyrus is involved in temporal memory for complex events, and that beta frequency has an enhancing effect on this type of performance when applied to the right angular gyrus. Importantly, the lack of effect for the left angular gyrus (both in terms of accuracy and confidence) suggests that while the representation of an event in memory involves the default mode network (as demonstrated by previous studies; see Renoult, Irish, Moscovitch, Rugg, 2019), the temporal positioning of the same memory appears to rely on different neural mechanisms. In other words, this may suggest that temporal positioning is a different/separate process from event representation. Future studies should further investigate the relationship between representation and temporal placement of complex events.

Publications. The results of this study are in preparation for submission:

Frisoni, M., Capotosto, P., Sestieri, C. (in preparation). Temporal memory for complex events is enhanced by parietal beta stimulation at the right angular gyrus.

4. Summary & Acknowledgments

Thanks to the BIAL Foundation grant, we have published 2 papers in two important journals such as Psychological Research and Memory. A third is under review. Importantly, the EEG and TMS studies are being prepared for submission to two high impact journals.

In addition, the results of the EEG study were presented at the ESCOP 2023 - 23rd Conference of the European Society for Cognitive Psychology, held in Porto on 06-09 September 2023. The BIAL Foundation was duly acknowledged in the papers and events.

Overall, I can say that the BIAL Foundation-funded project "Schema-based temporal memory in parietal cortex (SCHETEMP)" has been very productive and is providing us with groundbreaking knowledge.