Prior knowledge modulates the neural substrates of encoding and retrieving naturalistic events at short and long delays

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ABSTRACT

Congruence with prior knowledge and incongruence/novelty have long been identified as two prominent factors that, despite their opposing characteristics, can both enhance episodic memory. Using narrative film clip stimuli, this study investigated these effects in naturalistic event memories – examining behaviour and neural activation to help explain this paradox. Furthermore, we examined encoding, immediate retrieval, and one-week delayed retrieval to determine how these effects evolve over time. Behaviourally, both congruence with prior knowledge and incongruence/novelty enhanced memory for events, though incongruent events were recalled with more errors over time. During encoding, greater congruence with prior knowledge was correlated with medial pre-frontal cortex (mPFC) and parietal activation, suggesting that these areas may play a key role in linking current episodic processing with prior knowledge. Encoding of increasingly incongruent events, on the other hand, was correlated with increasing activation in, and functional connectivity between, the medial temporal lobe (MTL) and posterior sensory cortices. During immediate and delayed retrieval the mPFC and MTL each demonstrated functional connectivity that varied based on the congruence of events with prior knowledge; with connectivity between the MTL and occipital regions found for incongruent events, while congruent events were associated with functional connectivity between the mPFC and the inferior parietal lobules and middle frontal gyri. These results demonstrate patterns of neural activity and connectivity that shift based on the nature of the event being experienced or remembered, and that evolve over time. Furthermore, they suggest potential mechanisms by which both congruence with prior knowledge and incongruence/novelty may enhance memory, through mPFC and MTL functional connectivity, respectively.

1. Introduction

Creating and recalling memories of events depends on complex networks of brain regions, as incoming sensory information is transformed into meaningful percepts, and combined with relevant contextual, semantic, and affective information into a cohesive representation (Horner, Bisby, Bush, Lin, & Burgess, 2015; McKenzie et al., 2014; Rugg & Vilberg, 2012; St Jacques, Kragel, & Rubin, 2011). As such, memories reflect not only a record of the sensory input processed during a given event, but also the influence of past experiences (Bartlett, 1932). Prior knowledge and experiences may highlight relevant information, maximize the efficiency of new learning, expand memory capacity, and enable inferential processing (Alba & Hasher, 1983; Ghosh & Gilboa, 2014; Piaget, 1928; Preston & Eichenbaum, 2013; Wang & Morris, 2010), all of which allow our memories to efficaciously guide future behaviour. Here, prior knowledge refers to facts, concepts, schemas, and scripts; this includes general semantic knowledge, as well as personal semantic information and cultural knowledge, which are all thought to be developed through the extraction of consistencies from multiple related events, resulting in the retention of common features and the loss of details unique to any specific event (Brady & Oliva, 2008; Conway, 2009; Posner & Keele, 1968; Richards et al., 2014; Tulving, 1972).

Although congruence with prior knowledge often improves

comprehension and memory (for reviews see Alba & Hasher, 1983; van Kesteren, Ruiter, Fernández & Henson, 2012), and increases rates of learning (Sommer, 2017; Tse et al., 2007), it may also generalize or distort perception and memory (Friedman, 1979; Melo, Winocur, & Moscovitch, 1999; Spalding, Jones, Duff, Tranel, & Warren, 2015) particularly by biasing recall towards the 'average', such that stimuli and events are remembered as more prototypical (Richards et al., 2014; Hemmer & Steyvers, 2009; Konkle & Oliva, 2007). At the neural level, activity in the medial prefrontal cortex (mPFC) has been associated with increasing congruence between stimuli, during both encoding and retrieval (van Kesteren, Rijpkema, Ruiter, & Fernandez, 2010; van Kesteren et al., 2013). In addition, the mPFC is linked with both the enhancement (Liu, Grady, & Moscovitch, 2016; Maguire, Frith, & Morris, 1999; Tse et al., 2011; van Kesteren, Rijpkema, Ruiter, Morris, & Fernández, 2014) and generalization or distortion (Spalding et al., 2015; Warren, Jones, Duff, & Tranel, 2014; Berkers et al., 2017) of memory based on prior knowledge.

On the other hand, the novelty or incongruence of a stimulus with prior experiences is also known to enhance memory (Tulving, Markowitsch, Kapur, Habib, & Houle, 1994; Von Restorff, 1933, but see Poppenk, Köhler, & Moscovitch, 2010), with the overall distinctiveness of a stimulus thought to determine its memorability (McDaniel & Einstein, 1986). The medial temporal lobe (MTL), commonly associated with episodic memory in general (Nadel & Moscovitch, 1997; Scoville & Milner, 1957), is strongly linked with novelty in particular (Knight, 1996; Kumaran & Maguire, 2009; Lisman, Grace, & Street, 2005; Vinogradova, 2001). For example, the MTL responds most to sequences that generate and then violate expectations (Kumaran & Maguire, 2006, 2007), and tracks the total number of changes between studied items and similar lures (Duncan, Ketz, Inati, & Davachi, 2012). The importance of the MTL in the detection and encoding of novel or incongruent stimuli may be due to its ability to rapidly encode even arbitrary relations, unlike the neocortex, which gradually integrates new information with pre-exisiting representations (Cohen, 2015; McClelland, McNaughton, & O'Reilly, 1995; Moscovitch, 2008; O'Reilly, Bhattacharyya, Howard, & Ketz, 2014; Rolls, 2007). Although memory for arbitrary relations is often characterized as relying on the hippocampus specifically, studies on the mnemonic effects of incongruence with prior knowledge often report peaks across the MTL. For example, parahippocampal cortex activity is correlated with decreasing congruence of object-scene pairs (van Kesteren et al., 2013), while the learning of novel facts unrelated to prior academic knowledge is associated with MTL activation that encompasses both the hippocampus and parahippocampal cortex (van Kesteren et al., 2014). Similarly, the parahippocampal cortex is active during initial learning of a prediction task, when the information is novel and participants have not yet extracted commonalities from across the patterns in the task (Kumaran, Summerfield, Hassabis, & Maguire, 2009). Note that, although novelty is often investigated in isolation, the effects of novelty may themselves depend on prior knowledge since novelty often entails deviation from expectations developed through prior experiences (Carpenter & Grossberg, 1993), with maintenance of such context-sensitive expectations dependent on the integrity of the mPFC (Gilboa & Moscovitch, 2016).

The evidence outlined above suggests that congruence with prior knowledge and novelty, seemingly opposing constructs, may both improve memory, presumably through different neural processes (van Kesteren et al., 2012). Much of the imaging research conducted on these effects, however, has involved unrelated stimuli, paired-associates, or facts. The relevance of findings from such studies to memory for real-life narrative events remains to be shown. For example, previous research suggests an inhibitory relationship between the mPFC and MTLs (van Kesteren et al., 2012; van Kesteren et al., 2013; but see Preston & Eichenbaum, 2013; Chao et al., 2017; Schlichting & Preston, 2016; Zeithamova et al., 2012). For naturalistic event memories, we hypothesize that functional connectivity will exist between the mPFC and

MTLs to process the confluence of event-specific and semantic information that constitutes narrative events (Levine et al., 2002). Specifically, it has been suggested that mPFC-MTL functional connectivity supports the resolution of overlapping associations when moderate degrees of prior knowledge exist (Gilboa & Marlatte, 2017).

The effects of prior knowledge on episodic memory are further complicated by the fact that memories are not static; instead, information is stabilized, transformed, and/or forgotten over time (Chen et al., 2017; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Hardt, Nader, & Nadel, 2013; Winocur, Moscovitch, & Bontempi, 2010). There is a long-standing debate between theories that link the consolidation of memories with a transition from MTL-dependence to neocortical representation (Squire & Alvarez, 1995; Squire & Wixted, 2011; Takashima et al., 2006), and those that suggest that, as long as memories remain detailed, they continue to depend on the MTLs regardless of their age (Addis, Moscovitch, Crawley, & McAndrews, 2004; Moscovitch, Crawley, & McAndrews, 2004; Bonnici et al., 2012; Gilboa et al.,2004; Winocur & Moscovitch, 2011). Critically, recent evidence suggests that MTL-dependence at a given time-point may be modulated by congruence with prior knowledge. Both rodent (Tse et al., 2007) and human (Sommer, 2017) experiments suggest that paired-associates that are consistent with a previously learned schema become MTL-independent more quickly than schema-inconsistent pairs. Naturalistic events reveal memory transformation at a behavioural level – observable as characteristic changes in the way that memories are recalled over time (Sekeres et al., 2016; St-Laurent et al., 2014). As such, they are ideally suited for investigating corresponding transformations at the neural level, allowing us to untangle the interactions of time, memory quality, and congruence with prior knowledge.

Thus, the primary goals of this study were to investigate how congruence with prior knowledge affects neural activation during encoding and retrieval of complex narrative event memories, and to characterize how these effects evolve over the week following encoding. To these ends, we utilized film clips that varied with respect to congruence with prior knowledge, while measuring behaviour as well as neural activity across encoding, immediate retrieval, and delayed retrieval. Congruence was operationalized as the extent to which the story depicted in each clip reflected a typical sequence of events that participants might encounter in everyday life or in media (movies, television, books, etc.). Participants were shown 40 short narrative film clips during their first session in the magnetic resonance imaging (MRI) scanner, then were asked to recall half of the clips during an immediate retrieval session, followed by a second MRI session 7 days later during which they were asked to recall the other half of the film clips.

We hypothesized that event congruence would affect activity and connectivity across the brain at all time points, with increasing congruence between events and prior knowledge correlated with mPFC activity and incongruence correlated with activity in the MTLs, as hypothesized in van Kesteren et al.'s (2012) SLIMM model (schema-linked interactions between medial prefrontal and medial temporal regions). Furthermore, we hypothesized that the encoding of incongruent clips would be associated with greater mPFC-MTL functional connectivity, due to the greater integration demands in more incongruent events. We also expected to find greater MTL activation during the delayed-retrieval of incongruent events, compared with the delayed-retrieval of congruent events.

2. Materials and methods

2.1. Participants

Twenty healthy, right-handed participants (12 female; mean age = 24.1, SD = 2.8), were recruited through the participant database at Baycrest Hospital. Participants were fluent in English, and screened using a detailed health questionnaire to exclude psychiatric or neurological disorders, previous head injuries, or other health problems and/
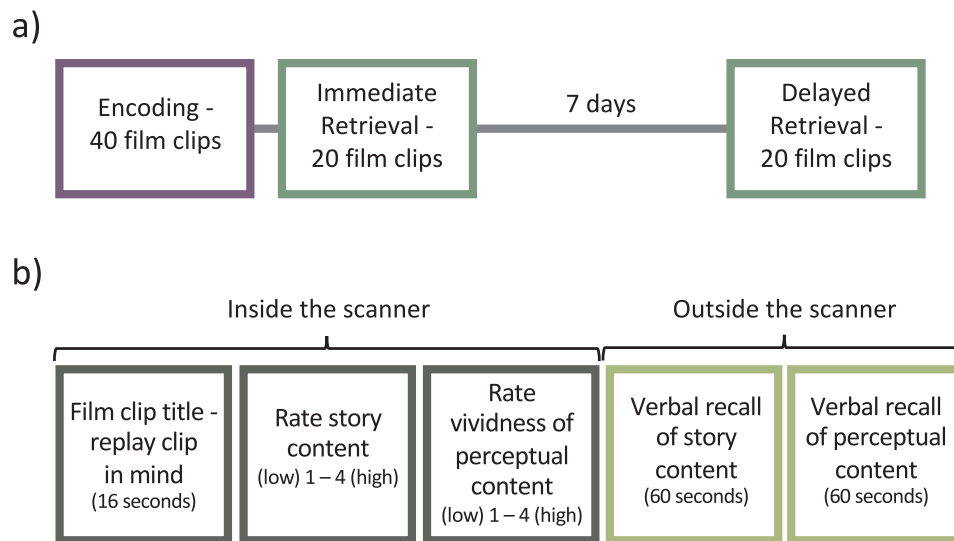
a)

| Encoding - 40 film clips | Immediate Retrieval - 20 film clips | 7 days | Delayed Retrieval - 20 film clips |

b)

Inside the scanner　　　　　　　Outside the scanner

| Film clip title - replay clip in mind (16 seconds) | Rate story content (low) 1 – 4 (high) | Rate vividness of perceptual content (low) 1 – 4 (high) | Verbal recall of story content (60 seconds) | Verbal recall of perceptual content (60 seconds) |

Fig. 1. Experimental Procedure. (a) General outline of encoding and retrieval. (b) Retrieval procedure. Immediate and delayed sessions each tested half of the encoded film clips, with the in-scanner retrieval of 20 clips followed by the post-scan retrieval procedure for those same 20 clips.

or medications that might affect cognitive function and brain activity, including strokes and cardiovascular disease. All procedures were approved by Baycrest's Research Ethics Board. All participants gave written informed consent, and were reimbursed $100 for their participation.

2.2. Stimuli

Forty film clips from St-Laurent et al. (2014) were used to test episodic memory. Film clip stimuli capture the dynamic narrative structure of real-world events, within a spatial-temporal context, while retaining the reproducibility and controlled nature of more traditional laboratory stimuli (Furman, Dorfman, Hasson, Davachi, & Dudai, 2007). All clips were 23 s in duration, taken from foreign films with limited or no dialogue, and have been used in other studies (Sekeres et al., 2016; St-Laurent et al., 2014). Each clip was analyzed for its content based on: visual complexity (includes ratings of background complexity, colour, movement, number of frame transitions, number of background characters), sound complexity (ratings of speech, music, background noise), story complexity (number of central characters, storyline complexity), and emotional content (degree of humour, sadness, cuteness, weirdness, and surprise). Three scorers (M.S., K.B., M.S-L.) independently rated each clip on each feature, assigning a score between 1 and 5, or a yes/no rating. Mean correlations between the three scorers were r = 0.79, r = 0.83, and r = 0.78. Composite scores for each feature category were averaged and transformed to z-scores. Each clip's z-scores were used to divide the 40 clips into two series of 20 clips, balanced across the feature categories. For each participant, each of the two series were tested at one of the retrieval delays – either immediately or seven days after encoding. The order of series tested at each delay was counterbalanced across participants.

Clips were also rated with respect to congruence with prior knowledge/experiences by sixteen independent participants (10 female; mean age = 25.6, SD = 3.1). Participants watched each clip, and then rated the clip's story/events on a scale of 1 (very typical) – 5 (very atypical). Typical stories were defined as 'similar to an event you would normally encounter in day to day life', and thus were congruent with participant's prior knowledge/experiences. Atypical stories were defined as 'very unusual and/or dissimilar to anything you would encounter in day to day life'. The raters were instructed that 'encountering' included not only experiences in one's own life, but also events experienced through books, movies, television, or other media. Ratings were consistent across participants (Cronbach alpha = 0.93),

with final congruence values determined by averaging across all participants, resulting in a continuous variable. Since the emotional content score that was used to counter-balance clips across different delays included ratings of 'surprise' and 'weirdness', and since clips that are incongruent with prior knowledge are, by definition, more surprising or weird, we also asked raters to assess emotional arousal. Raters assigned each clip a rating on a 9-point Likert scale ranging from 1 (calming, low arousal) to 9 (exciting, high arousal), and these ratings were converted to z-scores. Congruence ratings were not significantly correlated with either visual complexity (r = 0.18, p = 0.26), sound complexity (r = −0.22, p = 0.18), story complexity (r = 0.01, p = 0.94), or with these ratings of emotional arousal (r = 0.26, p = 0.11), see Fig. S1.

Neuroimaging analyses included all forty clips, each associated with its specific congruence rating, with additional analyses directly contrasting a group of the ten most congruent clips with a group of the ten most incongruent clips. For behavioural analyses, neutral clips (the ten clips with ratings in the centre of the scale) were also analyzed in order to provide a benchmark against which to test the effects on memory of both congruence and incongruence with prior knowledge. See Table S1 for a list of clips with their associated congruence ratings.

2.3. Experimental procedure

Encoding and retrieval sessions took place in the MRI scanner, while verbal recall sessions took place outside the scanner (Fig. 1). Participants encoded all forty film clips on the first day, followed by an immediate retrieval session (for 20 clips). Seven days later, participants returned to the MRI scanner for a delayed retrieval session (for the remaining 20 clips). Participants were instructed that this was a memory experiment and that they should pay attention to the title and content of each clip. They were also informed that they would be tested on their memory for half of the clips shortly after encoding, while their memory for the other half of the clips would be tested one week later. Participants performed a practice session outside of the scanner prior to beginning the study.

2.4. Encoding

During encoding the forty film clips were presented in randomized order. Each clip was given a title (e.g., "Boy, Girl and Balloon") that served as a cue in the retrieval portions of the experiment. The title appeared centrally on the screen for 4000 ms immediately before and after the clip. Clips were presented centrally on the screen with sound

delivered through a rimless Avotech headset. A fixation cross was presented for 4000 ms between each clip. Encoding was performed across four runs in the scanner, with 10 clips presented in each run.

2.5. Retrieval

As described above, one set of 20 clips was retrieved immediately after the encoding session, and the other set of 20 clips was retrieved after a 7d delay, with the retrieval order of sets counterbalanced across participants. In each retrieval session there were two runs of 10 clips each, with 2–3 of the most congruent and 2–3 of the most incongruent clips per run. For each in-scanner retrieval trial, participants were presented with the title of a clip centrally presented on the screen for a duration of 16000 ms, during which time they were instructed to re-experience the clip (visual and audio replay) in their mind from beginning to end. This timing was chosen based on pilot testing to determine the length of time participants required to replay the film clips in their minds (St-Laurent et al., 2014). In replaying these clip memories there seems to be some compression of time, as has been reported in replaying previously traveled routes in one's mind (Bonasia, Blommesteyn, & Moscovitch, 2016) and in recalling real-life events (Jeunehomme, Folville, Stawarczyk, van der Linden, & D'Argembeau, 2017) or events viewed in an episode of a television program (Chen et al., 2017). Next, they used a keypad to rate how well they had recalled the clip's story content, on a scale of 1–4. Story content referred to the general plot of the story and events central to the progression of the episode (Sekeres et al., 2016; Berntsen, 2002). A rating of '1' indicated recall of no story content, while a rating of '4' indicated participants believed that their memory contained all of the story elements. Next, participants rated the vividness of their memory's perceptual content (visual and auditory details) in a similar way. A rating of '1' indicated retrieval of no perceptual content, while a rating of '4' indicated a maximal level of vividness in perceptual content. Each clip's retrieval was separated by a 4000 ms fixation cross.

2.6. Post-scan retrieval

After each in-scanner retrieval session participants exited the scanner and completed the post-scan retrieval session in another room. Participants were presented with the title of each clip they had just retrieved in the MRI session, and were asked to verbally report the story and perceptual details they had recalled while in the scanner. The presentation order of clips was randomized within each retrieval and verbal recall session.

2.7. Scoring and behavioural analyses

Since in-scanner ratings of '1' indicated retrieval of no story or perceptual content, clips were classified as forgotten when participants provided ratings of '1' for both story and perceptual content. Ratings of story and perceptual content were highly correlated ($r = 0.79$, $p < 0.001$ for immediate retrieval; $r = 0.78$, $p < 0.001$ for 7d retrieval).

With respect to verbal free recall, two recordings were obtained for each clip to encourage participants to report everything they recalled about a clip's storyline and perceptual content. The recordings of verbal responses were transcribed, then recalled details were scored and tallied by a scorer blind to the delay and congruence rating of each clip. No points were assigned for repeated details or for unrelated information (i.e. opinions or speculations). Errors were also scored and tallied. Errors were considered to be any details that did not match the information presented in the clip. Participants were not penalized for failing to recall a detail. Thus, all analyzed errors are errors of commission, rather than errors of omission. See Sekeres, Anderson, Winocur, Moscovitch, and Grady (2016) for an alternate analysis of these data that differentiates between details that are central to the

progression of each episode and peripheral details that contribute to the 'richness' of each memory.

Behavioural data consisting of in-scanner ratings, numbers of details, and numbers of errors were averaged across groups of clips (congruent, neutral, incongruent) for each participant, at each delay. All analyses of behavioural data were conducted as repeated measures ANOVAs using R software. Significant effects were investigated using planned comparisons t-tests when they were consistent with *a priori* hypotheses, and post-hoc Tukey Honest Significant Difference (HSD) tests otherwise, to maintain the family wise error rate (FWE) at $p < 0.05$. One participant's verbal recall data from the 7d retrieval session were lost due to a software malfunction.

2.8. fMRI data acquisition

Anatomical and functional images were acquired with a 3 T Siemens TIM Trio MRI scanner and standard 32-channel array head coil at Baycrest Hospital. For the anatomical scans, a T1-weighted volumetric anatomical MRI (160 axial slices, TE = 2.63 ms, 1 mm thick, FOV = 256 cm) was acquired for each participant. The functional scans included thirty-six axial slices (3.5 mm thick, skip 0.5 mm), using a T2*-weighted pulse sequence with an echoplanar imaging (EPI) readout (TR = 2200 ms, TE = 27 ms, FOV = 225 mm, 96 × 96 matrix). Slices were obtained from an axial-oblique orientation, parallel to the Sylvian fissure.

2.9. fMRI data preprocessing

All pre-processing and statistical analyses described below were carried out using FSL. The data were skull stripped using the Brain Extraction Tool, high-pass filtered at 100 s, and motion corrected using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002). The data were spatially smoothed with a 6.0 mm full-width-at-half-maximum Gaussian kernel. Registration was carried out using FLIRT (Jenkinson et al., 2002; Jenkinson and Smith, 2001). Individual participants' functional data were first registered to their anatomical data using normal linear search and Boundary Based Registration. These data were then registered to MNI standard space (MNI 152 template) with a 2 × 2 × 2 mm voxel size using normal non-linear search with 12 degrees of freedom in FNIRT (Andersson, Jenkinson, & Smith, 2010). Encoding trials were modelled as 23 s blocks (the time that the film clips were being played), while retrieval trials were modelled as 16 s blocks, spanning the time that participants were replaying events in their mind's eye.

2.10. fMRI data analyses

In order to be included in analyses, each participant must have recalled at least 50% of the congruent and incongruent clips in each scanner retrieval session (min recalled = 5/10, max recalled = 10/10), and must have retrieved at least one congruent and one incongruent clip in each of the four retrieval runs. Three participants were excluded from fMRI analyses due to an insufficient number of clips recalled.

Across all analyses described below, statistical processing was carried out in three steps, using FEAT (fMRI Expert Analysis Tool, version 6.0). First, a general linear model (GLM) was applied at the level of each individual run. The specific explanatory variables (EV), used in each GLM will be described with their corresponding analyses. Each EV was convolved with a double-gamma HRF, included a temporal derivative, and had temporal filtering. The initial results for each individual run were thresholded at $z > 5.3$, then passed up to fixed effects analyses at the participant level, with each participant's results then passed up to a final mixed effects analysis at the group level (FMRIB's Local Analysis of Mixed Effects; FLAME 1). Group level analyses were thresholded at $z > 2.3$ across all voxels, then cluster corrected to maintain FWE at $p < 0.05$. This general procedure was carried out for three different types of analyses: parametric analyses using all 40 clips (each

clip associated with a specific congruence rating); seed-based functional connectivity analyses; and a direct contrast analysis comparing MTL activation for the ten most congruent and ten most incongruent clips.

All analyses described below include only subsequently remembered film clips, with forgotten clips modelled as 'null' events. Additional encoding analyses were conducted including all clips, whether subsequently remembered or forgotten. This analysis produced qualitatively equivalent results, such that clip perception demonstrated the same correlations between event congruence and patterns of neural activity, irrespective of subsequent memory. Analysis of 'forgotten' clips at retrieval was not carried out since participants had not recalled any relevant information during these time periods or engaged in any consistent cognitive task.

2.11. Parametric analyses

Parametric analyses were conducted to determine whether there were patterns of neural activation predicted by film clip congruence ratings, such that activation increased with either increasing or decreasing congruence of events with prior knowledge. In this GLM, all clips were given equal weight in the first EV, to characterize mean activity associated with encoding/recall. All clips were also included in a second EV, but in this case each clip was associated with a rating between 1 (most congruent) and 5 (most incongruent) in order to model the activity correlated with increasing/decreasing congruence. EV2 was orthogonalized with respect to EV1 to control for mean activation across all film clips, allowing us to isolate activation related to event congruence. Null events were included in a third EV. The second level (within participant) GLM included three EVs: encoding, immediate retrieval, and 7d retrieval. The third level (across participant) GLM included a single EV modeling the group mean.

2.12. Functional connectivity analyses

Whole-brain functional connectivity of the mPFC and MTL was explored during encoding and retrieval using the psychophysiological interaction (PPI) method implemented in FSL (O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012). The mPFC and MTL peaks from the encoding parametric analyses were used to investigate functional connectivity (mPFC: [−2, 56, 6]; MTL: [24, −38, −14]). The MTL peak, found in the right parahippocampal cortex but associated with activation that spread into the hippocampus, was identified as a local MTL maximum from within a large cluster peaking in the lateral occipital cortex.

The following general procedure was conducted for a PPI analysis at each time-point (encoding, immediate retrieval, 7d retrieval). (a) A spherical seed was created with a radius of 6 mm centred on either the mPFC or MTL peak. (b) This generic seed was then transformed into each subject's native space using the reverse transformation matrix from registration. (c) The time course of activity within each seed was extracted for each of the relevant runs, for each participant. (d) This time course was included in a GLM with five EVs. The first EV included all film clips, each associated with their specific congruence rating, while the second EV consisted of the relevant peak's time course. The third EV modelled the PPI, and was constructed from the interaction of EV1 and EV2 (zero centred and mean centred, respectively). The fourth EV included all clips (without congruence ratings) in order to model mean encoding activity, while the fifth EV modelled null events.

2.13. MTL region of interest (ROI) analysis

To test our hypothesis that congruent events would be associated with attenuated MTL activity at delayed retrieval, we conducted an analysis directly contrasting MTL activation during retrieval of the ten most congruent, and ten most incongruent, film clips. The MTL ROI was created using FSL's Harvard-Oxford cortical and subcortical

structural atlases, including hippocampal, parahippocampal, entorhinal, and perirhinal cortices on both the left and right side (Fig. S2). The ROI was applied before thresholding at the final (third) level of analysis in a GLM contrasting (congruent clips > incongruent clips) and vice versa. The GLM for the first level analysis in this case included four EVs modelling the activity associated with congruent clips, incongruent clips, neutral clips, and null events, respectively. As above, the second level analysis included three EVs: encoding, immediate retrieval, and 7d retrieval. The third level analysis included a single EV modelling the group mean. Note that, although neutral clips were included as a separate EV, our contrast of interest was between congruent and incongruent clips.

2.14. Subsequent memory analysis

Lastly, we tested the hypothesis that MTL activity at encoding would be predictive of subsequent memory for both congruent and incongruent clips. To test this hypothesis we used the right parahippocampal peak found in encoding analyses [24, −38, −14] with a 6 mm radius; this is the same seed that was used for functional connectivity analyses. We extracted activation within the seed during encoding (encoding > fixation), for congruent and incongruent clips separately. We then calculated the Pearson correlation coefficient between MTL encoding activation for each participant and the number of clips subsequently recalled by that participant. A one-tailed significance test was conducted due to the directionality of our hypothesis. One outlier was removed from the correlation due to that person's activity change being more than two standard deviations below the mean (MTL activity change for congruent clips = −0.11; both sets of results reported).

3. Results

3.1. Behavioural results

3.1.1. Both congruence with prior knowledge and incongruence enhance memory for film clips, although incongruent events are recalled with more errors over time

In order to test the effects of congruence with prior knowledge on memory for film clip events, we conducted a 3 × 2 repeated measures ANOVA with congruence (congruent, neutral, incongruent) and retrieval time (immediate, 7d) as independent variables, with number of clips forgotten as the dependent variable. There was no main effect of congruence ($F_{(2, 38)}$ = 2.20, p = 0.13), but a significant main effect of time ($F_{(1, 19)}$ = 66.40, p < 0.001) such that more clips were forgotten at 7d retrieval. There was also a significant interaction of congruence with time ($F_{(2, 38)}$ = 5.15, p = 0.01). Planned comparison t-tests revealed that at 7d retrieval, neutral clips were forgotten at a significantly higher rate than congruent clips ($t_{(19)}$ = 2.77, p = 0.01, cohen's d = 0.68) and at a marginally higher rate than incongruent clips ($t_{(19)}$ = 1.93, p = 0.07, cohen's d = 0.55) (Fig. 2a). Rates of forgetting for congruent and incongruent clips were equivalent ($t_{(19)}$ = 0.40, p = 0.69). No significant differences existed at immediate retrieval (all p's > 0.11). All subsequent analyses include only successfully remembered clips.

Next we investigated whether or not congruence affected the number of details correctly recalled for each clip. We conducted a 3 × 2 repeated measures ANOVA with congruence (congruent, neutral, incongruent) and retrieval time (immediate, 7d) as independent variables, and number of correctly recalled details as the dependent variable. There was a significant main effect of time ($F_{(1, 18)}$ = 40.81, p < 0.001) such that fewer details were recalled at 7d retrieval, but no significant main effect of congruence ($F_{(2, 36)}$ = 1.34, p = 0.27), and no significant interactions (all p's > 0.12) (Fig. 2b).

Our main hypothesis with respect to verbal recall focused on errors, since a prominent effect of prior knowledge is to distort memory for
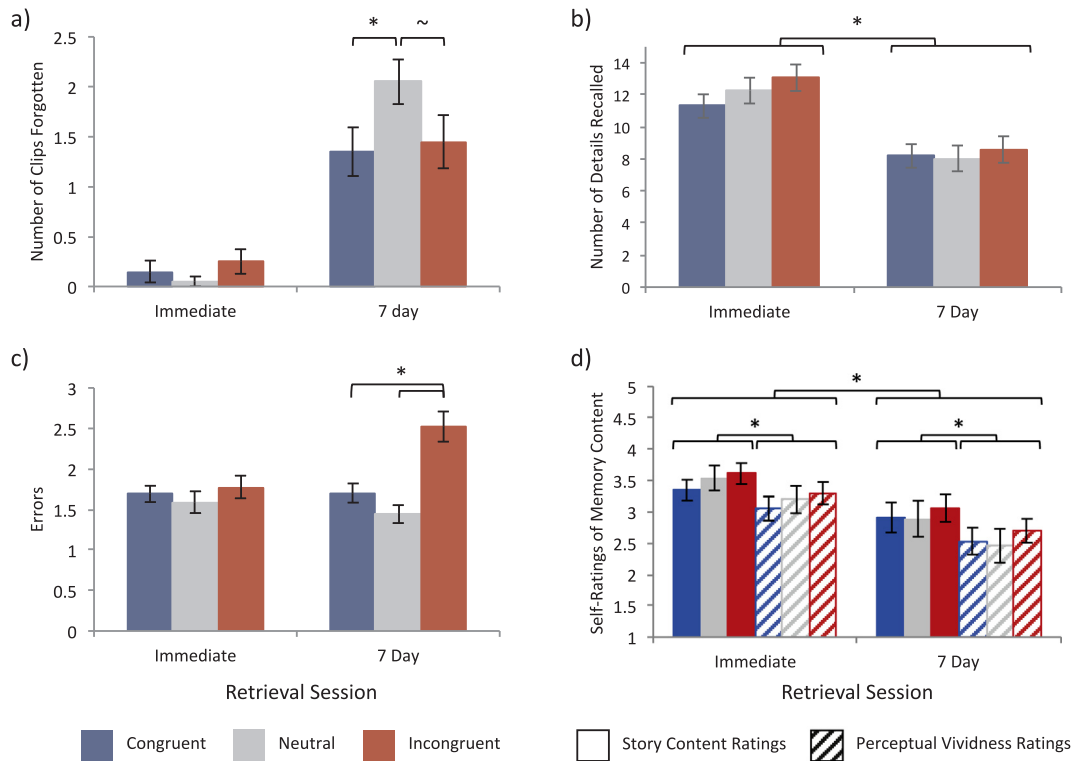
Fig. 2. Behavioural Retrieval Results. All results are categorized based on the congruence of film clip events with prior knowledge. (a) Mean number of clips forgotten at immediate and 7-day retrieval sessions. (b) Mean number of details correctly recalled during immediate and 7-day verbal retrieval sessions. (c) Mean number of errors made during immediate and 7-day verbal retrieval sessions. (d) Mean self-ratings of memory (ratings of story content recalled and ratings of perceptual vividness of memory) for immediate and 7-day retrieval. Error bars represent the standard error of the mean. ($^{~}$p < 0.10, *p < 0.05).

incongruent information. The mean number of errors made by participants at immediate retrieval was 1.69 SD = 0.94. The mean number of errors made by participants at delayed retrieval was 1.89 SD = 1.00. To investigate errors, we conducted a 3 × 2 repeated measures ANOVA with congruence (congruent, neutral, incongruent) and retrieval time (immediate, 7d) as independent variables and number of errors per clip as the dependent variable. This analysis revealed a significant main effect of congruence (F(2, 36) = 5.80, p = 0.007), no significant main effect of time (F(1, 18) = 0.52, p = 0.48), and a marginal interaction of time with congruence (F(2, 36) = 2.82, p = 0.07). Tukey HSD tests for the congruence main effect revealed that errors for incongruent clips were significantly higher than errors for neutral clips (p_{adj} = 0.01), whereas an equivalent number of errors was made for incongruent and congruent clips (p_{adj} = 0.10) and for congruent and neutral clips (p_{adj} = 0.69), when averaging across both retrieval time-points. Based on our a priori hypothesis that memory for incongruent events in particular would be distorted over time, measured as a greater number of errors made during delayed recall, we investigated the marginal time × congruence interaction. This analysis indicated that the congruence main effect (outlined above) was driven by differences at 7d retrieval, where there were significantly more errors for incongruent clips than for either neutral (t(18) = 2.89, p = 0.01, cohen's d = 0.46) or congruent clips (t(18) = 2.55, p = 0.02, cohen's d = 0.35). An equivalent number of errors was made for congruent and neutral clips at 7d retrieval (t(18) = 1.09, p = 0.29), and equivalent numbers of errors were made for all clips at immediate retrieval (all p's > 0.15) (Fig. 2c).

Last, we investigated whether or not congruence affected self-rated quality of memory (in-scanner ratings). We conducted a 3 × 2 × 2 repeated measures ANOVA with congruence (congruent, neutral, incongruent), retrieval time (immediate, 7d), and rating type (story content, perceptual vividness) as independent variables, and memory rating as the dependent variable. There was a significant main effect of time (F (1,18) = 55.87, p < 0.001) with ratings declining over the week

following encoding, a significant main effect of rating type (F(1, 18) = 59.19, p < 0.001) with higher ratings for story content, and a marginal main effect of congruence (F(2, 36) = 3.16, p = 0.06). There were no significant interactions (all p's > 0.43). The marginal main effect of congruence was not explored further since the magnitudes of the differences are small and unrelated to our hypotheses (Fig. 2d).

3.2. fMRI results

3.2.1. Encoding of congruent events is associated with mPFC activation; encoding of incongruent events is associated with greater MTL activation

Parametric analyses were conducted to determine if the encoding of film clip events was modulated by the congruence of those events with prior knowledge. This analysis included all forty film clips, each clip associated with a specific congruence rating on a continuous scale from most congruent (1) to most incongruent (5). Note that, since our film clips varied continuously on a scale from very congruent to very incongruent, decreasing congruence is equivalent to increasing incongruence/novelty.

As events increased in congruence, activity increased in the mPFC, posterior cingulate cortex, bilateral superior temporal gyri, and the right angular gyrus (Fig. 3a; Table 1a). Conversely, as events decreased in congruence, activity increased in a large cluster that extended into the MTL (parahippocampal cortex and hippocampus), occipital, temporal, and parietal cortices, as well as in smaller bilateral superior frontal gyrus clusters (Fig. 3a; Table 1a). Note that the peak of the posterior cluster is in the lateral occipital cortex, but this large cluster of activation extends through occipital/temporal/parietal cortices and into the MTLs, with the local MTL peak reported due to our specific MTL hypotheses. See Table S2 for a list of other local maxima within this large cluster.
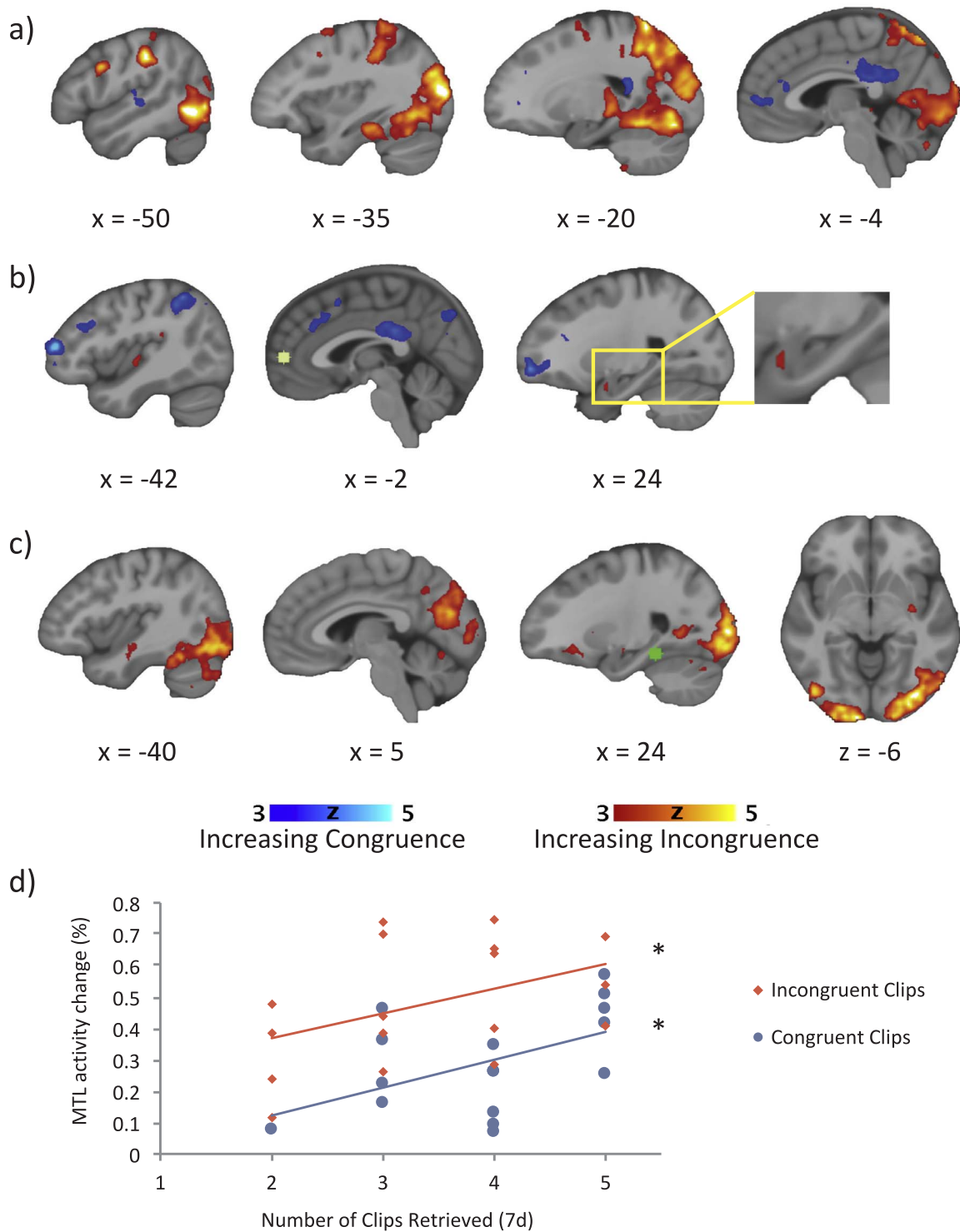
Fig. 3. Encoding Activation. (a) Activation during the encoding of film clip events that correlated either with increasing congruence or incongruence of the events with prior knowledge. (b) mPFC functional connectivity during encoding. Functional connectivity is shown for an mPFC seed (yellow) during encoding of film clip events that vary in congruence with prior knowledge. (c) MTL functional connectivity during encoding. Functional connectivity is shown for an MTL seed (green) during encoding of film clip events that vary in congruence with prior knowledge. Note that there were no significant MTL functional connectivity results for increasing congruence. (d) MTL activity at encoding and subsequent memory 7 days later. Each data point represents a single participant's MTL activity during the encoding of either congruent or incongruent film clip events (encoding > fixation), plotted against their mean number of events successfully recalled at 7d retrieval for that type of clip. Note that, out of the 10 most congruent and 10 most incongruent clips encoded by each participant, 5 are tested at each retrieval delay, resulting in a maximum of 5 clips retrieved in each category. (*p < 0.05) For fMRI figures, cool colours indicate areas whose activity increased with increasing congruence between film clip events and prior knowledge, while warm colours indicate areas whose activity increased with increasing incongruence. Colour intensity corresponds to the z-value of each voxel's activation. See Supplementary Fig. 4a and Table 3a for mean encoding results, averaging across all clips irrespective of congruence with prior knowledge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Encoding cluster peaks. All cluster statistics represent the results of parametric analyses at encoding, including all 40 film clips, each associated with a specific congruency rating. (a) Cluster peaks from parametric analyses at encoding where regional activity increased either with increasing or decreasing congruence of film clip events. Note that the lateral occipital cortex cluster seen with increasing incongruence extended into the parahippocampal and hippocampal cortices, thus the local peak within the MTL is listed below (see Table S2 for other local maxima within this cluster). (b) Cluster peaks from functional connectivity analyses using an mPFC seed [−2, 56, 6]. Names refer to brain regions whose functional connectivity to the mPFC increased either with increasing congruence or with increasing incongruence. (c) Cluster peaks from functional connectivity analyses using an MTL seed [24,−38,−14] (right parahippocampal cortex). Names refer to brain regions whose functional connectivity to the right parahippocampal cortex increased either with increasing congruence or with increasing incongruence.

Brain region	X (mm)	Y (mm)	Z (mm)	z-score	Cluster size (voxels)
(a) Parametric analyses					
Increasing congruence					
mPFC	−2	56	6	3.9	3253
R precuneus/posterior cingulate cortex	18	−40	20	4.6	3057
L superior temporal gyrus	−64	−26	4	4.3	1238
R superior temporal gyrus	60	−26	2	3.5	806
R angular gyrus	48	−56	50	3.9	667
Increasing Incongruence					
L lateral occipital cortex	−28	−84	20	6.1	48,484
MTL peak: R parahippocampal cortex	24	−38	−14		
L superior frontal gyrus	−28	0	66	4.5	1233
R superior frontal gyrus	22	0	60	4.2	989
L cerebellum	−14	−46	−52	4.8	613
(b) mPFC Functional Connectivity					
Increasing Congruence					
Posterior cingulate cortex	2	−26	34	4.2	1412
L supramarginal gyrus	−38	−46	44	4.4	5888
R insula	40	16	−4	4.4	5055
L dorsolateral prefrontal cortex	−34	58	16	5.0	3620
L cerebellum	−28	−66	−38	3.7	946
Increasing Incongruence					
R entorhinal cortex	24	0	−22	3.3	536
L insula	−42	−12	−2	3.4	498
(c) MTL Functional Connectivity					
Increasing Congruence					
–					
Increasing Incongruence					
L occipital pole	−14	−104	4	5.6	96,187

3.2.2. mPFC and MTL functional connectivity during encoding is modulated by the congruence of events with prior knowledge

The mPFC peak from the previous parametric results was taken as a seed for PPI analyses to investigate functional connectivity during encoding. These analyses revealed that, as the congruence of an event with prior knowledge increased, the mPFC was increasingly functionally connected with the posterior cingulate cortex, supramarginal gyrus, right insula, dorsolateral prefrontal cortex, and cerebellum. This same peak showed a very different pattern of connectivity when events were increasingly novel/incongruent with prior knowledge. In that case, the mPFC showed greater functional connectivity with the right entorhinal cortex (MTL area) and left insula. The entorhinal cortex cluster extended into the amygdala, indicating that incongruence may also be associated with increased mPFC-amygdala functional connectivity. We focus on MTL connectivity, however, since the peak is in the entorhinal cortex. Although mPFC-amygdala connectivity may be related to incongruent clips being inherently more surprising or weird, congruence ratings were not significantly correlated with emotional arousal, suggesting that the neural differences correlated with congruence across this study are unlikely to be driven by differences in

emotional arousal. See Fig. 3b for a visualization of all mPFC functional connectivity and Table 1b for a list of clusters that were functionally connected with the mPFC in either condition.

The local MTL peak from the parametric analyses, in the right parahippocampal cortex, was used as a seed to investigate MTL functional connectivity during encoding. In this case, we found no significant functional connectivity for increasing congruence. Incongruence, however, was correlated with increasing functional connectivity from the MTL seed to areas throughout the ventral visual stream and occipital cortex (peak in the left occipital pole; see Fig. 3c and Table 1c). Thus, the perception and encoding of increasingly incongruent events seems to be associated not only with increased activity in sensory areas (shown in parametric analyses above), but also with increased functional connectivity between these areas and the parahippocampal cortex. We conducted supplementary analyses to test for functional connectivity between the MTL seed and areas within an mPFC region of interest during encoding of incongruent events, to confirm the mPFC-MTL functional connectivity found above. Consistent with mPFC-seed results, we found increasing MTL-mPFC functional connectivity correlated with increasing incongruence, and no significant functional connectivity for increasing congruence (Fig. S3, Table S3d).

3.2.3. MTL activation at encoding is correlated with subsequent memory

To investigate the relationship between MTL activity at encoding and subsequent memory in this study, we assessed the correlation between activity in the MTL peak from parametric analyses (parahippocampal cortex; also used as the seed for functional connectivity analyses) and the number of congruent and incongruent film clips successfully recalled at 7d retrieval. Note that not enough film clips were forgotten at immediate retrieval (mean = 0.1 clips forgotten per participant) to conduct meaningful correlation analyses at that time point. For incongruent film clips, there was a positive correlation between MTL activity at encoding and subsequent memory one week later (r = 0.43, p = 0.04). The relationship was in the same direction for congruent clips, and is significant when a single outlier (activation more than 2 SDs below the mean) is removed (all data: r = 0.27, p = 0.14; without outlier: r = 0.51, p = 0.02). See Fig. 3d.

3.2.4. mPFC and MTL functional connectivity during retrieval is modulated by the congruence of events with prior knowledge

Parametric analyses did not reveal any brain regions whose overall activity during retrieval was directly correlated with increasing/decreasing congruence of events, but functional connectivity of both the mPFC and MTL was modulated by the congruence of events with prior knowledge. During immediate retrieval, increasing congruence between events and prior knowledge was correlated with increasing functional connectivity between the mPFC and the bilateral middle frontal gyri, posterior cingulate and paracingulate cortices, angular gyrus, intraparietal sulcus, and fusiform and occipital cortices. Incongruence, on the other hand, was correlated with increasing functional connectivity between this mPFC seed and the dorsomedial prefrontal cortex, precuneus, lateral occipital cortex and anterior temporal lobe (Fig. 4a). As was seen during encoding, increasing incongruence of events during immediate retrieval was correlated with enhanced functional connectivity between the MTL and the mPFC and occipital cortex, whereas no significant MTL functional connectivity emerged with increasing congruence between events and prior knowledge (Fig. 4b). See Table 2a for a list of clusters that were functionally connected with either the mPFC or MTL during immediate retrieval.

One week later, both the mPFC and MTL demonstrated different patterns of functional connectivity, however both were still modulated by the congruence of events with prior knowledge. Specifically, increasing congruence was correlated with increasing functional connectivity between the mPFC and bilateral middle frontal gyri, supramarginal gyrus, fusiform cortex, frontal operculum, and caudate. The
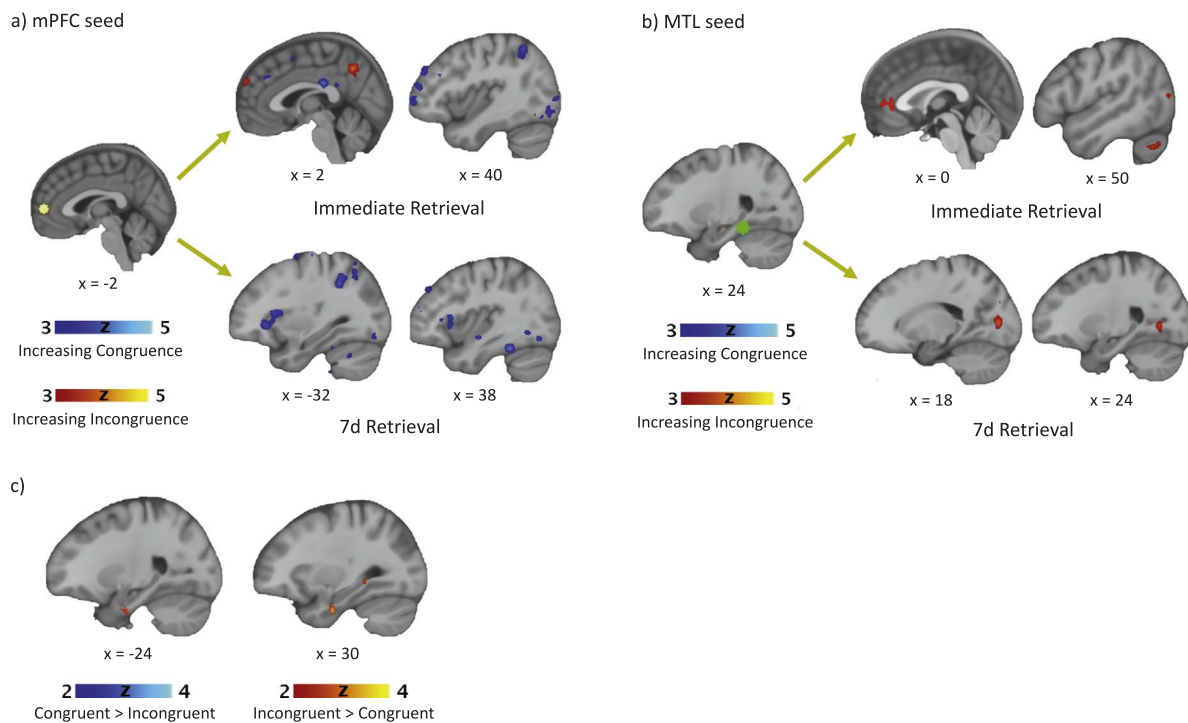
Fig. 4. Retrieval Activation. (a) mPFC functional connectivity during retrieval. Functional connectivity is shown for an mPFC seed (yellow) during immediate and 7d-delayed retrieval of film clip events. Cool colours indicate areas whose functional connectivity with the mPFC during retrieval increased with increasing congruence between the event being recalled and prior knowledge. Warm colours indicate areas whose functional connectivity with the mPFC during retrieval increased with increasing incongruence between the event being recalled and prior knowledge. Note that there was no significant mPFC functional connectivity associated with incongruence during the 7d-delayed retrieval session. (b) MTL functional connectivity during retrieval. Functional connectivity is shown for an MTL seed (green) during immediate and 7d-delayed retrieval of film clip events. Warm colours indicate areas whose functional connectivity with the MTL during retrieval increased with increasing event incongruency. Note that there was no significant MTL functional connectivity associated with retrieving congruent events, at either time-point. (c) MTL ROI analysis of activation during the 7d-delayed retrieval of incongruent vs. congruent clips. Voxels are thresholded at p < 0.005 uncorrected within the MTL ROI as explained in results ($2 < z < 4$ in figure). Note that no significant activation was found for the contrast (congruent > incongruent), nor for either contrast at immediate retrieval. For fMRI figures, colour intensity corresponds to the z-value of each voxel's activation. See Supplementary Fig. 4b and Table 3b, c for mean retrieval results, averaging across all clips irrespective of congruence with prior knowledge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mPFC demonstrated no significant functional connectivity correlated with incongruence (Fig. 4a). Conversely, the MTL seed demonstrated no significant functional connectivity correlated with congruence between events and prior knowledge. Instead, significant MTL-lingual gyrus functional connectivity was correlated with the retrieval of incongruent events (Fig. 4b). Thus, by one-week after encoding, the mPFC and MTL each showed patterns of functional connectivity for only congruent *or* incongruent events, respectively. See Table 2b for the list of clusters that were functionally connected with either the mPFC or the MTL during 7d retrieval.

3.2.5. Incongruent clips are associated with greater MTL activation during 7d retrieval

We next conducted direct contrast analyses within an MTL ROI to test the hypothesis that MTL activation would be equivalent during the retrieval of congruent and incongruent clips shortly after encoding, but that the retrieval of congruent clips would be associated with less MTL activation than incongruent clips at delayed retrieval. The results from our ROI analysis comparing the retrieval of the ten most congruent clips with the retrieval of the ten most incongruent clips were consistent with this hypothesis. Although there were no significant MTL differences based on congruence at immediate retrieval, bilateral MTL clusters showed significantly more activation during the 7d-retrieval of incongruent (vs. congruent) events (Fig. 4c). In particular, the recall of incongruent events was associated with greater activity in the bilateral entorhinal cortices, as well as in a small right posterior hippocampal cluster (Table 2c). These results should be interpreted cautiously since they were thresholded at p < 0.005 uncorrected. We report them here since the analysis was strongly motivated by evidence from the rodent

literature suggesting that, at remote time points, schema-consistent (congruent) memories are less dependent on the MTLs for retrieval than memories for schema-inconsistent items (Tse et al., 2007). To our knowledge, this is the first time that this effect has been shown for narrative event memories in humans. There were no MTL clusters that were more active during the retrieval of congruent > incongruent clips at either time point. There were also no differences at either retrieval time-point when testing within an mPFC ROI.

4. Discussion

The primary objective of this study was to further our understanding of neural activation underlying the encoding and retrieval of events that vary with respect to their congruence with prior knowledge, and to characterize how the effects of congruence evolve over time. Using dynamic narrative film clip stimuli, we demonstrate that both congruence and incongruence/novelty enhance memory for events, but that incongruent events are recalled with more errors over time. As hypothesized, the encoding of increasingly congruent events was correlated with increasing activation in the mPFC, while increasing incongruence was correlated with activation in the MTL, occipital lobes and ventral visual stream.

Functional connectivity of both the mPFC and MTL was modulated by congruence with prior knowledge, across encoding and retrieval at both time-points. In particular, increasing congruence was associated with greater mPFC-inferior parietal lobule functional connectivity at all time-points, greater mPFC-posterior cingulate cortex functional connectivity during encoding and immediate retrieval, and greater mPFC-middle frontal gyrus functional connectivity during both retrieval

Table 2

Retrieval cluster peaks. (a) Cluster peaks from functional connectivity analyses at immediate retrieval using an mPFC seed [−2, 56, 6] and an MTL seed [24, –38, –14] (right parahippocampal cortex). Names refer to brain regions whose functional connectivity to either the mPFC or the MTL increased either with increasing congruence or with increasing incongruence. (b) Cluster peaks from functional connectivity analyses at 7d-delayed retrieval using the same mPFC and MTL seeds. Names refer to brain regions whose functional connectivity to either the mPFC or the MTL increased either with increasing congruence or with increasing incongruence. (c) Cluster peaks from a direct contrast of activation during 7d-delayed retrieval, comparing the 10 clips most congruent with prior knowledge with the 10 most incongruent clips ([congruent > incongruent] and [incongruent > congruent]). An MTL ROI was applied before thresholding at p < 0.005 uncorrected.

Brain region	X (mm)	Y (mm)	Z (mm)	z-score	Cluster size (voxels)
(a) Immediate Retrieval – Functional Connectivity					
mPFC seed - Increasing Congruence					
Right middle frontal gyrus	46	48	16	3.8	2602
Left fusiform gyrus	−36	−72	−12	3.9	2073
Right occipital pole	36	−90	6	3.9	1516
Left precentral gyrus	−40	−12	64	3.8	1237
Right angular gyrus	40	−54	54	3.9	1122
Right paracingulate gyrus	10	26	42	3.5	695
Left intraparietal sulcus	−32	−54	46	3.7	591
Posterior cingulate cortex	0	−26	28	4.2	484
Left middle frontal gyrus	−40	6	32	4.0	470
Left middle frontal gyrus	−38	30	22	3.7	352
mPFC seed – Increasing Incongruence					
Right anterior temporal lobe	58	6	−28	3.5	472
Right dorsomedial prefrontal cortex	6	60	30	3.7	461
Left lateral occipital cortex	−44	−66	28	3.5	373
Right precuneus	4	−58	44	4.1	352
MTL seed – Increasing Congruence					
–					
MTL seed – Increasing Incongruence					
mPFC	0	38	6	3.3	656
Right cerebellum	50	−62	−36	3.5	437
Right lateral occipital cortex	50	−76	10	3.2	342
(b) 7d Retrieval – Functional Connectivity					
mPFC seed – Increasing Congruence					
Right fusiform cortex	38	−42	−22	4.2	19,567
Left supramarginal gyrus	−32	−46	38	3.9	3354
Right frontal operculum	36	20	12	3.7	1364
Right middle frontal gyrus	28	42	24	3.6	672
Right middle frontal gyrus	32	0	68	3.6	639
Left superior frontal gyrus	−22	−2	56	4.0	598
Right caudate	16	−2	20	3.4	466
mPFC seed – Increasing Incongruence					
–					
MTL seed – Increasing Congruence					
–					
MTL seed Increasing Incongruence					
Lingual gyrus	18	−80	8	4.0	1781
(c) Direct Contrast Analysis					
Congruent > Incongruent					
–					
Incongruent > Congruent					
R entorhinal cortex	30	−8	−30	3.3	22
L entorhinal cortex	−24	−10	−34	2.8	9
R hippocampus	32	−40	−4	2.7	6

sessions. Decreasing congruence between events and prior knowledge, on the other hand, was correlated with functional connectivity between the parahippocampal cortex and posterior sensory cortices at all time points, as well as mPFC-MTL functional connectivity during encoding and immediate retrieval. Lastly, congruent and incongruent events demonstrated equivalent MTL activation at immediate retrieval, while delayed recall of congruent events was associated with attenuated MTL activation, compared with recall of incongruent events.

Note that MTL activity during encoding was correlated with subsequent memory for both congruent and incongruent clips, while supplementary analyses of mean activation across all film clips revealed MTL activation during the encoding and retrieval of all events (Fig. S4). The differences based on congruence with prior knowledge that we outline here are not meant to suggest that the mPFC and MTL play roles only in memory for either congruent *or* incongruent events, respectively. Instead, they are meant to highlight ways in which either mPFC-based schematic/semantic processing or MTL-based novelty-triggered processing may be dominant depending on the nature of the event being encoded or retrieved.

4.1. Behaviour

Our first measures of behaviour were at immediate retrieval, when all film clips were forgotten at an equivalent (low) rate. One week later, however, clear benefits of both congruence and incongruence emerged with respect to overall memory for the film clips, with neutral clips forgotten at the highest rate. These results are compatible with van Kesteren et al.'s (2012) theory that experiencing something that is neither very novel, nor strongly related to prior experience, will fail to strongly engage either the event-specific (MTL-mediated) or prior knowledge-based 'schematic' (mPFC-mediated) memory systems, leading to poor memory. Novelty is thought to strengthen long-term potentiation and memory stabilization via the MTL system (Kumaran & Maguire, 2009; Frey et al., 1990; Li, Cullen, Anwyl, & Rowan, 2003). Prior knowledge, on the other hand, may guide perception and enhance memory through the engagement of higher order semantic representations or schemas (Wang & Morris, 2010; van Kesteren et al., 2012; Dudai, Karni, & Born, 2015). Thus, these two seemingly opposing factors have the convergent result of strengthening memory, but through different mechanisms. Interestingly, although both congruence and incongruence attenuated forgetting of the film clips generally, incongruent clips were recalled with more errors than congruent or neutral clips, particularly at delayed retrieval, in line with Bartlett's (1932) historic demonstration that unusual stories are susceptible to memory distortions over time.

4.2. Encoding

Encoding activity was strongly modulated by event congruence. As events increased in congruence across all forty clips, activation increased in the mPFC and posterior cingulate cortex. Conversely, as events became increasingly incongruent, activity increased across the bilateral MTLs, along the ventral visual stream, and throughout posterior occipital/parietal cortices. Since congruent and incongruent clips were equivalent with respect to sensory (visual, auditory) input, story complexity, and emotional arousal (Fig. S1), we suggest the differences observed here are likely to be due to the congruence/incongruence of the various events with participant's prior knowledge and experiences.

The encoding of congruent events elicited activity in areas often associated with the absence of task engagement (i.e. the default mode network). We do not think it likely, however, that the neural activity associated with congruence in this study reflects participants paying less attention to these more 'typical' clips since participants remembered an equivalent number of congruent and incongruent clips, and actually made fewer errors during the recall of congruent clips. Instead, activity in these 'default mode' regions is likely related to the

engagement of this network during activation of prior knowledge (Spreng et al., 2014; Binder, Desai, Graves, & Conant, 2009; Binder & Desai, 2011). Indeed, the mPFC and posterior cingulate cortex in particular – identified as 'hub regions' of the default mode network – have been linked to semantic functions along with the dorsomedial prefrontal subsystem (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010).

4.3. mPFC functional connectivity and increasing congruence between events and prior knowledge

Activation in the mPFC during the perception and encoding of congruent events was predicted based on the hypothesis that the mPFC detects congruence between current experiences and prior knowledge, activating relevant prior knowledge (which is presumably stored in distributed networks across other frontal, parietal, and temporal areas; Binder et al., 2009; Binder & Desai, 2011) to facilitate comprehension and/or bias processing (Preston & Eichenbaum, 2013; van Kesteren et al., 2012; Maguire et al., 1999; van Kesteren et al., 2010), and to enhance the integration of new event-specific information with prior knowledge (Sommer, 2017; Zeithamova, Dominick, & Preston, 2012; Schlichting, Mumford, & Preston, 2015; Chen et al., 2015).

Notably, functional connectivity between the mPFC and the inferior parietal lobule (angular and supramarginal gyri) was also correlated with increasing congruence, at all time-points. The specific peaks of functional connectivity with the mPFC were in the supramarginal gyrus for encoding and 7d retrieval, and in the angular gyrus for immediate retrieval. Consistent with this functional connectivity during the processing of clips that are congruent with prior knowledge, the inferior parietal lobule is commonly associated with semantic memory. Binder and Desai (2011) suggest that the inferior parietal lobule is a supramodal convergence area for semantic information, with a meta-analysis linking both the angular and supramarginal gyri with knowledge retrieval and conceptual integration (Binder et al., 2009). Indeed, van der Linden et al. (2017), using object stimuli, similarly linked activity in the angular gyrus during encoding and retrieval with memory for schema-related, semanticized memories (but see Cabeza, Ciaramelli, & Moscovitch, 2012; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Bellana, Liu, Anderson, Moscovitch, & Grady, 2015; Bonnici et al., 2016; Oliva & Torralba, 2007 for an alternative interpretation of inferior parietal lobule activity based on attention).

The posterior cingulate cortex and the bilateral middle frontal gyri also demonstrated functional connectivity with the mPFC that correlated with increasing event congruence. The posterior cingulate cortex, however, emerged only during the first day of the task (encoding and immediate retrieval), while the middle frontal gyri emerged only during retrieval sessions. In other studies, the posterior cingulate cortex is linked with both semantic processing (Binder et al., 2009; Fairhall & Caramazza, 2013) and episodic memory (Valenstein et al., 1987; Aggleton & Pearce, 2001; Vincent et al., 2006), perhaps due to the critical role semantic knowledge plays in facilitating comprehension of events (Maguire et al., 1999) and supporting episodic memory (van Kesteren et al., 2012). In particular, Bird et al. (2015) propose that the posterior cingulate cortex aids memory encoding and consolidation by strengthening the association between episodic details and semantic information. Our data are consistent with such a role in the encoding and initial strengthening of memories – we find mPFC-posterior cingulate cortex functional connectivity during encoding and immediate retrieval, but not during delayed retrieval one week after encoding. The middle frontal gyrus, on the other hand, is functionally connected to the mPFC during both immediate and delayed retrieval, consistent with other studies commonly associating the middle frontal gyrus with memory retrieval (Hayes et al., 2004; Lepage, Ghaffar, Nyberg, & Tulving, 2000), especially when an event is 'recollected' along with contextual information (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Burgess, Maguire, Spiers, & O'Keefe, 2001).

4.4. The MTL and increasing incongruence between events and prior knowledge

Our primary hypothesis with respect to decreasing congruence of film clips was that the encoding of events that are more incongruent with prior knowledge would be more dependent on MTL-based processing. Our data are consistent with this hypothesis, such that the encoding of increasingly incongruent events was associated specifically with an MTL peak in the parahippocampal cortex. Although the parahippocampal cortex is prominently linked with processing physical space (Aguirre, Detre, Alsop, & D'Esposito, 1996; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998), it is also associated with episodic memory generally (Hasson, Furman, Clark, Dudai, & Davachi, 2008; Maguire, 2001), as well as with decreasing congruence between stimuli (van Kesteren et al., 2013), and with learning novel information (van Kesteren et al., 2014; Kohler et al., 2002). The mnemonic relevance of the parahippocampal activation in this study is indicated by its correlation with subsequent memory for the film clips (Fig. 3d). The correlation between MTL activation and incongruence may reflect the need to encode the relations between the items, actions, context, etc., within the incongruent events, without a strong semantic framework to support encoding (Duncan et al., 2012; Rolls, 2007; O'Reilly and Rudy, 2001). These data provide evidence that even across a group of complex narrative events, all of which are presumably dependent on the MTL for encoding and retrieval (McDaniel & Einstein, 1986; Nadel & Moscovitch, 1997; Moscovitch et al., 2016; and see mean activation in Fig. S4), differences exist based on prior knowledge such that increasing incongruence is correlated with greater MTL activation.

Behaviourally, other studies have demonstrated enhanced processing and encoding of visual information when items are novel or unexpected based on the context (Friedman, 1979; Konkle & Oliva, 2007). This enhanced visual processing may be accomplished even without conscious awareness of having seen an incongruent item (Mudrik, Breska, Lamy, & Deouell, 2011) suggesting that incongruence with expectations may trigger increased perceptual processing both rapidly and subconsciously. Thus, although relying on prior knowledge (presumably through mPFC-based processing) may enhance the efficiency of perception and encoding for congruent events (Binder & Desai, 2011; Oliva & Torralba, 2007), processing seems to be more dependent on bottom-up sensory information when events are incongruent or novel. As predicted based on such behavioural data, our results demonstrate that increasing incongruence is associated not only with activation in the MTL, but also throughout the ventral visual stream and occipital cortices, and with enhanced functional connectivity between posterior sensory areas and a parahippocampal cortex seed. Since congruent and incongruent clips are equivalent with respect to sensory (visual, auditory) input (Fig. S1), the activity observed here may illustrate a neural mechanism underlying the enhanced perceptual processing of stimuli that are incongruent with prior knowledge and/or expectations (Friedman, 1979; Konkle & Oliva, 2007; Mudrik et al., 2011). Although MTL activation is often associated with activation in posterior neocortex during mnemonic processing (e.g., Adnan et al., 2015), our results specifically correlate increases in this functional connectivity with increasing incongruence between events and prior knowledge. Notably, incongruence was also correlated with enhanced MTL-posterior sensory cortex functional connectivity during immediate and delayed retrieval, with peaks in the lateral occipital cortex and lingual gyrus, respectively. Thus, enhanced connectivity between the MTL and classically 'sensory' areas during the mnemonic processing of incongruent events may also occur during retrieval, as suggested by behavioural evidence that memory for the visual details of items is more accurate when items are studied in incongruent contexts (Spalding et al., 2015).

Lastly, incongruence was also correlated with mPFC-MTL functional connectivity during encoding and immediate retrieval. Thus, although some previous research on schema-congruence and novelty has suggested an inhibitory relationship between the mPFC and MTLs (van

Kesteren et al., 2012), we find evidence instead for functional connectivity, consistent with some other studies (Sommer, 2017; Liu et al., 2016; Schlichting et al., 2015). The fact that we do not find evidence for inhibition between the mPFC and MTLs may be due to the complex mix of semantic and episodic information in the naturalistic film clip events (Levine et al., 2002), with even the most incongruent events having some relation to prior knowledge. When partial overlap exists between novel episodic information and semantic prior knowledge there may be greater need for both mPFC and MTL-mediated processing to resolve overlapping associations and contexts (Preston & Eichenbaum, 2013; Gilboa & Marlatte, 2017), with the balance of activation shifting based on the degree of congruence with prior knowledge.

4.5. Delayed retrieval

Rodent and human literature suggests that, although recent memories are dependent on the hippocampus irrespective of prior knowledge, memories that are congruent with a previously learned schema may become hippocampus-independent more rapidly than unrelated memories (Sommer, 2017; Tse et al., 2007; Brod, Lindenberger, Werkle-Bergner, & Shing, 2015). Consistent with this observation, we did not find differences in MTL activation based on congruence at immediate retrieval, while one week after encoding we observed attenuated MTL activation for retrieval of congruent clips compared to incongruent clips. This phenomenon, termed *accelerated consolidation*, may be due to the potentiation of direct connections between neocortical representations (van Kesteren et al., 2012), the schema-based enhancement of direct, or hippocampus-dependent, reactivation during rest or sleep (Dudai et al., 2015; van Dongen et al., 2011), and/or the decreased number of new connections and biological modifications necessary to integrate a new event into a relevant pre-existing cortical framework (Wang & Morris, 2010). Our data suggest that such mechanisms may also apply to the consolidation of narrative event memories, despite the fact that such naturalistic events generally demonstrate much more dependence on MTL-based encoding and retrieval.

4.6. Limitations

This study was limited by power, especially since three out of twenty participants did not recall enough film clips to be included in the fMRI analyses. Future research involving more participants and different types of naturalistic stimuli would be valuable for clarifying the patterns of behaviour and neural activation found in this investigation. This would be particularly useful in providing more conclusive evidence for, or against, the hypothesis of 'accelerated consolidation' since the attenuated MTL activation that we observed during the delayed retrieval of congruent clips was only evident at a threshold of $p < 0.005$ uncorrected.

Additionally, although prior knowledge is often shared within a culture – especially as defined for our film clip ratings, which refer to prior experiences not only in participants' personal lives but also events experienced through books, movies, television, or other media – meaningful differences are still likely to exist across individuals. These differences may have affected the patterns of neural activation measured in this study in ways that we did not have the power to explore. Future research focusing on these individual differences in episodic and semantic memory, and their relation to mPFC and MTL structure and function, may provide valuable insights into the neural underpinnings of memory for complex events.

5. Conclusion

Our findings illustrate that congruence with prior knowledge modulates the patterns of mPFC and MTL activity associated with encoding and retrieving naturalistic events. In particular, our data are consistent with theories associating the mPFC with the influence of

prior knowledge on the processing of one's current experiences, possibly via the activation of relevant semantic information or schemas stored in distributed networks throughout the cortex (van Kesteren et al., 2012; Moscovitch et al., 2016). With respect to functional connectivity, we found connectivity between the mPFC and various higher order semantic areas during the encoding and retrieval of events that are congruent with prior knowledge, while the MTL demonstrated connectivity with posterior sensory areas during both the encoding and retrieval of incongruent events. These findings provide novel insights into the neural mechanisms supporting memory for complex narrative events, thereby enhancing our understanding of memory function in real-world settings and across time.

Conflict of interest

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.nlm.2018.02.017.

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