



Spatial cueing in time–space synesthetes: An event-related brain potential study

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ABSTRACT

Some people report that they consistently and involuntarily associate time events, such as months of the year, with specific spatial locations; a condition referred to as time–space synesthesia. The present study investigated the manner in which such synesthetic time–space associations affect visuo-spatial attention via an endogenous cuing paradigm. Reaction times and ERPs were recorded as 12 time–space synesthetes and 12 control participants did a peripheral target detection task, cued by three different types of centrally presented cues: arrows pointing left or right, direction words “left” or “right”, and month names associated with either the left or the right side of the synesthete’s mental calendar (e.g., “October” or “May”). Cues were followed by probes on the left or right side of the screen, and participants responded to the probes with button presses. Behavioral and ERP data suggested that for synesthetes, month words functioned more effectively as cues to direct attention in space. In synesthetes but not controls, a comparison of ERPs to probes cued by months revealed effects of cue validity on the P3b component peaking 370 ms post-onset and on the subsequent positive slow wave (pSW) observed 600–900 ms post-onset (both larger for invalid probes). No effects of cue validity were observed on early visual potentials (N1) for probes cued by months. The findings suggest that in these time–space synesthetes cue validity influenced post-perceptual processes, such as stimulus evaluation and categorization, with no evidence for enhanced visual processing.

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1. Introduction

Synesthesia is a condition in which certain types of perceptual or conceptual stimuli evoke involuntary and consistent sensations in another, unstimulated and seemingly unrelated modality (Baron-Cohen & Harrison, 1997; Cytowic, 1989/2002; Hubbard, Arman, Ramachandran, & Boynton, 2005; Ramachandran & Hubbard, 2001, 2003). In time–space synesthesia, units of time are experienced as occupying specific spatial locations such that temporal sequences (e.g. the months of the year) are felt to be arranged in a particular shape. These spatial representations are sometimes convoluted and idiosyncratic, but display the test–retest consistency that is the hallmark of synesthesia (Cytowic, 1989/2002; Galton, 1880/1997; Smilek, Callejas, Dixon, & Merikle, 2007). More typically, time–space synesthetes report the 12 months of the year to be arranged in the shape of an oval, an oblong, or a circle (Brang, Teuscher, Ramachandran, & Coulson, 2010; Galton, 1880/1997).

Time–space synesthesia, along with other kinds of synesthetic spatial forms for sequences (e.g., the sensation that numbers, letters of the alphabet, etc. are aligned on a convoluted path), perhaps constitutes a borderline case of synesthesia, since it is an internal experience generated by a cognitive state, rather than by sensory stimulation. Some authors have either included (Galton, 1880/1997) or excluded (Dehaene, 1997) these associations between temporal units and spatial forms as an instance of synesthesia. However, in view of these individuals’ descriptions of the involuntary, consistent, and idiosyncratic nature of time–space associations, and given that they are often observed in people who report other, more canonical synesthetic experiences (e.g. colored letters, or colored hearing; e.g., Sagiv, Simner, Collins, Butterworth, & Ward, 2006), most researchers now do include time–space synesthesia as a valid form of the condition (e.g., Grossenbacher & Lovelace, 2001; Hubbard, Piazza, Pinel, & Dehaene, 2005; Price & Mentzoni, 2008; Sagiv et al., 2006; Smilek et al., 2007).

Hubbard and Teuscher (2010) propose that time–space synesthesia is caused by cross-activation in parietal cortex, an area known to be involved in the processing of both temporal quantities (Coull, Vidal, Nazarian, & Macar, 2004; Lewis & Miall, 2002) and abstract spatial maps (see also the discussion of number-form synesthesia by Hubbard, Arman, et al. (2005) and Hubbard, Piazza, et al.

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(2005)). Abstract spatial maps are represented in posterior superior parietal lobes, which have also been implicated in spatial abilities (Cohen & Andersen, 2002; Colby & Goldberg, 1999). Although the neural substrate of time–space synesthesia is not currently known, it likely involves a complex interplay of activity in the angular gyrus (representing spatial forms ranging from number-lines to calendars, e.g. Göbel, Walsh, & Rushworth, 2001; Spalding & Zangwill, 1950) and activity in other parietal structures (including the intraparietal sulcus and more generally the temporal parietal occipital junction; Ramachandran and Hubbard, 2001). Grapheme–color synesthesia has been shown to be accompanied by an increase in white matter connectivity between brain areas thought to be important for grapheme and color perception, respectively (Rouw & Scholte, 2007). Accordingly, it is possible that an analogous increase in connectivity is present in time–space synesthesia.

Given the important role played by the parietal lobes in orienting attention in space (Behrmann, Geng, & Shomstein, 2004; Posner & Petersen, 1990), one implication of Hubbard and Teuscher's (2010) model is that the hypothesized increased connectivity in parietal lobes in time–space synesthetes may affect spatial attention processes. Due to the habitual involuntary associations in individuals with this condition, temporal concepts may trigger shifts of visuo-spatial attention to their associated regions in space. For example, when thinking about October, a time–space synesthete might naturally direct her attention to the region of space that she associates with October. This is consistent with a spatial cuing study by Smilek et al. (2007). In this paradigm, a cue stimulus (e.g. an arrow) directs the subject to attend to a particular location on each trial, and a target is then presented either at the attended location (valid trials), or at an unattended location (invalid trials) (Posner, 1978). In the so-called Posner paradigm, responses to targets are faster and more accurate when they appear at the cued (i.e. valid) than un-cued (invalid) location (e.g., Cheal & Lyon, 1991; Posner, 1980). Smilek and colleagues (2007) used a variant of the Posner task in which a centrally presented cue was equally likely to be followed by valid and invalid targets (Friesen & Kingstone, 1998). In light of the uninformative nature of the cues, faster responses to targets in the cued locations have been interpreted as signaling the reflexive nature of the attentional shift (Jonides, 1981). To test the reflexive nature of synesthetic spatial forms, Smilek et al. (2007) presented month words that synesthetes associated with the left and the right side of space as nonpredictive cues in their task. That is, probes were equally likely to occur in the cued and un-cued locations. Smilek and colleagues found that in two of the four time–space synesthetes they tested, responses were faster for targets in cued locations. In spite of the fact that the cues provided no information that could help participants perform the target detection task, these synesthetes nonetheless shifted their attention to the cued region of space. Moreover, these cuing effects were evident both at a long cue-target SOA (600 ms) and at a short cue-target SOA (150 ms), where strategic influences on performance should be nonexistent, since volitional shifts of attention typically emerge at cue-target SOAs greater than 300 ms (e.g., Friesen & Kingstone, 1998). Consequently, Smilek et al. (2007) argued that the associations in time–space synesthesia are such that temporal concepts automatically trigger a shift of attention to the appropriate region of space.

One reason Smilek and colleagues (2007) did not observe a higher incidence of cuing effects, however, may be their use of nonpredictive cues. Previous research on visuo-spatial attention has suggested a dissociation of voluntary, *endogenous* processes engaged by cues which are symbolic, centrally presented, and predictive, from reflexive, *exogenous* processes induced by nonpredictive cues presented in the periphery (see Funes, Lupianez, & Milliken (2007) for review). When centrally presented symbolic

cues are nonpredictive, they do not typically facilitate responses to stimuli in the cued region of space, as there is simply no motivation for the subject to shift attention to the cued location if the target is just as likely to occur in the un-cued one (Stevens, Pashler, & Yantis, 2004, pp. 241–242). In light of this, it is surprising that Smilek et al. found any cuing effects at all. Furthermore, exogenous processes have been linked to the superior colliculus, whereas endogenous processes have been linked to parietal regions that have also been implicated in time–space synesthesia (Rafal, Posner, Friedmann, Inhoff, & Bernstein, 1988; Rafal & Henik, 1994, though cf. Bartolomeo & Chokron, 2002). Consequently, we used predictive endogenous cues in the present task, to test whether synesthesia would affect canonical endogenous attentional processes.

As in the case of classic spatial cuing effects, the observation of facilitation in a reaction time task can be interpreted as reflecting either the operation of a perceptual gating function during early stages of processing (Posner, 1980), or as reflecting attentional changes in later, post-perceptual stages of processing (Sperling, 1984; Sperling & Doshier, 1986). By recording event-related brain potentials (ERPs) in conjunction with a spatial cuing task, previous investigators have determined that spatial cuing effects result both from the operation of perceptual gating, as shown by the fact that cued targets elicit larger amplitude visual potentials (e.g., P1 and N1), and from the operation of attention in post-perceptual stages, as reflected in cuing effects on late positive components in the ERP (e.g. the P3b) (Eimer, 1994; Luck & Hillyard, 1994; Mangun & Hillyard, 1991).

The present study was intended to explore the time course of spatial cuing in time–space synesthetes and non-synesthetic controls by recording ERPs during a prototypical endogenous cuing task with cues that were symbolic, centrally presented, and informative. Three different types of cues were employed: arrows pointing left or right; direction words “left” and “right”; and time units associated with either the left or the right region of space (e.g., “October”, which in one of our synesthetes was associated with the left side of space, and “May” which was associated with the right). Arrow cues were included because they have previously been shown to be effective in ERP studies of endogenous cuing (e.g. Eimer, 1997); direction words, which are verbal stimuli associated with particular regions of ego-centrally defined space, were used because they could be expected to effectively direct spatial attention in synesthetes and non-synesthetes alike.

Further, a number of precautions were taken to ensure that any observed differences between the synesthetes' and controls' ERPs could be attributed to synesthesia, as opposed to greater motivation on the part of the synesthetes. For example, all cues (arrows, direction words, and months) were predictive, as probes occurred in the cued location 75% of the time. Previous research with the Posner paradigm has indicated that validity rates of 75–80% produce the largest cuing effects and ensure that participants comply with instructions to shift their attention in response to the cue (Bowman, Brown, Kertzman, Schwarz, & Robinson, 1993; Jonides, 1980; Posner & Cohen, 1984). Each non-synesthete was paired with a different synesthete, was told which month cued which region of space (left or right), and viewed the exact same stimuli as the synesthete with whom s/he was paired.

We predicted that both synesthetes and non-synesthetic controls would show a similar pattern of ERP cuing effects following arrow and direction-word cues, but that the two groups' brain response would differ for time-unit cues. Based on previous ERP studies using similar spatial cuing paradigms (e.g., Donchin & Coles, 1988; Eimer, 1997; Hillyard, Vogel, & Luck, 1998; Mangun, 1995; Perchet, Revol, Fournieret, Mauguier, & Garcia-Larrea, 2001), we focused our predictions on the N1 and P3b components, as well as a positive slow wave (pSW).

The posterior N1 component is a negative wave that peaks 150–200 ms post-stimulus onset and is influenced by spatial attention (e.g., Eimer, 1997; Hillyard et al., 1998). In studies in which stimuli were presented unpredictably to the right and left visual fields and subjects were asked to pay attention to the events in one field only, stimuli in the attended field elicited a larger amplitude N1 (150–190 ms) component than did stimuli in the unattended field (e.g., Hillyard et al., 1998; Mangun, 1995). Enlarged N1 components to stimuli at pre-cued or expected locations are also associated with speeded reactions or improved target detectability relative to unattended locations (e.g., Eimer, 1997).

The P3b component is a large positive peak often elicited in target detection paradigms. Other things being equal, P3b amplitude is sensitive to the probability of the eliciting stimulus: the rarer the event, the larger the P3b. (e.g., Donchin & Coles, 1988; Sutton, Brazen, Zubin, & John, 1965). As such, the validity of month cues could be expected to modulate the amplitude of the P3b in both synesthetes and non-synesthetes. However, P3b amplitude is also a function of stimulus salience, with more salient stimuli eliciting larger P3b (Donchin & Coles, 1988). As such, synesthetes' greater familiarity with the association between the month name and the cued region of space might be expected to give rise to larger P3b effects, as they might be more surprised by invalidly cued probes.

The positive slow wave (pSW) is a waveform following the P3b, with a low spatial frequency (<2 Hz), and a posterior topography reminiscent of the P3b (e.g., Perchet & Garcia-Larrea, 2000; Perchet et al., 2001). The pSW is only evoked by invalid trials and has been attributed to cue/target incompatibility (Perchet & Garcia-Larrea, 2000). It reflects further processing invoked by increased task demands, such as difficult perceptual (e.g., pattern recognition) or conceptual (e.g., arithmetic) mental operations, beyond the processing that underlies P3b (Ruchkin, Johnson, Mahaffey, & Sutton, 1988).

We have no reason to presume any fundamental differences in visuo-spatial attention processes between synesthetes and controls, and therefore we expected that arrows and direction words would yield similar cuing effects in synesthetes and controls. We did however expect differences between the two groups for the month cues. In synesthetes, their idiosyncratic involuntary associations between months and locations in space may allow month names to serve as effective cues to direct visuo-spatial attention. We therefore expected that in synesthetes, month names as cues could lead to a facilitation or cost in response times, depending on whether the month cue was followed by a target in the cued or un-cued location. Our predictions for ERPs during the task with month cues were based on the body of ERP research on visuo-spatial cuing effects discussed above. If time-unit cues operate during perceptual stages of processing in synesthetes, their ERP cuing effects should be evident on visual potentials of the ERP, that is, validly cued targets would elicit larger amplitude N1 components than invalidly cued targets. If time-unit cues operate during post-perceptual stages, spatial cuing effects are predicted to be evident in later endogenous components of the synesthete's ERPs such as the P3b and pSW.

2. Methods

2.1. Participants

Twelve time-space synesthetes and 12 controls participated in the experiment, either for cash or in order to get course credit for undergraduate classes at the University of California, San Diego, UCSD (all controls participated for course credit; five synesthetes participated for course credit and seven for payment). All participants had normal or corrected-to-normal vision, and none had any reported history of psychiatric or neurological disorder. Partic-

ipants' ages ranged between 18 and 31 (mean = 22.4 years synesthetes, 20.1 years controls, $t(22) = 1.1713$, $p = .2540$). Handedness was assessed via the Edinburgh Inventory (Oldfield, 1971), which yields a laterality quotient ranging from +1 (strongly right-handed) to -1. Participants were mostly right-handed (10 right, 2 left in both controls and synesthetes) as suggested by the average laterality quotient of +.33 in synesthetes and +.35 in controls. Note that in the data below, only 10 matched pairs were included in the analyses of the ERPs to the target probes in the month condition, due to excessive eye movement artifacts in two synesthetes. All other analyses involved 12 matched pairs (viz. analyses of ERPs to targets cued by arrows and direction words, analyses of all non-target ERPs, and all reaction time analyses).

Individuals were considered as non-synesthetic controls based on their responses on a general questionnaire regarding grapheme-color, sound-color, and time-space synesthesia. Control subjects consistently answered "no" to queries about whether they typically experienced color sensations when viewing particular letters or numbers, experienced color sensations when hearing particular sounds (speech or music), or whether they had a spatial representation for the months of the year.

Individuals were considered as synesthetic subjects when they reported having a spatial representation for months of the year in our general recruitment questionnaire. During a subsequent informal interview the experimenter asked subjects to give vivid descriptions of their calendars, and asked them whether their spatial calendars had been consistently the same since childhood. Due to our experimental paradigm, we only included individuals as synesthetic subjects if they reported that (1) they *always* experienced the months as being in the locations they indicated (regardless of whether they read the month name, heard the month name spoken, or thought about the month); (2) their calendars were projected in front of them (as opposed to surrounding their body); (3) the left-most month on their spatial calendar forms were later in the year than the right-most month (opposite to the more conventional left-to-right mapping of sequences); and (4) their calendars did not rotate with the passage of time. Individuals who participated in our experiment were asked a second time within a 6-month period to describe and draw a sketch of their calendars. One (additional) subject's data were not used because his calendar had rotated in the 4 months between the two measuring times.

In addition to subjective reports, 11 of the 12 synesthetes (due to technical difficulties one subject's data were unavailable) completed a computer program designed to compare the spatial consistency of their respective calendar within one testing session. This consistency test was designed in Macromedia Flash and is similar in function to that described in Smilek et al. (2007). Subjects were initially asked to use a mouse to place 12 small blue dots on a computer screen so as to reproduce the spatial arrangement they experienced for all 12 months. For this they were asked to project their calendars onto the screen, even if they normally experienced them as being wider than the screen. This original placement was followed by five test trials for each month (60 trials total), in which subjects were again prompted to place a dot at the location of each month, one at a time (see Fig. 1). The order in which the months were prompted during the test trials was randomized. Synesthetes' performance on this task was compared to that of a set 85 non-synesthetic individuals who took the same consistency test; all were UCSD undergraduate students who participated for course credit, and all responded "No," to our initial query about whether they had a spatial representation for months of the year. (None of these 85 non-synesthetes participated in the EEG experiment described below.)

Several synesthetes complained that defining a single location for each month was difficult since each of their months

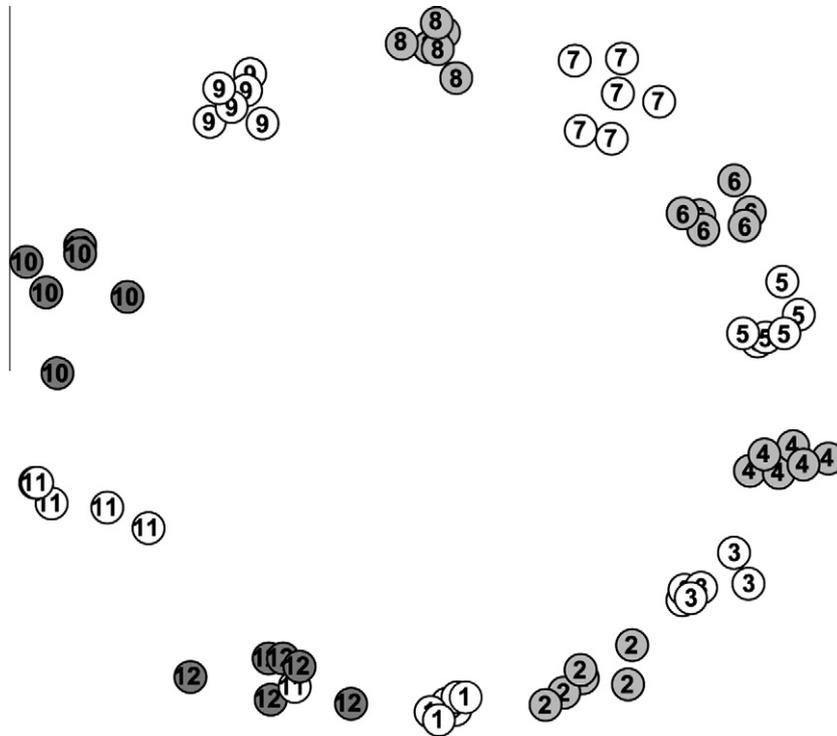


Fig. 1. Example of a synesthete's representation of the year: placements of each month by mouse-click over 6 trials (each number represents a month name, 1 = January to 12 = December).

encompassed an area of space, rather than a solitary point. In order to accommodate this understanding of a month's location as being a spatial region rather than a point in space, errors were defined as placements in the retesting phase that were closer to the original locus of *another* month than that of the presented month (e.g., an error was recorded if a subject was prompted to place 'March', but placed it closer to the original location of 'February' than to the original location of 'March'). An example of such an error is the one November (11) in the field of Decembers (12) in Fig. 1. Synesthetes produced fewer of these errors ($M = 12.5$, $SD = 9.8$) than controls ($M = 28.4$, $SD = 14.1$), $F(1, 94) = 12.96$, $p < .001$, suggesting the genuineness of spatially experienced calendars in these individuals.

2.2. Procedure

2.2.1. Stimulus presentation

Participants were seated in a comfortable chair at a distance of 54 in. from the 19-in. monitor in a sound-attenuated room. They were instructed to focus their eyes on a fixation cross during a target detection task. Cues consisted of arrows pointing left and right, direction words "left" and "right", and the names of 2 months that for the synesthetes were on the very left and the very right hand side of their mental calendar (e.g. "October" and "May"). The 2 month cues were thus tailored to each synesthete's individual representation. Arrow cues subtended .75 vertical \times 2.65 horizontal degrees of visual angle; direction word and month cues subtended 1° vertically and varied from 2.5 to 6.7 horizontal degrees, depending on the number of letters in the word. Each synesthete was matched with a control participant who viewed the exact same stimuli. Stimuli were presented with custom software designed for DOS operating system.

Cues were presented centrally for 200 ms followed by approximately 300 ms of blank screen (including a randomized latency jitter of ± 25 ms). After that a probe stimulus (either an X or an O) appeared either to the left or to the right of fixation (eccentricity:

2.2 degrees). Probes were presented for 150 ms and followed by 850 ms of blank screen. Participants were instructed to respond via button press with their right hand if an X (target) appeared on the right side of the screen, and with their left hand if an X appeared on the left side of the screen. They were instructed not to respond if an O (non-target) appeared on either side. Half of the probes required a response (targets), and half did not (non-targets). The inclusion of probes not requiring a response was intended to examine ERP effects that reflected the perceptual and categorical requirements of the task, without the requirements of response selection (see Eimer, 1997).

Each trial ended with the presentation of the word "blink" for 800 ms. This stimulus was presented centrally, and subtended 1×3.5 degrees of visual angle. It was intended to encourage participants to blink only when prompted, since blinking leads to artifactual activity in the EEG. The word "blink" was followed by 200 ms of blank screen. After that, a fixation cross was presented for 600 ms, followed by a blank screen for 100 ms (± 25 ms latency jitter), after which the next trial started with a new cue.

Both target and non-target probes appeared in the correctly cued location 75% of the time, and in the un-cued location 25%. Participants were told that probe stimuli were more likely to occur on the side signaled by the cue. Both synesthetes and control participants were informed of the side to which each month name corresponded. For the example of a synesthetic calendar where May was on the right side, subjects were told that "MAY means that in most cases (75%), the X or O will appear on the right side". For each cue type (arrows, direction words, or months) we presented a total of 100 trials in which the probe was a target (X), and 100 in which the probe was a non-target (O). Stimulus presentation was fully randomized.

2.2.2. Electrophysiological recording and analysis

As they performed this target detection task, participants' electroencephalograms (EEG) were recorded with an electrode cap

using 29 scalp sites arranged according to the International 10–20 system (Nuwer et al., 1999). Horizontal eye movements were measured with a bipolar derivation of electrodes placed at the outer canthi, in which the left horizontal eye electrode was referenced to the right horizontal eye electrode. Vertical eye movements and blinks were monitored with an electrode under the right eye. All electrodes were referenced on-line to the left mastoid and all impedances were maintained below 5 k Ω . The EEG was recorded and amplified with an SA Instruments isolated bioelectric amplifier at a bandpass of .01 and 100 Hz, and digitized on-line at 250 Hz.

ERPs were time-locked to the onset of the probes by extracting EEG epochs beginning 100 ms before probe onset, and continuing for 900 ms. The 100 ms before the probe served as the baseline. Two synesthetes were excluded from the analysis of ERPs time-locked to target probes (X's) following month cues, because, due to a combination of misses and eye movement artifacts, they had fewer than five trials for invalidly cued targets following month cues. For each of these synesthetes, the matching control subject was also excluded from the analysis. Consequently, the ANOVA for the target probes cued by months included only 10 participants in each group.

Epochs containing electrical activity due to non-neural sources were rejected prior to averaging (blinks, eye movements, amplifier drift, and blocking). This resulted in rejecting 23.5% of probes cued by arrows (24.3% in synesthetes and 22.7% in controls), 23% of probes cued by words (24% in synesthetes and 22% in controls), and 23.8% of probes cued by months (23% in synesthetes and 24.6% in controls).

Dependent measures involved three ERP components known to be modulated in attentional cuing paradigms, the posterior N1, the P3b, and the pSW, as well as the N3 component which was identified post-hoc. Because the latency of the P3b is known to vary as a function of the difficulty of stimulus evaluation (Zani & Proverbio, 2003), we used a measure of the peak amplitude of the P3b between 300 and 450 ms post-stimulus onset. All other analyses involved mean amplitude measurements because those are more resistant to noise. All analyses used typical time windows over electrode sites where each component is known to be focused, essentially treating them as regions-of-interest effects. N1 was measured as the mean amplitude in the 150–200 ms window over occipito-temporal channels TP7, TP8, T5, T6, O1, O2 (as in Vogel & Luck, 2000). P3b and pSW (600–900 ms) were measured over centro-parietal channels (C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4) where the P3b is known to be focused (as in Luck, 2005). The N3 component, identified post-hoc, was measured 300–450 ms over all 29 channels. For analyses of target stimuli, only the correct responses were included.

We performed separate analyses for each of the cue types (arrows, direction words, months) for reaction time as well as ERP analyses. As cue validity effects were predicted for the N1 and P3b, these components were measured for each of the cue types (arrows, direction words, months). The pSW was evident only for probes cued by months, and thus was not assessed in the other two conditions. Likewise, the N3 modulation was observed only for probes cued by direction words, and thus was not measured in the other conditions.

Mean reaction times of all correct responses to the targets were subjected to a 2 \times 2 repeated measures ANOVA with the between-participants factor Group (synesthetes/controls), and within-participants factor Validity (valid/invalid). ERP measurements were subjected to a repeated measures ANOVA with between-participants factor Group (synesthetes/controls), and within-participants factors Validity (valid/invalid) and Electrodes (six sites for N1; 9 for P3b; 29 for N3; 9 for pSW). *p*-Values have been adjusted with the Greenhouse–Geisser (GG) correction for violation of sphericity (Greenhouse & Geisser, 1959). For clarity, we report the original degrees of freedom (*viz.*, before the GG correction).

3. Results

3.1. Behavioral responses

3.1.1. Accuracy

Task accuracy was very high overall. The average hit rate for probes following arrow cues was 96%. Analysis revealed no effects of Group or Validity on the hit rate [Group $F(1, 22) = .62$, $p = .44$; Validity $F(1, 22) = 1.01$, $p = .32$; Group \times Validity $F(1, 22) = .68$, $p = .42$]. The average hit rate for probes following word cues was also 96%, and the analysis revealed no effects of Group or Validity [Group $F(1, 22) = 1.19$, $p = .29$; Validity $F(1, 22) = 1.45$, $p = .24$; Group \times Validity $F(1, 22) = 1.04$, $p = .32$]. Similarly, the average hit rate for probes following month cues was 96%. The analysis revealed no effects of Group or Validity [Group $F(1, 22) = .87$, $p = .36$; Validity $F(1, 22) = 1.02$, $p = .32$; Group \times Validity $F(1, 22) = .98$, $p = .33$].

3.1.2. Reaction times to probes following arrow cues (<-, ->)

The analysis of reaction times to probes following arrow cues revealed a main effect of Validity (see Fig. 2), with reaction times being on average 81 ms faster after valid ($M = 362$, $SD = 55$) than invalid cues ($M = 443$, $SD = 101$) [$F(1, 22) = 25.39$, $p < .001$]. There was no main effect of Group [$F(1, 22) = .82$, $p = .37$], and no interaction between Group and Validity [$F(1, 22) = 1.63$, $p = .21$]. That is, the cuing effects for arrows were similar in the two experimental groups, synesthetes and controls.

3.1.3. Reaction times to probes following direction-word cues (Left, Right)

The analysis of reaction times to probes following direction-word cues revealed a main effect of Validity (see Fig. 2), with reaction times being on average 35 ms faster after valid ($M = 382$, $SD = 54$) than invalid cues ($M = 417$, $SD = 59$) [$F(1, 22) = 14.87$, $p < .001$]. There was no main effect of Group [$F(1, 22) = .10$, $p = .75$], and no interaction between Group and Validity [Group \times Validity $F(1, 22) = 1.29$, $p = .27$].

3.1.4. Reaction times to probes following month cues (e.g., October, May)

The analysis of reaction times to probes following month cues revealed a main effect of Validity (see Fig. 2), with reaction times being on average 38 ms faster after valid ($M = 384$, $SD = 55$) than invalid cues ($M = 422$, $SD = 87$), [$F(1, 22) = 11.32$, $p = .003$]. Although there was no main effect of Group [$F(1, 22) = .35$, $p = .56$], there was a significant interaction between Group and Validity [$F(1, 22) = 4.38$, $p = .05$], due to a larger effect of Validity in synesthetes than in controls.

The interaction between Group and Validity motivated separate analyses of reaction times for targets cued by months in each of the groups, *i.e.* synesthetes and controls. For the synesthetes, there was a main effect for Validity, with reaction times being on average 62 ms faster after valid ($M = 378$, $SD = 47$) than invalid cues ($M = 440$, $SD = 108$) [$F(1, 11) = 8.47$, $p < .01$]. A similar trend was observed in the controls, as reaction times were on average 15 ms faster after valid ($M = 388$, $SD = 63$) than invalid cues ($M = 403$, $SD = 56$), though this difference was not significant [Validity $F(1, 11) = 3.35$, $p = .09$].

3.2. ERP measures

3.2.1. Probes following arrow cues

Probes following arrow cues elicited a negative peak 180 ms post-onset over occipito-temporal sites (N1), and a posterior positivity peaking 400 ms post-onset (P3b). As hypothesized, N1

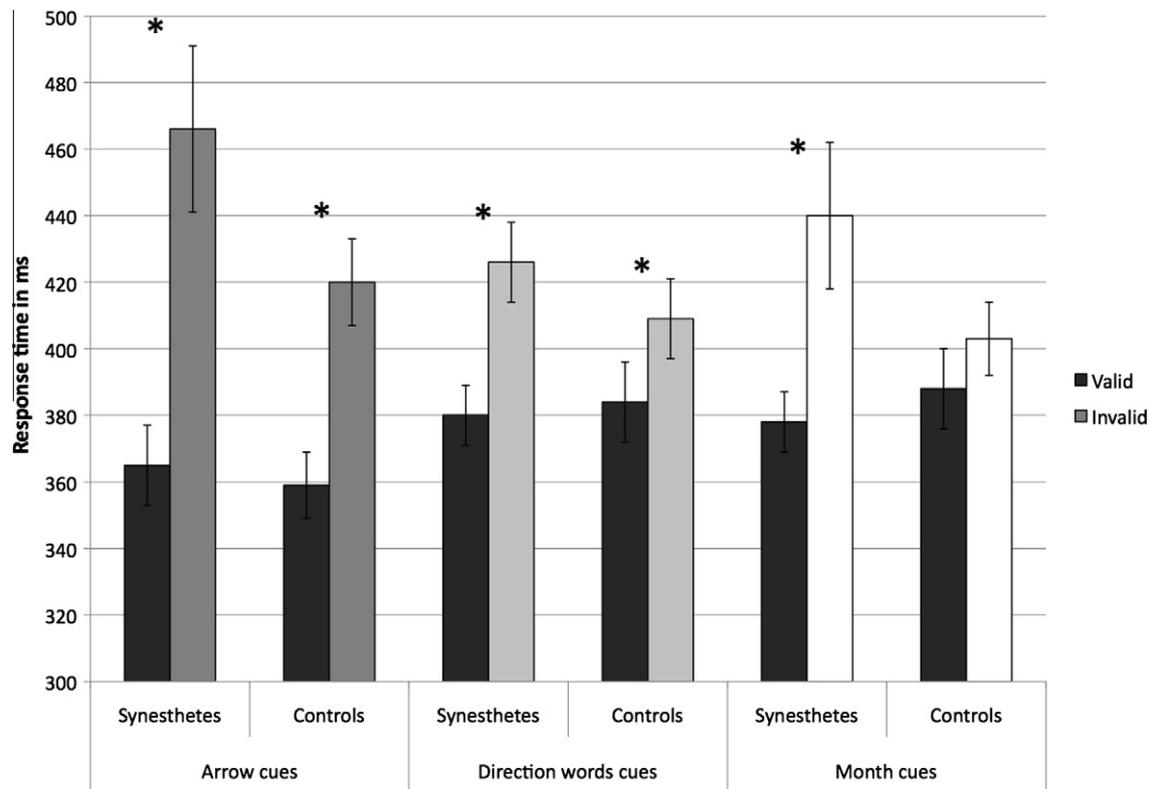


Fig. 2. Reaction times to targets following valid vs. invalid arrow cues, direction-word cues, and month cues. * Statistically significant ($p < .05$) differences are marked with an asterisk. The error bars represent standard error of the mean.

amplitude was larger for probes following valid cues, while P3b amplitude was larger for probes following (less probable) invalid cues. ERPs to valid and invalid probes converged approximately 600 ms post-stimulus onset. To assess the statistical significance of these differences, N1 and P3b components were measured as outlined in the Methods section, and subjected to repeated measures ANOVA with factors Group, Validity, and Electrode. Results of these analyses are shown in Table 1.¹

Analysis revealed no evidence that ERP effects following arrow cues differed as a function of Group (see Table 1). That is, there were no differences between synesthetes and control subjects. Target probes (X's) elicited a negativity over posterior sites that peaked approximately 180 ms post-onset (N1). Fig. 3 displays these early visual potential effects on target probes (X's) and non-target probes (O's), collapsed across synesthetes and controls. ERP waveforms are shown for electrode T5, electrodes where the N1 component is prominent (Vogel & Luck, 2000). This scalp site is well situated to pick up activity in extra-striate cortices (important generators for the N1 component, Clark, Fan, & Hillyard, 1995). As shown in Fig. 3, the N1 elicited by valid probes was 1 μV larger than that for invalid probes. Later portions of the waveform included a positivity peaking approximately 400 ms post-onset (P3b). Analysis suggested that the P3b elicited by invalidly cued targets was 2.2 μV more positive than those to validly cued targets. Similarly, ERPs to non-target probes (O's) were 1.3 μV more negative for valid than invalid probes in the interval of the N1 (Fig. 3); and were 2.2 μV more positive for invalid than valid probes in the interval of the P3b.

Table 1

Omnibus analysis of ERP effects (N1 mean amplitudes and P3b peak amplitudes) time-locked to target (X) and non-target (O) probes following arrow cues. Non-significant interactions between experimental factors and electrode site have been omitted from all tables in order to conserve space. Likewise, in all tables, p -Values have been adjusted with the Greenhouse–Geisser (GG) correction for violation of sphericity (Greenhouse and Geisser, 1959) arrow cues (<- / ->).

Component	Probe	Factors	F-Value	df	p-Value (GG)
N1	X	Group	1.36	1, 22	.26, ns
N1	X	Validity	7.54	1, 22	<.05*
N1	X	Group \times Validity	1.36	1, 22	.26, ns
N1	O	Group	.78	1, 22	.39, ns
N1	O	Validity	11.42	1, 22	<.05*
N1	O	Group \times Validity	.27	1, 22	.61, ns
P3b	X	Group	.06	1, 22	.80, ns
P3b	X	Validity	15.37	1, 22	<.001*
P3b	X	Group \times Validity	.04	1, 22	.85, ns
P3b	O	Group	.09	1, 22	.78, ns
P3b	O	Validity	4.15	1, 22	.05*
P3b	O	Group \times Validity	.00	1, 22	.985, ns

3.2.2. Probes following direction-word cues

Probes cued by direction words elicited a posterior N1 component 150–200 ms post-stimulus onset, followed by a parietally focused P3b peaking approximately 400 ms post-onset. Moreover, invalidly cued probes elicited a fronto-central negativity 300–450 ms that was particularly prominent to target items (see Fig. 3). As in the case of probes cued by arrows, ERPs to valid and invalid probes converged by 600 ms post-stimulus onset. The N1 and P3b components were measured and subjected to the same analyses as were probes cued by arrows. An unexpected effect, the N3 was measured and subjected to post-hoc analysis as outlined in the Methods. Results of these analyses are presented in Table 2.

¹ Non-significant interactions between experimental factors and electrode site have been omitted from all tables in order to conserve space.

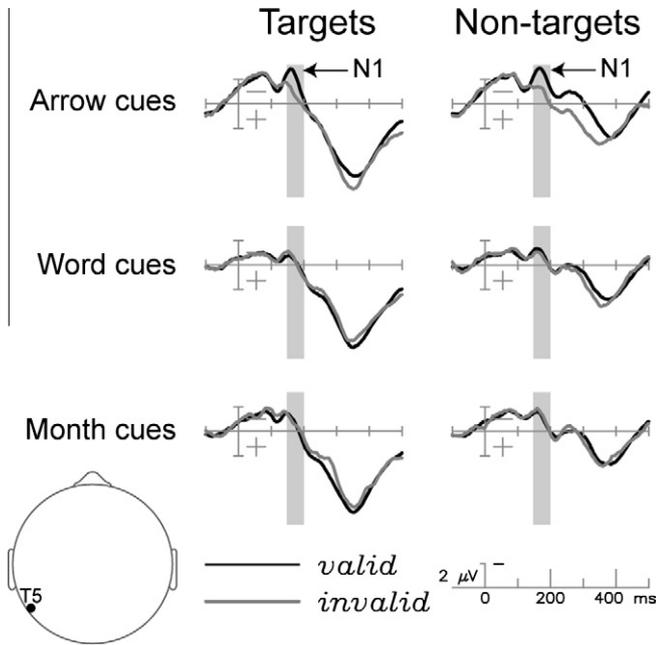


Fig. 3. Early visual potential (N1) effects on target (left hand column) and non-target (right hand column) probes, collapsed across synesthetes and controls. Time (from 100 ms before to 500 ms after probe onset) is plotted on the x-axis. This time window was chosen to highlight the early perceptual effects. Voltage is plotted on the y-axis. In all figures, negative voltage is plotted upwards by convention. ERP waveforms are shown for electrode T5, an electrode site where the N1 component is prominent. The top row represents the brain response to probes cued by arrows, the middle row to probes cued by direction words, and the bottom row to probes cued by months. For arrows, the N1 was larger for valid than invalid probes. This was not the case for probes cued by direction words or months.

Table 2
Omnibus analysis of ERP effects (N1 mean amplitudes, P3b peak amplitudes, and N3 mean amplitudes) time-locked to target (X) and non-target (O) probes following direction-word cues direction word cues (“right”/“left”).

Component	Probe	Factors	F-Value	df	p-Value (GG)
N1	X	Group	.24	1, 22	.63, ns
N1	X	Validity	.35	1, 22	.56, ns
N1	X	Group × Validity	1.64	1, 22	.21, ns
N1	O	Group	.48	1, 22	.49, ns
N1	O	Validity	2.32	1, 22	.14, ns
N1	O	Group × Validity	.01	1, 22	.94, ns
P3b	X	Group	.23	1, 22	.64, ns
P3b	X	Validity	.01	1, 22	.94, ns
P3b	X	Group × Validity	.55	1, 22	.47, ns
P3b	O	Group	.06	1, 22	.80, ns
P3b	O	Validity	.32	1, 22	.58, ns
P3b	O	Group × Validity	.77	1, 22	.39, ns
N3	X	Group	.02	1, 22	.89, ns
N3	X	Validity	7.15	1, 22	<.05*
N3	X	Validity × Electrode	3.57	28, 616	<.01**
N3	X	Group × Validity	.47	1, 22	.50, ns
N3	O	Group	.13	1, 22	.72, ns
N3	O	Validity	.02	1, 22	.89, ns
N3	O	Validity × Electrode	3.54	28, 616	<.05*
N3	O	Group × Validity	.61	1, 22	.44, ns

As in the case of the arrow cues, none of the Validity ERP effects following direction-word cues varied as a function of Group (see Table 2); that is, there were no differences between synesthetes and control subjects. Target probes (X’s) cued by direction words (“left” vs. “right”) elicited an N1 component (see Fig. 3, middle panel) whose amplitude was similar for valid and invalid probes (see Table 2). Target probes also elicited a posterior positivity peaking approximately 400 ms post-onset (P3b), which did not differ as a function of Validity (see Table 2). Validity modulated the amplitude of ERPs to target probes principally in the interval between

300 and 450 ms post-onset (N3), as invalid probes elicited more negative waveforms than did valid probes over frontocentral electrode sites (see Table 2). Fig. 4 displays N3 effect on target probes (X’s) following word cues, collapsed across synesthetes and controls. This effect was especially prominent at the fronto-central midline channel (FCz) shown in Fig. 4. More information on the scalp distribution of this negativity is shown in the topographic map in Fig. 4, which represents the difference between invalid and valid trials.

ERPs to non-target probes (O’s) were somewhat similar to those for the targets (Fig. 4). Neither the N1 nor the P3b analyses revealed significant Validity effects (see Table 2). There was, however, a spatially restricted Validity effect on the N3 as suggested by the interaction between Validity and Electrode (see Table 2). Though no peak was evident in the waveforms, invalid non-target probes elicited more negative ERPs over fronto-central electrodes (see Fig. 4, bottom panel).

3.2.3. Probes following month cues

Probes cued by months elicited a posterior N1 component 150–200 ms post-stimulus onset, followed by a parietally focused P3b peaking approximately 400 ms post-onset (Fig. 5). A unique pattern in the ERPs to target probes (X’s) following month cues, in contrast to those following either arrows or direction-word cues, was the presence of validity effects on the latter portion of the epoch (600–900 ms post-onset; Fig. 5, top panel). While this portion of the waveform may reflect a combination of the slow wave known to follow the P3 component, and contingent negative variation (CNV) related to anticipation of the onset of the next trial, for simplicity’s sake we refer to it here as a positive slow wave (pSW).

The N1, the P3b, and the pSW were measured and subjected to the analyses outlined in the Methods section (results are presented in Table 3). As noted above, two synesthetes were excluded from the analysis of ERPs time-locked to target probes (X’s) following month cues, because, due to a combination of misses and eye

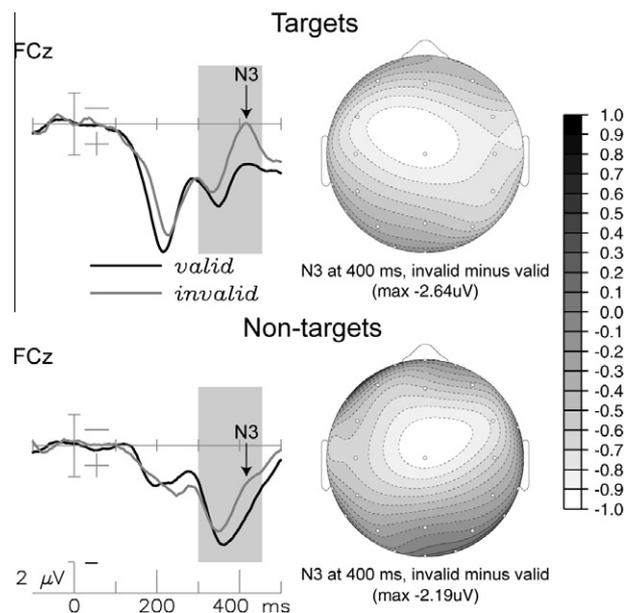


Fig. 4. N3 effect on target (top) and non-target (bottom) probes following direction-word cues recorded at the FCz (fronto-central midline) electrode, collapsed across synesthetes and controls. As in Fig. 3, ERP waveforms are shown from 100 ms before to 500 ms after probe onset. Relative to validly cued probes, invalidly cued probes elicited more negative ERPs between 300 and 450 ms. The fronto-central distribution of this negativity is shown in the topographic maps, which represent the difference between invalid and valid trials 400 ms after the onset of target probes (top) and non-target probes (bottom).

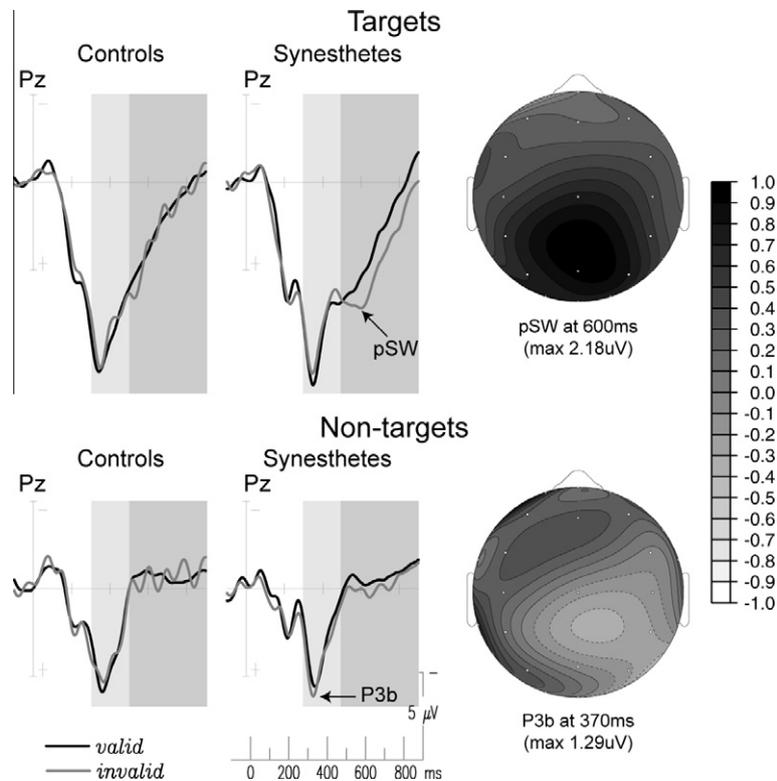


Fig. 5. ERPs to target (top) and non-target (bottom) probes following month cues for controls (left) and synesthetes (right) at midline parietal channel Pz. The entire epoch from 100 ms before to 900 ms after probe onset is shown to highlight the relatively late onset of these effects. Shaded areas indicate the time window measured for the P3b (light gray), and the pSW (dark gray). Apparent validity effects in controls' ERPs were not significant. Arrows indicate the significant P3b effect to non-target probes, and marginal pSW effect on target probes, both in synesthetes' ERPs. The topographic maps show the scalp distribution of the pSW effect in synesthetes 600 ms after target onset (top), and the distribution of the P3b effect in synesthetes 370 ms after the onset of non-target probes (bottom).

Table 3

Omnibus analysis of ERP effects (N1 mean amplitudes, P3b peak amplitudes, and pSW mean amplitudes) time-locked to target (X) and non-target (O) probes following month cues (e.g., "October"/"May").

Component	Probe	Factors	F-Value	df	p-Value (GG)
N1	X	Group	.09	1, 18	.76, ns
N1	X	Validity	.03	1, 18	.86, ns
N1	X	Group × Validity	.22	1, 18	.63, ns
N1	O	Group	.31	1, 22	.58, ns
N1	O	Validity	4.08	1, 22	.06, ns
N1	O	Group × Validity	2.41	1, 22	.13, ns
P3b	X	Group	.08	1, 18	.78, ns
P3b	X	Validity	.65	1, 18	.43, ns
P3b	X	Group × Validity	.28	1, 18	.61, ns
P3b	O	Group	.49	1, 22	.49, ns
P3b	O	Validity	2.76	1, 22	.11, ns
P3b	O	Group × Validity	4.27	1, 22	.05*
pSW	X	Group	1.27	1, 18	.27, ns
pSW	X	Validity	.79	1, 18	.39, ns
pSW	X	Group × Validity	2.89	1, 18	.11, ns
pSW	X	Group × Validity × Electrode	2.71	8, 144	.05*
pSW	O	Group	.63	1, 22	.43, ns
pSW	O	Validity	.35	1, 22	.56, ns
pSW	O	Group × Validity	.02	1, 22	.89, ns

movement artifacts, they had fewer than five trials for invalidly cued targets following month cues. For each of these synesthetes, the matching control subject was also excluded from the analysis (the remaining participants all had more than 20 trials). Consequently, the ANOVA for the target probes included only 10 participants in each group. The ANOVA for the non-target probes (O's), however, included all 12 participants in each group.

As for ERPs to probes following direction words, the amplitude of the N1 to target probes (X's) following month cues were not modulated by Validity (see Table 3 and Fig. 3). Despite the trend towards an interaction between the Group and Validity factors, post-hoc analyses of data collected from each group of participants revealed no significant N1 effects (in synesthetes, the N1 was on average .37 μV more negative for valid than invalid trials; for controls the N1 was on average .46 μV more negative for invalid than valid trials).

Although analyses of ERPs to non-target probes (O's) suggested a trend towards an effect of Validity on the N1, this trend is in contrast to the usual N1 pattern of being more negative for valid than invalid trials (e.g., Hillyard et al., 1998; Mangun, 1995), with invalid probes eliciting ERPs that were on average .35 μV more negative than those elicited by valid probes. Post-hoc analyses of N1s elicited by non-targets in each of the two groups revealed no significant Validity effects (in synesthetes, the N1 was .03 μV more negative for invalid than valid trials, for controls the N1 was .7 μV more negative for invalid than valid trials).

In both groups, target probes (X's) cued by months elicited a P3b peaking 359 ms after stimulus onset, and non-target probes (O's) elicited a P3b peaking 370 ms post-stimulus onset. While no group differences were evident in our measurements of the P3b peak amplitude to target probes (X's), analysis of the non-target probes (O's) did reveal statistically significant differences in validity effects between the two groups' ERPs (see Group × Validity interaction in Table 3). The interaction reflects a larger P3b to invalid trials in synesthetes and to valid trials in controls (see bottom panel in Fig. 5). Separate analysis of the peak amplitude of the P3b in synesthetes revealed that ERPs to invalid probes were 1.1 μV more positive than ERPs to valid ones ($F(1, 11) = 6.75$,

$p < .05$). Comparable analysis of the controls' data revealed no evidence of a Validity effect ($F(1, 11) = .08, p = .7$), though there was a trend towards an interaction between Validity and Electrodes ($F(8, 88) = 2.14, p = .09$).

The pSW to target probes differed reliably as a function of group (see Group \times Validity \times Electrode interaction in Table 3). Post-hoc analyses suggested that in synesthetes there was a trend toward the pSW being more positive (1.5 μ V difference) for invalid than valid targets ($F(1, 9) = 4.05, p = .07$). There was no evidence of Validity effects in ERPs recorded from controls, invalid cues being .5 μ V less positive than valid cues ($F(1, 9) = .28, p = .61$). Fig. 5 (top panel) shows ERPs to targets at midline parietal site Pz where the pSW is focused. The topographic map in Fig. 5 shows valid trials subtracted from invalid trials in synesthetes at 600 ms after the onset of the target probes, and highlights the centro-parietal distribution of this response. The pSW for non-target probes (O's) was not modulated by Validity and did not vary as a function of Group (see Table 3).

4. Discussion

The present study utilized an endogenous cuing paradigm in order to investigate the influence of time–space associations on visuo-spatial attention in time–space synesthetes and neurotypical controls. Reaction times and ERPs were recorded as 12 time–space synesthetes and 12 matched control participants did a peripheral target detection task when cued by three different sorts of centrally presented cues: arrows pointing either leftwards or rightwards, direction words “left” and “right”, and month names (e.g. “October” or “May”) that each time–space synesthete associated with either the left or the right visual field. This paradigm allowed us to see whether time–units can cue spatial locations in synesthetes, and how ERP effects of the time–unit cues compared to those elicited by the arrow and direction-word cues.

As predicted, the reaction time data suggested differences between synesthetes and controls in the month condition, but not in the other cue conditions. Consistent with an extensive body of previous research using the Posner paradigm (reviewed in Yantis, 1998), both synesthetes and controls showed on average faster reaction times after valid than invalid targets in the arrow and direction-word conditions. By contrast, in the month cue condition, synesthetes were significantly faster after valid than invalid cues, whereas control participants were not. This finding suggests that months worked as endogenous cues for synesthetes but not controls, and demonstrates the psychological reality of the time–space mappings reported by synesthetes. The present data are in line with previous studies of other types of synesthesia, using priming or Stroop paradigms to provide behavioral evidence of synesthetic associations. For instance, grapheme–color synesthetes are faster to name color patches when those are congruent with the synesthetic color induced by an alphanumeric prime (Mattingley, Rich, Yelland & Bradshaw, 2001; Rich & Mattingley, 2003). Similarly, when color–grapheme synesthetes are presented with numbers or letters in colors congruent or incongruent with their photisms and are asked to name the color of the grapheme, they exhibit faster reaction times for the congruent stimuli (Dixon, Smilek, Cudahy, & Merikle, 2000; Mills, Boteler, & Oliver, 1999; Odgaard, Flowers, & Bradman, 1999). These types of tasks have been proposed to serve as an objective cognitive marker for synesthesia (Odgaard et al., 1999).

ERP data also revealed predicted similarities in the two groups' processing of probes cued by arrows and direction words, and differences in their processing of probes cued by months.

4.1. Arrow cuing

In both synesthetes and controls attentional cuing by arrows enhanced the amplitude of N1 elicited by valid probes compared

to invalid probes for both targets that required a response (X's), and non-targets (O's) that did not. Further, for both targets and non-targets, invalid probes elicited more positive P3b. Indeed, the pattern of attention effects observed in the arrow condition was very similar to that described by other ERP researchers using a similar paradigm (e.g. Eimer, 1994). Larger amplitude N1 to valid targets is typically interpreted as reflecting enhanced visual processing of objects at the attended location (Luck, 1995), while effects in the later portion of the waveform (i.e. P3b) presumably reflect attentional enhancement of post-perceptual processes such as stimulus evaluation and categorization (Eimer, 1994; Mangun & Hillyard, 1991).

4.2. Direction word cuing

Both subject groups showed similar effects for probes cued by direction words: a fronto-central negativity 300–450 ms post-onset (N3) that was larger for invalid probes. Our failure to observe a significant validity effect on the P3b amplitude may be related to temporal overlap with the N3, such that the negative-going N3 effect over central sites partially cancels out the positive-going P3b effect over central and parietal sites.² The observation of N3 effects for direction words but not for arrows or months suggests that visuo-spatial cuing by these linguistic spatial expressions involved different neuro-cognitive processes than cuing by the other two cue types. Our finding of large direction word ERP cuing effects is in keeping with the report that the words “left” and “right” have elicited behavioral cuing effects even when they were completely non-predictive of probe location (Hommel, Pratt, Colzato, & Godijn, 2001), suggesting they are particularly effective attentional cues.

4.3. Month cuing

For probes cued by months, ERP effects differed between time–space synesthetes who spontaneously experienced the association of the month names with particular regions of space, and control subjects for whom those associations were a construct of the experimenter. In synesthetes, invalid non-target probes (O's) elicited slightly more positive P3b than valid, while invalid target probes (X's) elicited a more positive pSW than valid. Neither cuing effect was evident in control subjects. In addition to the significant effects yielded by the ANOVA, a look at validity effects on the pSW component for each individual subject (Fig. 6) indicated that more synesthetes (9 out of 10) than controls (5 out of 10) showed at least a trend towards a more positive pSW for targets following invalid than valid month cues, $\chi^2(1) = 3.81, p = .05$. These data suggest that month cues served to direct synesthetes' but not controls' attention to the relevant region of space.

Our results from a larger sample of 12 synesthetes thus replicate Smilek et al.'s (2007) behavioral findings with four synesthetes, in showing that time units, such as the name of a month, can direct spatial attention in time–space synesthetes. However, our paradigm was designed to reveal more controlled, endogenous cuing than the covert attentional shifts targeted by Smilek and colleagues. Whereas Smilek et al. employed both a short (150 ms) and a long (600 ms) cue–target SOA, we used only the latter (approximately 500 ms). Perhaps more importantly, whereas the cues in the study by Smilek et al. were uninformative (i.e. targets were equally likely to appear on the left as they were on the right), the cues in the present study were valid 75% of the time. Our

² Consistent with this claim, the mean amplitude N3 analysis of all 29 electrode sites did reveal an interaction between validity and electrode. The P3b analysis was focused over a smaller number of electrode sites and therefore may have lacked the power to detect the much smaller differences in the amplitude of the posterior positivity (see Table 2).

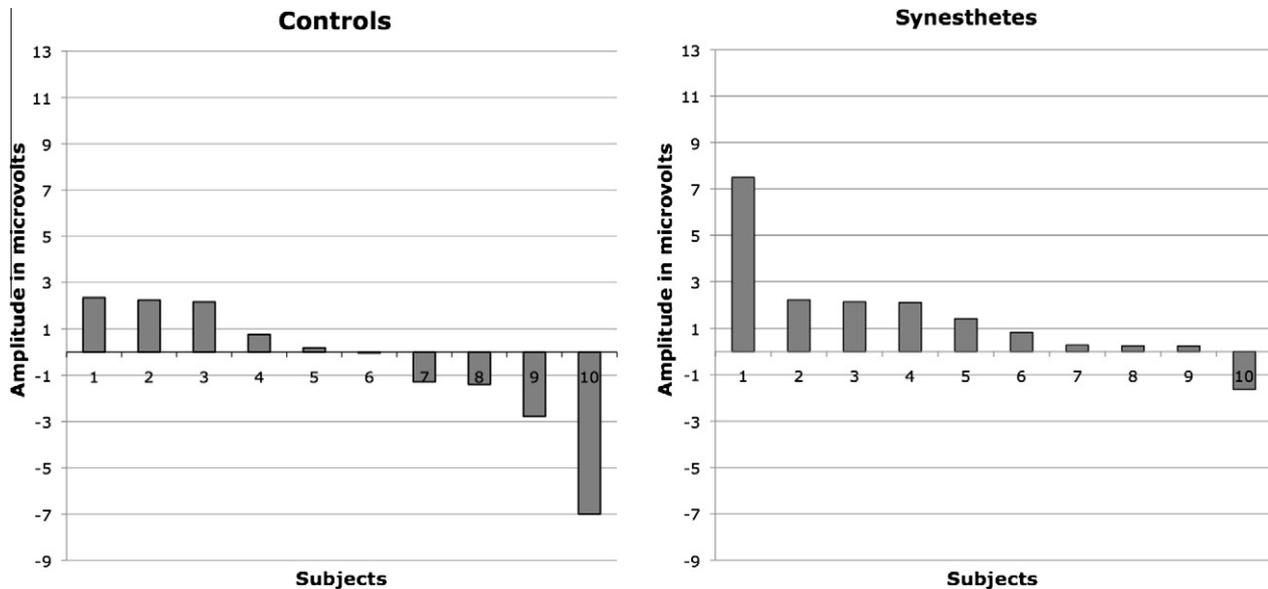


Fig. 6. Month cue validity effects on pSW mean amplitudes for target probes (X's). Each bar represents the size (in μV) of the difference wave obtained by subtracting ERPs to validly cued targets from invalidly cued targets in each of 10 synesthetes (left) and 10 controls (right).

observation of a higher incidence of cuing effects (e.g., the pSW effect was evident in 9 out of 10 synesthetes tested), than Smilek and colleagues (two out of four synesthetes tested) may thus reflect a greater involvement of prototypical endogenous attentional processes in the neural substrate of time–space synesthesia.

4.4. Interpretation of ERP effects

In sum, the present study showed that both time–space synesthetes and matched controls responded faster to valid than invalid targets cued by arrows and direction words, while only time–space synesthetes showed validity effects when months of the year served as cues. Similarly, while ERP validity effects of arrows and direction words were evident in both groups of participants, only time–space synesthetes showed validity effects when cued by months of the year. Further, arrow cues impacted visual discrimination processes indexed by the N1 component as well as those indexed by later ERP components such as the P3b. By contrast, the month cues impacted only the post-perceptual processes indexed by the P3b to non-target probes 370 ms after stimulus onset, and the pSW to targets 600–900 ms post-onset. It is important to acknowledge, however, that results of the present study are based on a relatively small sample of synesthetes who may not be entirely representative of the condition.

4.5. N1

The ERP data in the present study speak to the nature of attentional cuing effects in our sample of synesthetes. Whereas N1 effects indicative of enhanced visual processing were evident for probes cued by arrows, they were not evident for probes cued by months. The two sorts of cues thus function differently in the allocation of attention, as arrow cues influenced perceptual processing of probes indexed by the N1, while month cues primarily influenced post-perceptual processes indexed by the P3b and the pSW.

Our failure to observe N1 attention effects with month cues might be attributable to various aspects of the conduct of our study. For example, the location of probes on the screen only matched the direction (left or right) of the corresponding month cues in each synesthete's spatial calendar, and may not have matched their exact location in 2-d space. Further, because we re-

cruited synesthetes who reported that month–space associations were experienced irrespective of whether they read the month name, heard the month name spoken, or thought about the month, our sample was biased towards relatively high-level synesthetes with conceptual inducers. N1 effects might be observed with either more precise alignment between probe stimuli and synesthetes' calendars, and/or a different sample of synesthetes.

Direction words did not give rise to N1 effects, either, raising the possibility that null effects in both the month and the direction-word conditions reflect the demands of interpreting a verbal cue. Although verbal cues are clearly effective in sustained attention paradigms (see e.g. Luck, Woodman, & Vogel (2000) for a review), they may function less efficiently in endogenous cuing paradigms that require participants to shift their attention to different regions on each trial. The greater complexity of interpreting a symbolic (verbal) cue over an iconic one, such as an arrow, may lead to more variability in the timing of attentional shifts prompted by those verbal cues. Variability in timing would limit the power of ERPs, which rely on the assumption that the time course of brain activity is similar from person to person and from trial to trial. As indicated in Table 3, several N1 effects in the month condition approached significance. However, the tendency was in the predicted direction for synesthetes (the N1 was $.37 \mu\text{V}$ more negative for valid than invalid trials), while it was in the opposite direction for controls (N1 was $.46 \mu\text{V}$ less negative for valid than invalid trials). Moreover, marginal N1 differences in the month condition (Table 3) contrast with robust N1 effects for both groups in the arrow condition (Table 1). Data suggest that endogenous cuing by arrows enabled the attentional system to act earlier in the processing stream than cuing either by the direction words or the month names.

4.6. N3

Although the time course of direction word and month cuing was fairly similar, the two kinds of verbal cues gave rise to qualitatively different cuing effects. When cued by months, probes elicited validity effects on the P3b and pSW components in synesthetes (discussed below). When cued by direction words, probes elicited validity effects in both groups on the N3, a negative-going ERP component observed in the same time window as

the P3b effect. These data indicate that the endogenous cuing we observed in synesthetes is qualitatively different from that provided by verbal cues “left” and “right”. Perhaps because direction words “left” and “right” are strongly integrated with hand actions – as they were in our task – they more readily affect processes of response selection than did the pairings of month names with particular regions of the computer monitor. Indeed for the control participants, the month mappings were dictated by the experimenter, and actually went against the normal tendency to associate earlier months of the year with the left-hand side of space (Gevers, Reynvoet, & Fias, 2003). For our time–space synesthetes, the mappings between month names and spatial regions were meaningful, but perhaps not associated with movements in ego-centric space. Rather, these time–space associations are used to help conceptualize time, and to organize events within time-lines, much as most people use paper- or computer-based calendars and planners.

4.7. P3b

In synesthetes, the earliest month cuing effect was observed on the P3b component for non-targets.³ The most widely accepted functional characterization of this component is that it reflects a context updating process in which the participant revises her internal model of the context for action (Donchin & Coles, 1988). The P3b has multiple sources with major contributions from bilateral temporo-parietal cortices (Ebmeier et al., 1995; Menon et al., 1997; Polich, 2002). In light of its neural generators, Knight & Scabini (1998) have suggested P3b indexes the transfer of information from the temporoparietal junction to the hippocampus and other structures implicated in memory updating. Its elicitation in the present study is consistent with the proposal that time–space synesthetes have a spatial calendar representation in long-term memory, while the controls do not. For controls, the appearance of a probe in an un-cued location was unexpected in light of information recently conveyed by the experimenters, but did not lead to a robust P3b effect. For synesthetes, however, the appearance of probes in un-cued locations was unexpected not only in the context of the experiment, but went against expectations derived from a lifetime of experience with their spatial calendars.

4.8. pSW

Interestingly, the largest ERP validity effect in synesthetes (the pSW) was observed 600–900 ms after the onset of the target probes, at least 100 ms after the slowest reaction times to these stimuli. Parietal positivities like those in the present study have previously been associated with target detection tasks that lead to a complex subsidiary task. A variety of underlying cognitive correlates have been proposed, including decision processing (Johnson & Donchin, 1985), response selection (Falkenstein, Hohnsbein, & Hoormann, 1994; Naylor, Halliday, Callaway, Yano, & Walton, 1987; Perchet & Garcia-Larrea, 2000; Ruchkin et al., 1988), and response evaluation (Falkenstein et al., 1994; Ruchkin, Johnson, Canoune, Ritter, and Hammer, 1990; Stuss & Picton, 1978). Data from the present study suggest the pSW was related to response evaluation, as it occurred after the response and was only observed in trials where a response was required.

³ The reason that the P3b effect was only observed in the non-target condition for the months may be due to our exclusion of two synesthetes from the analysis of the target condition since they showed excessive artifacts (eye-movements, blinks) specifically in the invalidly cued month condition. The analysis of target probes was thus less powerful than the analysis of non-targets, both because there were fewer participants in the former (10 vs. 12), and because the synesthetes who were excluded from the target analysis were those whose behavior (viz. eye movements and blinks) suggested they were particularly disturbed by the target’s appearance in the un-cued location.

García-Larrea and Cézanne-Bert (1998) have noted that the scalp topography of the pSW is highly similar to that of the P3b, and suggested that there is a great deal of overlap in the underlying neural generators of these effects. Similarly, Zani and Proverbio (2003) have argued that, like the P3b, the pSW reflects cognitive updating and comparison with models stored in memory. Its elicitation in synesthetes but not controls likewise underlines the existence of a stored spatial calendar in synesthetes but not controls. In synesthetes, the larger pSW to invalid target probes presumably reflected their spontaneous evaluation of those items as occurring in the wrong region of space, and is in keeping with reports that synesthetic associations often have a strong affective component.

Our finding that time-unit cuing acts at a relatively late stage of processing may be related to evidence that the so-called SNARC effect also arises at a relatively late stage (Keus, Jenks, & Schwarz, 2005; Keus & Schwarz, 2005). The SNARC effect (Spatial Numerical Association of Response Codes) is the finding that when asked to judge whether a given number is odd or even, participants respond faster to small numbers with their left hand, and faster to large numbers with their right (Dehaene, Bossini, & Giraux, 1993). The SNARC effect has typically been interpreted as reflecting a parietally mediated mapping between numerical and spatial representations in a mental number line in which numbers are mapped onto a horizontal line running from the left side of space to the right. ERP studies using the SNARC paradigm suggest this effect arises when participants attempt to map their mental representations of number onto an appropriate response (Keus et al., 2005). Analogously, we suggest that time-unit cuing effects observed in the present study arose during stimulus evaluation as well as response evaluation.

In conclusion, our finding that month cues served to effectively direct spatial attention in time–space synesthetes is thus consistent with predictions of Hubbard and Teuscher’s (2010) model of time–space synesthesia as resulting from cross-activation between parietal regions that mediate the representation of ordered sets of temporal units and spatial cognition.

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