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Episodic simulation and empathy in older adults and patients with unilateral medial temporal lobe excisions

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ABSTRACT

Recent work shows that vividly imagining oneself helping others in situations of need (episodic simulation) increases one's willingness to help. The mechanisms underlying this effect are unclear, though it is known that the medial temporal lobe (MTL) is critical for supporting episodic simulation in general. Therefore, individuals who have compromised MTL functioning, such as older adults and those who have undergone resection of medial temporal lobe tissue as treatment for epilepsy (mTLE patients), may not show the prosocial effects of episodic simulation. Our lab previously found that older adults and mTLE patients are impaired on a problem-solving task that requires the simulation of hypothetical scenarios. Using similar logic in the present study, we predicted that older adults and mTLE patients would show reduced effects of episodic simulation on their empathic concern for, and willingness to help, people in hypothetical situations of need, compared to young adults and age-matched healthy controls, respectively. We also predicted that the subjective vividness and the amount of contextspecific detail in imagined helping events would correlate with willingness to help and empathic concern. Participants read brief stories describing individuals in situations of need, and after each story either imagined themselves helping the person or performed a filler task. We analyzed the details in participants' oral descriptions of their imagined helping events and also collected subjective ratings of vividness, willingness to help, and empathic concern. Episodic simulation significantly boosted willingness to help in all groups except for mTLE patients, and it increased empathic concern in young adults and healthy controls but not in older adults or mTLE patients. While the level of context-specific detail in participants' oral descriptions of imaged events was unrelated to willingness to help and empathic concern, the effects of episodic simulation on these measures was completely mediated by subjective vividness, though to a significantly lesser degree among mTLE patients. These results increase our understanding not only of how episodic simulation works in healthy people, but also of the social and emotional consequences of compromised MTL functioning.

1. Introduction

Episodic recollection has been shown to contribute to various other functions such as imagining future events (Mullally and Maguire, 2014; Schacter et al., 2012), open-ended problem-solving (Sheldon et al., 2011; Sheldon et al., 2015), economic decision-making (Benoit et al., 2011; Palombo et al., 2015), and theory of mind (Ciaramelli et al., 2013; Cohn et al., 2015; Rabin and Rosenbaum, 2012). The medial temporal lobe (MTL), among other regions, is crucial for episodic memory (for review see Eichenbaum et al., 2012; Moscovitch et al., 2016; Sheldon and Levine, 2016). The links between the MTL and the diverse

aforementioned functions have important implications for everyday life, especially among individuals with compromised autobiographical memory and MTL functioning, such as older adults (e.g., Driscoll et al., 2003; Jernigan et al., 2001; Raz et al., 2005) and people with MTL epilepsy (mTLE; e.g., St-Laurent et al., 2014; St-Laurent et al., 2009). The mechanisms underlying many of these MTL-mediated phenomena are not yet clearly understood, but the vivid imagination of specific scenarios (*episodic simulation*) seems to be a key feature. Behavioural and functional neuroimaging research indicates a very strong relationship between the retrieval of contextual detail from prior experience and simulating such detail in service of other cognitive functions (Madore

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et al., 2019; Rubin et al., 2014; Schacter et al., 2012). While other brain regions are implicated in these processes, the primary aim of the present study is to examine how critical the MTL is for enabling episodic simulation to influence prosocial intentions and empathy.

Previous work by Gaesser and Schacter (2014) demonstrated that when healthy young adults vividly imagined themselves helping strangers in specific scenarios of need, they later reported being more willing to help in those scenarios. Importantly, this prosocial effect of episodic simulation surpassed the effect of merely thinking about and enumerating ways to help, which did not increase willingness to help above "baseline" levels (Gaesser and Schacter, 2014, Exp. 2; Gaesser et al., 2017a). Participants' ratings of the vividness of their imagined helping events correlated with their self-reported willingness to help. Furthermore, manipulating the familiarity of the location in which the helping episode takes place has been shown to heighten the subjective detail and subsequently increase willingness to help (Gaesser et al., 2018). Vividness ratings continued to predict willingness to help even when accounting for individual differences in empathic and prosocial traits (Gaesser et al., 2018).

In other words, imagining these helping scenarios does not increase willingness to help solely by priming conceptual knowledge about helping; there is something special about imagining episodes that are specific in time and place from a first-person perspective (or even from someone else's perspective, for that matter; see Gaesser et al., 2015) that enhances motivation. This notion dovetails with earlier work showing that people are more likely to do things they have imagined concretely as opposed to abstractly (e.g., Gollwitzer and Brandstatter, 1997; McCrea et al., 2008), perhaps because context-specific detail increases the subjective plausibility and likelihood of the scenario or task in question (e.g., D'Argembeau and Van der Linden, 2012; Szpunar and Schacter, 2013). Interestingly, fMRI experiments have found that MTL activity correlates with the vividness of episodic memories and imagined events (Addis et al., 2004; Addis et al., 2011; Addis and Schacter, 2008; Gilboa et al., 2004). It is possible, therefore, that the enhancement of willingness to help by episodic simulation is related to an MTL-mediated increase in the vividness of the imagined helping event. If so, people with MTL damage or dysfunction should show a reduced effect of episodic simulation on willingness to help, after imagining themselves helping, compared to control groups in which the MTL is intact. In addition, a mediation analysis should show that the effect of episodic simulation on willingness to help is significantly mediated by the scenario in question being represented more vividly in the mind of the prospective helper, compared to a condition in which he or she had not previously imagined helping. Last, this mediating effect of vividness should be stronger among those with intact MTL function.

The secondary aim of the present study was to get a clearer idea of how vividness contributes to willingness to help. While previous studies on healthy individuals have found correlations between participants' willingness to help and their ratings of the vividness of their imagined events (e.g., Gaesser et al., 2017b; Gaesser et al., 2018; Gaesser and Schacter, 2014), it is unclear whether the role of vividness in that relationship is related to a broader phenomenological impression or whether it truly reflects an aggregate of episodic details specific to the context of the imagined event (see Gaesser et al., 2015). After all, MTL activity is related not only to subjective ratings of vividness and amount of detail but also to other phenomenological features, such as emotionality and personal significance (Addis et al., 2004, 2011; Addis and Schacter, 2008; Gilboa et al., 2004). Also, to our knowledge, no previously published work has directly compared subjective ratings of detail to context-specific details, at least not with respect to imagined events. Addis et al. (2007) found that in healthy participants only subjective ratings of remembered events were positively, but not significantly, correlated with context-specific details on the Autobiographical Interview (AI; Levine et al., 2002), a test designed to distinguish between episodic and other details in narratives of events; among MTL patients, however, vividness and episodic details were negatively

correlated though, again, not significantly so. One way to ascertain the role of context-specific detail *per se* is to analyze participants' imagined events with a proven measure based on the AI.

Originally developed as a tool for analyzing narratives of autobiographical memories, the AI has since been adapted successfully to the analysis of imagined events in both healthy and clinical populations (e. g., Addis et al., 2008; Brown et al., 2014; Lechowicz et al., 2016; Sheldon et al., 2011). In the AI method, a participant describes a memory (or imagined event) in as much detail as possible, while being recorded. The transcript is then segmented into chunks of information and each chunk is classified as either an "internal" or "external" detail. Internal details convey information specific to the spatiotemporal context in which the event takes place, while external details convey more general information (see Method section for examples). Previous experiments with the AI show that older adults and people with mTLE generate fewer internal (i.e., context-specific, or episodic), but not external (i.e., acontextual, or non-episodic) details, compared to young adults and healthy controls, respectively (e.g., Addis et al., 2010; Addis et al., 2008; Lechowicz et al., 2016; Levine et al., 2002; Sheldon et al., 2011; St-Laurent et al., 2014, 2009). Moreover, the number of internal details in imagined events is related to participants' performance on a social problem-solving task (Sheldon et al., 2011, 2015). Since these groups exhibit deterioration and damage to the MTL (e.g., Addis et al., 2007; Jernigan et al., 2001; Raz et al., 2005; St-Laurent et al., 2009), reduced internal detail production may reflect impaired MTL functioning. This relationship is supported by the finding that healthy adults who are formally trained with an "episodic specificity induction" produce more internal details, and this benefit is associated with increased MTL activity (Madore et al., 2016). Using the AI in the present study, therefore, may provide a proxy measure of the degree to which the MTL contributes to the effect of episodic simulation on willingness to help via the generation of context-specific detail.

We compared the performance of individuals who had undergone total unilateral resection of the medial temporal lobe as treatment for intractable epilepsy (mTLE patients) and healthy controls on an episodic simulation task adapted from Gaesser and Schacter (2014). We also compared young and older adults, since previous work has found that older adults resemble mTLE patients on episodic simulation tasks, though the deficit is not as severe (e.g., Addis et al., 2010; Lechowicz et al., 2016; Sheldon et al., 2011), and each group has its own strengths and limitations regarding specificity and degree of MTL damage. While the MTL is not the only brain region involved in episodic simulation (for example, the ventromedial prefrontal cortex is also known to be important; Addis, 2018; Bertossi et al., 2016; Verfaellie et al., 2019), it was our focus in the present study. We chose to follow in the theoretical footsteps of Sheldon et al. (2011), who investigated the relationship between episodic simulation and open-ended problem-solving in the same two populations from which we sampled here: older adults and mTLE patients. To the extent performance is comparable between these groups, it suggests a common underlying dysfunction; to the extent that performance differs, it suggests that some other factors may be implicated.

Participants read short vignettes describing individuals in situations of need and, for each vignette, were asked either to vividly imagine themselves helping the person in need, or to perform an unrelated control task (to allow collection of "baseline" measures). Participants also described each event they imagined, so we could analyze transcripts according to the AI method. Last, participants used rating scales to answer questions about the vignettes they had seen, such as how willing they would be to help the person in each scenario, how vividly they had imagined each helping event, and the degree to which they experienced various emotions. These emotion ratings were used to calculate an index of "empathic concern" (see Method section). As with willingness to help, we predicted that older adults and mTLE patients would show a reduced effect of episodic simulation on empathic concern compared to their respective control groups, and that the effect of episodic simulation on empathic concern would be significantly mediated by the subjective vividness of imagined helping events. We measured empathic concern in addition to willingness to help because 1) we theorized it would capture a relatively more affective dimension of prosocial intent; and 2) we suspected it may be less prone to potential demand characteristics, as it is an aggregate of several other ratings. Last, we predicted that older adults and mTLE patients would produce fewer internal details compared to controls, and that internal details would be related to willingness to help and to empathic concern.

2. Experiment 1 method

2.1. Participants

Our target total sample size for the aging experiment was 62, based on a power analysis performed on data from a contemporary study that used a very similar paradigm (Gaesser et al., 2017b). Altogether, we recruited 30 young and 43 older adults from the University of Toronto and surrounding community, but excluded two young and two older adults because they failed to comply with task instructions (i.e., on at least half of the trials they described imagined events but did not include themselves helping). Another four older adults were excluded because their willingness to help ratings were at ceiling even in the baseline condition. In addition, we administered the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) to our older adult participants, and excluded three who scored below an independently validated cut-off score for screening out individuals who might have mild cognitive impairment (i.e., a MoCA score below 23 out of 30; see Carson et al., 2018). Thus, our final sample consisted of 28 young (20 females, age range: 17–34 years old, M = 19.0, SD = 3.32) and 34 older adults (23 females, age range: 65–81 years old, M = 73.2, SD = 4.73). Inclusion criteria required fluency in English, no prior diagnosis of a psychiatric or neurological condition, and normal or corrected-to-normal hearing and vision. Young adults were compensated with course credit if enrolled in an introductory psychology course at the University of Toronto, or with \$20 otherwise. Older adults were compensated with \$32 according to the standards in our department. Our experiment protocol was approved by the University of Toronto Research Ethics Board (protocol #31031).

2.2. Materials & design

2.2.1. Vignettes

Eight single-sentence vignettes served as the bases for participants' imagined events, each featuring a nondescript individual in a specific situation of need (adapted from Gaesser and Schacter, 2014). The vignettes were presented one at a time on a computer screen, in black text against a grey background, using E-Prime 2.0 (Psychology Software Tools Inc. Release candidate version 2.0.10.242). They were randomly and equally assigned to conditions, for a total of eight trials (four per condition), with presentation order counterbalanced across participants.

2.2.2. Adapted Autobiographical Interview (AI) transcript scoring

Participants' oral descriptions of imagined events were transcribed and analyzed according to guidelines established by Levine et al. (2002) and adapted by others for use with imagined events (e.g., Addis et al., 2008; Sheldon et al., 2011). First, the text was segmented into chunks, with each chunk defined as a single observation, fact, thought, emotion, or judgment. These were then classified as either "internal" details (i.e., specific to the context of the event being imagined, such as perceptual details; references to a particular time or place; moment-by-moment happenings in the unfolding of the narrative; any thoughts or emotions the participant imagined themselves having) or "external" details (i.e., not specific to the event being imagined, such as factual knowledge; repeated details). After scoring, we counted the total number of internal details in each transcript and also tallied the subcategories of internal details (time, place, perceptual, emotion-thought, event). We counted external details as well but did not distinguish among subcategories, as they were of no theoretical interest. To establish inter-rater reliability, another person, blind to the purpose of the study and to which group of participants produced the transcripts, scored a third of the transcripts. Intraclass correlation coefficients indicated high inter-rater reliability (young adults: internal and external details = .981 and .922, respectively; older adults: internal and external details = 0.956 and 0.839, respectively; for a similar procedure and values see Sheldon et al., 2011).

2.2.3. Trait empathy

We administered two self-report measures of trait empathy to identify possible age-related group differences as they might obscure group differences in the effect of episodic simulation on willingness to help or empathic concern. Participants completed the 16-item Toronto Empathy Questionnaire (TEQ), which is designed to tap into a single trait empathy factor shared by various empathy measures (Spreng et al., 2009). The TEQ has high internal consistency (Cronbach's $\alpha = 0.85$) and test-retest reliability (r = 0.81, p < .001), correlates with behavioural measures of social inference, such as the "Reading the Mind in the Eyes" Test (Baron-Cohen et al., 2001), and has been used in previous aging studies (e.g., Gould and MacNeil Gautreau, 2014). Participants also completed the widely-used Interpersonal Reactivity Index (IRI; Davis, 1980), and our focus was on the empathic concern subscale (IRI-EC), since it is intended to reflect the respondent's tendency to feel compassion, warmth, and concern for other individuals (Davis, 1983).

2.2.4. Procedure

Participants gave written consent to be involved in the study, and were seated at a computer in a well-lit room. The experimenter told them they would view a series of short stories adapted from the media, and that after reading each one they would either imagine themselves helping the person in the story or think of as many words as possible starting with a certain letter that would be provided (see Supplementary Material for task instructions).

2.2.5. Task block

After instructions were given, participants were told they would later need to answer questions about the vignettes, their reactions to them, and what they had done after reading each one. Then the experimenter guided participants through several practice trials to ensure that they understood and were comfortable with everything that was required of them, especially imagining and orally describing hypothetical scenarios. No ratings were collected on practice trials. When participants were finished practicing, the experimenter remained in the room and allowed participants to work in silence as the computer guided them through each of eight trials (four *imagine* and four *words* trials intermixed), and only interacted with participants when it was time to record their oral responses.

On a given trial, a vignette would appear in the centre of the screen for 10s, followed by brief instructions depending on which task condition the vignette had been assigned to (*imagine*: "Imagine an event in which you help this person. Try to make it as vivid as possible"; *words*: "Think of as many words as you can that begin with the letter ****"). Instructions remained on screen until participants pressed the ENTER key to indicate they were ready to begin the trial.

2.2.5.1. "Imagine" trials. On imagine trials, the screen became blank for 60 s while participants closed their eyes and imagined helping the person mentioned in the vignette. After 60 s, the computer played a bell sound and displayed a message instructing participants to provide a verbal description of what they had imagined. The experimenter recorded the description using a handheld digital recording device. Once participants were finished, the experimenter terminated the recording and pressed a key on the computer to advance to the next trial. If on a given trial participants needed longer than 3 min to finish describing what they imagined, they were allowed it, but then only the first 3 min of the transcript was used in subsequent analyses.

2.2.5.2. "Words" trials. On words trials, the screen read, "Please say each word out loud" and, for 2 min, participants spoke words out loud that began with whichever letter had been given in the preceding instructions. The letter was randomly selected from a set based on previous studies on phonemic fluency (Ferrett et al., 2014; Sheldon and Moscovitch, 2012). The experimenter digitally recorded the responses. After 2 min, a new letter was presented and participants generated new words for another 2 min. When they finished, the experimenter terminated the recording and pressed a key to advance to the next trial. Note that words trials provided a baseline by controlling for the effects of exposure to the vignette and, importantly, administering the phonemic fluency task is expected to recruit brain regions other than the hippocampus (Sheldon and Moscovitch, 2012), such as lateral frontal cortex (e.g., Smirni et al., 2017; Troyer et al., 1997; Tupak et al., 2012), making it less likely that participants will imagine themselves helping or mind-wander (Andrews-Hanna et al., 2014).

Whenever a trial was finished, the screen became blank for 2.5 s; then the next vignette appeared on the screen. After a block of four trials had passed (two *imagine* and two *words* trials, in counterbalanced order), there came a question block.

2.3. Question block

In the question block, the vignettes were displayed again, one by one, but this time participants answered a series of questions on the computer after each vignette. Participants used 7-point rating scales to indicate how willing they would be to help (1 = not at all willing; 7 = very willing). They also rated the degree to which the scenario made them experience various emotions (*compassionate, sympathetic, tender, warm*; 1 = not at all; 7 = very much) when they first saw it during the task block; these ratings were averaged together to form an index of empathic concern (as per Batson, 2011; Batson et al., 1997). Participants also rated how vivid each event was when they imagined it during the task block: "The imagined scene in your mind was?" (1 = vague; 7 = detailed). See Supplementary Material for descriptions of other ratings collected but not reported here. The question block was self-paced.

After the first question block, participants completed a second trial block and question block. We split the eight trials into two blocks of four so that older adults (and, later, mTLE patients) would have an easier time remembering what they imagined and experienced for each vignette when making their ratings in the question blocks.

Last, participants completed the TEQ and the IRI. The entire session typically lasted about 2 h.

3. Experiment 1 results

3.1. Trait empathy

Independent samples t-tests revealed no significant difference between young adults (YAs) and older adults (OAs) on the TEQ (OAs: M = 46.2, SE = 1.24; YAs: M = 49.1, SE = 1.24), $t_{(60)} = -1.66$, p = .103, nor on the IRI-EC (OAs: M = 21.1, SE = 3.98; YAs: M = 19.9, SE = 4.39), $t_{(60)} = 1.12$, p = .266, indicating that the groups were well-matched on levels of trait empathy.

3.2. Willingness to help, empathic concern, and vividness

We ran a two-way mixed ANOVA with task condition (2: *imagine*; *words*) as a within-participants variable, age group (2: OAs; YAs) as a between-participants variable, willingness to help as the dependent

variable, and gender as a covariate (since females were overrepresented in both groups). We found a main effect of task, $F_{(1, 59)} = 15.60$, p < .001, $\eta^2_p = .209$, with willingness to help being greater in the *imagine* condition compared to the *words* condition (see Fig. 1), essentially replicating Gaesser and Schacter (2014, Exp. 1). We also detected a significant effect of age group ($F_{(1, 59)} = 10.19$, p = .002, $\eta^2_p = .147$), with OAs being more willing to help than YAs overall, but no interaction between task condition and age group ($F_{(1, 59)} = 1.47$, p = .230, $\eta^2_p = .024$), meaning that, contrary to our prediction, the ES effect was not stronger in YA compared to OA. Means are as follows: in the *imagine* condition, YAs M = 5.21, SD = 1.11; OAs M = 5.78, SD = 0.97; and in the *words* condition, YAs M = 4.4, SD = 1.05; OAs M = 5.29, SD = 1.04 (see Supplementary Material for exploration of baseline differences). There was no effect of the gender covariate ($F_{(1,59)} = 0.81$, p = .373).

A second ANOVA specified as above, except with empathic concern as the dependent variable, showed that empathic concern was significantly higher in the *imagine* condition, $F_{(1, 60)} = 11.96$, p = .001, $\eta_p^2 = .169$, and among OAs, $F_{(1, 60)} = 4.91$, p = .031, $\eta_p^2 = .077$. We also found a significant interaction between task and age group, $F_{(1)}$ $_{60} = 5.30$, p = .025, $\eta^2_p = .082$, which indicated that the difference in empathic concern between tasks was greater in YAs than in OAs (see Fig. 1). Post-hoc paired-samples t-tests, conducted separately for each age group, revealed that YAs' empathic concern was significantly higher in the *imagine* condition compared to the *words* condition, $t_{(27)} = 4.38$, p < .001, while OAs' was not, $t_{(33)} = 1.63$, p = .226. Means are as follows: in the *imagine* condition, YAs M = 4.18, SD = 1.18; OAs M = 4.42, SD = 0.86; and in the words condition, YAs M = 3.46, SD = 1.12; OAs M = 4.19, SD = 0.93 (see Supplementary Material for exploration of baseline differences). There was also a significant effect of the gender covariate indicating that empathic concern was greater among women $(F_{(1,59)} = 5.04, p = .029, \eta^2_p = .079).$

We ran a third ANOVA with vividness as the dependent variable to verify that our episodic simulation task boosted vividness as compared to any spontaneous mental imagery associated with the vignettes in the *words* condition. This was confirmed with a main effect of the *imagine* condition, $F_{(1,60)} = 37.41$, p < .001. There was no effect of age group, $F_{(1,60)} = 1.31$, p = .257, and no interaction, $F_{(1,60)} = 0.610$, p = .438. Means are as follows: in the *imagine* condition, YAs M = 5.16, SD = 1.03; OAs M = 5.33, SD = 1.05; and in the *words* condition, YAs M = 3.44, SD = 1.57; OAs M = 3.94, SD = 1.94. There was no effect of the gender covariate ($F_{(1,59)} = 1.11$, p = .296).

3.3. Mediation analyses

Next, we ran two mediation analyses to test our predictions about the mediating role of vividness for both willingness to help and empathic concern. In each of our mediation models, the *a* path refers to the effect of episodic simulation on vividness; the *b* path refers to the effect of vividness on willingness to help (or empathic concern); the c' and c paths refer to the effect of episodic simulation on willingness to help (or empathic concern) with and without accounting for the mediating effect of vividness, respectively; and the product of the *a* and *b* paths (*ab*) is equivalent to the mediating effect of vividness (or c - c'). We specified our models using the MLmed macro for SPSS (Rockwood and Hayes, 2017), which automatically provides an estimate of *ab* (the mediation effect) with 95% confidence intervals generated using 10,000 Monte Carlo samples (Bauer et al., 2006; Zhang et al., 2009), and can also provide an index of moderated mediation (Bauer et al., 2006; Hayes, 2015). Episodic simulation was specified as the predictor and represented by a binary variable (1 = imagine condition; 0 = words condition), willingness to help (or empathic concern) was the outcome variable, vividness was a mediator, and a binary variable for age group (1 = OA;0 = YA) was a potential moderator of the *a* path (that is, the effect of episodic simulation on vividness). It is also important to note that, for our mediation analyses, we adopted a multi-level modeling approach, nesting individual trials within participants (with a random intercept for

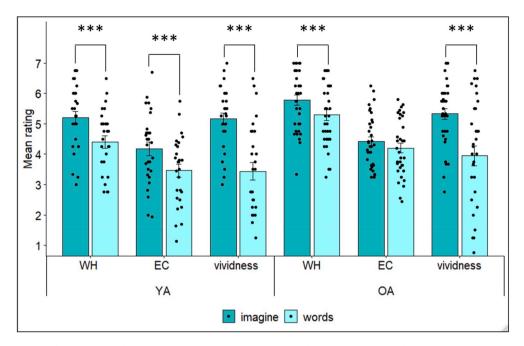


Fig. 1. Mean willingness to help (WH), empathic concern (EC), and subjective vividness by age group and condition. ***p < .001. Error bars represent the SE.

the effect of participant) instead of averaging over trials for each participant, which made the tests more sensitive and allowed us to examine relationships at the trial level (Bauer et al., 2006; Zhang et al., 2009; for a similar approach, without mediation, see Gaesser and Schacter, 2014).

In the model for willingness to help, we found that episodic simulation was a significant predictor of vividness ($\beta = 1.72$, SE = 0.20, p < .001) with no moderating effect of being an older adult (estimate = -0.08, 95% CI = [-0.26, 0.09]) consistent with our participant-level ANOVA. Vividness was a significant predictor of willingness to help ($\beta = 0.31$, SE = 0.05, p < .001; see Fig. 2), replicating previous work (Gaesser et al., 2015, 2017a; 2018; Gaesser and Schacter, 2014). The effect of episodic simulation on willingness to help was completely mediated by vividness ($\beta = 0.54$, SE = 0.10, p < .001), as the *c*' path (the effect of episodic simulation on willingness to help after accounting for vividness) was non-significant ($\beta = .17$, SE = 0.15, p = .248; see Fig. 2). Note that, when the moderated mediation component of the model was excluded, the effect of episodic simulation on willingness to help (i.e., the *c* path) was significant ($\beta = 0.67$, SE = 0.14, p < .001).

Similar results were found in the model for empathic concern. Episodic simulation was a significant predictor of vividness ($\beta = 1.72$, SE = 0.20, p < .001) with no moderating effect of being an older adult (estimate = -0.05, 95% CI = [-0.17, 0.06]), vividness was a significant predictor of empathic concern ($\beta = 0.20$, SE = 0.04, p < .001), and

completely mediated the effect of episodic simulation on empathic concern ($\beta = 0.35$, SE = 0.08, p < .001), as the *c*' path was non-significant ($\beta = 0.13$, SE = 0.12, p = .292). Note that, when the moderated mediation component of the model was excluded, the effect of episodic simulation on empathic concern (i.e., the *c* path) was significant ($\beta = 0.45$, SE = 0.11, p < .001).

3.4. Internal and external details in transcripts of imagined helping events

Note that verbal descriptions (and therefore internal and external details) were collected for *imagine* trials only. A mixed ANOVA with detail type (internal vs. external) as a within-participant measure and age group as a between-participant measure revealed that participants produced significantly more internal than external details, $F_{(1,60)} = 206.99$, p < .001, and that YAs produced more details than OAs, $F_{(1,60)} = 12.85$, p = .001. Importantly, there was also a significant interaction between age group and detail type, $F_{(1,60)} = 20.05$, p < .001, consistent with our expectation that the groups would differ on internal details in particular. Post-hoc independent samples t-tests revealed that, as expected, YAs produced significantly more internal details in their descriptions of imagined helping events (M = 34.0, SD = 10.22) compared to OAs (M = 22.2, SD = 11.21), $t_{(60)} = 4.28$, p < .001, but the age groups did not differ with respect to external details (YAs M = 10.58, SD = 5.32; OAs M = 9.9, SD = 4.51), $t_{(60)} = 0.551$, p = .583 (post-hoc p's

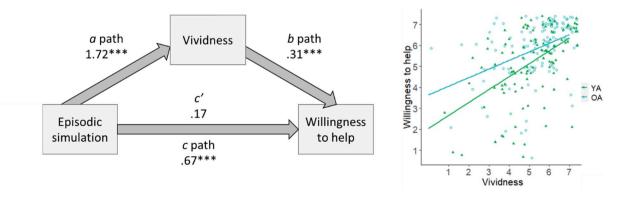


Fig. 2. Mediation analysis in YAs and OAs, with scatterplot for willingness to help and vividness. All values are beta coefficients. ***p < .001.

corrected for multiple comparisons as per Holm [1979]; see Fig. 3). These findings were expected and are generally consistent with previous studies using the AI method to assess the imagined events of YAs and OAs, although sometimes OAs generate more external details compared to YAs (e.g., Addis et al., 2010; Addis et al., 2008; Levine et al., 2002; but see Sheldon et al., 2011).

Next, we were interested in whether internal details predicted willingness to help or empathic concern, whether they correlated with subjective vividness ratings, and whether any of these relationships varied between YAs and OAs, especially given that YAs produced significantly more internal details compared to OAs. To address these questions, we ran a multi-level model (with a random slope for the effect of participant) on all of the trials from the imagine condition. The number of internal details was the outcome variable, and the predictors were willingness to help, empathic concern, vividness, and a binary variable for age group (1 = OA; 0 = YA) along with terms representing the interaction between age group and each of the other three predictors. After accounting for the negative effect of being an OA on the number of internal details ($\beta = -19.69$, SE = 6.65, p = .004), no other predictor was significant, except for the term representing the interaction between age group and empathic concern ($\beta = 3.26$, SE = 1.17, p = .006). Running separate models for OAs and YAs, with empathic concern as the predictor and internal details as the outcome, revealed that empathic concern was significantly related to internal details in OAs $(\beta = 2.49, SE = 0.67, p < .001)$ but not in YAs $(\beta = 0.07, SE = 0.66, p < .001)$ p = .911; post-hoc p's adjusted for multiple comparisons as per Holm [1979]). When we ran the full model again, as specified above, only with external details as the outcome variable instead of internal details, no predictor was significant (all p's > 0.303). Analyses of subtypes of internal details can be found in the Supplementary Material.

3.5. Auxiliary analyses

We also compared OAs and YAs on their performance in the phonemic fluency task used in the *words* condition. We conducted this analysis primarily to help alleviate potential concerns that group differences in episodic simulation could be due to frontal lobe issues in OAs, as phonemic fluency is known to involve frontal regions (e.g., Madden et al., 2019; Manenti et al., 2013; Smirni et al., 2017; Troyer et al., 1997; Tupak et al., 2012). Beyond this purpose, we had no predictions for the phonemic fluency data. First, we found that OAs produced significantly more words (M = 23.38, SD = 5.66) than did YAs (M = 19.99, SD = 5.62), $t_{(60)} = 2.35$, p = .022. When we excluded repeated words and other errors, however, there was no longer a significant difference (OAs: M = 20.60, SD = 5.09; YAs: M = 18.74, SD = 5.27), $t_{(60)} = 1.41$, p = .165. Either way, the results are consistent with the notion that frontal lobe function was *not* significantly impaired among our OA participants (see Supplementary Material for additional descriptive statistics).

Next, to address potential concerns about demand characteristics (e. g., participants may have believed they were expected to be more willing to help in the *imagine* condition), we took advantage of our block design and, for OAs and YAs separately, compared all measures between the first and second block. If demand characteristics influenced our results, we would expect them to emerge on later trials when the participant was better acquainted with the task. These analyses revealed that YAs produced significantly more internal details in their descriptions of imagined helping events in the first block (M = 36.86, SD = 12.26) compared to the second (M = 31.38, SD = 10.45), $t_{(27)} = 3.49$, p = .002, and that OAs generated significantly more words in the phonemic fluency task in the second block (M = 24.34, SD = 6.46) compared to the first (M = 22.41, SD = 5.52), $t_{(33)} = -2.81$, p = .008. We attribute these differences to simple effects of fatigue and practice, respectively, that can be expected in any experiment. Critically, there were no significant differences regarding willingness to help or empathic concern (see Supplementary Material), which we believe addresses and alleviates, albeit indirectly, potential concerns that demand characteristics may have been at play. There were also no significant differences for subjective vividness.

4. Experiment 1 discussion

While our prediction that episodic simulation would have a greater effect on empathic concern in young compared to older adults was borne out by the data, our prediction regarding willingness to help was not, as episodic simulation increased willingness to help to a similar degree in both groups. This finding, however, replicates that of Gaesser et al. (2017b), who saw a similar increase in young and older adults when episodic simulation was compared to a baseline condition. The same study only found a difference between young and older adults when

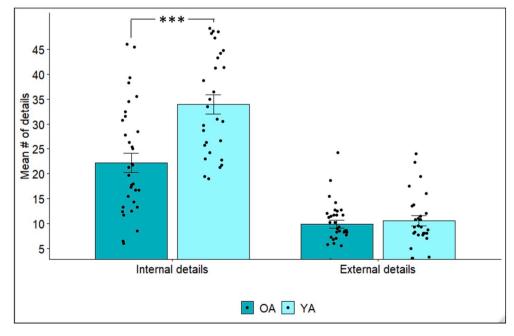


Fig. 3. Mean number of details in transcripts of imagined helping events, by age group. Error bars represent the SE. ***p < .001.

episodic simulation was compared to a condition involving directed retrieval of conceptual helping information (Gaesser et al., 2017b). Second, our mediation analyses indicated that vividness completely mediated the effects of episodic simulation on willingness to help and empathic concern, but there was no moderating effect of age. Third, while our prediction that young adults would produce more internal details than older adults was borne out by the data, we found that internal details were unrelated to vividness or to willingness to help, and were related to empathic concern only among older adults.

First, it is worth noting that the larger effect of episodic simulation on empathic concern among young adults was due to older adults expressing significantly more empathic concern in the words condition. In other words, the older adults had less room for improvement, and the interaction effect may be best described as a phenomenon wherein episodic simulation allows young adults to catch up to the level of empathic concern that older adults already exhibit at baseline. Importantly, we did not find significant age-related differences in trait empathy, suggesting that it is the act of considering the specific circumstances of other people, whether or not the situation is represented episodically, that distinguishes young and older adults when it comes to expressing empathy. This difference may be related to the fact that older adults, naturally, tend to have accumulated a wider variety of life experiences compared to young adults, and are therefore able to express empathic concern in relation to the hypothetical scenarios used in this study by drawing on crystallized, conceptual knowledge (Ardelt, 2010; Moore et al., 2015), without needing to engage in episodic simulation. Thus, if older adults do have some mild level of MTL deterioration (suggested by their production of fewer internal details), they are able to compensate for any adverse effects this may have on their ability to empathize with others by drawing on their extensive prior knowledge (e. g., Umanath and Marsh, 2014).

In the literature on the adapted AI, we and others have taken the number of internal details as an objective expression of the vividness of recollection. Thus, we were surprised to find 1) internal details were not related to vividness ratings in either age group; and 2) despite the age difference in internal details, age was not a significant moderator in analyses showing vividness to be a strong mediator of the relationship between episodic simulation and both willingness to help and empathic concern; and 3) internal details were related to empathic concern only among older adults. One clue to interpreting these results can be found in a neuroimaging study in which subjective detail ratings were related to different neural substrates in young and older adults (Addis et al., 2011). Specifically, in both remembered and imagined events, subjective detail ratings in young adults were related to activity in the MTL and other medial regions affiliated with the brain's autobiographical memory network, whereas in older adults they were related to the lateral temporal cortex, the insula, and the cerebellum (Addis et al., 2011), structures that do not typically mediate detailed episodic memory. Also, while the authors of that study found no significant difference in detail ratings between young and older adults, they did find that older adults rated episodes as being more emotional and more personally significant compared to young adults (Addis et al., 2011). In light of these findings, our results suggest that the subjective, phenomenological experience of episodic simulation is more important for its role in willingness to help and empathy than context-specific detail as measured by the AI. The fact that internal details were significantly related to empathic concern only among older adults may indicate that older adults were more motivated to generate internal details when describing episodes they found particularly emotional. Indeed, motivation is an important factor to consider, given that older adults have been shown to be capable of producing more internal details after undergoing an "episodic specificity induction" training session (Madore et al., 2016). Future research should clarify these issues by measuring brain activity, as well as physiological indices of emotional responsivity, in young and older adults during tasks involving episodic simulation and the expression of empathy.

The potential explanations we have suggested above can be

addressed to some degree in Experiment 2 by comparing individuals with MTL excisions to age-matched healthy controls. First, we can be relatively certain that the MTL will be playing less of a role in supporting phenomenological features of imagined helping events in these patients, because each of them has a significant and uniform amount of MTL tissue excised from one hemisphere. Second, given that the patient and control groups are not only matched very closely for age, but do not include anyone over the age of 65 (which was our criterion for inclusion in the older adult group in Experiment 1), any compensatory benefit of greater life experience accumulated with age should have relatively little bearing on the results of Experiment 2. Note that our controlling for age in Experiment 2 also addresses the possibility that age-related differences in Experiment 1 could be related to issues with the frontal lobe or frontoparietal circuitry (e.g., Campbell et al., 2012; Grady, 2008; Manenti et al., 2013; Troyer et al., 1997) that our analysis of the phonemic fluency data was not sensitive enough to detect.

5. Experiment 2 method

The materials, design, and procedure for Experiment 2 were identical to those of Experiment 1; the only methodological difference was in the sample collected. Interclass correlation coefficients for inter-rater reliability on the adapted AI scoring were 0.920 and 0.822 for healthy controls and 0.926 and 0.844 for mTLE patients, for internal and external details, respectively.

5.1. Participants

Through the epilepsy clinic at Toronto Western Hospital, we recruited 16 mTLE patients (11 females; M age = 37.6, SD = 11.7; M years of education = 15.3, SD = 2.3) who had undergone unilateral anterior temporal lobectomy for the treatment of intractable epilepsy a minimum of six months previously and who had been seizure-free for that post-resection interval. These resections included the entirety of the amygdala, hippocampus, and anterior parahippocampal gyrus as well as neocortical resections of 4–5 cm from the temporal pole on the inferior temporal gyrus, 2–3 cm on the middle temporal gyrus and 1–2 cm on the superior temporal gyrus. Note that while there were eight patients with left-sided resections and eight with right, previous work from our lab has found that laterality is not a significant factor with respect to autobiographical memory deficits (Sheldon et al., 2011; St-Laurent et al., 2009; Viskontas et al., 2000). In addition, as alluded to above, all patients had had the same amount of hippocampal tissue resected (i.e., all of it) from the epileptogenic hemisphere. These participants were compensated with coffee shop gift cards preloaded with \$25, in accordance with pre-established standards in our lab at Toronto Western Hospital. Through the University of Toronto community, we recruited 16 healthy controls matched to the patients, on an individual basis, for age, sex, and years of education (11 females; M age = 37.1, SD = 11.7; M years of education = 16.3, SD = 2.7), and with no history of psychiatric or neurological conditions. These participants were compensated with \$32, according to the standards of our department (see above). Our experiment protocol was approved by the University Health Network Research Ethics Board.

6. Experiment 2 results

6.1. Trait empathy

As in Experiment 1, we did not observe any significant differences when comparing patients to controls on the TEQ (mTLE patients: M = 47.7, SE = 1.63; healthy controls: M = 50.1, SE = 1.19), $t_{(30)} = 1.21$, p = .237, or on the IRI-EC (mTLE patients: M = 20.7, SE = 4.98; healthy controls: M = 20.8, SE = 3.45), $t_{(30)} = 0.09$, p = .933, and thus the groups were well-matched on levels of trait empathy.

6.2. Willingness to help, empathic concern, and vividness

A mixed ANOVA, specified the same way as in Experiment 1, showed a marginally significant effect of episodic simulation on willingness to help, $F_{(1,29)} = 3.80$, p = .061, $\eta^2_p = .116$, but no effect of group, $F_{(1,29)} = 0.156$, p = .696. There was, however, an interaction between task and group, $F_{(1,29)} = 4.22$, p = .049, $\eta^2_p = .127$. Post-hoc paired samples t-tests showed that willingness to help was significantly higher in the *imagine* vs. *words* condition among healthy controls, $t_{(15)} = 4.29$, p = .003, but not among mTLE patients, $t_{(15)} = 0.59$, p = .695 (see Fig. 4). Means are as follows: in the imagine condition, healthy controls M = 5.76, SD = 0.71; mTLE patients M = 5.42, SD = 1.2; and in the words condition, healthy controls M = 4.67, SD = 0.83; mTLE patients M = 5.22, SD = 1.04. There was no significant effect of the gender covariate ($F_{(1,29)} = 0.007$, p = .933).

A second ANOVA, this time with empathic concern as the dependent variable, showed no significant effect of task, $F_{(1,29)} = 0.234$, p = .632, nor of group, $F_{(1,29)} = 0.02$, p = .882, but did show a significant interaction between the two, $F_{(1,29)} = 4.77$, p = .037, $\eta^2_p = .141$. As above, we ran two sets of post-hoc tests. As with willingness to help, the first set showed that empathic concern was significantly higher in the *imagine* vs. *words* condition among healthy controls, $t_{(15)} = 2.91$, p = .043, but not among mTLE patients, $t_{(15)} = -0.49$, p = .634 (see Fig. 4). Means are as follows: in the *imagine* condition, healthy controls M = 4.43, SD = 0.57; mTLE patients M = 3.99, SD = 1.13; and in the *words* condition, healthy controls M = 4.13, SD = 1.14. There was no significant effect of the gender covariate ($F_{(1,29)} = 0.274$, p = .604).

As in Experiment 1, we ran a third ANOVA to verify that episodic simulation increased the vividness of any spontaneous mental imagery associated with the helping scenarios. We found a significant main effect of the *imagine* condition, $F_{(1,29)} = 21.26$, p < .001, $\eta^2_p = .423$, and, while there was no main effect of participant group, $F_{(1,29)} = 0.592$, p = .448, there was a significant interaction between task and group, $F_{(1,29)} = 11.41$, p = .002, $\eta^2_p = .282$. Post-hoc paired samples t-tests (corrected for multiple comparisons as per Holm [1979]) indicated this was due to episodic simulation inducing a larger increase in vividness in controls, t (15) = 6.16, p < .001, compared to patients, t (15) = 2.26, p = .039 (see Fig. 4). Means are as follows: in the *imagine* condition,

healthy controls M = 5.59, SD = 0.91; mTLE patients M = 4.91, SD = 1.19; and in the *words* condition, healthy controls M = 2.73, SD = 1.89; mTLE patients M = 4.06, SD = 1.67. There was no significant effect of the gender covariate ($F_{(1,29)} = 2.24$, p = .146).

6.3. Mediation analysis

As in Experiment 1, we ran a multi-level moderated mediation analysis with episodic simulation as the predictor, willingness to help as the outcome, vividness as the mediator, and a binary moderator variable for participant group (1 = healthy control; 0 = mTLE patient). We were unable to run an analogous moderated mediation analysis for empathic concern because, consistent with our participant-level ANOVA, the relationship between episodic simulation and empathic concern before accounting for vividness (i.e., the *c* path) was not significant ($\beta = .26$, SE = 0.15, p = .089). To check whether vividness predicted empathic concern outside of a mediation model, we ran a regression model with vividness, participant group, and their interaction term as predictors, and empathic concern as the outcome variable, collapsing across imagine and words trials to allow for greater statistical power and fewer degrees of freedom. This analysis confirmed that vividness significantly predicted empathic concern (β = .28, SE = 0.06, p < .001), with no significant effect of the interaction term ($\beta = 0.03$, SE = 0.08, p = .695).

In the mediation model for willingness to help, episodic simulation was a significant predictor of vividness, but there was a significant moderating effect of being an mTLE patient (estimate = .59, 95% CI = [0.29, 0.95]) consistent with our participant-level ANOVA. Specifically, the effect of episodic simulation on vividness was significantly greater for healthy controls (β = 2.88, SE = 0.26, p < .001) than it was for mTLE patients ($\beta = 0.84$, SE = 0.26, p = .001). Regardless of group membership, vividness was a significant predictor of willingness to help $(\beta = .29, SE = 0.06, p < .001; see Fig. 5)$, again replicating previous work (Gaesser et al., 2015, 2017a; 2018; Gaesser and Schacter, 2014) and our Experiment 1. The effect of episodic simulation on willingness to help was completely mediated by vividness, as the c' path (the effect of episodic simulation on willingness to help after accounting for vividness) was non-significant ($\beta = .10$, SE = 0.22, p = .637; see Fig. 5). Importantly, however, as indicated by the index of moderated mediation reported above, the mediating effect of vividness was significantly

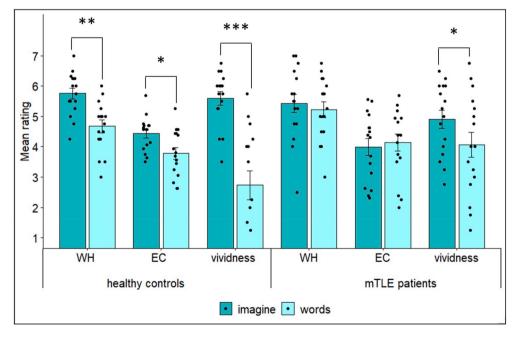


Fig. 4. Participants' ratings of willingness to help (WH), empathic concern (EC), and vividness by group and task. Error bars represent the SE. Post-hoc t-tests within groups: ***p < .001, *p < .01, *p < .05.

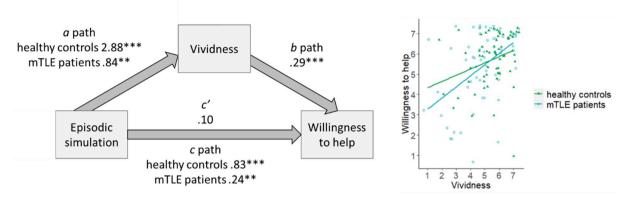


Fig. 5. Mediation analysis in healthy controls and mTLE patients, with scatterplot for willingness to help and vividness. All values are beta coefficients. ***p < .001, **p < .01.

greater for healthy controls ($\beta = 0.83$, SE = 0.20, p < .001) than it was for mTLE patients ($\beta = 0.24$, SE = 0.09, p = .009). Note that, when the moderated mediation component of the model was excluded, the effect of episodic simulation on willingness to help (i.e., the *c* path) was significant ($\beta = 0.64$, SE = 0.19, p = .001). Altogether, these results indicate that the diminished effect of episodic simulation on willingness to help in mTLE patients, compared to healthy controls, is driven by a diminished effect of episodic simulation on the vividness of imagined events in mTLE patients.

6.4. Internal and external details in transcripts of imagined helping events

Regarding the transcripts, an ANOVA showed main effects of detail type, $F_{(1,30)} = 57.28$, p < .001; and of being a healthy control, $F_{(1,30)} = 8.39$, p = .007; along with an interaction between the two, $F_{(1,30)} = 10.31$, p = .003. Post-hoc t-tests confirmed, as predicted, that controls produced more internal details (M = 26.67, SD = 7.73) than mTLE patients (M = 15.75, SD = 8.26), $t_{(30)} = 3.858$, p = .001, but the groups did not differ on external details (controls: M = 13.02, SD = 6.47; patients: M = 10.23, SD = 7.76), t (30) = 1.101, p = .280 (post-hoc p's corrected for multiple comparisons as per Holm [1979]). Next, we used a multi-level model with the same specifications as in Experiment 1, to examine whether internal details were related to vividness, willingness to help, and empathic concern, and whether these relationships differed by participant group. None of the variables predicted, nor interacted with participant group to predict, internal details. In an analogous model with external details as the outcome variable, empathic concern significantly predicted fewer external details ($\beta = -1.79$, SE = 0.77, p = .022) but interacted with identification as a healthy control to predict more external details ($\beta = 3.78$, SE = 1.09, p < .001). Running separate models for controls and patients, with empathic concern as the predictor and external details as the outcome, revealed that empathic concern was marginally related to external details in controls ($\beta = 1.57$, SE = 0.72, p = .070 [p = .035 uncorrected]) but not in patients $(\beta = -0.64, SE = 0.57, p = .264;$ post-hoc p's adjusted for multiple comparisons as per Holm [1979]). Analyses of subtypes of internal details can be found in the Supplementary Material.

6.5. Auxiliary analyses

To be consistent with Experiment 1, we compared mTLE patients and healthy controls on their performance in the phonemic fluency task. There was no significant difference in the total number of words generated, $t_{(29)} = -1.80$, p = .083, so we did not conduct any further analyses (see Supplementary Material for descriptive statistics).

As in Experiment 1, we compared all measures, for mTLE patients

and healthy controls separately, between the first and second block. Healthy controls generated more words in the phonemic fluency task in the second block (M = 24.93, SD = 6.01) compared to the first (M = 23.17, SD = 5.85), $t_{(14)}$ = -2.66, p = .019, as did mTLE patients (first block: M = 18.84, SD = 7.19; second block: M = 21.19, SD = 6.33), $t_{(15)}$ = -3.54, p = .003. We assert that these are simple practice effects, as can be expected in any experiment. More importantly, there were no significant differences regarding willingness to help or empathic concern (see Supplementary Material), and we believe this helps address potential concerns about demand characteristics. There were also no significant differences for subjective vividness.

6.6. Exploratory analysis: age of seizure onset

Previous work from our lab (Cohn et al., 2015) and in other labs (e.g., Giovagnoli, 2014; Sidhu et al., 2015) has found that earlier age of seizure onset in mTLE patients is associated with greater impairments in memory and in theory of mind. In addition, the early years of life are known to be a critical period for social development (e.g., Anderson et al., 2018), so we were curious whether age of seizure onset was playing an unanticipated role in our present sample, even with the extent of resected hippocampal tissue being the same for all the patients. We computed a difference score for each mTLE patient by subtracting his or her mean willingness to help rating in the words condition from that in imagine condition; the same was done for empathic concern. We then ran a simple correlation and found that age of onset was significantly correlated with difference scores for willingness to help (r = .643, $R^2 = 0.414$, p = .01; see Fig. 6), a relationship that remained significant after controlling for the effect of age in a partial correlation (r = .561, p = .037). The results for empathic concern, however, were not significant (p's \ge 0.383).

7. Experiment 2 discussion

We had predicted that healthy controls, compared to mTLE patients, would produce a greater number of internal details in their descriptions of imagined helping events, and that this would be accompanied by a more pronounced effect of episodic simulation on both willingness to help and empathic concern in controls. Each of these predictions were borne out by the data. In fact, among mTLE patients, episodic simulation did not significantly increase willingness to help, nor empathic concern. Our predictions regarding the mediating role of vividness were also fulfilled, at least for willingness to help. Not only did vividness mediate the effect of episodic simulation on willingness to help, but its mediation was significantly weaker in mTLE patients compared to controls. This result dovetails with our finding that episodic simulation influenced

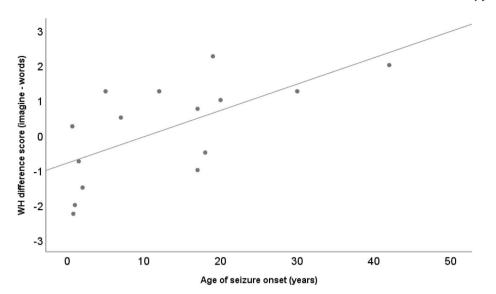


Fig. 6. Willingness to help (WH) difference score (mean imagine rating - mean words rating) plotted against age of seizure onset.

vividness ratings to a lesser degree in the mTLE group, but is complicated by the fact that mTLE patients' vividness ratings appear to be higher at baseline (even if they are not significantly so) than those of controls.

There are at least two plausible explanations as to why our mTLE patients gave relatively high vividness ratings at baseline. One is that they are so severely impaired in their ability to mentally render episodes in detail, and in their ability to recognize this lack of detail, that they not only rated scenarios in the *imagine* condition as being as vivid as those in the *words* condition, but they rated both as quite vivid (whereas controls rated scenarios in the *words* condition as much less vivid).

A second, and more interesting, possibility has to do with greater emotional reactivity on the part of mTLE patients. This idea is supported by a recent study on moral decision-making in (non-epileptic) MTL patients (McCormick et al., 2016). In that study, MTL patients were less likely than healthy controls to endorse "cold-blooded" utilitarian responses to highly sensitive moral dilemmas and, when interviewed afterward, cited emotional reasons for this behaviour. Further, they also exhibited more intense skin conductance in response to these scenarios, compared to controls, "corroborating" their oral accounts of emotional aversion (McCormick et al., 2016). Similarly, in the present study, our mTLE patients may have responded to our "helping" scenarios more emotionally, such that they experienced relatively vivid imagery even in the baseline condition. After all, another moral decision-making study, among healthy individuals, found links between "emotional" (as opposed to utilitarian) responses and spontaneous imagery of the individuals in the hypothetical scenarios suffering (Amit and Greene, 2012). Perhaps subjective, phenomenological qualities are more important for prosocial responding than are context-specific details. Indeed, we did not find internal details to be related to either willingness to help or empathic concern in either mTLE patients or healthy controls. Moreover, our mediation analysis showed that the effect of episodic simulation on willingness to help was fully mediated by subjective vividness. Thus, much as in Experiment 1, where episodic simulation apparently allowed young adults to catch up to older adults in terms of empathic concern, episodic simulation may have allowed healthy controls to catch up to mTLE patients in both willingness to help and empathic concern. This interpretation is consistent with reports from other labs of temporal lobe epilepsy patients giving significantly higher ratings of emotional arousal in response to both narratives (Múnera et al., 2015) and scenes (Ciuffini et al., 2018; Hennion et al., 2015) when compared to healthy controls.

These findings, however, are qualified by the results of our

exploratory analysis on age of seizure onset. We found that mTLE patients who did not develop seizures until later in life (roughly speaking, after childhood) performed more similarly to healthy controls with respect to the effect of episodic simulation on willingness to help. While these data mesh with other work linking earlier age of onset to greater difficulties both with psychosocial functioning in general and with theory of mind in particular (for review see Bora and Meletti, 2016), we did not find the same pattern with respect to empathic concern. Broadly speaking, these findings may indicate a relatively stronger influence of MTL function on one's emotional reactivity (e.g., Ciuffini et al., 2018; Hennion et al., 2015; Múnera et al., 2015) compared to one's hypothetical willingness to help, which may be more strongly influenced by environmental factors. Experiencing seizures in public, or among one's peers, early in one's life may have unforeseen social and emotional consequences that, depending on a variety of environmental factors, could either enhance or impede empathic responding and be closely intertwined with the patient's quality of life and perceived support (e.g., Aydemir et al., 2004; Giovagnoli and Avanzini, 2000; Giovagnoli et al., 2013; Lehrner et al., 1999).

Most important for the present investigation, however, is that the mTLE patients in Experiment 2 performed similarly to the older adults in Experiment 1, at least with respect to internal detail production and the effect of episodic simulation on empathic concern. Not only does this mirror previous studies (Addis et al., 2010, 2008; Lechowicz et al., 2016; Levine et al., 2002; Sheldon et al., 2011, 2015; St-Laurent et al., 2014, 2009), but it suggests that the difference we observed between young and older adults, in the effect of episodic simulation on empathic concern, is related, in part, to deteriorating MTL function.

8. General discussion

We found that, in healthy young, older, and middle-aged (control) adults, episodic simulation can significantly increase one's willingness to help people in situations of need, replicating previous work (Gaesser et al., 2015, 2017a; 2018; Gaesser and Schacter, 2014). Such an increase, however, may depend on whether episodic simulation is compared to a "baseline" condition or a condition that involves directed retrieval of conceptual helping information (cf. Gaesser et al., 2017b). We also found that episodic simulation can increase empathic concern in healthy young and middle-aged adults, but has no significant effect on the empathic concern of older adults or mTLE patients, both of whom express a relatively high level of empathic concern even without the use of episodic simulation. We again replicated previous work showing that

participants' ratings of the vividness of their imagined helping events is associated with their willingness to help, and showed that vividness is also related to empathic concern. Further, we showed that the positive effects of episodic simulation on willingness to help are completely mediated by vividness in all of our participants. As predicted, however, the mediation was significantly weaker in mTLE patients compared to healthy controls, due to a diminished effect of episodic simulation on vividness in the mTLE group. Last, while our predictions regarding diminished production of internal (context-specific) details in older adults and mTLE patients were supported, we did not find a strong relationship between internal details and either willingness to help, empathic concern, or even vividness. Rather, our findings highlight the importance of subjective, phenomenological aspects of episodic simulation.

Previous work has shown that the overall positive valence of the imagined event increases willingness to help (Gaesser et al., 2017a), but the present study is the first to test and demonstrate an increase specifically in empathic concern as a consequence of episodic simulation, at least in young and middle-aged adults. While empathic concern and willingness to help are closely related constructs, they are clearly not synonymous given our finding that, in older adults, episodic simulation influenced willingness to help but not empathic concern. Indeed, willingness to help suggests a controlled and planned exercise of volition, which may or may not be influenced by emotion, while empathic concern represents a more affective construct, being the average of several different emotional reactions (compassion, sympathy, tenderness, warmth; Batson, 2011; Batson et al., 1997). One of the broader implications of our findings is the notion that, while episodic simulation can influence various psychological functions, from empathizing to economic decision-making to open-ended problem-solving (e.g., Benoit et al., 2011; Boyer, 2008; Gaesser and Schacter, 2014; Palombo et al., 2015; Rubin et al., 2014; Sheldon et al., 2011, 2015), the underlying mechanisms may be quite different depending on the specific cognitive and emotional parameters associated with the task at hand. Perhaps solving problems and making judgments or decisions that are less emotionally charged or value-based benefits more from the mental construction of context-specific detail, while the resolution of emotional or interpersonal dilemmas is more clearly informed by the subjective vividness with which hypothetical outcomes can be represented. Interestingly, while there is evidence that the effect of episodic simulation on temporal discounting is associated with the subjective vividness of imagined events (Peters and Büchel, 2010), that study found increased activation not in the hippocampus but in other nodes of the autobiographical memory network such as the retrosplenial, ventromedial prefrontal, and left parietal cortices. The parietal cortex in particular has been associated with the richness of semantic information (e.g., Ferreira et al., 2015). In addition, while Benoit et al. (2011) also showed that episodic simulation decreases temporal discounting, and that this was associated with hippocampal activity, they found that the effect was strongest when imagined events were rated with higher emotional intensity. Hence, our study harmonizes with other voices in the literature proclaiming that understanding the subjective qualities of imagined events is paramount to understanding the effects of episodic simulation on tasks involving judgment and decision-making. Just as important is the delineation of the roles played by different brain areas within the autobiographical memory network.

That being said, and regardless of which subjective quality is carrying the day, the similar performance of older adults and mTLE patients, compared to their respective control groups, suggests that the positive effects of episodic simulation on empathic concern and willingness to help, in healthy young adults, are related, in part to MTL function, as we suspected. This interpretation is consistent with previous work on episodic simulation, which indicates that both older adults and mTLE patients are impaired in their ability to imagine detailed, contextspecific events (Addis et al., 2010, 2008; Lechowicz et al., 2016; Sheldon et al., 2011, 2015). As we have acknowledged earlier, the MTL is not the only brain region implicated in episodic simulation, and it is not the only the brain region affected by aging. Therefore, it is conceivable that the differences we saw in OAs could be related to frontal lobe issues (e.g., Campbell et al., 2012; Grady, 2008; Manenti et al., 2013; Troyer et al., 1997). While assessing frontal lobe functioning is beyond the scope of the present study, we note that OAs did *not* show a deficit on our phonemic fluency task, which is known to rely on lateral frontal regions (e. g., Madden et al., 2019; Manenti et al., 2013; Smirni et al., 2017; Troyer et al., 1997; Tupak et al., 2012). What is more puzzling, however, is that the reason the older adults and mTLE patients in the present study showed smaller effects of episodic simulation compared to their respective control groups is that they gave higher ratings of empathic concern and willingness to help at baseline (even if not significantly higher, in the case of the patients). In the next section, we discuss possible explanations for this phenomenon.

First, as we discussed earlier, mTLE patients may respond more emotionally to scenario-based stimuli than do healthy controls (e.g., Ciuffini et al., 2018; Hennion et al., 2015; Múnera et al., 2015). Though the literature is inconsistent in this regard (cf. Beadle et al., 2013; Craver et al., 2016), differences in etiology may have important implications for social cognition and emotional decision-making. For example, a 30-year-old who has had recurrent seizures since childhood prior to MTL surgery may have had very different social and emotional experiences compared to someone who has been relatively healthy until sustaining an anoxic brain injury in adulthood (see Experiment 2 discussion). Such individual differences may also explain why the patients in our study responded more emotionally than those in others, and future research is needed to delineate such differences more clearly.

With respect to older adults, there is evidence that they, too, respond more emotionally than young adults (e.g., Albouy and Décaudin, 2018; Fernández-Aguilar et al., 2018). Such behaviour may be related to greater life experience and prior knowledge (Ardelt, 2010; Carstensen, 2006; Moore et al., 2015; Umanath and Marsh, 2014; see also Gaesser and Schacter, 2014, Exp. 3), as well as a positivity bias (for reviews see Carstensen and DeLiema, 2018; Carstensen and Mikels, 2005) which may influence empathy. Another possibility is that older adults take a more rule-oriented (or "deontological") approach to making judgments in hypothetical social situations (e.g., "one must always help those in need"), instead of considering the plausibility or desirability (among other factors) of helping on a case-by-case basis, which may have led some of their ratings to be lower, as were those of young adults (for examples of deontological decision-making in older adults, see Lim and Yu, 2015; McNair et al., 2018).

Such an approach may also have been taken by our mTLE patients, though perhaps for different reasons. There is behavioural and neuroimaging evidence from both healthy and clinical samples that the MTL is important for responding to idiosyncratic, open-ended problems that require creative, context-specific solutions (e.g., Madore et al., 2019; Rubin et al., 2014; Sheldon et al., 2011, 2015). Indeed, our findings related to MTL impairment in the present manuscript nicely converge with emerging evidence in healthy individuals showing that activity within the MTL subsystem, specifically in the parahippocampus and hippocampus, predicted willingness to help when participants imagined and remembered helping events (Gaesser et al., in press), suggesting a direct link between episodic processing in the MTL and prosocial intentions. Nevertheless, the MTL not only supports episodic simulation (Andrews-Hanna et al., 2014) but is also associated with individual differences in creativity (Beaty et al., 2014), acting in concert with a frontoparietal network to support goal-directed cognition (Spreng et al., 2010) and divergent thinking (Beaty et al., 2015). Future research should employ neuroimaging techniques to examine how the MTL interacts with other systems, and with the frontoparietal network in particular, to contribute to the prosocial effects of episodic simulation. Moreover, future studies using a neuroimaging approach may shed additional light on the unique contributions and interplay among vividness, internal detail, emotionality, and other aspects of imagined

events.

Last, we did not find an association between subjective vividness and internal details in any participant group, which was somewhat surprising. Other studies, however, have also reported a dissociation between these two variables (e.g., Addis et al., 2007, 2011; Kirwan et al., 2008; Levine et al., 2009). Recent work suggests that indeed they are supported by different neural substrates, with the hippocampus being sensitive to subjective vividness and lateral parietal cortex being sensitive to internal details (Thakral et al., in press). It is noteworthy, given our hypothesis of the role of the hippocampus in episodic simulation and prosociality, that in our study it is subjective vividness, not internal details, that mediates the effect of episodic simulation on willingness to help. It may be that subjective vividness ratings reflect the salience (Cooper et al., 2019) or availability (D'Angiulli et al., 2013) of internal details, regardless of their number.

What we can say conclusively is that, while episodic simulation leads to greater willingness to help and empathic concern in healthy individuals, this effect appears to rely more on the subjective vividness of imagined events than on context-specific detail that can be measured by independent observers. In MTL patients, the link between vividness and some prosocial behaviours and attitudes may be compromised. This is not to detract from the importance of previous work linking contextspecific detail to open-ended problem-solving (e.g., Sheldon et al., 2011, 2015) or concrete (as opposed to abstract) construal to future intentions (e.g., Gollwitzer and Brandstatter, 1997; McCrea et al., 2008). Rather, it underscores the value of also studying the subjective, phenomenological features of imagined events. Future research on episodic simulation should also investigate more concrete measures of prosocial responding, as well as moral decision-making, to paint a more complete picture of the role of the MTL in the everyday lives in healthy controls and in people with compromised MTL functioning, be it due to trauma or normal aging.

Declaration of competing interest

None of the authors have any conflicts of interest to declare.

CRediT authorship contribution statement

Caspian Sawczak: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing original draft, Writing - review & editing, Visualization. Mary Pat McAndrews: Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition. Brendan Gaesser: Writing - review & editing, Supervision. Morris Moscovitch: Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2019.107243.

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