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Neurophysiological correlates of memory for experienced and imagined events

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Abstract

Changes in slow cortical potentials within EEG were monitored while autobiographical memories of experienced and imagined event were generated and then held in mind for a short period. The generation of both kinds of memory led to significantly larger negative dc shifts over left versus right frontal regions, and this was interpreted as a reflection of substantial left frontal activation. The generation phase was also associated with greater right versus left negative dc shifts over posterior occipital regions. This pattern replicates and extends previous findings from our laboratory. In addition, however, experienced memories were associated with significantly larger negative dc shifts over occipito-temporal regions than imagined events. Furthermore, during the hold-in-mind period, imagined events led to larger negative dc shifts over left frontal regions than experienced events. These findings suggest that memories for imagined and experienced events may share control processes that mediate construction of memories but that they differ in the types of content of the memories: memories of experienced events contain sensory–perceptual episodic knowledge stored in occipital networks whereas memories for imagined events contain generic imagery generated from frontal networks.

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1. Introduction

The present work is part of larger project concerned with the neurophysiological characteristics of autobiographical memory [1,2]. The term “autobiographical memory” refers to memory for the experiences of a person’s life (episodic memories) and also to more abstract, conceptual, autobiographical knowledge such as the names of friends and colleagues, places where one has worked, towns lived in, schools attended, goals attained or abandoned, etc. [3]. Autobiographical knowledge provides a context for sensory–perceptual episodic memories and the combination of the two in an act of remembering constitutes a specific autobiographical memory [4]. The fundamentally constructive nature of autobiographical remembering is a form of complex higher order cognition which engages neural networks in both long- and short-term (working) memory and which, centrally, involves the self. In Conway and Pleydell-Pearce [3] model of autobiographical memory,

memories are viewed as transitory mental constructions effortfully generated and maintained in the *self memory system* (SMS). The SMS consists of the *working self* (currently active goal hierarchy and mental models of the self) and the *autobiographical knowledge base*, i.e. representations of episodic memories and autobiographical knowledge. This dynamic and complicated system is disrupted by many different types of brain damage and psychiatric illness [5], and is mediated by complex interlocking neural networks [6]. Topographically, these networks are widely distributed in the brain [2]. More generally, however, and even in intact memory systems, the constructed nature of autobiographical memories means that they are intrinsically prone to error and in extreme cases, i.e. confabulation, may be wholly false. Here we are interested in neurophysiological differences between false but plausible ‘memories’—memories for imagined events—and autobiographical memories for experienced events.

The construction of autobiographical memories is effortful and retrieval times (RTs) are highly variable: in the range 3–9 s with mean RTs at approximately 5 s. Because of these latencies, imaging techniques with coarse temporal resolution, e.g. PET and fMRI, cannot identify the points

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at which different networks become involved in the construction process. Thus, PET and fMRI have good spatial resolution and can effectively identify which neuroanatomical sites become active during an episode of remembering, but do not provide precise information about when specific structures become active. Because we are interested in the dynamics of memory construction we have developed a programme of research using the fine temporal resolution of EEG. At the same time we also draw on findings using imaging techniques with better spatial resolution, PET and fMRI (see [2]), and so have powerful convergent evidence for the *dynamic localisation* (Luria, 1976) of autobiographical remembering. The dynamic localisation of autobiographical remembering was demonstrated by Conway et al. [1] who found enhanced neurophysiological activity within EEG recorded from electrodes overlying left frontal lobe during the construction of autobiographical memories (prior to formation of an actual memory). When, a memory was formed, however, enhanced EEG activity was detected at electrodes located over posterior temporal and occipital lobes. This pattern of activation of networks in left prefrontal cortex (PFC) during retrieval followed by additional temporo-occipital activation once a memory was formed and held in mind appears to be highly characteristic of autobiographical remembering. The question addressed by the present study was whether or not the same pattern is present in the generation of plausible but false autobiographical memories.

In the following sections we report how slow potential shifts within EEG reflect the process of memory construction and the dynamic localisation of the SMS. Slow potentials are measured using dc electroencephalography and many studies have shown that negative-going slow potential shifts recorded at the scalp are primarily a reflection of activation within underlying cortical regions [7–18]. For this reason, these slow shifts are often described as ‘slow cortical potentials’, SCPs [19]. While the hypothesis that negativity reflects activation is not always correct (e.g. [20]), the vast majority of relevant papers support this interpretation, and the topographic distribution of SCPs invoked by many tasks is commonly consistent with other imaging procedures ([21]; see also [1]). Our concern here is with contrasting the patterns of SCPs in the generation of autobiographical memories for experienced events (and thus replicating [1]) with the patterns of SCPs detected in the generation of mental representations of imagined events.

2. Methods

2.1. Participants

There were 20 participants, 16 women and 4 men with an average age of 30.6 years and the range was 25–47 years. Data from a further six participants were rejected on grounds of excessive numbers of trials associated with body and eye-movement artefacts.

2.2. Procedure and design

Fig. 1 illustrates the sequence of events which occurred on each trial of the study. Participants sat at a viewing distance of 70 cm from a computer screen. Each trial began with either the memory instruction “Real Memory” or “Imagined Memory” which remained on the screen for 3 s, and was replaced by a 1 s period during which the screen was dark. The instruction “Pull for Cue” appeared, and participants were instructed to pull back two joysticks simultaneously, one in each hand, thereby minimising the risk of asymmetric movement-related potentials contaminating the retrieval phase [1]. This was followed by another 1 s duration dark screen, which in turn was succeeded by a fixation stimulus “-----” presented for 3 s. A lower case cue word (e.g. camera or museum) was then presented and remained on screen until participants indicated, with a bimanual response, that they had retrieved/generated a memory, or were unable to provide a memory (see ahead).

Participants were asked to ensure that all memories, whether experienced or imagined, were associated with the cue word and were at least 6 months old. The imagined memories were to be constructed of real people, places, goals, etc., and to be constructed in such a way as to be plausible if described to close family or friends. When a bimanual response was made, the cue word was replaced by a small red circle, which subtended 0.29° of visual angle. The circle remained on the screen for 7.5 s, during which time participants were asked to fixate it, and hold in mind the memory (or wait patiently if no memory had been formed). The red circle was then replaced by an equivalent sized green circle, which remained for 2 s, during which the memory was to be released from mind. At the end of the 2 s ‘release phase’, participants were prompted to type a brief description/title of their memory using the keyboard provided. If no memory had been found, pressing the ‘Return’ key would lead to onset of the next trial.

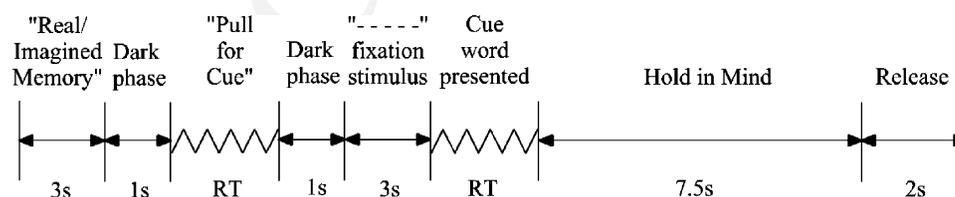


Fig. 1. Schema of events and their timings occurring on a single trial.

156 All text was presented in a mono-spaced font, in white
 157 against a black screen background at the vertical and hori-
 158 zontal centre of the screen. Each letter subtended a maximum
 159 of $0.25^\circ \times 0.33^\circ$ of visual angle. There were 84 cue words
 160 in total (taken from [1]), 12 of which were used as practice

161 trials. Of the remaining 72 cues, half named to objects, e.g. 161
 162 camera, and the other half to locations, e.g. museum. These 162
 163 two subgroups were further divided into sets of 18 trials, 163
 164 which required real and imagined memories and this latter 164
 165 factor was counterbalanced across participants. Trials were 165

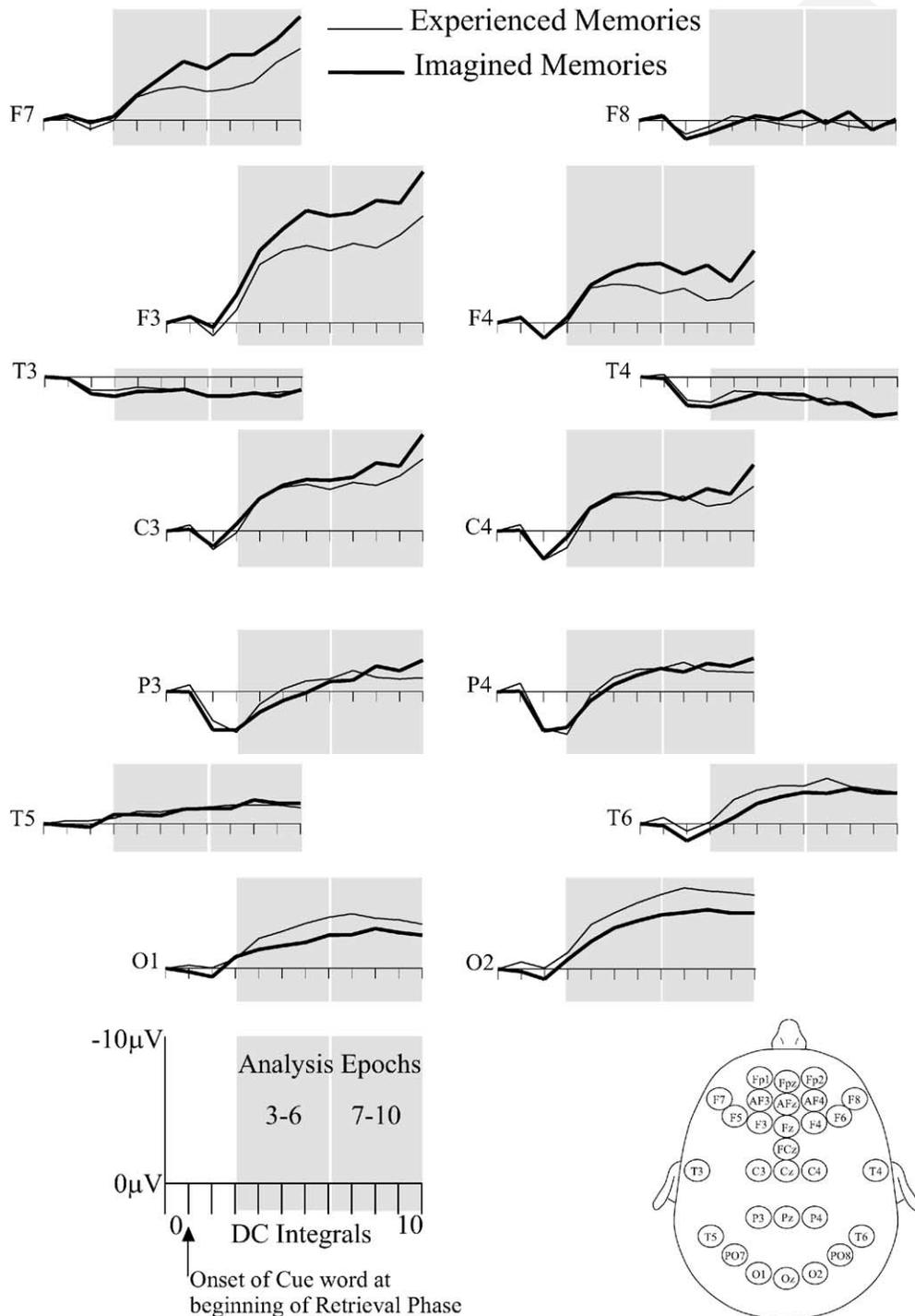


Fig. 2. Slow potentials within 10 equal duration integrals spanning the period between cue onset and bimanual response indicating actual retrieval of experienced memories (thin trace) and imagined memories (thick trace). Only data from selected electrodes are displayed. Note left frontal negativity and right posterior negativity. The two shaded regions indicate epochs for which mean amplitude measures were derived for purposes of statistical analysis. Locations of all electrodes employed in the study are illustrated bottom right.

run in blocks of 12, during which 6 imagined and 6 experienced memories were cued in random order. A short rest was provided between each block. The experimental procedure lasted approximately 2 h.

Electroencephalographic data were recorded using silver–silver chloride electrodes located within an elastic electrode cap, at 30 locations according to the International 10–20 system co-ordinates (see Fig. 2). All scalp electrodes were referred to linked mastoids. Vertical and horizontal electro-oculogram (VEOG and HEOG) were recorded from electrodes located above and below the right eye and at the outer canthi. Data were acquired using a Neuroscan dc amplifier (bandpass 0–30 Hz) and digitised at 200 Hz in all channels. Slow dc shifts spanning the entire experimental session (commonly regarded as ‘drift’ artefact, see Simons et al., 1982) were modelled by polynomial coefficients up to 10th order and were then removed from raw trials [22]. After applying this procedure, all trials on which any electrode displayed a shift greater than $\pm 30 \mu\text{V}$ for more than 5% of the total duration of that trial, were discarded from the analysis. The group of 20 participants reported here had at least 20 surviving trials for both conditions. Trials on which large eye-movements were made were rejected on the basis of visual inspection. Effects of eye-movements were also corrected using regression coefficients [23] derived after all channels had been subjected to a post hoc digital filter with a 5 s time constant (Elbert and Rockstroh, 1980; Ruchkin, 1993). This ensured that slow dc shifts at EOG and EEG electrodes did not lead to inflated or erroneous correction coefficients.

In all cases, statistical significance was assessed using repeated measures analysis of variance (ANOVA) with epsilon corrections for violations of sphericity where appropriate. Three-way ANOVAs were restricted to homotopic electrodes (e.g. O1/O2) and involved 2 levels of memory instruction, 2 levels of hemisphere and 11 levels of ‘region’ (e.g. O1 + O2 = occipital region). Thus, significant differences between homotopic pairs are indicated by a significant interaction between hemisphere and region. A further two-way ANOVA involved 30 levels of electrode and 2 levels of memory instruction. In all statistics reported here, effects of memory cue were examined after data were re-scaled in order to counteract non-additive effects of source strength changes upon ANOVA [24]. However, some of the hypotheses tested here actually predict changes in source strength. For this reason, we also report significant condition effects for ‘untransformed’ data in the absence of the correction.

3. Results

3.1. Behavioural data

For memories of experienced events there were 84.4% artefact-free trials compared to 80.3% for memories of imagined events, a reliable difference, $F(1, 19) = 5.7$, $MS_e =$

3.92 ($P < 0.05$ for all effects reported here). If trials rejected on the grounds of unacceptable drift and artefact are ignored, this reliable difference remains and shows that generating memories of imagined experiences was more difficult than recalling memories of experienced events. This is because participants were more likely to report failure to produce a memory for imaginary versus real trials. Consistent with this, imagined memories (5722 ms) took significantly longer to retrieve than memories of experienced events (5095 ms), $F(1, 19) = 6.5$, $MS_e = 3.92$. Overall then memories of imagined events were constructed less frequently and took longer generate than memories of experienced events.

3.2. SCPs associated with retrieval

Analysis of EEG data focused upon SCPs during the retrieval and ‘hold-in-mind’ phases. Examination of changes during the retrieval phase is made more difficult given the unpredictable length of this period. In order to deal with this problem, the interval between cue onset and bimanual response was divided into 10 equal duration epochs (integrals) on each individual trial and for each participant. Thus, a 5 s retrieval latency provides 1000 points at a sample rate of 200 Hz, or 10 epochs of 500 ms. On most trials, this division led to a remainder number of points, and the policy was to avoid the remainder points in the period immediately prior to response. The mean duration of each integral for experienced and imagined memories was 507 and 570 ms, respectively. Reliable SCPs within these integrals are shown in Fig. 2 (retrieval phase) and Fig. 3 (hold-in-mind phase). Fig. 2 shows substantially greater left versus right frontal negativity during the retrieval phase for both experienced and imagined memories. The traces also suggest greater right versus left hemisphere negativity over occipito-temporal regions.

Data within the retrieval phase were then divided into early and late epochs; the early phase comprising integrals 3–6, and the late phase comprising integrals 7–10. A single mean dc amplitude was then calculated for each of these phases, and each was baselined to the mean amplitude over a 1 s period prior to cue onset. A three-way ANOVA, with 2 levels of memory (experienced and imagined), 11 levels of homotopic region (e.g. AF3 + AF4 are the anterior frontal region), and 2 levels of hemisphere was applied to each phase. The interaction between region and hemisphere was significant for both the early, $F(10, 190) = 7.2$, $MS_e = 3.91$, and late phases, $F(10, 190) = 9.7$, $MS_e = 6.3$. Exploration of interactions employed analysis of simple main effects (ANOSME). In the early phase ANOSME revealed significantly greater left than right hemisphere negativity at two frontal regions: AF3 > AF4 and F3 > F4. In the late phase, significantly greater left than right hemisphere negativity was found at the following homotopic pairs: AF3 > AF4, F7 > F8, F5 > F6 and F3 > F4. Significantly greater negativity over right than left hemisphere regions was found over the occipital region (O2 > O1), in both the early and late phases of memory construction. There were no signifi-

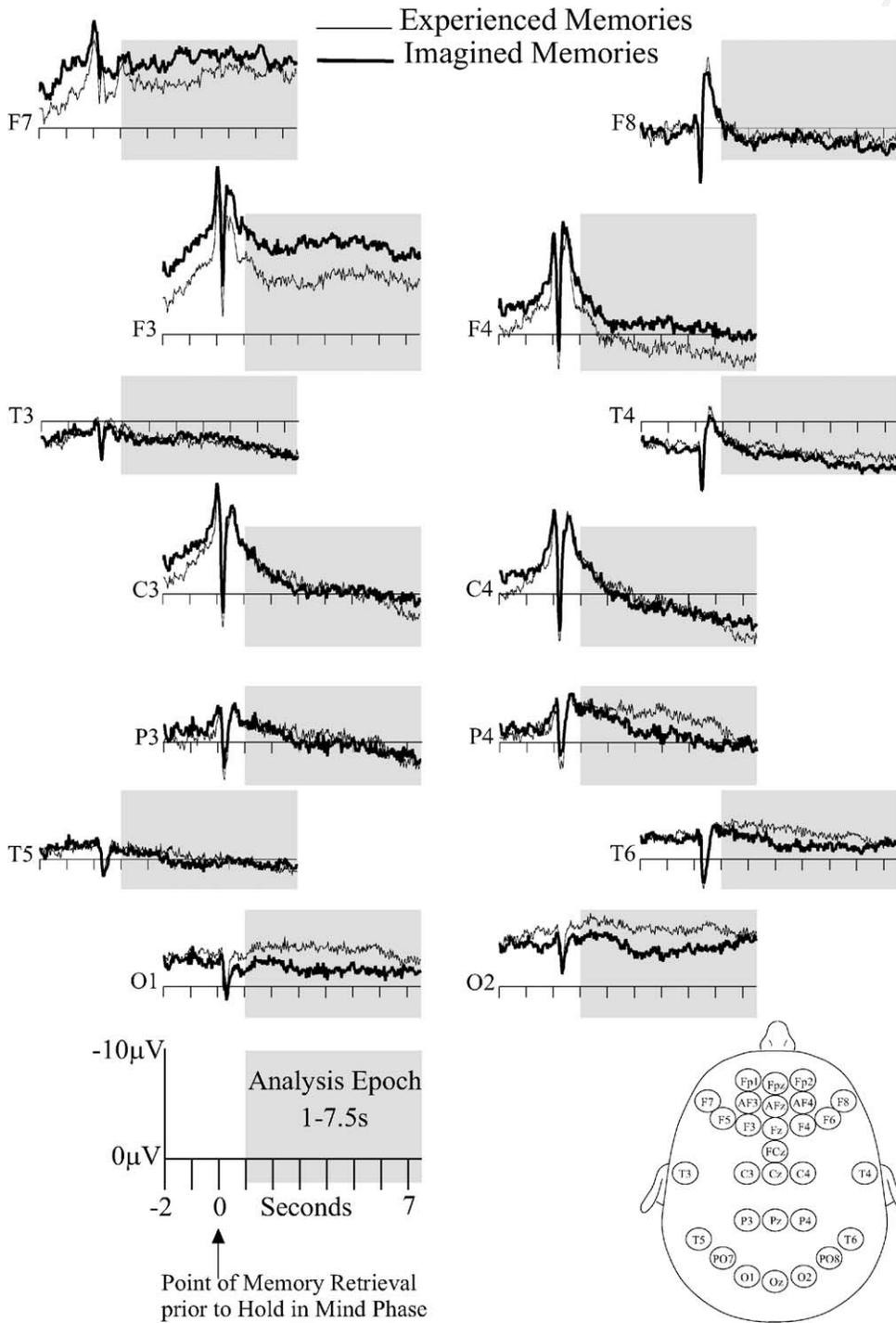


Fig. 3. Slow potentials observed when experienced and imagined memories were held in mind over a 7.5s period. Traces begin 2s prior to bimanual response indicating actual retrieval. Only data from selected electrodes are displayed. Note that experienced memories are associated with greater posterior negativity, whereas imagined memories are associated with greater left frontal negativity, particularly at electrode F3. Shaded regions indicate epochs for which mean amplitude measures were derived for purposes of statistical analysis. Locations of all electrodes employed in the study are illustrated bottom right.

272 icant effects of memory instruction during either the early
 273 or late retrieval phase, even after comparison in a two-way
 274 ANOVA with 30 electrodes \times 2 levels of memory. The left
 275 frontal negativity during retrieval replicated our earlier work

[1] which also found extensive left PFC activation during
 the memory retrieval phase. The significant activity over
 the right occipital region, which in the previous study was
 only observed as a memory was formed and then held in

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280 mind, suggests early access to sensory–perceptual visual au-
281 tobiographical knowledge stored in occipital networks. It
282 is perhaps worth noting in this respect that mean retrieval
283 times for memories of experienced events were faster in the
284 present study than those observed in previous studies (see
285 [2]).

286 3.3. SCPs associated with holding a memory in mind

287 Fig. 3 shows the SCPs during the hold-in-mind phase.
288 Analysis of this phase involved computing a mean dc ampli-
289 tude over a period 1000–7500 ms post-bimanual response.
290 This amplitude measure was baselined with respect to a 1 s
291 period prior to cue onset. A three-way ANOVA revealed
292 a significant interaction between region and hemisphere,
293 $F(10, 190) = 11.5$, $MS_e = 12.4$. Analysis of simple main
294 effects found greater left than right hemisphere negativity
295 frontally ($AF3 > AF4$, $F7 > F8$, $F5 > F6$ and $F3 >$
296 $F4$), but, in a reversal of these effects, greater right than
297 left hemisphere negativity was detected at electrodes over-
298 lying the occipital region ($O2 > O1$). In contrast to the re-
299 trieval phase, the hold-in-mind phase revealed a significant
300 interaction between memory and region, $F(10, 190) = 3.9$,
301 $MS_e = 4.5$. ANOSME indicated significantly greater nega-
302 tivity for experienced than imagined memories over occip-
303 ital and occipito-temporal regions ($O1 + O2$, $PO7 + PO8$).
304 A two-way ANOVA with 30 levels of electrode and 2 lev-
305 els of memory was also performed. This yielded a signifi-
306 cant two-way interaction, $F(10, 190) = 2.7$, $MS_e = 2.4$ and
307 ANOSME here revealed greater negativity for experienced
308 over imagined memories at electrodes $PO8$, $O1$, $O2$ and Oz .
309 An identical two-way ANOVA applied to data not subjected
310 to McCarthy and Wood [24] correction found a significant
311 interaction between electrode and memory: $F(29, 551) =$
312 2.9 , $P < 0.05$, $MS_e = 2.43$. Post hoc analysis revealed
313 that in addition to the findings described above, imaginary
314 memories were associated with greater negativity than real
315 memories at the left frontal electrode $F3$.

316 4. Discussion

317 The central finding of the present study was that the pat-
318 terns of changes in SCPs for memories of experienced and
319 imagined events could be differentiated, although both also
320 shared some neurophysiological characteristics. During the
321 phase of memory construction both experienced and imag-
322 ined events were associated with sharp increases in activa-
323 tion in left PFC networks. This finding is highly consistent
324 with the waveforms observed by Conway et al. [1] in their
325 SCP study of autobiographical memory retrieval. In fact, as
326 the methodology is virtually identical the present findings
327 replicate those of the earlier study. According to Conway
328 et al. [1] this left PFC activity so characteristic of the re-
329 trieval phase in the construction of autobiographical memo-
330 ries reflects the operation of control processes and especially

of the working self in elaborating cues, probing the knowl- 331
edge base and evaluating the relevance of accessed knowl- 332
edge. What is novel and of special interest in the present 333
data is that the left PFC activation is most intense during 334
the active maintenance of plausible false memories. Upon 335
reflection this is, perhaps, not so surprising as presumably 336
the creation of a novel and false representation out of au- 337
tobiographical knowledge pre-stored in long-term memory 338
would be effortful and temporally extended. In contrast, for 339
some autobiographical memories, especially those that have 340
received high amounts of rehearsal, construction may be less 341
effortful and occur more quickly (as indeed was found to be 342
the case). For rehearsed memories it is possible that some 343
form of mental model is, eventually, retained in long-term 344
memory and accessing this leads to a relatively undemand- 345
ing construction process. Nonetheless, it is apparent that 346
many of the same neural networks must be active in the 347
construction/retrieval phase for imagined and experienced 348
events. 349

What differentiates the two construction processes in 350
terms of topography is the degree to which they activate 351
posterior networks in the temporal and occipital lobes (more 352
dominant in the right than in the left cortical hemisphere). 353
In the present study this posterior activity was greatest in 354
the construction of real autobiographical memories and 355
occurred during retrieval and hold-in-mind phases. Accord- 356
ing to Conway et al. [2] this occipital–temporal activation 357
indicates access of networks that store sensory–perceptual 358
episodic knowledge that constitute the visual imagery so 359
endemic in autobiographical remembering (see [4]). This 360
suggests a relatively simple explanation of the overall pat- 361
tern of findings: namely that autobiographical memories 362
featured visual imagery whereas confabulated memories of 363
imagined events did not and hence the difference in pos- 364
terior activations. This, of course, would not explain the 365
differences in left PLC activation, but nevertheless may 366
seem a good account of the occipital–temporal differences. 367
There are, however, several reasons for doubting the im- 368
agery hypothesis. For example, the topographic differences 369
described above were obtained with data scaled by vec- 370
tor length and, therefore, source strength changes within a 371
common imagery system are unlikely to account for these 372
findings. Moreover, clarity ratings of memories (collected 373
but not reported above), found that visual images were 374
endemic in the construction of both types of memory. In 375
other studies contrasting SCP changes in the generation of 376
images with the corresponding changes in the generation 377
of autobiographical memories we have found a type of 378
generic autobiographical imagery to be common in both 379
tasks and in imagery to be associated with increased frontal 380
activation. Such frontal activation for imagined events was 381
found in the present study during the hold-a-memory in 382
mind phase. We suggest that qualitatively different types of 383
images occur in the two tasks: in autobiographical memory 384
the images are episodic, event-specific, knowledge rep- 385
resentations derived from sensory–perceptual experience, 386

387 they are “experience-near”; in contrast the images in imag-
 388 ined events are generic and, possibly, derived from episodic
 389 representation, they are “experience-distant”.

390 In summary then, we have found memory for imagined
 391 and experienced events to draw upon the highly similar brain
 392 regions during construction. These regions are located in
 393 left PFC and may reflect the operation of control process in
 394 accessing and evaluating knowledge in long-term memory.
 395 They are more intensely active in the constructive mainte-
 396 nance of memories for imagined than experienced events,
 397 but are nonetheless highly active in the latter too. In con-
 398 trast, posterior activation of temporal-occipital networks was
 399 more intense in the construction of memories for experi-
 400 enced than imagined events and this may reflect the access
 401 of autobiographical imagery.

402 Uncited references

403 [25–32].

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