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The objectification of overlearned sequences: A new view of spatial sequence synesthesia

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ABSTRACT

In the phenomenon of spatial sequence synesthesia (SSS), subjects can articulate explicit spatial locations for sequences such as numbers, letters, weekdays, months, years, and other overlearned series. Similarly, abstract sequences can take on implicit spatial representations in non-synesthetes, as evidenced by the spatial numerical association of response codes (SNARC) effect. An open question is whether the two findings represent different degrees of the same condition, or different conditions. To address this, we developed computer programs to quantify three-dimensional (3D) month-form coordinates in 571 self-reported spatial sequence synesthetes; this approach opens the door for the first time to quantified large-scale analysis. First, despite the common assumption that month-forms tend to be elliptical, we find this to be true in only a minority of cases. Second, we find that 27% of month forms are in the shape of lines, consistent with the assumed shape of implicit spatial forms in the SNARC effect. Next, we find that the majority of month forms are biased in a left-to-right direction, also consistent with the directional bias in the SNARC effect (in Western speakers). Collectively, these findings support the possibility that SSS is directly related to the sequence representations in non-synesthetes. While the search for neural correlates has concentrated on areas in the parietal lobe involved in numeric manipulation and coordinate systems, we propose that the basis of this synesthesia may be the close proximity of temporal lobe regions implicated in sequence coding and visual object representation.

1. Introduction

Spatial sequence synesthesia (SSS) is a condition in which abstract sequences are automatically conceived as having physical two- or three-dimensional (2D or 3D) structures, like real-world objects (Galton, 1880, 1883; Bertillon, 1880; Seymour, 1980; Seron et al., 1992; Hubbard et al., 2005b; Sagiv et al., 2006; Cytowic and Eagleman, 2009). The conceived structures have typically been reported to bend, loop or zigzag in a variety of idiosyncratic shapes. Sir Francis Galton pointed out that the forms

> "are stated in all cases to have been in existence… as long back as the memory extends; they come 'into view quite independently' of the will, and their shape and position… are nearly invariable (Galton, 1883)".

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Digits of the numberline, letters of the alphabet, days of the week and months of the year are especially common forms, as are other ordinal sequences such as shoe sizes, Indian caste system, temperatures, historical eras, and prime time television line-ups (Seymour, 1980; Seron et al., 1992; Sagiv et al., 2006; Cytowic and Eagleman, 2009; Hubbard et al., 2005b). Even blind subjects can purportedly experience spatial sequence synesthesia (Wheeler, 1920). Some individuals possess a form for only one sequence; others have forms for more than a dozen (Hubbard et al., this issue, 2009; Cytowic and Eagleman, 2009).

Two important clues about the neural basis of spatial sequence synesthesia deserve highlighting at the outset: (1) spatial forms are composed of stimulus sets that are sequential and overlearned, and (2) the forms typically possess an internal coordinate system that allows different perspectives upon it, suggesting that forms are ''reified'', or coded as physical objects by the brain. We will turn to each of these points in turn and then combine them for a new theory about the neural basis of SSS.

1.1. *What is special about sequences?*

There has previously been an assumption that spatial sequence synesthesia is fundamentally tied to concepts of time. For example, Smilek and colleagues described the spatialization of months, weeks, and years under the term ''time-space synesthesia'' (Smilek et al., 2007). Despite the seduction of connecting ''time'' and ''space'' (as has been successful in physics), the linkage here erroneously intimates that *temporality* is the basis of the forms, rather than the *sequentiality* of the stimuli. The large variety of other spatialized sequences (alphabets, shoe sizes, caste systems, etc) indicates that time is not the critical property in question – instead, it is ordinality. Therefore this sentence hopes to represent the literature's final usage of the term ''time-space synesthesia.''

Instead, the elements that compose spatial forms implicate something unique about the neural basis of overlearned sequences. It has been long noted that the learned ordinal sequence is also a typical trigger for color synesthesias (Shanon, 1982; Rich et al., 2005), suggesting a possible common neural origin between grapheme-color synesthesia and SSS (Seron et al., 1992). In support of this hypothesis, many synesthetes experience their overlearned sequences with both color and location (Sagiv et al., 2006; Cytowic and Eagleman, 2009). Collectively, the properties of these types of synesthesia implicate something unique about the neural coding of overlearned sequences. Below, we will present data that point to the brain areas that are involved.

1.2. *What is the coordinate system of the forms? The case for reification*

Although forms are often thought of as fixed forms in relation to the body space, it is commonly reported that synesthetes can mentally take on different perspectives, ''zooming in and out'' or ''moving around'' the form (Galton, 1880; Seron et al., 1992; Cytowic and Eagleman, 2009). Even as viewers look right or left, ''up to'' or ''down on'' the configuration, relationships between elements within the form are reported to remain constant. For example, Jarick and colleagues describe a synesthete who imagines herself on one side of her form when she is cued by an auditory cue, and imagines herself on a different side of the form when she is triggered by a visual cue (Jarick et al., this issue, 2009). Another synesthete likens what she privately calls her ''memory maps'' to a geographical map that allows her to take in an overall view without much detail, and then zoom in on a specific enlarged region of interest (Cytowic and Eagleman, 2009).

This ability to change perspectives is often left out of theoretical frameworks, and is mentioned more often as a curiosity. However, this capacity to change points of view may serve as a critical clue. Specifically, it indicates that spatial forms do not have to be defined in coordinates fixed to the body (ego-centric coordinates), but instead consist of their own internal coordinate system, thus having the properties of an *object*. Therefore it may be useful to understand SSS as a type of *reification*, which the Oxford English Dictionary defines as ''the mental conversion of a person or abstract concept into a thing.'' (Note that reification is also used in Gestalt psychology, in which a percept contains more explicit spatial information than the sensory stimulus on which it is based, as in Kanizsa figures; Eagleman, 2001). In other words, typical synesthetes describe forms that have the properties of fixed, real objects; that is, forms are described in object-coordinates instead of ego-coordinates. One synesthete describes his weekdays as follows: ''The members are aligned in fixed positions according to each other, but their absolute locations are not determined.''

It has been previously suggested that the key to understanding spatial sequences will be to understand the spatial coordinate systems in the parietal cortex – specifically in the intraparietal sulcus (IPS) (Hubbard et al., 2005b; Tang et al., 2008). However, the reification of the sequences instead suggests a search in the parts of the brain involved in representing objects – namely, the ventral visual stream in the temporal lobes (see General discussion).

But how can this description of reified sequences encompass the variety of descriptions offered by synesthetes, some of whom describe a form fixed in front of them, some of whom describe a dynamically changing perspective on their form? To understand this, visualize your car parked right in front of you. Although you do not see it physically there (as you would with a hallucination), you will have little trouble pointing to the front and back of your imagined car, the rear wheel, the driver's side window, and so on. The car has 3D object-based coordinates in your mental space. Since the driver's side might be your preferential (default) viewpoint, you might be the type to always describe your car from that single, static point of view (which could give the impression that the car is based in ego-centric coordinates). Alternatively, you might be the type to ''move around'' your car, ''zooming in'' on details when you chose to. Some contexts might induce you to visualize yourself on the driver's side, while others will suggest the point of view from the passenger side. This description of your imagined car accords with descriptions of overlearned sequences: the forms are often imagined from a default point of view in relation to the body, but can also be experienced from different perspectives.

To understand what this reification tells us about the mental representation of sequences, we now turn to the mapping of mental timelines in non-synesthetes.

1.3. *Implicit mapping of sequences to space in non-synesthetes*

Even non-synesthetes appear to have a non-conscious internal spatial representation of sequences. This is exemplified by the ignominiously named spatial numerical association of response codes (SNARC) effect, in which subjects respond more quickly to small numbers with their left hand, and to larger numbers with their right hand (Dehaene et al., 1993; Fias, 1996). Moreover, when subjects are asked to cross their hands, their responses cross too—being faster to a small number with the right hand now on the left half of space—indicating that it is not the hand but the side of space that matters (Dehaene et al., 1993, but see Wood et al., 2006). A similar finding occurs with eye movements: subjects look faster to the left when responding to small numbers and to the right when numbers are large. The direction of the effect may be sensitive to cultural experience: Iranian subjects, who write from right-to-left, show the SNARC effect in the reverse direction (Dehaene et al., 1993). The SNARC effect, replicated in many laboratories, suggests that numbers are automatically associated with positions in space, supporting the idea that a spatially organized internal numberline exists in synesthetes and non-synesthetes alike (Hubbard et al., 2005b).

A natural first assumption was that the SNARC effect was related to numbers in particular, and hence brain areas specifically involved in numeric computation (including verbally, visually and abstractly; Plodowski et al., 2003; Hubbard et al., 2005b). However, SNARC effects have now been reported in non-synesthetes for months of the year, days of the week and letters of the alphabet (Gevers et al., 2003, 2004, 2006; Price, this issue, 2009), suggesting that the effect is tied to overlearned sequences in general. In the more general framework, early members of a sequence show left-hand reaction time advantages, and late members show right-hand advantages.

1.4. *Is synesthesia a different degree of the same thing, or a different phenomenon?*

The generalized SNARC effect in non-synesthetes and the spatial forms of synesthetes raises the question of whether the spatial representation of sequences is the same phenomenon in synesthetes and non-synesthetes (Hubbard et al., 2005b). In other words, is SSS simply an exaggerated form of the cross-talk present in all brains? Circumstantial evidence supports this hypothesis: for example, the spatialization of ordinal sequences in both synesthetes and non-synesthetes appears to have logarithmic compression of successively larger numbers (i.e., there is more resolution to 12, 13 and 14 than to 112, 113 and 114; Cytowic and Eagleman, 2009).

To more directly explore whether the spatialization in synesthetes and non-synesthetes represents the same phenomenon, Price and Mentzoni (2008) asked whether synesthetes have a SNARC effect that is defined by the idiosyncratic details of their forms. They found that the left- versus right-hand reaction time depended on how the form was oriented in space—for example, subjects with later months on the left of midline showed a left-handed reaction time advantage for later months (Price and Mentzoni, 2008). However, they did not find a reaction time advantage for months that were farthest from the spatial midline versus those were close, suggesting the possibility that the SNARC effect reflects more about binary association between stimuli and response categories than about the detailed structure of spatial representations (Santens and Gevers, 2008; Price, this issue, 2009).

To move forward our understanding of these issues, we performed an analysis of 571 month forms from self-reported spatial sequence synesthetes. This allows us to quantify the statistical properties of month forms in search of trends and commonalities. Additionally, these data allow us to compare the characteristics of synesthetes to the properties of the SNARC effect. The existence of a generalized SNARC effect seems to favor of a relationship between SNARC and SSS; on the other hand, the interpretation of the similarities must be taken cautiously. After all, while the SNARC effect is thought to be robustly left-to-right in Western non-synesthetes, it is not the case that all synesthetes have a left-to-right representation in their forms. In other words, researchers commence papers about the SNARC effect with sentences such as ‘‘We spontaneously associate numbers with space: we think of small numbers as being lower and to the left of us, and larger numbers as being further up and to the right of us’’ (Wood and Fischer, 2008). But the question remains whether such a description will apply, on average, for spatial sequence synesthetes. If yes, then it may be possible that SSS is an exaggeration of normal neural cross-talk. If no, it may be a separate phenomenon. To answer this question, we here report on a large-scale examination of month forms.

2. Methods

Because previous methods of data collection have relied on descriptions (Galton, 1880; Seymour, 1980; Cytowic, 2002), questionnaires (Seron et al., 1992; Sagiv et al., 2006) and/or interview (Price and Mentzoni, 2008), there has been no systematic way to study the similarities, differences, patterns, and changes in number forms in 3D coordinates. Many synesthetes report that simple line drawings fail to convey the panorama and depth they sense. As one wrote, ‘‘[my paper] drawings aren’t accurate because in my mind they are 3D: either lying flat in a single plane or else coming at me at an angle and crisscrossing through other horizontal planes.’’

To address this problem, we developed virtual reality software (WorldViz software, python programming language) that allows synesthetes to physically place sequences in the positions where they perceive them in 3D space. Fig. 1a, b illustrates the spatial forms of two sisters.

To broaden the reach of this approach, we next developed an internet-enabled version using javascript (Fig. 1c). This program was incorporated into the Synesthesia Battery (www.synesthete.org), a free online battery of tests and questionnaires for the study, verification, and quantification of synesthesia (Eagleman et al., 2007). We have currently only

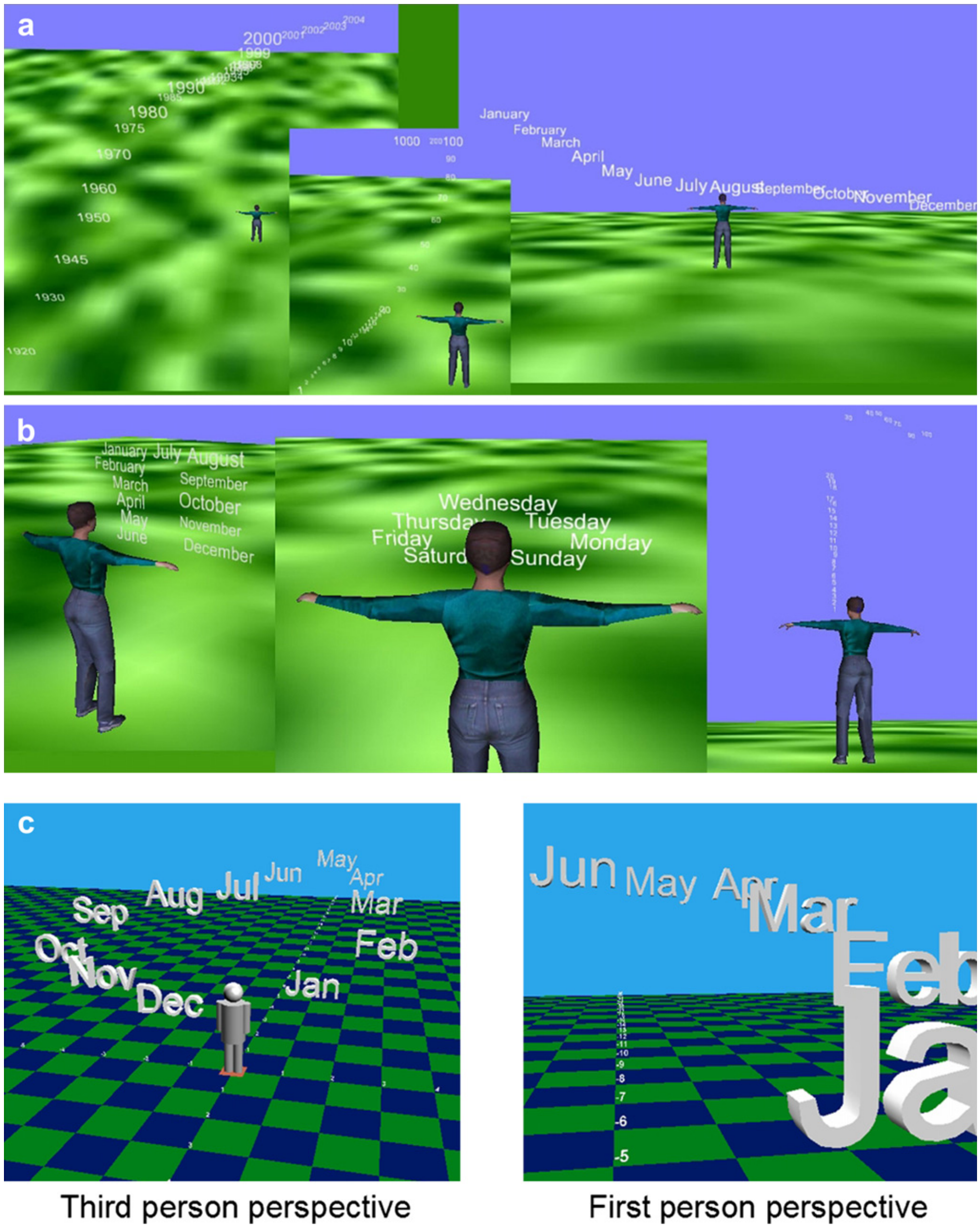

Fig. 1 – Capturing reified sequences in 3 dimensional coordinates. (a, b) Spatial forms for two sisters who grew up in same household (data captured in laboratory, programmed in WorldViz virtual reality software). Top row: older sister, bottom row: younger sister. Note that even though the sisters were raised in the same household, there is no similarity between their forms, weighing against the possibility that number forms are something synesthetes learn from their parents or from exposure to an unusual calendar during their childhood. (c) Reified sequence of a representative subject using the spatial sequence program on the Synesthesia Battery (data captured online, programmed in javascript, www.synesthete.org).

launched the month version of the program; weekdays, numbers and years will follow soon.

In both versions of the program participants are represented in a 3D space by an avatar. Using the mouse or keyboard, subjects can select each month and change its coordinates in the x, y or z axes, as well as its size. Additionally, they can change the position of the camera, orbit the camera around the scene in three dimensions, and toggle their perspective between third and first person (see Fig. 1c). All months are viewed on the screen at once.

Note that this method of quantifying 3D coordinates introduces at least two advantages. First, it can open the door to quantifiable verification of SSS. For example, the Synesthesia Battery is designed to automatically email subjects one year after initial testing to assess retest consistency. At that time, the distances between the original and retested coordinates will be quantified. Our expectation based on previous experience (Eagleman et al., 2007) is that we will be able to identify a bimodal distribution between genuine synesthetes and malingerers; a threshold will be chosen that optimally discriminates the two groups. As of this writing, the consistency retesting has not been done, which means that the current data is non-verified and presumably polluted with an unknown number of malingerers. Further, we have no way of knowing whether some participants began the task but did not complete it; therefore we automatically exclude data sets for which 2 or more of the months are left in the same arbitrary position in which they were automatically placed at the start of the program. Given the concerns about self-reported data, even in a sample size this large, we restrict ourselves at this time to general observations.

The second advantage of quantifying in 3D space is the ability to identify patterns across the spatial coordinates of different subjects. In the same way that color-grapheme synesthetes may display some amount of imprinting from exposure to patterns seen in everyday life (Witthoft and Winawer, 2006), there may be the possibility of similar influences on spatial forms—as seen, for example, in the frequent placement of numerals 1–12 in a clocklike pattern (Galton, 1883; Hubbard et al., 2005b; Seron et al., 1992). Below we will identify several common features of month forms. Finally, the flip side of identifying patterns is quantifying individual differences. The importance of such differences has been previously noted by investigators (Hubbard et al., 2005a; Smilek et al., 2007), although they consented that their sample sizes were too small to draw conclusions about those differences.

3. Results: large-scale characterization of spatial sequence synesthesia

3.1. *Varieties of shape motifs*

Using the program on synesthete.org, we have collected data from 571 subjects who claimed to have SSS. Because this data is based on self-report and is currently unverified by consistency testing, it should be interpreted with appropriate caution. It will be further refined by retests in the coming years, but in the meantime we hope that the signal-to-noise ratio is sufficient to capture a rough picture of the underlying distributions.

We first turned to understanding the common shapes that were found in month forms. An independent judge naïve to the goals of the study divided the 571 forms into categories of her own choosing, as illustrated by representative examples in Fig. 2. Not shown is an example of the group ‘‘unclassified,’’ which served as a catch-all class for shapes that were not readily classifiable.

As can be seen in the top row, ellipses were a common shape for month forms (Galton, 1880; Smilek et al., 2007; Price and Mentzoni, 2008; Cytowic and Eagleman, 2009), a motif which accords with the cyclical nature of the year. However, we immediately noticed many fewer elliptical shapes than expected. Depending on our method for classifying ellipses (detailed in the next section), we found only between 94 and 110 ellipses, meaning that despite the prevalence of their reports in the literature, fewer than 20% of the month forms were actually classifiable this way.

Perhaps surprisingly, the most common shape of month-form (26.6%) fell into the category of a line (which includes straight lines, bent-lines, and zigzags). As one straight-line synesthete described it: ‘‘My sequences always go to the right, away from me. Number lines are kind of a pain because, to me, the negative numbers are backwards.... They [months, weekdays, numbers] get smaller and smaller as they go higher (or, for negatives, lower), to the point where I finally can’t see them anymore.’’ The fact that lines crop up so commonly suggests the interesting possibility of selection bias in previous reports on spatial sequence synesthesia: often, when investigators are trying to determine whether a subject is synesthetic, they are impressed by striking and unusual shapes and pursue such reports further. On the other hand, when a subject testifies, ‘‘In my mind, the months proceed from left to right in a line,’’ she is often dropped from further analysis given the uncertainty of whether she is simply reporting what has been previously seen on a calendar. Therefore, the possibility is raised that many genuine spatial sequence synesthetes in fact see their forms as lines (Cohen Kadosh and Henik, 2007b); if this is validated by future research, it suggests a closer relationship with non-synesthetes (and thus with the SNARC effect) than previously expected.

The next most common motifs were U-shapes (12.4%), triangles (4.4%), star-shapes (2.1%), squares (1.9%) and S-shapes (.35%). Encouraged not to over-categorize, the judge put almost 30% of the shapes under the label of ‘‘unclassified,’’ most often because they were hybrids of other categories—for example, a hybrid of a circle/triangle, a circle/line, and so on.

3.2. *Ellipses and their directions*

Because of the attention previously paid to elliptical month forms in the literature (Seymour, 1980; Smilek et al., 2007; Price and Mentzoni, 2008), we next turned to these in more detail. To appropriately classify shapes that were primarily elliptical, we identified them with two independent techniques. First, and most simply, the independent judge labeled those she found to be elliptical—this method yielded 110 ellipses. A second, more rigorous approach was applied to the 3D coordinates of the forms: first, the spatial distance between each month and its nearest ordinal neighbors was calculated (e.g., for May, the distances to April and June). If, for every month, these two distances were among its shortest three distances to any month, *and* December was close to January (within one standard deviation of the average inter-month distance for that participant), then the form was considered to be elliptical. This second, slightly more draconian method selected 94 ellipses (16.5%), all of which had also appeared in the judge’s selection.

Using the more conservative subset of 94, we characterized which ellipses ran clockwise and which counterclockwise. Seventy one (75.6%) moved in a clockwise direction, and twenty three (24.4%) ran counterclockwise. The fact that one quarter of the ellipses ran counterclockwise casts at least some doubt on the possibility that subjects are imprinting on clock faces.

Finally, we selected those ellipses which lay primarily in the XY plane (i.e., an ellipse arranged in front of the avatar like a large clock, $n = 48$), and assessed Galton’s claim that January is not necessarily the topmost month of spatial forms (Galton,

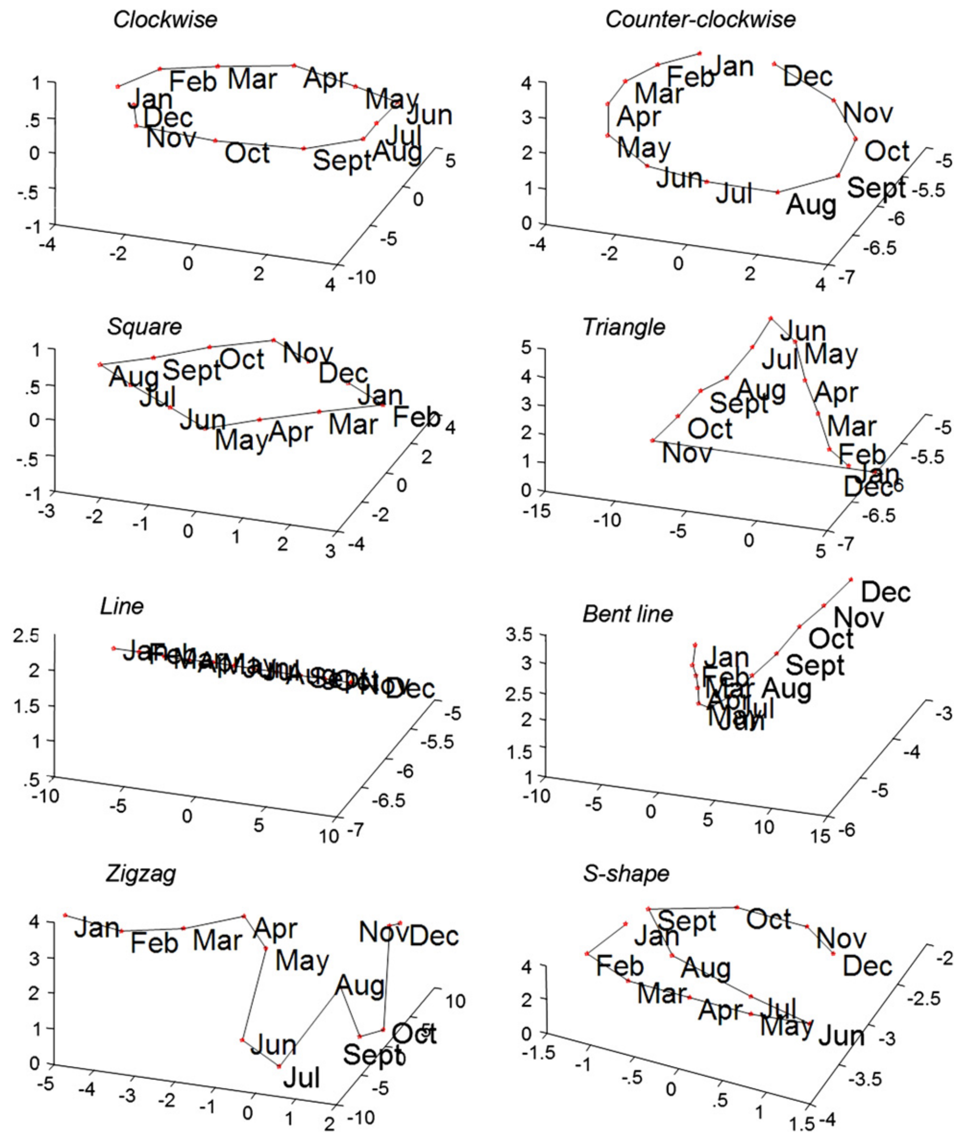

Fig. 2 – A selection of some common shape motifs of month-forms.

1880). For each form, we calculated the location of January in relation to the center of gravity of the circle. Indeed, Galton was correct: there appears to be no overall pattern to the location of January (Fig. 3), casting further doubt on the possibility that subjects are mapping their months onto an imprinted representation of a clock.

3.3. *Left-to-right bias*

As mentioned above, the SNARC effect in non-synesthetes for numbers, months, days and letters suggests a spatial representation of ordinal sequences from left to right (Gevers et al., 2003, 2004, 2006). Will we find the same left-to-right representation in synesthetes? If not, this might indicate a fundamental difference in the representations of synesthetes and controls, rather than a different degree of the same thing. If so, it may support a common underlying basis.

To address this question, we engineered two techniques to measure the left/right bias for all month-forms. First, we defined a bias index: the distance of each month from the vertical midline was computed; for early months (January–June), these distances were positive if the months were on the left of midline, and negative otherwise, and for later months this was reversed. In other words, if a participant's January through June were on the left side of the midline while July through December were on the right, the directional index would be strongly positive; in the flipped case, it is negative; if there were an even distribution of early and late months on either side of the midline, the index would be close to zero.

As shown in Fig. 4a, 62% of subjects show a left-to-right directional bias. Although this is not a vast majority, it allows the possibility that SSS and the SNARC effect could be degrees of the same phenomenon, because we would expect, *on average*, to find a left-to-right bias in a random sampling of

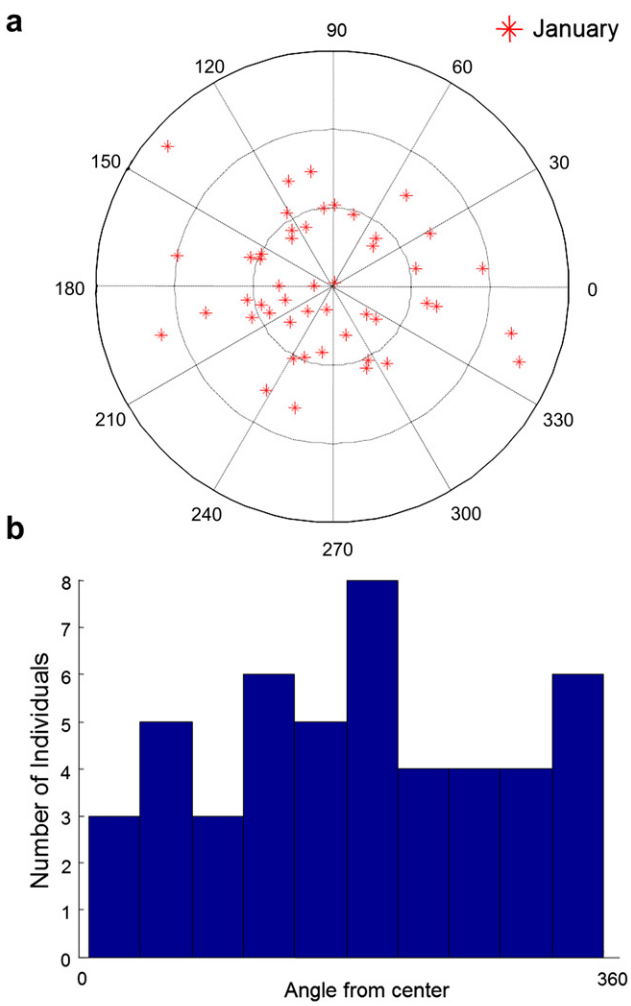

Fig. 3 – The top of the year is not necessarily the top of the form. (a) Each red dot represents the angle and radius of January in relation to the center of gravity of an elliptical month form. $n = 48$. (b) Summary histogram.

non-synesthetic subjects who implicitly hold similar representations to the ones found here.

The fact that there are biases in the right-to-left direction as well is consistent with several previous reports in which some subjects have early months on the left of midline, and some have early months on the right (Galton, 1880; Smilek et al., 2007; Price and Mentzoni, 2008). However, since the previous studies had sample sizes of four or less, it was difficult to know how this variability would express in larger populations. Note that all participants were asked to volunteer their native language, and of those whose responded (538 of 571), only four reported right-to-left languages (3 Hebrew and 1 Arabic). Also, note that the Synesthesia Battery is currently administered entirely in English, and therefore all participants require at least a basic knowledge of this left-to-right language to take the tests.

We next utilized a second technique to measure the directional bias element-by-element. Within each form, we determined for every month (e.g., April) whether the subsequent month (e.g., May) was spatially positioned to the right or left (or aligned). When analyzing the data this way, a similar result emerged: months February through December are 62.5% more likely to be to the right rather than the left of their previous month (Fig. 4b). In other words, the individual elements tend to move in a left-to-right direction. Not surprisingly, the one exception to the trend is January, which tends to be to the left of December rather than to its right.

Note that especially with elliptical forms, there may be an interesting conflation between where an element is in relation to midline (e.g., to the left) compared to where it is in relation to its previous neighbor (e.g., to the right). Speculatively, this may shed light on why Price and colleagues have concluded that the SNARC effect is not sensitive to the spatial details of the reported forms, only to left-right polarity (Price and Mentzoni, 2008; Price, this issue, 2009). It may be that spatial details *do* matter, but that all the aspects (lateralization as well as neighborhood relations) must be taken into account.

In the General discussion (below), we will suggest how these results shed light on the relationship of spatial sequence synesthesia to effects found in non-synesthetes. But first we will turn to a novel proposal for the neural basis.

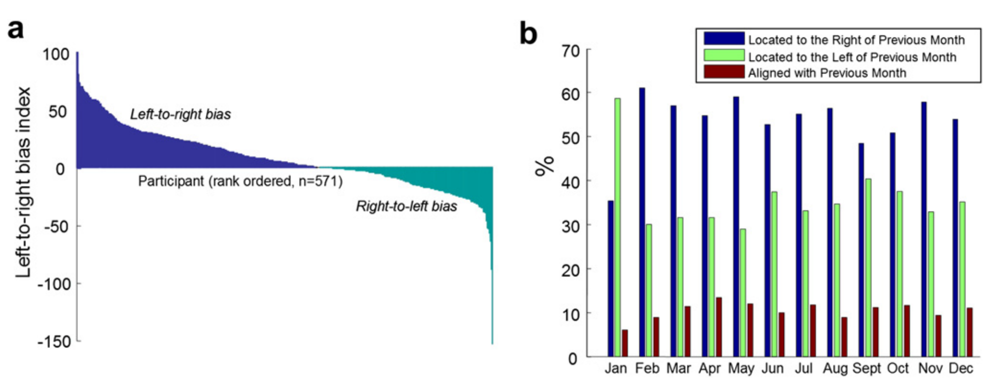

Fig. 4 – Measuring left-to-right bias in month forms. (a) Lateralization analysis. A bias index quantifies the degree to which early months are on the left of midline and later months on the right (see text for details). The majority of month forms (62%) had a left-to-right bias. $n = 571$. (b) Element-by-element analysis. Bars show the percentage of time in which any given month is found to the right or left of the previous month in the sequence. The majority of months move in a left-to-right direction with respect to their neighbors in the sequence. $n = 571$.

4. Neural mechanisms

4.1. The neural basis of overlearned sequences

As discussed earlier, overlearned ordinal sequences seem to be the key trigger for SSS (Shanon, 1982; Rich et al., 2005; Seron et al., 1992; Cytowic and Eagleman, 2009). But what is special about these sequences, neurally speaking? Are there special neural networks that seem to process these sequences explicitly, and, if so, what does this indicate about the neural basis of SSS?

Inspired by this question, we recently set out to elucidate the neural areas involved specifically in the encoding of ordinal categories. Using functional magnetic resonance imaging (fMRI), we discovered that stimuli belonging to a ordinal category (e.g., letters, numbers, weekdays, months) involve right-hemispheric activation in the middle temporal gyrus (rMTG) (Pariyadath et al., 2008). In contrast, words belonging to non-ordinal categories (e.g., names of fruits, animals, cars and furniture) activate left-hemisphere areas typically implicated in language processing (Cohen and Dehaene, 2004; Cohen et al., 2003). We therefore propose the hypothesis that a critical neural area in spatial sequence synesthesia is the right middle temporal gyrus, as will be detailed below.

It is important to note that our hypothesis is quite different from a previous proposal that SSS involves the IPS, a brain region involved not only in spatial processing but also in the representation of numerical quantity (Hubbard et al., 2005b; Tang et al., 2008). We will therefore spend a few moments addressing the IPS hypothesis.

Activity in the IPS is modulated by numerical magnitude judgments (e.g., assessing the numerical distance between numbers; Piazza et al., 2004, 2007; Pinel et al., 2001), irrespective of how the magnitude is conveyed (e.g., digits, dot patterns, a sequence of single events, etc; Fias et al., 2003; Cohen Kadosh et al., 2007a; Piazza et al., 2007). In patients, lesions of the IPS impair normal ability for quantity comparison (Dehaene et al., 2003). These data from humans accord well with monkey electrophysiology in the same region, in which individual neurons appear to encode magnitude judgments (Nieder, 2005; Nieder and Miller, 2004). Collectively, these studies make clear that the IPS is involved in processing numerical quantity.

But does the IPS encode ordinal sequences, such as letters, weekdays and months? Several studies suggest not: these have found stronger activation in the IPS during number processing than during processing of other ordinal dimensions such as letters of the alphabet (Eger et al., 2003), body part position (Le Clec et al., 2000), or animal ferocity (Thioux et al., 2005). In other words, these studies suggest that the IPS does not process ordinal sequences in general, but numerosity or magnitude judgments in particular. Recently, Fias et al. (2007) challenged this view, demonstrating that the IPS is active not only when comparing numerical magnitude, but also alphabetical magnitude (''which of these two letters appears *later* in the alphabet?''; Fias et al., 2007). Note that this result does not demonstrate that the IPS is involved in encoding individual letters, only that it can be involved in comparing the relative magnitude between letters. In a related study, Ischebeck et al. (2008) asked subjects to verbally generate the names of numbers or months (in scrambled or canonical order), and also animal names (Ischebeck et al., 2008). Under certain conditions, they found that the IPS (along with the rMTG) was as activated by month generation as by number generation, which led them to suggest that the IPS can process months as well as numerical quantity. Again, note that in the context of the experiment, the task of generating cardinal versus scrambled sequences requires attention to relative ordering; therefore, their result does not establish that individual months are encoded by the IPS, only that attention to relative positioning activates this area.

Thus, although the evidence is clear that IPS is involved in numerosity, this region seems ill-suited to serve as the basis of sequence-based synesthesias. This is for a simple reason: the IPS is found to be activated only in paradigms involving quantity, magnitude or ordering tasks (such as comparing which of two stimuli comes later in a sequence). The critical point is that quantity, magnitude or ordering judgments do not appear to be the triggering stimuli for synesthesia; to our knowledge, there is not a single reported case in which synesthesia is elicited by such tasks. Instead, typical synesthesia is triggered simply by individual elements of sequences, such as a weekday, month, letter or number. Such straightforward stimuli map more directly onto the presentation of stimuli in the study of Pariyadath et al. (2008), not the magnitude comparison studies that activate the IPS.

In summary, then, we suggest that the critical neural areas involved in SSS will not be the intraparietal regions involved in comparison judgments, but instead areas involved in the elements of ordinal sequences, such as the right middle temporal gyrus. Of course, both of these regions may play a part; future studies will be needed to refine our understanding of their respective roles.

4.2. The neural basis of reification

As discussed above, the IPS processes not only comparative numerical judgments, but also spatial coordinates, and this has previously led to a suggestion that perhaps this area serves as the basis for SSS (Hubbard et al., 2005b; Tang et al., 2008). We speculate that such a model is likely to be incomplete. Instead, the fact that sequences are reified (turned into objects) suggests that areas of the brain involved in visual object representation may play the critical role. The areas most involved in visual object representation, generally speaking, are found in the ventral surface of the temporal lobe (Gauthier et al., 1999; Gross et al., 1969; Sergent et al., 1992; Peissig and Tarr, 2007).

Given the proximity of the middle temporal gyrus 'sequence area' (Pariyadath et al., 2008) to the inferior temporal lobe, we propose a new hypothesis for the basis of SSS, depicted in Fig. 5. Specifically, we hypothesize cross-talk between areas involved in sequences and those involved in object representation. The degree of cross-talk may determine, with some sort of non-linear thresholding, whether a person experiences the relationship explicitly (synesthetes) or implicitly (non-synesthetes).

Fig. 5 – A new hypothesis for the neural basis of spatial sequence synesthesia. *Red*: an area in the middle temporal gyrus recently implicated in the coding of overlearned sequences (Pariyadath et al., 2008). *Blue*: the inferior temporal lobe, an area implicated in visual object representation. The proximity of the two areas suggests the possibility that cross talk between them results in the objectification of sequences.

This hypothesis is not exclusive with a possible involvement of other areas (such as the IPS), but it directs the emphasis onto the ''objecthood'' of overlearned sequences. It may well be that the IPS plays a role in the mental rotations and translations as synesthetes ''move around'' their spatial forms; indeed, the dorsal-stream role of the IPS seems well-suited to that task (Colby and Duhamel, 1996; Gauthier et al., 2002; Kawamichi et al., 2007; Podzebenko et al., 2005; Tagaris et al., 1996; Hubbard et al., 2005b). But as for the number form itself, ventral stream areas such as the inferior temporal lobe appear the most likely candidate for sequence reification.

5. General discussion

There has been an ongoing discussion about whether spatial sequences should qualify as a form of synesthesia. At first glance, the objectification of sequences does not seem to fit the definition of synesthesia as a sensory coupling; however, the fact that the inducers are the same as the more well-studied color synesthesia seems to implicate it as a related phenomenon. In this case, the overlearned sequences trigger an experience of objecthood, in the same way that experiences of shape, texture, color, and illumination can also be triggered by sequences (Eagleman and Goodale, 2009). Therefore it seems appropriate to classify the automatic objectification of sequences as a form of synesthesia.

An open question is whether the implicit spatial mapping illustrated in non-synesthetes by phenomena such as the SNARC effect represents the same phenomenon. To address this possibility, we examined month-forms from 571 self-reported synesthetes, and found several pieces of evidence that can be interpreted to weigh in favor of a shared basis between the SNARC effect and SSS.

First, most month forms appear to proceed generally in a left-to-right direction (Fig. 4). This means that if non-synesthetes happened to possess implicit versions of the spatial forms that synesthetes experience explicitly, we would expect to find, on average, a left-to-right SNARC effect in the population.

Further, when examining the variety of shape motifs in month forms, we found a surprisingly high percentage of lines (26.6%, either straight or with slight bends). Although elliptical month-forms were found, they were less common (<20%) than would be expected from their emphasis in the extant literature (Seymour, 1980; Price and Mentzoni 2008; Smilek et al., 2007). In contrast, linear month-forms are hardly mentioned in the literature. We speculate that this absence may reflect an unconscious selection bias: previous investigators, searching for surprising spatial forms that could convince skeptics based on pure exoticism, may have been uncertain whether to include subjects who reported straight lines. If we take our data to indicate that there are more linear month-forms than previously reported, this may suggest a closer relationship with non-synesthetes (and the SNARC effect) than expected.

This possibility raises an interesting question: if SSS is simply an exaggeration of normal neural cross-talk in everyone, is it possible that some fraction of non-synesthetes have implicit month forms that are elliptical, U-shaped, S-shaped, or so on? In tests of the SNARC effect, there is a good deal of variability among subjects (e.g., compare Gevers et al., 2003 with Price and Mentzoni, 2008). Might it be possible that non-synesthetic subjects who do not show a standard SNARC effect are in fact harboring spatial forms of more interesting shapes, like their more famous synesthetic counterparts? In other words, the existence of the SNARC effect in non-synesthetes does not require that the underlying structure is a straight left-to-right line – it only requires that the representations, on average, are biased from left-to-right, just as we have found in our sample (Fig. 4).

Collectively, therefore, the average properties we find in month forms appear roughly consistent with the characteristics found in the SNARC effect. While the present findings cannot conclusively establish that SNARC and SSS represent the same phenomenon, they certainly do not rule against it. Further, we have raised the possibility that the unseen month-forms that underlie the SNARC effect in normals may well consist not only of straight lines, but more generally of the variety of forms seen in synesthetes.

If synesthetes and non-synesthetes share a common neural basis for their mappings between sequence and objecthood, what is that basis? The search has heretofore been focused on areas of the brain such as the parietal lobe (Hubbard et al., 2005b; Tang et al., 2008), which is involved in both numeric computations and spatial coordinate systems. However, given the new discovery of temporal lobe areas involved in overlearned sequences (Pariyadath et al., 2008) and the well-known role of the inferior temporal lobe in object representation (Peissig and Tarr, 2007), we have proposed a critical role for these neighboring temporal regions (Fig. 5).

Why the putative neural cross-talk should cross the threshold of conscious awareness in some, and not in others, is currently unknown. One possibility is that the difference results from individual differences in the vividness of the visual imagery, which is known to vary widely in the population (McKelvie and Rohrberg, 1978; Lotze et al., 1999; Howard et al., 1998; Cui et al., 2007). This long-considered possibility (Seron et al., 1992), while unlikely to serve as a complete explanation, is consistent with two reports in this issue that spatial sequence synesthetes show superior imagery both in self-report (Price, this issue, 2009) and in behavioral tasks such as mental rotation (Simner et al., this issue, 2009). Another, non-exclusive possibility for why a subset of the population has vividly conscious access to sequential spatial mappings is an inherited genetic component, as is thought to occur in colored sequence synesthesia (Ward and Simner, 2005; Cytowic and Eagleman, 2009; Nelson et al., in preparation).

We wish to emphasize again that the data in this paper relies on self-reported synesthetes. However, there are several reasons to believe that the results may nonetheless contain a sufficiently high signal-to-noise ratio. First, the size of the sample ($n = 571$) lends itself to washing out noise from malingerers. Second, the testing process is somewhat lengthy (average time to complete is 12 min, not including registering for the Synesthesia Battery and filling out the questionnaires), and this time investment can be generally assumed to reduce the enthusiasm of malingerers. Relatedly, we have excluded any data sets for which two or more of the months are left in the same arbitrary position in which they were automatically placed at the start of the program; this eliminates any malingerers who were unwilling to devote their time to work through the full session. There are of course limitations inherent in data based on self-report, but we hope that the population reported here is sufficiently large to allow us to at least discern some general patterns not previously detected.

In closing, some simple observations can help us refine our understanding and constrain future theories. First, note that for a learned sequence to trigger synesthetic experience, it is not required for the sequence to have a beginning or end. For example, the fact that years commonly trigger spatial forms (Fig. 1a) indicates that the important characteristic is simply ordinality, irrespective of whether the sequence possesses beginnings, endings, or a cyclical nature. Second, an obvious feature that deserves to be explicitly highlighted is that close spatial relationships are maintained between neighboring elements in a sequence – or what we term 'sequentiotopy'. In other words, a synesthete could *in theory* experience Wednesday as the spatial neighbor to Saturday – but instead sequential elements almost always are positioned as neighbors in space (i.e., Wednesday typically ends up between Tuesday and Thursday). Topography is a theme of sensory organization: consider retinotopy in the visual system, tonotopy in the auditory system, and somotatopy in the somatosensory system. Thus, as sequences are learned, it appears they may become mapped onto other ''topic'' structures, such as an ellipse or a line. This simple observation may serve as a future clue to the details of the neurobiology. Finally, while consistency over time has served as the gold standard for determining the genuineness of synesthesia, certain spatial sequences (e.g., years, ages) may prove to be an exception to that rule, as spatial forms are sometimes reported to change or ''grow'' through time. One synesthete remarked that number forms relating to her age grew from their terminal end ''like a vine''. That is, at a young age, her future years faded into the foreground; by age 23, the psychophysical space had enlarged for later years (Cytowic, 2002). Thus, any complete theory of SSS will have to address how ongoing experience can dynamically modify spatial mappings.

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REFERENCES

Bertillon J. De la vision des nombres. *La Nature*, 378: 196–198, 1880.
Cohen Kadosh R, Cohen Kadosh K, Kaas A, Henik A, and Goebel R. Notation-dependent and -independent representations of numbers in the parietal lobes. *Neuron*, 53: 307–314, 2007a.
Cohen Kadosh R and Henik A. Can synaesthesia research inform cognitive science? *Trends in Cognitive Sciences*, 11: 177–184, 2007b.
Cohen L and Dehaene S. Specialization within the ventral stream: the case for the visual word form area. *NeuroImage*, 22: 466–476, 2004.
Cohen L, Martinaud O, Lemer C, Lehericy S, Samson Y, Obadia M, et al. Visual word recognition in the left and right hemispheres: anatomical and functional correlates of peripheral alexias. *Cerebral Cortex*, 13: 1313–1333, 2003.
Colby CL and Duhamel JR. Spatial representations for action in parietal cortex. *Brain Research. Cognitive Brain Research*, 5: 105–115, 1996.
Cui X, Yang D, Jeter C, Montague PR, and Eagleman DM. Vividness of mental imagery: individual variation can be measured objectively. *Vision Research*, 47: 474–478, 2007.
Cytowic RE. *Synaesthesia: a Union of the Senses*. Cambridge, MA: MIT Press, 2002.
Cytowic RE and Eagleman DM. *Wednesday is Indigo Blue: Discovering the Brain of Synesthesia*. Cambridge, MA: MIT Press, 2009.
Dehaene S, Bossini S, and Giraux P. The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, 122: 371–396, 1993.
Dehaene S, Piazza M, Pinel P, and Cohen L. Three parietal circuits for number processing. *Cognitive Neuropsychology*, 20: 487–506, 2003.
Eagleman DM. Visual illusions and neurobiology. *Nature Reviews Neuroscience*, 2: 920–926, 2001.
Eagleman DM and Goodale MA. Why color synesthesia involves more than color. *Trends in Cognitive Sciences*, 13: 288–292, 2009.
Eagleman DM, Kagan AD, Nelson SS, Sagaram D, and Sarma AK. A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods*, 159: 139–145, 2007.
Eger E, Sterzer P, Russ MO, Giraud AL, and Kleinschmidt A. A supramodal number representation in human intraparietal cortex. *Neuron*, 37: 719–725, 2003.

Fias W. The importance of magnitude information in numerical processing: evidence from the SNARC effect. *Mathematical Cognition*, 2: 95–110, 1996.

Fias W, Lammertyn J, Caessens B, and Orban GA. Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. *The Journal of Neuroscience*, 27: 8952–8956, 2007.

Fias W, Lammertyn J, Reynvoet B, Dupont P, and Orban GA. Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience*, 15: 47–56, 2003.

Galton F. Visualized numerals. *Nature*, 21: 252–256, 1880.

Galton F. *Enquiries into Human Faculty and its Development*, 1883.

Gauthier I, Hayward WG, Tarr MJ, Anderson AW, Skudlarski P, and Gore JC. Bold activity during mental rotation and viewpoint-dependent object recognition. *Neuron*, 34: 161–171, 2002.

Gauthier I, Tarr MJ, Anderson AW, Skudlarski P, and Gore JC. Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nature Neuroscience*, 2: 568–573, 1999.

Gevers W, Lammertyn J, Notebaert W, Verguts T, and Fias W. Automatic response activation of implicit spatial information: evidence from the SNARC effect. *Acta Psychologica*, 122: 221–233, 2006.

Gevers W, Reynvoet B, and Fias W. The mental representation of ordinal sequences is spatially organized. *Cognition*, 87, 2003.

Gevers W, Reynvoet B, and Fias W. The mental representation of ordinal sequences is spatially organized: evidence from days of the week. *Cortex*, 40: 171–172, 2004.

Gross CG, Bender DB, and Rocha-Miranda CE. Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, 166: 1303–1306, 1969.

Howard RJ, Ffytche DH, Barnes J, McKeefry D, Ha Y, Woodruff PW, et al. The functional anatomy of imagining and perceiving colour. *Neuroreport*, 9: 1019–1023, 1998.

Hubbard EM, Arman AC, Ramachandran VS, and Boynton GM. Individual differences among grapheme-color synesthetes: brain-behavior correlations. *Neuron*, 45: 975–985, 2005a.

Hubbard EM, Piazza M, Pinel P, and Dehaene S. Interactions between number and space in parietal cortex. *Nature Reviews. Neuroscience*, 6: 435–448, 2005b.

Hubbard EM, Ranzini M, Piazza M, and Dehaene S. What information is critical to elicit interference in number-form synesthesia? *Cortex*, 45: 1200–1216, 2009.

Ischebeck A, Heim S, Siedentopf C, Zamarian L, Schocke M, Kremser C, et al. Are numbers special? Comparing the generation of verbal materials from ordered categories (months) to numbers and other categories (animals) in an fMRI study. *Human Brain Mapping*, 29: 894–909, 2008.

Jarick M, Dixon MJ, Stewart MT, Maxwell EC, and Smilek D. A different outlook on time: visual and auditory month names elicit different mental vantage points for a time-space synaesthete. *Cortex*, 45: 1217–1228, 2009.

Kawamichi H, Kikuchi Y, Noriuchi M, Senoo A, and Ueno S. Distinct neural correlates underlying two- and three-dimensional mental rotations using three-dimensional objects. *Brain Research*, 1144: 117–126, 2007.

Le Clec HG, Dehaene S, Cohen L, Mehler J, Dupoux E, Poline JB, et al. Distinct cortical areas for names of numbers and body parts independent of language and input modality. *NeuroImage*, 12: 381–391, 2000.

Lotze M, Montoya P, Erb M, Hulsmann E, Flor H, Klose U, et al. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal of Cognitive Neuroscience*, 11: 491–501, 1999.

McKelvie SJ and Rohrberg MM. Individual differences in reported visual imagery and cognitive performance. *Perceptual and Motor Skills*, 46: 451–458, 1978.

Nelson S, Sarma AK, Shete S, Yu RK, Intwala A, Leal SM, et al. The genetics of colored sequence synesthesia: evidence of linkage to chromosome 16q, in preparation.

Nieder A. Counting on neurons: the neurobiology of numerical competence. *Nature Reviews. Neuroscience*, 6: 177–190, 2005.

Nieder A and Miller EK. A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences of the United States of America*, 101: 7457–7462, 2004.

Pariyadath V, Churchill SJ, and Eagleman DM. Why overlearned sequences are special: distinct neural networks in the right hemisphere for ordinal sequences. *Nature Precedings*, 2008.

Peissig JJ and Tarr MJ. Visual object recognition: do we know more now than we did 20 years ago? *Annual Review of Psychology*, 58: 75–96, 2007.

Piazza M, Izard V, Pinel P, Le Bihan D, and Dehaene S. Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, 44: 547–555, 2004.

Piazza M, Pinel P, Le Bihan D, and Dehaene S. A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron*, 53: 293–305, 2007.

Pinel P, Dehaene S, Riviere D, and LeBihan D. Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage*, 14: 1013–1026, 2001.

Plodowski A, Swainson R, Jackson GM, Rorden C, and Jackson SR. Mental representation of number in different numerical forms. *Current Biology*, 13: 2045–2050, 2003.

Podzebenko K, Egan GF, and Watson JD. Real and imaginary rotary motion processing: functional parcellation of the human parietal lobe revealed by fMRI. *Journal of Cognitive Neuroscience*, 17: 24–36, 2005.

Price MC. Spatial forms and mental imagery. *Cortex*, 45: 1229–1245, 2009.

Price MC and Mentzoni RA. Where is January? The month-SNARC effect in sequence-form synaesthetes. *Cortex*, 44: 890–907, 2008.

Rich AN, Bradshaw JL, and Mattingley JB. A systematic, large-scale study of synaesthesia: implications for the role of early experience in lexical-colour associations. *Cognition*, 98: 53–84, 2005.

Sagiv N, Simner J, Collins J, Butterworth B, and Ward J. What is the relationship between synaesthesia and visuo-spatial number forms? *Cognition*, 101: 114–128, 2006.

Santens S and Gevers W. The SNARC effect does not imply a mental number line. *Cognition*, 108: 263–270, 2008.

Sergent J, Ohta S, and MacDonald B. Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, 115: 15–36, 1992.

Seron X, Pesenti M, Noe?l MP, Deloche G, and Cornet JA. Images of numbers, or ''When 98 is upper left and 6 sky blue''. *Cognition*, 44: 159–196, 1992.

Seymour PHK. Internal representations of months: an experimental analysis of spatial forms. *Psychological Research*, 42: 255–273, 1980.

Shanon B. Colour associates to semantic linear orders. *Psychological Research*, 44: 75–83, 1982.

Simner J, Mayo N, and Spiller M. A foundation for savantism? Visuo-spatial synaesthetes present with cognitive benefits. *Cortex*, 45: 1246–1260, 2009.

Smilek D, Callejas A, Dixon MJ, and Merikle PM. Ovals of time: time-space associations in synaesthesia. *Consciousness and Cognition*, 16: 507–519, 2007.

Tagaris GA, Kim SG, Strupp JP, Andersen P, Ugurbil K, and Georgopoulos AP. Quantitative relations between parietal activation and performance in mental rotation. *Neuroreport*, 7: 773–776, 1996.

Tang J, Ward J, and Butterworth B. Number forms in the brain. *Journal of Cognitive Neuroscience*, 2008.

Thioux M, Pesenti M, Costes N, De Volder A, and Seron X. Task-independent semantic activation for numbers and animals. *Brain Research. Cognitive Brain Research*, 24: 284–290, 2005.

Ward J and Simner J. Is synaesthesia an x-linked dominant trait with lethality in males? *Perception*, 34: 611–623, 2005.
Wheeler RH. *The Synaesthesia of a Blind Subject*. University of Oregon Publications, 5, 1920.
Witthoft N and Winawer J. Synesthetic colors determined by having colored refrigerator magnets in childhood. *Cortex*, 42: 175–183, 2006.
Wood G and Fischer MH. Numbers, space, and action – from finger counting to the mental number line and beyond. *Cortex*, 44: 353–358, 2008.
Wood G, Nuerk HC, and Willmes K. Crossed hands and the SNARC effect: a failure to replicate Dehaene, Bossini and Giraux (1993). *Cortex*, 42: 1069–1079, 2006. Discussion 1119–23.