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Left mediotemporal structures mediate the retrieval of episodic autobiographical mental images

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The aim of this functional magnetic resonance imaging (fMRI) study was to investigate the neuroanatomical substrates associated with the process of mental generation of specific (i.e., exemplar) and episodic autobiographical (i.e., an image of a unique life episode connected with an object) images. The fMRI paradigm in this experiment included a non-image generation baseline and two activation conditions requiring the generation of either specific or episodic autobiographical images. Image generation times and brain activation were recorded. Behavioral results showed that generating specific mental images took significantly less than generating episodic autobiographical images. Individuals generated specific images that were well distinct from the episodic autobiographical ones, semantic in nature without an episodic reference. Episodic autobiographical images did not show a significant bias towards preferential retrieval from any particular life period but were retrieved from across the entire life span. Conjunction analysis of the fMRI data showed that the two image generation conditions significantly activated a common set of neural structures, including mediofrontal areas. This shared pattern of activation might be the result of an underlying similar format and characteristics (e.g., richness in details) between the two types of images and might reflect the involvement of similar cognitive processes. Distinct patterns of significant activation were also present. Activation in the right parietal regions, cuneus, precuneus and left temporal regions was associated solely with the generation of specific images. Regions more specifically devoted to episodic memory retrieval and imagery, such as the left parahippocampal gyrus and precuneus, and the posterior cingulate cortex bilaterally, were significantly activated exclusively by the generation of episodic autobiographical images.

Keywords: Mental image generation; fMRI; Specific image; Autobiographical image; Episodic; Imagery

Introduction

There is experimental evidence that different types of mental images can be generated based on conceptual retrieval of concrete nouns from long-term memory (Cornoldi et al., 1989; Helstrup et al., 1997; De Beni and Pazzaglia, 1995). Behavioral differences (i.e., different generation times, vividness and goodness ratings, performance in memory recall) exist in generating, for example, general (i.e., a prototype), specific (i.e., an exemplar), contextual (i.e., an exemplar within a given spatial context) and episodic autobiographical (i.e., an image of a unique life episode connected with an object) images following presentation of concrete verbal stimuli. Among these types of image, the episodic autobiographical ones were those receiving the highest judgements for goodness (i.e., how complete and easy to form is the generated image) and vividness (i.e., how clear, detailed and visually defined is the generated image), took longer to generate and were those best recalled during memory tests (De Beni and Pazzaglia, 1995). These findings confirmed previous evidence that in retrieval tasks, there was a memory advantage provided by self-reference during the encoding of verbal material (Rogers et al., 1977). These studies have also shown that, when participants are well instructed, specific and episodic autobiographical images are well distinct, and individuals can inhibit irrelevant information to meet task requirements (Cornoldi et al., 1989). Specific images, although occasionally might refer to autobiographical material, maintain a semantic connotation without any episodic context. Episodic autobiographical images, instead, are clearly referred to a single life event connected with an object and not to repeated events (Conway and Pleydell-Pearce, 2000).

The finding of behavioral differences when individuals are requested to generate different types of images might reflect either reliance on different cognitive processes and/or mediation of different brain structures. This latter hypothesis finds support in evidence from neuroimaging studies which have shown differences in regional brain activation in association with the generation of different types of mental images (Ishai et al., 2000; Lambert et al., 2002; Gardini et al., 2005). The generation of mental images from concrete nouns, compared with passive

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listening of abstract nouns (considered difficult to image), activated the left fusiform gyrus, the premotor area and the anterior cingulate gyrus (D'Esposito et al., 1997). A hemispheric specialization for prototypical and multi-part types of images has also been put forward (e.g., Doricchi et al., 1995; Kosslyn et al., 1995). Evidence was found suggesting that both hemispheres might be devoted to the generation of global images, while only the left hemisphere would be more involved in adding visual details to a global shape (Kosslyn, 1988). A different scenario is offered by evidence contrasting general and specific images. Different pathways were detected with functional magnetic resonance imaging (fMRI) in the generation of general versus specific images (Gardini et al., 2005). General images activated the cuneus bilaterally, the cingulate and postcentral gyri in the left hemisphere and the sub-gyral region of the temporal lobe, the superior frontal gyrus, the insula and the middle occipital gyrus in the right hemisphere. Specific mental images activated the left superior frontal gyrus and the medial dorsal nucleus of the right thalamus. The finding of activation in distinct neural structures was interpreted as reflecting the difference in cognitive processes contributing to the generation of these two types of images and the involvement of the thalamus in the generation of specific images as related to its role in attention and retrieval of details.

No functional imaging studies have yet addressed the distinction between specific and episodic autobiographical mental images. The episodic and autobiographical nature of this latter type of image, for its direct reference to the self and the involvement of episodic memory retrieval, might rely on neuronal structures associated with autobiographical memory mechanisms. Several functional neuroimaging studies have addressed the question of which neuronal structures support the retrieval of autobiographical memory. In a review of several functional imaging studies, Maguire (2001) identified a network including the left hippocampal-frontal lobe areas as specifically involved in autobiographical retrieval and these regions appear to be part of a larger, and predominantly left sided, memory retrieval network, which includes the retrosplenial cortex, the parahippocampal gyrus, the temporo-parietal junction, the temporal pole and the cerebellum. Within autobiographical memory, however, a distinction should be made between the semantic and episodic character of recollections. Episodic memory has the unique characteristic of enabling individuals to project themselves back in the past and recollect previously experienced events as such, with a peculiar sense of re-experience called autonoetic awareness, while semantic personal memory consists of factual information lacking any specific context (Schacter and Tulving, 1994; Gardiner, 2001; Piolino et al., 2004; Ivanoiu et al., 2004). In this framework, episodic and semantic autobiographical memories are fundamentally different and dissociable during the process of recollection. A PET study found that memory for autobiographical events (the "episodic" aspects) activated specifically the left hippocampus, the left temporal pole and the medial prefrontal cortex, whereas the parieto-temporal junction was activated bilaterally by retrieval of personal facts (semantic) (Maguire and Mummery, 1999). A further distinction is that between episodic autobiographical memory and general episodic memory. A recent review of neuroimaging findings has shown that the right mid-dorsolateral prefrontal cortex supports the retrieval of non-personal episodic memory, whereas ventromedial prefrontal regions, predominantly on the left side, are associated with the retrieval of autobiographical events (Gilboa, 2004).

Although the studies above have contributed to clarify the neurobiological substrates associated with autobiographical memory retrieval, no study has investigated what brain regions support the mental generation of images referring to a unique episodic autobiographical event related to a particular object.

The aim of the present fMRI experiment was to investigate whether the cognitive distinction between specific and episodic autobiographical mental images arises from their association with different brain circuits. The following paragraph contains an explanatory description of what was meant by specific and episodic autobiographical images as detailed to the participants. A *specific image* was defined as the visual representation of a particular exemplar of an object (e.g., Ferrari Testarossa, if requested to generate a specific image of a car). An *episodic autobiographical image* was defined as the visual representation of a single unique life episode, spatially and temporally defined, connected to a given object (e.g., the visual representation of when I was once in Maranello, I was looking at a Ferrari Testarossa and I took a picture of it, if requested to generate an episodic autobiographical image of a car). Episodic autobiographical mental images have been defined by Kosslyn (1994) as particular instances of specific images. Undoubtedly, episodic autobiographical images and specific images, both require the generation of very detailed items, and based on this shared format, their generation might be supported by the same anatomical structures. There are, however, substantial differences as well, mostly related to the episodic nature of the episodic autobiographical images and the semantic/conceptual nature of the specific images. It is possible, therefore, that in addition to a common set of structures, episodic autobiographical images might additionally activate regions supporting episodic autobiographical retrieval, whereas specific images might show additional activation in regions which are involved in the retrieval of factual information.

Materials and methods

Participants

Fourteen healthy right-handed volunteers, four men and ten women, participated in this study (mean age of 37.93 years, SD = 8.89, age range 20–51; mean education of 16 years, SD = 3.08, education range 11–20). They were part of the medical and technical staff of the Aberdeen Royal Infirmary and the University of Aberdeen (UK). They were all British and had English as first language. The present study received ethical approval by the Grampian Health Board and University of Aberdeen joint Ethics Committee.

Material

Material and procedure were derived from the methodology used by Cornoldi et al. (1989). A pool of two hundred and five concrete nouns was utilized during the mental image generation conditions. For the baseline condition, one hundred pseudo-words were used. Words were selected amongst items that 30 undergraduate students had judged as having a medium–high familiarity and imagery value. Stimuli were rated on a 7-point Likert type scale (with 1 indicating low imagery and familiarity and 7 indicating high imagery and familiarity), and only words with mean imagery and familiarity values higher than 3.5 were used. The mean