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Automatic numerical-spatial association in synaesthesia: An fMRI investigation

Isabel Arend[a,*], Sarit Ashkenazi[b], Kenneth Yuen[c], Shiran Ofir[a], Avishai Henik[a]

[a] Department of Psychology and Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Israel
[b] Department of Education, Hebrew University of Jerusalem, Israel
[c] Neuroimaging Center (NIC), Focus Program Translational Neuroscience, Johannes Gutenberg University Medical Center, Mainz, Germany

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ABSTRACT

A horizontal mental number line (MNL) is used to describe how quantities are represented across space. In humans, the neural correlates associated with such a representation are found in different areas of the posterior parietal cortex, especially, the intraparietal sulcus (IPS). In a phenomenon known as number-space synaesthesia, individuals visualise numbers in specific spatial locations. The experience of a MNL for number-space synaesthetes is explicit, idiosyncratic, and highly stable over time. It remains an open question whether the mechanisms underlying numerical-spatial association are shared by synaesthetes and nonsynaesthetes. We address the neural correlates of number-space association by examining the brain response in a number-space synaestheste (MkM) whose MNL differs dramatically in its ordinality and direction from that of a control group. MkM and 15 nonsynaesthetes compared the physical size of two numbers, while ignoring their numerical value, during an event-related functional magnetic resonance imaging session (fMRI). Two factors were analysed: the numerical distance effect (NDE; e.g., 2–4 small distance vs. 1–6 large distance), and the size congruity effect (e.g., 2–8 congruent vs. 2–8 incongruent). Only for MkM, the NDE elicited significant activity in the left and right IPS, supramarginal gyrus (bilateral), and in the left angular gyrus. These results strongly support the role of the parietal cortex in the automatic coding of space and quantity in number-space synaesthesia, even when numerical values are task-irrelevant.

1. Automatic numerical-spatial association in synaesthesia: an fMRI investigation

In both human and nonhuman primates, numbers have been shown to be strongly associated with space (Dehaene et al., 1993; Drucker and Brannon, 2014). In the normal population this association is implicit; however, in a phenomenon known as number-space synaesthesia (NSS), this association is explicit, idiosyncratic, automatic, and highly stable over time (Arend et al., 2013; Gertner et al., 2013b; Jarick et al., 2009, 2011; Piazza et al., 2006). Graphic examples of NSS have been documented in the literature (Galton, 1880; Gertner et al., 2009; Piazza et al., 2006). NSS has also been shown to frequently co-occur with other types of synaesthesia such as grapheme-colour (Sagiv et al., 2006).

NSS constitutes a window into the cognitive and neural mechanisms of numerical-spatial association. Does the processing of numerical information in synaesthetes recruit a distinct or overlapping neural circuitry relative to nonsynaesthetes? One hypothesis addressing the origins of number-space synaesthesia postulates that the number-space association arises from the overlapping neural structures responsible for coding space and quantities (Hubbard et al., 2005). The suggestion is that parietal areas that are responsible for processing numbers and space in nonsynaesthetes would also be activated in the case of overlearned sequences in synaesthetes. That is, numerical processing would be quantitatively – not qualitatively – different in synaesthetes relative to nonsynaesthetes. For example, the intraparietal sulcus (IPS) has been shown to code different aspects of number processing such as symbolic and nonsymbolic dimensions (Dehaene et al., 2003) and the semantic distance between quantities in number comparison tasks (Piazza et al., 2004; Pinel et al., 2001). Although attractive, this hypothesis has not yet received support from brain imaging protocols. Previous studies addressing the neural mechanisms of synaesthesia have mainly focused on grapheme-colour synaesthesia (Cohen Kadosh et al., 2007; Rich et al., 2006; Rouw and Scholte, 2007; Sperling et al., 2006); therefore, the neural correlates of number processing in synaesthesia have not yet been systematically explored.

Tang et al. (2008) were the first to use a functional magnetic resonance imaging (fMRI) protocol to address the neural basis of

* Correspondence to: Department of Psychology, Ben-Gurion University of the Negev, P.O.B. 653, Beer Sheva, Israel.
E-mail address: arend.psy@gmail.com (I. Arend).

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number-space synaesthesia. They examined whether number-space associations represent the cardinality (e.g., three buses) or the ordinality (e.g., the third bus) of numbers. The idea was inspired by the fact that sequences in NSS are consistent with an ordinal representation of objects, such as the order of numbers or the order of letters, weekdays, and months. In the cardinal task used by Tang and colleagues, subjects needed to decide whether the numerical value matched that of the number of Xs in a string (e.g., xx3x or xx2x for compatible and incompatible stimuli, respectively), and in the ordinal task, subjects needed to decide whether the number was in the correct position within the string (e.g., x2xx and xxx2 for compatible and incompatible pairs, respectively). Brain imaging results showed that only the ordinal task elicited significant bilateral IPS activity for the synaesthete group but not for the control group, suggesting that a mental number line in synaesthesia is ordinal in nature. We believe this conclusion is rather premature. It is important to note that the synaesthete group only showed effects of ordinality in parietal areas when the stimuli were judged from left-to-right, and such a left-to-right arrangement was consistent with the synaesthetic representation. It is possible that reading habits (left-to-right scanning) may have elicited more parietal activity, considering that the parietal cortex responds to saccadic eye movements. This possibility is highlighted by the fact that all synaesthetes presented with a left-to-right association; therefore, their numerical-spatial representation could not be studied in isolation from reading (scanning) habits. Reading habits might have contributed to the effect in parietal areas, especially for synaesthetes. In addition, number-space synaesthetes report that the visualization they experience for a specific number and its corresponding spatial location occurs when a single number is presented, strengthening the argument that quantity information, and not ordinality, is an important aspect of number-space association in synaesthesia. To summarize, it is possible that the effects reported by Tang and colleagues (2008) may be derived by the ordinality of numbers imposed by the task requirements. However, we disagree with the authors' main claim that the mental number line in synaesthesia is ordinal in nature.

2. The present study

We addressed the neural basis of NSS by examining the neural correlates of number-space association in a rare case: a number-space synaesthete, MkM, who vividly experiences even and odd numbers in the left and right sides of space (see Fig. 1). This single case study constitutes a unique opportunity to examine the neural signature of quantity representation in synaesthesia when the synaesthetic MNL differs dramatically from that of a nonsynaesthete. MkM's representation offers a great opportunity to examine the following questions: 1) whether the automatic processing of number-space association will recruit number-relevant areas such as the IPS, the angular gyrus, and the supramarginal gyrus; and 2) whether the ordinal nature of the synaesthetic mental number line is what triggers IPS activity. The idea of ordinal representation implies that numbers (or any other concept such as letters or weekdays) are represented along a horizontal vector in which small numbers "come first" and large numbers "come later." Because MkM's number representation consists of splitting even and odd numbers across the left and right sides of space, small and large numbers are not arranged in terms of their ordinality along a horizontal line.

To study whether the synaesthetic number-space association elicits activity in number-related areas for MkM under conditions of autonomous processing, we used a physical-size comparison task ("Report which stimulus is physically larger"; Henik and Tzelgov, 1982). In this type of task, two numbers are presented in different physical sizes. In congruent trials, the size and the value of the number match (e.g., 2 4), and in incongruent trials, the size and the value of the numbers are mismatched (e.g., 2 4). The size congruity effect (SiCE) is derived by the difference in response times for congruent relative to incongruent

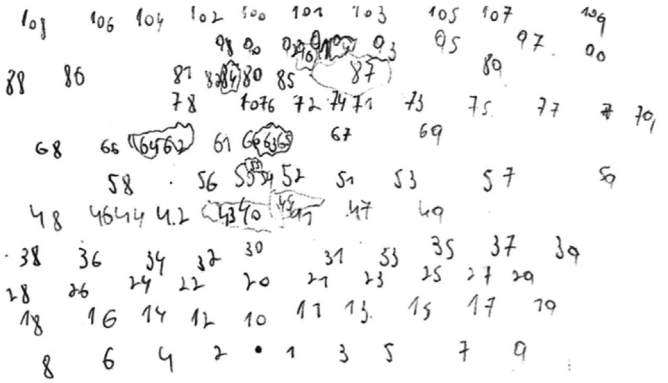

Fig. 1. Hand drawing of the synaesthete's numerical-spatial association.

trials. Our number pairs were selected to analyse the numerical distance effect (NDE).

2.1. The numerical distance effect

In humans, one of the classical ways to examine the behavioural manifestation of the MNL is by analysing the semantic distance of numbers through the so-called numerical distance effect (NDE; Moyer and Landauer, 1967). The NDE shows that, when deciding which number is the numerically larger, response times to large numerical distances (e.g., pair 1 6) are faster relative to response times to small numerical distances (e.g., pair 2 4). The NDE has been consistently observed even when the numbers are task irrelevant. Henik and Tzelgov (1982) used a physical comparison task to address the automatic processing of numbers. As expected, responses for congruent pairs were faster than for incongruent pairs. The NDE affected the SiCE such that the SiCE was found to be larger for large relative to small numerical distances, illustrating the automatic processing of numerical-spatial information.

To this day, the NDE is a valuable tool used for investigating the cognitive aspects of number-space association in synaesthesia. In number-space synaesthetes, the NDE is found to be larger when the arrangement of the stimulus matches that of the synaesthetic representation (Gertner et al., 2009). That is, the NDE for synaesthetes representing numbers from left-to-right, will be larger when the display contains number pairs from left-to-right (e.g., 2 – 4) than from right-to-left (e.g., 4 – 2). The NDE of number-space synaesthetes also reflects the automatic coding of numerical quantities that occurs across different mental number line representations (Piazza et al., 2006). To the best of our knowledge, this is the first time that an fMRI protocol has been used to access task-irrelevant NDE in nonsynaesthetes. Previous studies have examined the NDE when number was a task-relevant dimension (Pinel et al., 2001, 2004; Kaufmann et al., 2005). A few studies used passive viewing of single digits or non-symbolic quantities (array of dots) to address quantity coding in the parietal cortex (Ansari et al., 2006; Cohen Kadosh et al., 2007; Piazza et al., 2004). These studies are in agreement with the idea that quantities are represented in the parietal cortex in the absence of an explicit task.

3. Method

3.1. Participants

MkM is a 28-year-old right-handed man, with normal visual acuity who presents with number-space synaesthesia. He became aware of his sequence-space synaesthesia when he was describing his experience to one of his friends three years before testing. He reports that he was surprised to discover that not everyone experienced numbers in the way that he does. Fig. 1 shows MkM's hand-drawn number-space representation. He reports having a strong "feeling" that, for example,