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Research report

Neuroanatomical basis of number synaesthesias: A voxel-based morphometry study

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ABSTRACT

In synaesthesia, a specific sensory dimension leads to an involuntary sensation in another sensory dimension not commonly associated with it; for example, synaesthetes may experience a specific colour when listening or thinking of numbers or letters. Large-scale behavioural studies provide a rich description of different synaesthesia phenotypes, and a great amount of research has been oriented to uncovering whether a single or multiple brain mechanisms underlie these various synaesthesia phenotypes. Interestingly, most of the synaesthetic inducers are conceptual stimuli such as numbers, letters, and months. However, the impact of these concepts on the synaesthetic brain remains largely unexplored. Numbers appear as the most typical inducer in two common types of synaesthesia: grapheme-colour and sequence-space. Numbers are symbols that denote quantity information and their processing recruits a specific neural network. Therefore, numbers may play an important role in the brain mechanisms underlying some types of synaesthesia. We used voxel-based morphometry (VBM) to compare grey matter (GM) volume in synaesthetes and controls. Relative to controls, synaesthetes showed increase in GM in the right amygdala and in the left cerebellum. Within the synaesthete group, comparing synaesthetes who reported numbers as the inducer with synaesthetes who reported other stimuli as the inducer revealed increase in GM in the left angular gyrus, which is associated with the verbal aspect of number processing. These results reveal neuroanatomical differences between synaesthetes and controls, and show the impact of the type of inducer in the synaesthetic brain. We discuss these findings in line with current neurobiological models of synaesthesia.

1. Introduction

In the phenomenon called synaesthesia, the stimulation of one sensory modality (inducer) results in association of other additional percept (concurrent) not usually associated with it. For example, viewing or hearing letters may evoke colours, or hearing a musical tone may evoke a certain smell. The prevalence of synaesthesia has been found to be higher than the

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4% reported by Simner (2007). It is assumed by some researchers that synaesthesia stems from neurodevelopmental differences in the maturation of the brain, which produce an abnormal connection or ‘cross talk’ between brain areas. Abnormal ‘cross talk’ between brain areas would arise from incomplete pruning during development (i.e., some connections that would normally be eliminated are maintained), or from dis-inhibition in the normal adult brain.

Large-scale behavioural studies have shown a mosaic composed of different synaesthesia phenotypes (Novich, Cheng, & Eagleman, 2011). The different synaesthetic subtypes can be grouped into clusters depending on the inducer (i.e., the dimension that triggers the synaesthetic experience) and the concurrent (i.e., the dimension that is associated with the inducer) that define the specific experience. The grouping of different synaesthesia subtypes into clusters suggests a non-random organization. That is, some types of synaesthesia (e.g., colour sequences) are more likely to occur independently from other types of synaesthesias (e.g., grapheme-colour). According to Simner et al. (2006), around 88% of synaesthetic experiences are triggered by conceptual information such as numbers, letters, weekdays and months. It is important to note that this estimate was based on two studies based on self-report: one conducted on university students and the other conducted on English speaking visitors of the London museum. Only a small percentage of grapheme-colour synaesthetes are sensitive to the low-level features of the inducer (Hubbard & Ramachandran, 2005) and therefore synaesthesia seems to be highly linked to the processing of high-level concepts (Simner, 2007). Up until the present, it is still unknown to what extent the neural mechanisms of different synaesthetic phenotypes are influenced by the coding of specific concepts in the brain. Numbers are special concepts. Processing of numerical information is shared among species (Cantlon, Platt, & Brannon, 2009; Dehaene, Dehaene-Lambertz, & Cohen, 1998). That is, the processing of numerical information has evolved with the organisms' ability to manipulate some kind of quantity information. Numbers are basic elements of our daily life. From an early age, functioning in the world would be highly challenging unless individuals are capable of manipulating numerical symbols. Numbers are symbols that denote magnitude information and as such, they interact with other dimensions such as space, time and physical size (Bueti & Walsh, 2009; Walsh, 2003). Finally, a specific neural network for processing numbers has been identified (Dehaene, Molko, Cohen, & Wilson, 2004; for a recent review see; Arsalidou & Taylor, 2011). We know that, for example, the intraparietal sulcus (IPS) is responsible for coding quantity information independently of the format (i.e., verbal or non-verbal).

Whereas the IPS is responsible for coding quantity information, the left angular gyrus was found to be associated with the linguistic aspects of number and arithmetic processing (Dehaene, Piazza, Pinel, & Cohen, 2003), and to host spatial-numerical representation (Göbel, Walsh, & Rushworth, 2001). A number-form area has been also identified in the inferior temporal cortex (Dehaene, 2011; Grotheer, Ambrus, & Kovács, 2016; Shum et al., 2013), demonstrating the selectivity of neurons within the ventral cortex to learnt concepts. Ramachandran and Hubbard (2001) were the first to outline the possibility (see description for the cross-activation model below) that certain types of synaesthesia involving numerical information may arise due to cross-talk between the left angular gyrus and the adjacent superior temporal cortex that could be involved in late stages of colour processing (Zeki & Marini, 1998).

Attempts to address the neural correlates of synaesthetic experience have been made in particular by using voxel-based morphometry (VBM) analysis (Hänggi, Beeli, Oechslin, & Jäncke, 2008; Jäncke, Beeli, Eulig, & Hänggi, 2009; Melero et al., 2013; Rouw & Scholte, 2010; Weiss & Fink, 2009). VBM allows comparing the local concentration of grey matter (GM) volume between different groups of subjects. Even though these studies have been cited in the current literature as providing evidence for differences between the synaesthetic and the non-synaesthetic brain (for a review see Rouw, Scholte, & Colizoli, 2011), the validity of these findings has been recently questioned. That is, results from both functional and structural imaging cannot be considered in isolation from the critical issue involving statistical inference in neuroimaging research (Hupé, 2015). Recently, Hupé and Dojat (2015) performed a critical review on fMRI and structural imaging data, mainly focussing on grapheme-colour synaesthesia. According to their detailed evaluation, the published brain imaging studies do not provide sufficient evidence to support the claim that a neural basis of grapheme-colour synaesthesia has been identified. They bring to light the fact that when a more conservative and rigorous approach (both methodological and statistical) is used to evaluate the levels of brain activation, most reports fail to support their claims. One example is the claim that colour centres are differently activated in grapheme-colour synaesthesia. When a hypothesis-driven analysis is carried, out only 2/9 studies show the involvement of colour regions in grapheme-colour synaesthesia. According to Hupé and Dojat, the majority of studies provide only coordinates for voxels that have passed a disputable, arbitrary statistical threshold (see also Hupé, Bordier, & Dojat, 2012). This critical review brings up the fact that there is still no consensus in the literature with respect to the neural correlates of synaesthesia. This review also highlights the importance of following a strict methodological and statistical approach when using neuroimaging techniques to study the neural basis of a heterogeneous and multi-dimensional phenomenon as synaesthesia. Therefore, it also endorses the importance of approaching the study of synaesthesia using larger sample sizes in which different types of synaesthesias can be examined with the same brain imaging protocol.

In terms of studying synaesthesia as a heterogeneous phenomenon, Rouw and Scholte (2010) applied an interesting approach of examining individual differences by looking at anatomical changes between projectors and associators. Projector synaesthetes describe their experience as occurring outside of their bodies, whereas associators describe their experience as occurring in their mind's eye. Rouw and Scholte identified an increase in GM volume/density in areas involved in acting ‘outside the world’ (e.g., visual areas, auditory cortex and motor cortex) in projectors. In associators, an increase in GM was identified in the hippocampus, parahippocampal gyrus, amygdala and in the angular gyrus, that is, areas