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Gender identity better than sex explains individual differences in episodic and semantic components of autobiographical memory: An fMRI study

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ABSTRACT

Advances in the literature of sex-related differences in autobiographical memory increasingly tend to highlight the importance of psychosocial factors such as gender identity, which may explain these differences better than sex as a biological factor. To date, however, none of these behavioral studies have investigated this hypothesis using neuroimaging. The purpose of this fMRI study is to examine for the first time sex and gender identity-related differences in episodic and semantic autobiographical memory in healthy participants ($M=19$, $W=18$). No sex-related differences were found; however, sex-related effects of masculine and feminine gender identity were identified in men and women independently. These results confirm the hypothesis that differences in episodic and semantic autobiographical memory are best explained by gender but are an interaction between biological sex and gender identity and extend these findings to the field of neuroimaging. We discuss the importance of hormonal factors to be taken into consideration in the future.

1. Introduction

An increasing number of studies show that between-subject differences in autobiographical memory (AM) are better explained by gender, identified as a social source of variance, than sex, identified as a biological source of variance (Compère et al., 2018; Grysman and Fivush, 2016; Grysman et al., 2016; Grysman, 2014, 2016; Grysman et al., 2017). These studies usually discuss behavioral differences, which mainly concern the phenomenology and/or emotional aspects of AMs. However, to our knowledge, no study has yet investigated the neuronal substrates of these differences rely on.

The most widely acknowledged models of AM conceive it as a dynamic reconstruction of past events in which self-information is stored at different levels of abstraction (Conway and Pleydell-Pearce, 2000; Conway et al., 2004). Two levels of storage of self-related memories are usually distinguished:

- *Episodic autobiographical memory (EAM)*, the most specific level of self-information, that allows the recollection of memories with the feeling of traveling back in time to relive the personal experience by

recalling many details related to the context and occurrence of the event (Tulving, 2005), and;

- *Semantic autobiographical memory (SAM)* that refers to factual knowledge about oneself or the recall of general events, i.e., either repeated events (e.g., walking my dog every morning) or events extended over time (e.g., my last Christmas holidays in New York).

This hierarchical organization of AM is supported by the fact that neuroimaging has shown evidence of distinct patterns of activation for each type of autobiographical content (Martinelli et al., 2013; Svoboda et al., 2006). Moreover, one of the peculiarities of this conception of AM is that it suggests a complex and bidirectional relation between the concept of self and memory (Addis et al., 2004; Conway, 2005; Klein and Lax, 2010). This organization of AM, confirmed by investigations in experimental psychology, neuropsychology, and cognitive neuroscience, allows individuals to enjoy a sense of continuity in time on which the feeling of personal identity rests (Addis and Tippett, 2008; Prebble et al., 2013).

Being a man or a woman is an essential part of who we are, and allows us to predict a person's behavior, preferences, and social expect-

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tations (Garcia-Falgueras, 2014). Indeed, sex is one of the most salient social categories in our societies and is associated with several social assessments (Grysmann and Hudson, 2013). Thus, data from research in cognitive psychosociology suggest that individuals actively form gender schemas through their social relationships, which, in turn, define their behavioral choices. Moreover, being a man or a woman goes with some hormonal and genetic features that can also have consequences on the brain and cognition (Mann et al., 1990; Sacher et al., 2013). These differences are reported by neurobiological studies on animals for which human cultural explanations cannot be used to explain the observed differences (Andreano and Cahill, 2009). In summary, the sex-related differences in cognition reported in the literature could, therefore, reflect the influence of a set of multiple factors and distinguishing between these different sources of influence is a compelling but complex scientific issue.

From the biological perspective, sex hormones are one of the most interesting explanatory avenue proposed by the literature since they are known to influence behavior and cognition. Notably, Wassell et al. (2015) showed that the concentration of sex hormones affects the strength and vividness of mental imagery, whose fundamental role in episodic memory is well known. From the social perspective, social stereotypes are also known to have an impact on cognition (for an illustration of this influence, the stereotype threat effect, see, for example, Wraga et al., 2007).

In the clinical and scientific literature, the word “sex” often refers to biological aspects expressed in a dichotomous way, whereas “gender” generally refers to the psycho-social and behavioral aspects that go beyond this binary categorization. However, like “sex”, “gender” also tends to be expressed in a dichotomous way in most Western societies. Because of this, these terms are sometimes used interchangeably, although the word “gender” is preferably chosen to refer to a psychological variable, namely the combination of an individual’s self-concept and their role in society (Andreano and Cahill, 2009). Nevertheless, most of these studies report gender-related differences by asking participants to identify themselves as male or female and use this identification as a basis for comparison. We will therefore refer to the results of these studies as sex differences and will use the term gender differences later in this introduction to describe the results of the few studies that directly investigated participants’ gender identities.

Overall, the literature shows evidence of performance differences in several cognitive functions between men and woman (e.g., visuospatial skills and written language comprehension, see Weber et al., 2014), one of which is episodic memory (for a review, see Herlitz and Rehnman, 2008). It has often been suggested that this female advantage is related to women’s superior verbal abilities (e.g., Herlitz and Rehnman, 2008), even if their episodic memory advantage extends to non-verbal stimuli (e.g., faces, pictures, smells, Maitland et al., 2004) and manipulated contexts that minimize the use of verbal strategies (Lewin and Herlitz, 2002). Another hypothesis of this female advantage is linked to the feminine stereotype that women are more emotional than men (Lockenhoff et al., 2014); therefore, it is argued, women recall more emotional material than men (Davis, 1999). However, sex-related differences also appear with neutral material; therefore, different emotion management cannot by itself explain the female advantage shown in memory (Bloise and Johnson, 2007).

The same explanatory hypotheses of behavioral differences between men and women are found in AM. Thus, women are assigned better performances in EAM than men, not only quantitatively, i.e., in terms of the number of details provided or speed or number of memories recalled (Davis, 1999; Pillemer et al., 2003; Pohl et al., 2005; Skowronski et al., 1991), especially those of an emotional nature (Friedman and Pines, 1991; Fuentes and Desrocher, 2013; Herz and Cupchik, 1992), but also qualitatively, i.e., when investigating the content of autobiographical narratives of personal memories (e.g., more interdependent memory narratives for women, Grysmann and Hudson, 2013). These behavioral data are also supported by neuroimaging

data suggesting that women may persist with the elaboration of AMs to a greater extent than men (Manns et al., 2018), and that sex-differences in emotional memory are underlined by differences in the amygdala (Cahill et al., 2004).

The literature on sex-related differences in SAM is sparser. Fuentes and Desrocher’s (2013) study investigated the production of semantic details (i.e., details that refer to a specific event recalled but which are part of general knowledge or personal knowledge not specific to the event, e.g., the names of the acquaintances present at the event) during the recollection of EAMs and showed no sex-related differences in the production of this type of details. However, since the methodology used in the study did not study SAM per se, it is difficult to adjudicate for or against the existence of sex-related differences in SAM.

To our knowledge, only four studies have used functional neuroimaging to study sex related-differences in autobiographical recall. All demonstrated common and distinct neural mechanisms underlying the recall in men and women, the results varying slightly according to the methodologies employed.

In the first study (Piefke et al., 2005), participants were asked to recall EAMs in response to cues obtained from a previous semi-structured autobiographical interview. The results showed that only the left parahippocampal region was activated significantly more in men while the right dorsolateral prefrontal cortex (DLPFC) and insula were more activated in women. As no behavioral sex-related differences were observed, the authors interpreted their data as suggesting the use of cognitive strategies that were different but of comparable efficiency, in that women may rely more on temporal context while men rely on the spatial context during recall. The second study (St. Jacques et al., 2011) used an experimental design enabling to contrast recent AMs retrieved from visual versus verbal cues. The findings showed that men exhibit an activation pattern reflecting greater reliving and vivacity of the experience of remembering (i.e., greater activation in the hippocampus, retrosplenial and occipital cortex) when presented with visual versus verbal cues, while women did not show any difference between these two activation patterns, and, again, without any sex-related behavioral differences in the features of the recalled memories. The design of the third study (Young et al., 2013) was similar to that of the first one mentioned above, except that the control task was a semantic memory task of categorical fluency. Unlike the previous two studies, behavioral analyses showed evidence of behavioral sex-related differences regarding the valence of recalled AMs, in that women recalled more negative memories than men. All valences combined, women had increased activity in the DLPFC, left anterior dorsal insula, and right precuneus in comparison to men. Women also showed increased activity in the dorsolateral cortex and hippocampus bilaterally, and men only in the right hippocampus when comparing positive versus negative memories. Because of these valence-dependent results, the authors of the study suggested an alternative interpretation, namely that these differences indicated greater emotional control in women and were intended to minimize the evocation and intensity of negative AMs. Therefore, the first three studies favored the explanatory hypothesis of differences in strategies during the recall of AMs over differences related to the emotional processing of AM content when interpreting their results. However, some regions with increased activation in women (e.g., the insula or DLPFC, Piefke et al., 2005, Young et al., 2013) are well known to be involved in emotion processing or to support emotional regulation strategies (Goldin et al., 2008). Accordingly, the last and fourth study conducted to date (Compère et al., 2016) applied a method designed to minimize the differences in strategies between men and women. It used a control task (i.e., asking participants to imagine a non-personal mental scene) in order to remove from AM retrieval more basic retrieval strategies that may be subject to individual differences. The rationale behind this choice was that basic strategies at play during AM (e.g., the use of more visual or verbal strategies) would also be elicited by this control task, allowing the analyses to document differences in emotional processing and not differences in these strategies. Besides, while

the three early studies only investigated differences in EAM, the latter investigated separately sex-related differences in EAM and SAM separately using neuroimaging for the first time. While no sex-related behavioral differences were observed, this study evidenced that women had greater activation in the dorsal anterior cingulate cortex, left inferior parietal cortex, and left precentral gyrus compared to men in SAM only, which was interpreted by the authors as expressing differences in the implementation of emotional regulation strategies.

To summarize, all these findings suggest that different neuronal activation patterns in men and women underlie the use of different strategies related, at least partly, to emotional aspects of AMs. Some research indicates a link between emotional regulation strategies and social expectations (Kring and Gordon, 1998), implying that gender identity as a social construct could also influence these performance differences.

Grysmann and Fivush's team was the first to investigate whether the effects of gender in AM reflect exposure to cultural norms that can be modulated by gender identity. They defined gender identity as the feeling of endorsing gender-typical behaviors and the value attributed to this typicality (Grysmann et al., 2016). This concept attempts to account for the fact that, although individuals define themselves as members of a gender category, the importance given to this category in self-representation varies, as does the degree to which they think they conform to gender stereotypes. The rationale for studies investigating this concept is that individuals who claim to have stereotypical gender traits are more motivated to engage in gender-stereotypical activities (Grysmann and Fivush, 2016). Bem (1974) demonstrated that masculine and feminine gender identities are independent continuums, a result that has been replicated multiple times since then (for a review, see Grysmann and Fivush, 2016). Grysmann and Fivush's team showed that both gender stereotype scales (i.e., masculine and feminine, Spence and Helmreich, 1979) predicted participants' EAM phenomenology and content, regardless of their sex (Grysmann et al., 2016; Grysmann et al., 2017). Thus, the more participants identified themselves as feminine, the higher the quality of memories and their valence, i.e., events were recalled with more details, more vividly, more often shared; conversely, the more participants affiliated themselves with masculine gender stereotypes, the more they rated their memories as rich in sensory details (Grysmann and Fivush, 2016). However, all of these studies focused on the episodic component of AM. Therefore, in a previous publication, we extended this work by investigating the effects of sex and gender identity not only on EAM but also on SAM (Compère et al., 2018). This latter study replicated that gender identity was a better predictor than sex of between-participant differences in AM. Moreover, feminine gender identity was associated with differences in emotional aspects of EAMs and more abstract forms of knowledge about self, whereas masculine gender identity was, in line with previous studies, associated with more restricted effects. In addition, although novel and therefore requiring replication, our previous results suggested that some effects of masculine and feminine gender identity could be modulated by the participants' sex, suggesting a possible interaction between sources of biological and social variance whose separate influences on performances in AM have been evidenced (see for example, Schmader, 2002; Wassell et al., 2015). We therefore asked the sample of participants who had evidenced behavioural differences in AM in this previous study (Compère et al., 2018) to undertake another autobiographical task in fMRI to determine which interpretations were reinforced or invalidated by neuroimaging data.

As suggested by the results of our previously published behavioral data (Compère et al., 2018), we hypothesized that inter-individual differences in AM activation patterns would be better explained by gender identity than by sex. Behaviorally and in neuroimaging, we expected to replicate the previously obtained results in the same sample, i.e., that feminine gender identity would be associated with differences in emotional aspects of memories and that there would be significant interactions between sex and gender identity. In other words, given the results obtained in our former study, we expected that feminine gender

identity would be associated with higher activations in areas related to emotional processing and the use of emotion regulation strategies. Given the lack of previous neuroimaging studies conducted on gender-related effects in AM, we based the main hypothesis on the established sex-related effect in AM. We expected that the more participants had a feminine gender identity, the more they would exhibit an activation pattern matching that of women, i.e., greater activation in the dorso-lateral cortex and insula. In comparison, the more participants had a masculine gender identity, the more they were expected to exhibit an activation pattern matching that of men, i.e., with greater activation in hippocampal and parahippocampal regions.

2. Method

2.1. Participants

Fifty psychiatrically and medically healthy, right-handed (according to the Edinburgh Handedness Inventory, Oldfield, 1971) native French speakers between the ages of 18 and 38 years (25 males) participated in this study. Volunteers were recruited from the community via ads posted online and were evaluated at the Sainte-Anne Hospital. All participants gave their informed written consent to this protocol, which was approved by the ethics committee CPP Ile de France Paris 3 (n° Am7280-5-2981). Volunteers underwent medical and psychiatric screening evaluations that included the Mini-International Neuropsychiatric Interview (Sheehan and Lecrubier, 1998). Exclusion criteria included major medical or neurological disorders, a history of substance abuse, and exposure to any medication likely to influence cognitive function. Participants received financial compensation for their participation.

Following the discovery of contraindications to MRI scanning, protocol drop-out or MRI dysfunction at the time of acquisition, not all participant MRIs were collected or included in the analyses. As a result, data from 19 men and 18 women were analyzed as part of these results. Table 1 presents the means and standard deviations for age and years of education by sex of the participants involved in these analyses. The differences observed in our sample did not allow us to conclude that there were significant differences between men and women on age and years of education.

2.2. Gender assessment

Gender identity was assessed at a first screening visit two weeks before the fMRI scan. The Bem Sex Role Inventory (BSRI, Bem, 1974; French Adaptation, Alain, 1987) consists of 60 self-rated personality related items empirically identified by Bem as associated with gender stereotypes in North American and European culture. There are 20 masculine items, 20 feminine items, and 20 items that are gender neutral. Ratings are made on a scale ranging from 1 (never true of oneself) to 7 (always true of oneself). The inventory contains two independent scales for the domains of masculinity and femininity. The theoretical assumption of this widely used inventory is that both men and women have masculine and feminine gender attributes. Table 1 presents the means and standard deviations for masculine and feminine gender identity scores. Only the masculine gender identity score differed significantly between-group, meaning that men had a stronger masculine gender identity than women. This lack of sex difference in feminine gender identity score is consistent with previous results reported in two separate samples with an age range matching the one in this study (18-29, Grysmann, 2018; Grysmann and Fivush, 2016) using another scale highly correlated with the BSRI (Reilly et al., 2016).

2.3. Material

The items displayed during AM and control tasks were adjectives describing personality traits. For the selection of this material, we translated Bem's (1974) and Kirby and Gardner's (1972) lists of adjectives.

Table 1
Means (standard deviations) and analyses of the group effect on the population demographic data (BSRI = Bem sex role inventory).

	Participants		Group effect
	Men (n=19)	Women (n=18)	
Age	25.26 (± 3.23)	24.22 (± 4.57)	$t(30.45) = 0.80, p = 0.43$
Years of education	14.95 (± 1.58)	14.17 (± 1.79)	$t(33.91) = 1.40, p = 0.17$
BSRI masculine score	4.68 (± 0.56)	4.19 (± 0.78)	$t(30.75) = 2.20, p = 0.04$
BSRI feminine score	4.89 (± 0.47)	5.15 (± 0.58)	$t(32.68) = -1.48, p = 0.15$

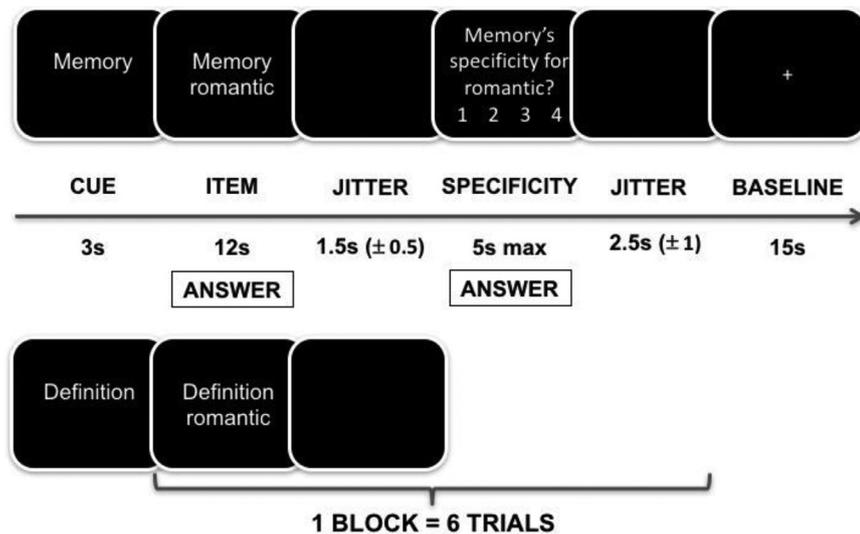


Fig. 1. Example of blocks in each condition of the fMRI autobiographical memory task.

From this translation, we created two lists of 98 items each and presented each list to two different sets of 50 participants (25 men and 25 women, therefore 100 participants in total). Participants were asked to evaluate each personality trait of their list on a scale of 1 to 5 along four dimensions: how well they understood the meaning of the item, if it described a man or a woman preferentially, if its valence was positive or negative and how hard it was to recall an AM using this item as a cue. This pre-test allowed us to discard items that might have been misunderstood or whose meaning was ambiguous. We then grouped the remaining items by gender characteristics (feminine, masculine or neutral) and valence (positive or negative).

From the adjectives whose spelling was the same in the masculine and feminine form, we created 8 lists of 6 items (half were positive/negative and one-third masculine/neutral/feminine), controlling that the frequencies of the items (Lexique 3.80, New et al., 2004) were the same according to their characteristics (gender and valence) from one list to another (see Table S1).

2.4. fMRI autobiographical memory task

The fMRI task distinguished two conditions. As this study aimed to document sex/gender differences in AM exclusively, i.e., the memory of self-referenced information, the AM condition was compared to a control condition designed to control for the retrieval of knowledge that was abstract/general but not self-related. The experimental condition was an AM recall task in which the participants had to recall, mentally, the most specific AM as possible, and the control condition was a definition task in which participants had to produce, mentally, a verbal definition as close as possible to a typical dictionary definition. Young et al. (2013) used a similar semantic memory control condition but preference was given here to a definition task that used the same cues as those used in the AM task, thus making it possible to control for basic retrieval and emotion processing and giving us an insight into participants' understanding of the material.

Before scanning, participants performed two training sessions on different items from those used at the time of the acquisition after an explanation of the instructions. Both training sessions corresponded to the protocol used during scanning, except that the first one provided additional feedback when the computer program did not identify a valid response (e.g., "answer faster" or "only one response is allowed"). Additionally, participants were instructed about the different types of AMs they might retrieve (according to conventional definitions used in the AM literature, e.g., Conway and Pleydell-Pearce, 2000; Martinelli et al., 2013; Prebble et al., 2013; Renoult et al., 2012) and were informed that their goal was to recall EAMs. A specific memory was defined as a memory that concerned unique, specific personal events characterized by both a precise spatial and temporal context and external and internal details remembered vividly, demanding mental time travel and the re-experiencing of the event (e.g., the performance of La Traviata that I attended at the Opera Garnier in February). If not specific, other AMs, called generic ones, were defined as memories of events we know about but we do not remember in which specific context they happened, they may concern either repeated (e.g., walking my dog every morning) or extended events (e.g., the weekend I went to Porto with my brother) that are retrieved without reliving a specific instance.

A computerized version of the experimental task was developed for use during fMRI. Visual stimuli display was provided by a mirror fixed on the head coil and adjusted by the participants so that they could comfortably see the material appearing behind them. Each block started with a cue displayed for 3 s indicating which task that they were about to perform (see Fig. 1) and then consisted of 6 trials. At the beginning of each trial, the item about which the participant had to recall a memory or think of a verbal definition was displayed for 12 s. During this item display, participants had to press the first button of an fMRI-compatible device with four response buttons as soon as they had identified a memory or a definition that fitted the criteria explained in the instructions and then continue to relive the memory in all its details or continue to work on the definition initiated until the end of the item display.

When a valid answer was recorded (i.e., when participants gave one answer during the time available), the on-screen white item became grey, while when recording an invalid response, the item became red to allow participants to identify their mistake. In the AM condition, when participants gave a valid answer, they additionally had to say how specific the memory recalled was. When they pressed the first button, participants indicated that they could not identify a specific event and that the only thing that came to their mind was a factual description about themselves. They pressed the second button when they were able to identify a generic event (i.e., either extended events that lasted more than 24 h, or repeated events). When they managed to recall an EAM (i.e., a specific, unique memory that occurred at a specific time and place, lasting less than a day, whose recall was associated with many details) or a very specific EAM (i.e., EAM criteria but in addition, participants were able to focus on a brief moment of the event that lasted a few seconds or minutes and felt as if they were reliving it fully in all its details), they pressed the third and fourth buttons respectively. Participants had a maximum of 5 s to indicate the specificity of their memory, but the task continued as soon as an answer was given. They were informed that their answer had been recorded by a green round feedback appearing around the selected answer on the screen.

All participants saw the same 48 adjectives in each condition. Each list was pseudo-randomly assigned to a block, was seen only once in each condition and never appeared twice in the same run or in two consecutive runs. The order of the blocks was pseudo-randomized in each group and the order of the items within a block was random. Scanning was divided into 4 runs with a duration of less than 10 min and each run consisted of 4 blocks (2 in each condition) and 2 baselines during which participants had to think of nothing specific.

Following the scan, the experimenter presented participants with all of the AM cue words again, in the same order as during the scan. Participants were asked if they remembered if they had had a memory (i.e., if they had provided an answer) and which specificity level they had chosen for this AM. Only debriefing data collected from AMs whose specificity level recalled matched the recorded one during scanning were analyzed.

Depending on the AM specificity level, participants had to specify some information about the AM. In the case of contextualized memories (2, 3 and 4), participants had to indicate their age at the occurrence of the event, their perspective in the mental imagery of the event (actor or observer), if the memory was unique, lasted less than 24 h and was located in time and space. This was done to verify that the AMs remembered truly met the criteria of the category they belonged to. Moreover, participants had to evaluate on Likert scales ranging from 1 to 5 the valence associated with the AM (1 = very negative, 5 = very positive) and from 0 to 5 the level of detail in time and space position (0 = no contextual information, 5 = very specific details). For episodic AMs (i.e., whose specificity level was rated as 3 or 4), participants were asked to use Likert scales ranging from 0 to 5 to evaluate the specificity level of sensory details (0 = no details, 5 = details with very high precision), how significant the event for them (0 = not significant, 5 = very significant), how vividly they relived the AM (0 = no impression of reliving the memory, 5 = reliving the event as a mental movie), the emotional intensity of the AM (0 = non-emotional AM, 5 = emotionally very intense AM), how much they talked or thought about the AM (0 = never talked or thought about the event since it happened, 5 = the participant talked or thought about this event very often since it occurred) and how old they were when they last talked or thought about this event, the importance of the AM for them (0 = not important, 5 = very important), the vividness of mental images (0 = no mental images of the event, 5 = numerous mental images of the event).

2.5. fMRI data acquisition

The fMRI scans were obtained using a 3T GE 750 MR scanner, with a twelve-channel receiver coil array (GE Healthcare, USA). Gradient-

recalled, echoplanar imaging (EPI) was used for fMRI with the following parameters: $42 \times 3 \text{ mm}^2$ sequential slices acquired axially with no gap, repetition time (TR) = 2,000 ms, echo time (TE) = 30 ms, flip angle = 90° , matrix = 64×64 , field of view (FOV) = 24 cm, voxel volume = $4 \times 4 \times 3 \text{ mm}^3$. Because the display duration of the response screens was determined by participants' response time, run duration and number of acquired volumes varied slightly from one participant to another. High-resolution T1 weighted anatomical fMRI scans ($136 \times 1.2 \text{ mm}$ slices acquired axially, TR = 11184 ms, TE = 4.25 ms, flip angle = 15° , matrix = 512×512 , field of view (FOV) = 25 cm, in-plane resolution = 0.5 mm^2) were also acquired for co-registration with the EPI series.

2.6. Assessment of behavioral performance during fMRI

Behavioral data were analyzed using R (version 3.3.1). Potential group and gender identity differences in the number of definitions given, in the memories recalled at each specificity level (episodic: 3 and 4, and, semantic: 1 and 2) and characteristics of the memories according to their specificity level, were assessed using linear and logistic mixed-effects models, with participants as a random factor. First, we modeled the effect of participants' sex to determine whether there were differences between men and women on each dependent variable (DV) (DV ~ sex). Then we investigated the effects of masculine and feminine gender identities on men and women (DV ~ sex * masculine BSRI, DV ~ sex * feminine BSRI), before investigating the effects of masculine and feminine gender identities irrespective of participants' sex (DV ~ masculine BSRI, DV ~ feminine BSRI).

2.7. fMRI processing and analysis

2.7.1. Preprocessing

Image preprocessing and analysis were performed using SPM 12 (*Statistical Parametric Mapping*, Wellcome Department of Imaging Neuroscience, London, UK, Friston et al., 2007). Image preprocessing consisted, in order, of within-subject realignment, coregistration between the anatomical and functional images when necessary, spatial normalization using a standard model included in the SPM12 software based on the segmentation of different tissues (Ashburner and Friston, 2005) and smoothing using a 8 mm full-width at half-maximum Gaussian kernel. After preprocessing, the 4 runs were concatenated one after the other in their order of acquisition.

2.7.2. First-level analysis

Regressors modeling the task and motion parameters were used in the model. The first-level model was designed to identify differences between the two experimental conditions (AM and definition) by distinguishing different types of AMs according to the level of specificity of the memories (memories whose specificity was evaluated at 3 or 4: EAM; memories whose specificity was evaluated at 1 or 2: SAM). For this purpose, the 3 main effects-of-interest were modeled independently at the first level: definition, EAMs and SAMs. Given that Young et al. (2013) had obtained interesting results based on the valence of specific memories when investigating sex-related differences, we also separated the negative and positive valence of EAMs, SAMs and definition. Therefore, we considered that memories recalled on the basis of positive valence cues were positive memories, that memories recalled on the basis of negative cues were negative and so on for definitions. This assumption was verified during analyses of the behavioral data collected during the debriefing showing that the cues' valence significantly predicted the valence of the memories recalled during fMRI acquisition ($\beta = 1.25, p > 0.001$), as suggested by previous literature (Schulkind and Woldorf, 2005; Sheldon and Donahue, 2017). The entire 12 s window of the item display was included. In addition to regressors modeling the main effects, each design matrix included regressors modeling rating selection, rejected trials (i.e., when participants did not give an an-

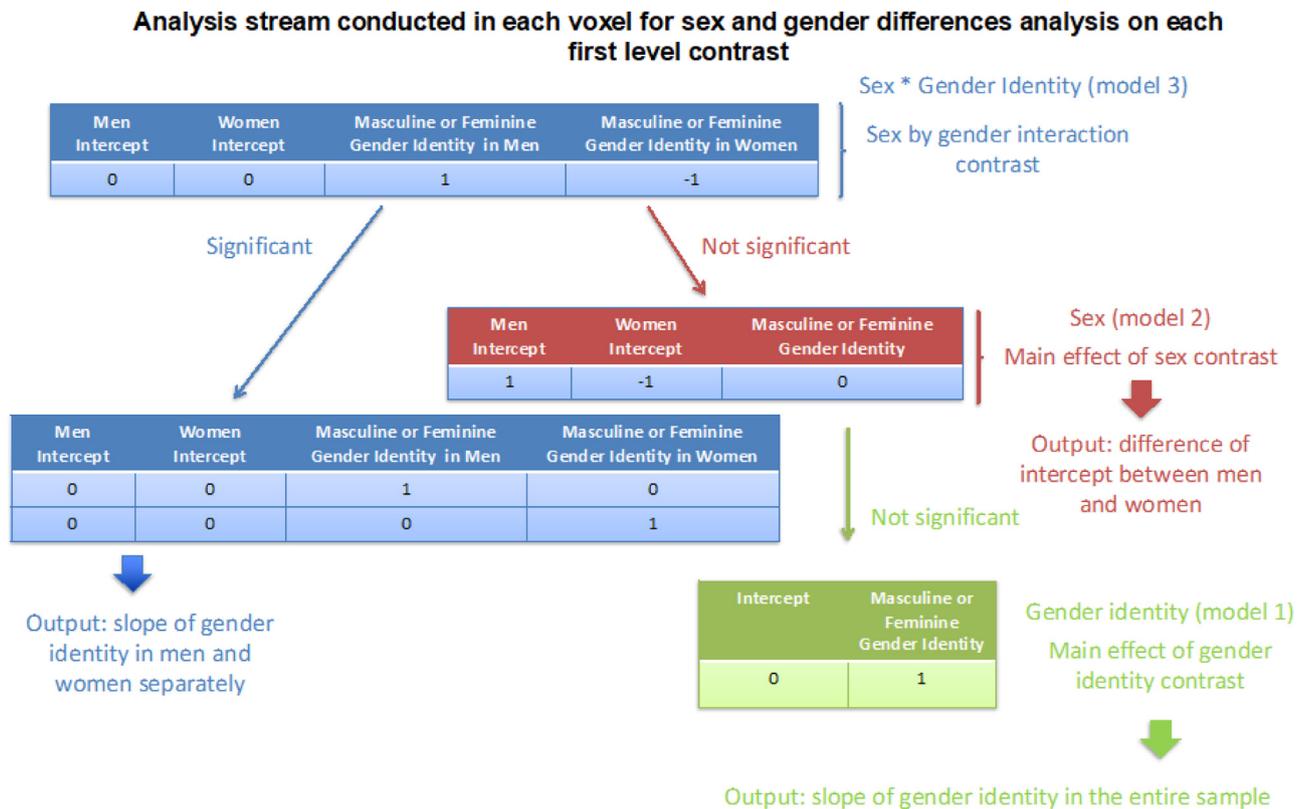


Fig. 2. Second level analyses and contrasts to investigate sex and gender identity interaction, carried out on masculine and feminine gender identity separately.

swer) and motor responses during memory and definition and memories' specificity ratings events. The display of the cues at the beginning of each block, and the baselines, were also each modeled as a regressors, i.e., their contribution to the variance of the signal was taken in to account in the model, but they were not included in the contrast analysis.

In addition to motion parameters, another type of confound regressors was also modeled, namely signal from regions identified as cerebrospinal fluid and white matter (one regressor each) during the normalization performed which allowed the segmentation of the different tissues because we did not use a high-pass filter given that the timing of a condition in a run with our protocol corresponded to the frequencies conventionally used (128 s period) to filter physiological effects (e.g., heartbeat, breathing, warm up, ...). We assumed that the modulations of the signal observed in the ventricles and the white matter reflected other processes than brain activity variation related to the cognitive mechanisms used to carry out the tasks of our experimental paradigm (Behzadi et al., 2007).

The regression coefficient for each regressor was estimated voxel by voxel by the software SPM12 on the basis of a convolution by the hemodynamic response curve of the design matrix using the algorithm "Expectation Maximization". This algorithm is formally equivalent to the covariance component estimation method using the "Restricted Maximum Likelihood" method to account for temporal correlation effects in the BOLD signal (Friston et al., 2002a, b).

The regression coefficients thus obtained, which reflect the contribution to the signal of the different sources of variance considered in the model, were subjected to contrasts defined a priori to highlight the mnemonic processes of interest. Images of these contrast values were formed for each participant and were subjected to a second-level analysis to account for inter-individual variability as a random factor (Holmes and Friston, 1998).

We made 9 contrasts of interests at the first level: EAMs vs. definition, SAMs vs. definition and EAMs vs. SAMs, each on every memory

combined regardless of their valence, then restricted to positive and negative memories independently.

2.7.3. Second-level analysis

At the group level, we first investigated the effects directly related to the experimental paradigm. For this, we performed t tests (Student, undefined, 1908) to determine which voxels had a level of activity significantly different from 0 on each of our first-level contrasts. The statistical threshold used was $p < .05$ corrected for multiple comparisons (Family Wise Error Correction - FWE, Worsley et al., 1996).

Second, we investigated the main effects of sex, masculine and feminine gender identity separately ($p < .05$ FWE correction).

Third, we investigated the interaction between sex and gender identity (see Fig. 2). To this end, we modeled the effects of sex – as intercepts and the effects of gender – a continuous covariate – as slopes in a multiple regression framework, following Jeanette Mumford's guidelines (http://mumford.fmripower.org/mean_centering/). We thus had to consider that the effect of gender identity could differ with respect to the sex as previous behavioral results suggested (Compère et al., 2018), e.g., that activation in a given brain area might increase with feminine gender identity in men and decrease in women. In such brain areas, the main effect of sex is irrelevant and the effect of gender has to be described for each sex. Thus, we first modeled the interaction between sex and masculine or feminine gender identity separately (model 3) and created a mask of clusters in which this interaction was significant (cluster forming threshold $p < 0.05$ FWE clusterwise correction). Inside this mask, we assessed the main effect of masculine or feminine gender identity separately for men and women. Outside this model 3 mask, as the interaction between sex and gender identity is non-significant, a more relevant model should include one slope: the effect of gender identity that does not differ between sexes. The remaining question is whether the effect of sex is relevant or not to describe the link between brain activations and our two factors. Indeed, if the difference between the intercepts is not significant in a model with two intercepts

Table 2
Behavioral characteristics of the study samples.

	Percent	Sex Effect	Masculine Gender Identity Effect	Interaction between Sex and Masculine Gender Identity	Feminine Gender Identity Effect	Interaction between Sex and Feminine Gender Identity
Autobiographical memories recalled						
Percent of all memories recalled (regardless of memories' specificity ratings)						
All	95.23	$\beta=0.79$,	$\beta=-0.34$, $p=0.47$	$\beta=2.59$, $p=0.01$	$\beta=-0.37$, $p=0.57$	$\beta=2.41$, $p=0.05$
Men	92.65	$p=0.27$	$\beta=-1.80$, $p=0.03$			
Women	97.81		$\beta=0.79$, $p=0.22$			

Table 3
Properties of EAMs and SAMs by sex and valence and analyzes of sex and gender identity effects and interaction.

	Mean(Std)	Sex Effect	Masculine Gender Identity Effect	Interaction between Sex and Masculine Gender Identity	Feminine Gender Identity Effect	Interaction between Sex and Feminine Gender Identity
Episodic Autobiographical Memories						
Valence of the event						
All	3.07(± 1.12)	$\beta=-0.21$, $p=0.14$	$\beta=0.21$, $p=0.03$	$\beta=0.16$, $p=0.47$	$\beta=0.27$, $p=0.03$	$\beta=-0.004$, $p=0.97$
Men	3.18(± 1.15)					
Women	2.98(± 1.10)					
Negative Episodic Autobiographical Memories						
Recall frequency						
All	1.31(± 1.46)	$\beta=0.01$, $p=0.96$	$\beta=0.09$, $p=0.63$	$\beta=0.98$, $p=0.045$	$\beta=0.51$, $p=0.03$	$\beta=0.02$, $p=0.97$
Men	1.30(± 1.37)		$\beta=-0.66$, $p=0.12$			
Women	1.32(± 1.54)		$\beta=0.33$, $p=0.15$			
Positive Episodic Autobiographical Memories						
Emotional Intensity						
All	1.72(± 1.82)	$\beta=0.39$, $p=0.30$	$\beta=-0.18$, $p=0.49$	$\beta=0.22$, $p=0.71$	$\beta=0.71$, $p=0.03$	$\beta=0.06$, $p=0.93$
Men	1.53(± 1.74)					
Women	1.91(± 1.91)					
Valence of the event						
All	3.65(± 0.97)	$\beta=-0.29$, $p=0.13$	$\beta=0.21$, $p=0.13$	$\beta=0.55$, $p=0.06$	$\beta=0.45$, $p=0.008$	$\beta=-0.11$, $p=0.72$
Men	3.81(± 0.90)					
Women	3.48(± 1.02)					
Personal relevance						
All	1.69(± 1.90)	$\beta=-0.22$, $p=0.63$	$\beta=0.10$, $p=0.74$	$\beta=-0.36$, $p=0.62$	$\beta=0.88$, $p=0.02$	$\beta=0.11$, $p=0.89$
Men	1.77(± 1.98)					
Women	1.62(± 1.83)					

and one slope, a more accurate model should only include one intercept and one slope. Thus, we modeled the effect of sex with a different intercept for men and women and gender identity with one slope (model 2). We created a mask of clusters in which the effect of sex was significant (cluster forming threshold $p < 0.001$, $p < 0.05$ FWE clusterwise correction). Inside this model 2 mask, we assessed the effect of masculine or feminine gender identity. Finally, in the regions concerned by neither of these two masks (models 3 & 2), we assessed the effect of masculine or feminine gender identity by testing for the slope in a model using a single intercept for all participants (model 1) (Fig. 2).

3. Results

3.1. Behavioral results

Participants' general task performances are presented in Table 2 and S1 (supplementary materials). There was no significant difference related to sex in the performance. Additionally, no differences were found in the number of memories recalled for each specificity type (episodic or semantic). However, the more men had a masculine gender identity, the less they recalled memories all types combined, and the more women had a feminine gender identity, the faster they were at recalling episodic and semantic memories combined but also more specifically negative and positive EAMs.

The main properties of memory recall are presented in Table 3 (see Table S3 for an exhaustive list of all analyses performed). Sex was not a significant predictor of any memories' properties. For specific memory recall (AMs whose specificity was rated as 3 or 4), only masculine and feminine gender identity were significant predictors of memories'

valence ($\beta=0.21$, $p=0.03$, and, $\beta=0.27$, $p=0.03$, respectively) revealing that the more all participants had a masculine or a feminine gender identity, the more they recalled positive memories. Regarding negative EAMs, the more participants had a masculine gender identity, the more they recalled memories with a high emotional intensity ($\beta=0.63$, $p=0.02$) and the more they had a feminine gender identity, the more they recalled negative EAMs ($\beta=0.51$, $p=0.03$). For positive EAMs, the more participants had a feminine gender identity, the more they recalled memories with a high emotional intensity ($\beta=0.71$, $p=0.03$), a positive valence ($\beta=0.45$, $p=0.008$), and personal relevance ($\beta=0.88$, $p=0.02$), and the less women recalled sensorial details ($\beta=-0.93$, $p=0.03$). For positive general memory recall (AMs whose specificity was rated as 1 or 2), the more men had a feminine gender identity, the more they recalled SAMs with a positive valence ($\beta=0.68$, $p=0.02$).

3.2. Imaging results

In the combined sample (Table S4), the mean BOLD activity was higher in the episodic AM recall versus the definition condition in the left DLPFC, bilateral angular cortex, left precuneus, bilateral cerebellum, right caudate, left parahippocampus, right middle temporal gyrus, right anterior cingulate cortex, and right cerebellum and in the semantic AM recall versus the definition in the bilateral ventrolateral prefrontal cortex (VLPFC), bilateral DLPFC, bilateral angular gyrus, left precuneus, left cerebellum and superior medial frontal cortex.

In the group comparison of all contrasts, there was no significant difference between sexes. However, there was a main effect of masculine gender identity in the left angular gyrus in the EAM recall versus the definition condition contrast, in that the more all participants had

Results of second level analysis on the first level EAM versus SAM contrast

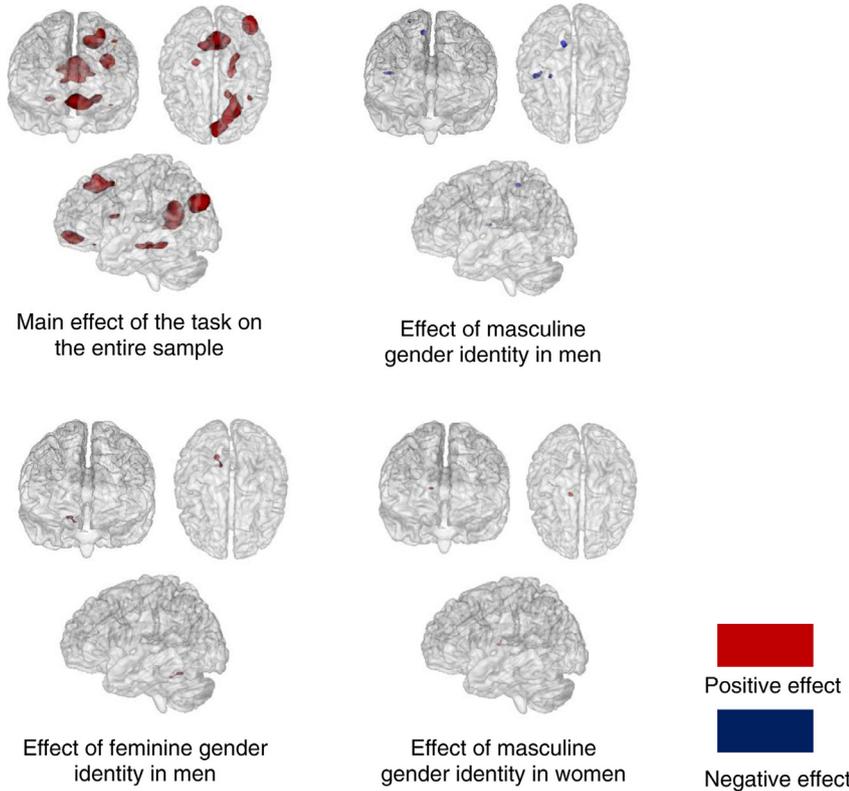


Fig. 3. Statistical parametric maps showing significant activation changes in the EAM versus SAM contrast.

Table 4

Region where hemodynamic activity main effect of masculine gender identity score is significant for the different contrasts performed.

Area	Cluster size	MNI coordinates			Masculine gender identity effect
		x	y	z	
EAMs versus definition					
L Angular G	1	-34	-52	22	$\beta=0.12, T=5.43$

Cluster size refers to the number of contiguous voxels for which the voxel *t* value corresponds to $p < 0.05$ (FWE corrected); G, gyrus; L, left.

a masculine gender identity, the more activation they had in the left angular gyrus (Table 4). Moreover, interaction between sex and masculine gender identity was significant in the contrast EAM versus SAM with a significant effect of masculine gender identity (Table 5) in the right superior frontal gyrus, the left superior temporal gyrus, the right insula, the right precuneus and the left middle occipital gyrus, in men, in that the more men had a masculine gender identity, the less those areas were activated while the more women had a masculine gender identity, the more their right thalamus was activated (Fig. 3). In the contrast positive EAM vs. positive SAM, the more men had a masculine gender identity, the less their right DLPFC, supramarginal gyrus, precuneus, left temporal superior gyrus, precentral gyrus, middle occipital gyrus, anterior cingulate cortex and pars opercularis inferior frontal gyrus and their supplementary motor area bilaterally were activated. In the contrast positive SAM versus positive definition, the more men had a masculine gender identity, the more their left caudate nucleus was activated. Finally, the feminine gender identity effect was significant in men in the EAM versus SAM contrast and the negative EAM and negative SAM contrast (Table 6). In the EAM versus SAM contrast, the more men had a feminine gender identity, the more their right cerebellum was activated (Fig. 3) while in the negative EAM and negative SAM

contrast, the more men had a feminine gender identity, the more their right cerebellum and right supramarginal gyrus were activated.

4. Discussion

4.1. Overview of results

Our results highlight that, in accordance with previous behavioral studies that investigated sex and gender related effects in AM (Compère et al., 2018; Gryzman and Fivush, 2016; Gryzman et al., 2016, 2017), the between-participant differences in AM are better explained by gender identity than by sex and extend these results to the field of neuroimaging. Indeed, behaviorally as in neuroimaging, no significant main effect of sex was found in this study; only main effects of gender identity or interactions between sex and gender identity reached the threshold of significance.

4.2. Autobiographical memory network identification

In the entire sample, activation patterns observed in EAMs contrast versus definition and SAM versus definition were observed in regions that were previously identified as belonging to the AM network, including the limbic system (hippocampus and hippocampal formation), medial cortical structures (medial prefrontal cortex, precuneus and posterior cingulate cortex/precuneus) and medial temporal gyrus (Martinelli et al., 2013; Svoboda et al., 2006). Moreover, the contrast between EAM versus SAM showed significant activation in more posterior and limbic structures (i.e., occipital regions and hippocampus) which was expected considering the shift from anterior to posterior regions associated with the gradient of increasing level of specificity of self-relevant information described in the literature (Martinelli et al., 2013; Svoboda et al., 2006).

Table 5

Regions where hemodynamic activity interaction between sex and masculine gender identity score is significant for the different contrasts performed.

Area	Cluster size	MNI coordinates			Masculine gender identity effect	
		x	y	z	Men	Women
EAMs vs. SAMs						
R Superior Frontal G	2	26	-8	66	$\beta = -0.55, T=5.98$	$\beta = 0.15, T=5.94$
R Thalamus	3	18	-12	10		
L Superior Temporal G	1	-58	-24	6	$\beta = -0.49, T=5.77$	
R Insula	5	42	-12	14	$\beta = -0.46, T=5.73$	
R Precuneus	5	10	-40	58	$\beta = -0.41, T=5.71$	
L Middle Occipital G	1	-46	-72	10	$\beta = -0.36, T=5.48$	
L Superior Temporal G	1	-42	-40	18	$\beta = -0.32, T=5.46$	
Positive EAMs vs. Positive SAMs						
R DLPFC	36	30	-12	70	$\beta = -0.68, T=7.49$	
R Supramarginal G	12	58	-16	38	$\beta = -0.66, T=6.51$	
R Precuneus	14	-2	24	50	$\beta = -0.65, T=6.28$	
L Superior Temporal G	13	-54	-20	10	$\beta = -1.14, T=6.09$	
L Precentral G	2	-22	20	74	$\beta = -0.53, T=6.08$	
B Supplementary Motor Area	8	2	0	54	$\beta = -0.89, T=5.83$	
L Middle Occipital G	1	-54	-72	-2	$\beta = -0.62, T=5.76$	
L Anterior Cingulate C	2	-10	20	30	$\beta = -0.61, T=5.71$	
L Pars Opercularis Inferior Frontal G	1	-46	12	14	$\beta = -0.58, T=5.70$	
L Superior Temporal G	2	-42	-36	18	$\beta = -0.49, T=5.48$	
Positive SAMs vs. Positive Definition						
L Caudate Nucleus	5	-2	4	6	$\beta = 1.12, T=6.06$	

Coordinates, cluster size and abbreviations correspond to those in Table 4. B, bilateral; C, cortex; DLPFC, dorso-lateral prefrontal cortex; R, right.

Table 6

Regions where hemodynamic activity is significantly correlated with the feminine gender identity score in men or women for the different contrasts performed.

Area	Cluster size	MNI coordinates			Feminine gender identity effect	
		x	y	z	Men	Women
EAMs vs. SAMs						
R Cerebellum	4	22	-64	-22	$\beta = 0.65, T=5.61$	
R Cerebellum	2	14	-52	-26	$\beta = 0.44, T=5.52$	
Negative EAMs vs. Negative SAMs						
R Cerebellum	7	22	-64	-22	$\beta = 1.08, T=5.65$	
R Supramarginal G	1	26	-52	18	$\beta = 0.46, T=5.58$	

Coordinates, cluster size correspond to those in Tables 4 and 5.

4.3. Feminine gender identity effect

One of our hypotheses was that we expected to replicate in neuroimaging the main result obtained from various behavioral studies (Grysmann and Fivush, 2016; Grysmann et al., 2016, 2017) including the one conducted on the same sample used in this study, but using a different set of behavioral tasks (Compère et al., 2018), namely that feminine gender identity is primarily associated with differences in emotional aspects of memories. This result was verified on the features of self-assessed memories: the more participants had a feminine gender identity, the more positive the valence of EAMs was, the more often negative EAMs were recalled, or the more emotional intensity and personal relevance of positive EAMs were important. Although Grysmann and Fivush team used another measure of gender identity (Spence and Helmreich, 1979) that is nonetheless highly correlated with the one that we used (Reilly et al., 2016), they also showed that the more participants identified with feminine stereotypes, the higher the quality and valence of memories and the more affect was expressed in the narratives (Grysmann and Fivush, 2016; Grysmann et al., 2016, 2017). Along the same lines, the behavioral results obtained in the same sample and with the same tool measuring gender identity as the one used in this study (but different behavioral tasks) were also congruent as they showed a positive link between feminine gender identity and the specificity and emotional intensity of EAMs (Compère et al., 2018).

Nevertheless, these results did not extend to data in neuroimaging where masculine gender identity effects were predominantly found, with the exception of a significant feminine gender identity effect only in men in the cerebellum for the contrast of EAMs versus SAMs and in the right supramarginal gyrus for the same contrast restricted to negative memories.

A surprising outcome is that we have no effect of feminine gender identity in the whole sample or in women. However, this can be due because this study did not control for fluctuation in ovarian hormones. It has been shown, for example, that the phase of the menstrual cycle in women influenced the recognition and memory of emotions, behaviorally (Bryant et al., 2011; Conway et al., 2007; Derntl et al., 2013, 2008; Ertman et al., 2011; Ferree et al., 2011; Gasbarri et al., 2008; Guapo et al., 2009; Soni et al., 2013) and in neuroimaging (Dan et al., 2019). Therefore, given the significant emotional component of AMs, one possible explanation for the lack of significant outcome in women in this study may be that the women's hormonal status was not considered, generating additional variability in the women sample. In turn, the main limitation of the fact that sex-specific effects have a strictly biological origin and those specific to gender identity a strictly social one is that these factors are usually inevitably confounded in a control sample (i.e., even though gender identity may be the only generator of between-subject variance, sex related differences could still be significant because of the statistical inclination of women to self-attribute feminine gen-

der stereotypes and vice versa). While feminine gender identity was not significantly different between men and women in this sample, most likely due to the age of our sample (see Gryzman, 2018; Gryzman and Fivush, 2016, for similar results), women still had a higher descriptive feminine gender identity score than men. Therefore, some additional noise in the women sample might explain why only so few feminine gender identity effects reached significance. Moreover, some work supporting that cerebral activation is influenced by the menstrual cycle without behavioral performance being affected (Pletzer et al., 2019) suggests the existence of adaptive strategies aiming at minimizing the influence of menstrual cycle on behavior. Naturally, given the novelty of this protocol, it is difficult to propose a strong explanatory hypothesis and the one suggested is just one possible explanation that would need to be tested directly by a protocol that controls for the impact of hormones and/or menstrual cycle on the variability in activation patterns in women. We therefore strongly suggest that future studies pay more attention to this variable in their future designs.

4.4. Masculine gender identity effect

4.4.1. Episodic autobiographical memory

All samples combined, there was a main effect of masculine gender identity in the EAMs versus definition contrast: the more participants identified with masculine stereotypes, the left angular gyrus was activated.

However, most of the results reaching the significance threshold were interactions between masculine gender identity and sex. In the EAMs versus SAMs contrast, the more participants identified with masculine stereotypes, the less activations the men had in the right superior frontal gyrus, left superior temporal gyrus, right insula and left median occipital gyrus while more women had activations in the right thalamus. Behaviorally, in general, the more men had a masculine gender identity, the less they recalled AMs, which is firstly congruent with the literature reporting that men recall fewer autobiographical events than women in limited time tests (Canli et al., 2002; Davis, 1999) and, secondly, may be related to the diminished activation of the frontal cortex in men with a strong masculine gender identity. It has been demonstrated that the prefrontal cortex is more active during the initial search for a memory than during its elaboration (Daselaar et al., 2008). A lower activation of the prefrontal cortex in these participants could thus translate into in less effort provided at the time of searching for a memory to recall and may explain their lower recall performance. In addition, these results also relate to the activation patterns observed in previous studies investigating the effects of sex on EAMs that reported that women had greater activations in the insula, prefrontal cortex and precuneus in comparison with men (Piefke and Fink, 2005; Young et al., 2013). These new findings suggest that previous results reported in the literature investigating sex-related differences in AM may be partially underpinned by gender identity specific effects confounded with sex.

In the same contrast (EAMs versus SAMs) but restricted to positive AMs, the more men identified themselves with masculine stereotypes, the less activation they exhibited in the right DLPFC, right supra-marginal gyrus, right precuneus, left superior temporal gyrus, right precentral gyrus, left medial occipital gyrus, left anterior cingulate cortex and left inferior frontal gyrus. A lower activation of the right supra-marginal, left precentral gyrus, supplementary motor area, and left anterior cingulate seems then to be more specific to memories with a positive valence.

4.4.2. Semantic autobiographical memory

Although the primary purpose of our task was to investigate sex and gender-related differences in EAMs since participants were explicitly asked to search for the most specific memories available, we also analyzed activation patterns associated with SAMs when participants did not achieve the level of specificity required. When men identified with

masculine stereotypes, they exhibited more activation in caudate nuclei in the contrast positive SAMs versus definition. To our knowledge, only one study has investigated sex-related differences in SAM using fMRI (Compère et al., 2016) and did not report sex differences in activation of this structure. However, the methodology used in the latter protocol was different from the one used here in that it aimed to directly test differences in emotional processing of AMs, did not consider memories' valence and did not investigate gender-related differences. Nevertheless, the results of this current study replicate and confirm that sex and gender-related differences also exist in more abstract forms of AM (Compère et al., 2016, 2018).

5. Conclusion, limits and perspectives

Overall, our main findings confirm previous behavioral studies suggesting that i. differences between men and women in AM are better explained by gender identity rather than sex; ii. biological (i.e., sex) and social (i.e., gender identity) factors can interact; iii. These effects have an impact at different levels of abstraction in AM, and; iv. Extend those results to the field of neuroimaging.

We acknowledge that the main limitation of this study is the small sample size considered here. We recognize that gender identity is a complex phenomenon, with various cognitive and social aspects, the effects of which, to be entirely understood and identified, require a larger sample. Thus, we hope that the results from this research will pave the way for groundbreaking avenues of research and will facilitate the securing of funding for future studies to collect data from larger samples to enable a more accurate and advanced study of this phenomenon. We also argue that another limitation of this study is that it did not consider the phase of the menstrual cycle in women and that this might have led to the unsatisfactory validation of our second hypothesis linking feminine gender identity to emotional aspects of memories regarding fMRI data. Researchers should, therefore, consider the impact of sex hormones in their design when studying sex and gender differences in AM. Another potential limitation of this study is that we used the valence of cues to presume the valence of memories. Although these variables were strongly associated, this choice was guided by the fact that we asked participants to assess the valence of their memories after the scan at the time of debriefing, which resulted in a large amount of missing data. To ensure that future analyses in the field are more precise and therefore based on actual valence ratings of memories and not a proxy for them, we recommend that future studies collect those ratings during the scan.

The existence of gender-related differences and the interaction effect of sex and gender identity has possible implications for the understanding of psychiatric disorders with an uneven prevalence ratio between men and women and in which a key feature of symptomatology is overgeneralization in AM. Indeed, several psychiatric conditions such as depression (Eid et al., 2019) or post-traumatic stress disorder (Breslau, 1997) are characterized by a higher prevalence of these disorders in women. We argue that given the importance of gender identity-related differences in AM, these sex-differences in prevalence may also be related to psychosocial factors since the definition of gender roles is culturally determined (Block, 1973; Reilly et al., 2016). Thus, the impact of gender identity in AM needs to be better identified and explained to understand better its role in the etiology and maintenance of psychiatric disorders affecting mostly women.

Data and code availability statement

Data and code will be available from the authors on request

Credit authorship contribution statement

Laurie Compère: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Data curation, Writing - original

draft, Visualization, Project administration. **Sylvain Charron**: Methodology, Software, Formal analysis, Investigation, Data curation, Writing - review & editing. **Thierry Gallarda**: Resources, Funding acquisition. **Eirini Rari**: Funding acquisition, Investigation. **Stéphanie Lion**: Investigation, Project administration. **Marion Nys**: Data curation. **Adèle Anssens**: Data curation. **Sandrine Coussinoux**: Investigation. **Sébastien Machefaux**: Resources. **Catherine Oppenheim**: Resources, Writing - review & editing. **Pascale Piolino**: Conceptualization, Writing - review & editing, Supervision.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117507.

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