Neural Basis of the Sound-Symbolic Crossmodal Correspondence Between Auditory Pseudowords and Visual Shapes

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ABSTRACT

Sound symbolism refers to the association between the sounds of words and their meanings, often studied using the crossmodal correspondence between auditory pseudowords, e.g. ‘takete’ or ‘maluma’, and pointed or rounded visual shapes, respectively. In a functional magnetic resonance imaging study, participants were presented with pseudoword-shape pairs that were sound-symbolically congruent or incongruent. We found no significant congruency effects in the blood oxygenation level-dependent (BOLD) signal when participants were attending to visual shapes. Rather, during attention to auditory pseudowords, we observed greater BOLD activity for incongruent compared to congruent audiovisual pairs bilaterally in the intraparietal sulcus and supramarginal gyrus, and in the left middle frontal gyrus. We compared this activity to independent functional contrasts designed to test potential underlying mechanisms, but found no evidence for semantic mediation, and only limited evidence for multisensory integration and magnitude estimation. Instead, we suggest that the observed incongruency effects are likely to reflect phonological processing and/or multisensory attention. These findings advance our understanding of sound-to-meaning mapping in the brain.

Keywords: multisensory; magnitude; semantic; phonology; attention; congruency effect

INTRODUCTION

A central question in language research is how words convey meaning. Although the relationship between the sound and meaning of a word is often considered primarily arbitrary (de Saussure, 1916/2009; Pinker, 1999; Jackendoff, 2002; but see also Joseph, 2015), there is also evidence that similar sound-meaning mappings occur reliably in a variety of natural languages (Blasi et al., 2016). Such mappings are termed 'sound-symbolic' (e.g., Svantesson, 2017). The idea that words can convey meaning via auditory resemblance to their referents has a long history, an early discussion being found in Plato's Cratylus Dialog (see Ademollo, 2011). A clear example of sound-meaning mapping is onomatopoeia, in which the sound of a word mimics the sound that the word represents (Catricalà & Guidi, 2015; Schmidtke et al., 2014), for example: 'fizzle', 'bang', or 'splash'. The sound-symbolic relation in onomatopoeia is within-modal (i.e., word sounds are used to index sound-related meanings). In addition, many languages possess a distinct class of words, variously known as ideophones or mimetics, whose phonological structure is reliably mapped not only within-modally to sound-related meanings, but also crossmodally to other sensory domains (Blasi et al., 2016; Dingemanse, 2012), i.e., word sounds can index visual, tactile, or other sensory meanings. For example, Japanese has a rich lexicon of mimetics including '*kirakira'* (flickering light), '*pika'* (a flash of light), and '*nurunuru'* (the tactile sensation of sliminess: Akita & Tsujimura, 2016; Kita, 1997). While sound symbolism (or 'iconicity') is often presented in opposition to arbitrariness of sound-meaning mapping, it is important to note that the two concepts are not mutually exclusive features of language (Lockwood & Dingemanse, 2015).

Crossmodal correspondences refer to associations between ostensibly unrelated stimulus features in different sensory modalities (Spence, 2011). For example, high- and low-pitched auditory stimuli tend to be matched with visual stimuli at high and low spatial elevation, respectively (e.g., Bernstein & Edelstein, 1971; Ben-Artzi & Marks, 1995; Evans & Treisman, 2010; Lacey et al., 2016; Jamal et al., 2017), and with small- and large-sized visual stimuli, respectively (Gallace & Spence, 2006; Evans & Treisman, 2010). Sound symbolism is often studied by examining the crossmodal correspondence between auditorily-presented pseudowords and visual features, such as two-dimensional visual shapes: e.g. 'takete' or 'kiki' are matched with shapes that have pointed contours whereas 'maluma' or 'bouba' are matched with shapes that have

rounded contours (Köhler, 1929, 1947; Ramachandran & Hubbard, 2001). In this kind of audiovisual pairing, the shapes can be considered as representing potential referents or meanings for the pseudowords[1]. Interestingly, individuals with synesthesia appear to be more sensitive than non-synesthetes to sound-symbolic, but not lower-level (e.g. pitch-elevation and pitch-size) crossmodal correspondences (Lacey et al., 2016).

Despite extensive behavioral investigations of sound symbolism and of crossmodal correspondences, their underlying neural basis remains unclear. Our approach in the current functional magnetic resonance imaging (fMRI) study was to consider a number of proposed mechanisms and to compare the blood oxygenation level-dependent (BOLD) signal during a sound-symbolic task with that during separate tasks comprising functional contrasts designed to reflect each potential mechanism. The selection of these functional contrasts, as in our prior study of the pitch-elevation crossmodal correspondence (McCormick et al., 2018), was based on suggestions by Spence (2011), who proposed that crossmodal correspondences may be rooted in statistical, structural or semantic mechanisms.

According to Spence (2011), one possible explanation for sound symbolism is that the relationships between sound-symbolic words and their visual or semantic referents reflect audiovisual statistical regularities in the natural environment that are integrated into a single perceptual object, for example, the sight of a stone thrown into water and the sound of it splashing might give rise to the onomatopoeic sound-to-meaning correspondence mentioned above. Such regularities may also underlie other crossmodal correspondences (Spence, 2011), for example that between high/low auditory pitch and high/low auditory and visual elevation (Jamal et al., 2017), since high-pitched sounds tend to emanate from high locations and low-pitched sounds from low locations (Parise et al., 2014). Thus, sound symbolism might be related to a more general multisensory integration process in which auditory and visual features are linked (Ković et al., 2010) and which may also underlie other crossmodal correspondences (Sidhu & Pexman, 2018). If so, neural activity related to sound-symbolic processing might co-localize

[1] Since pseudowords, by definition, have no referent, their ‘meaning’ depends on what is offered for consideration. Here, and traditionally, pointed and rounded shapes have been offered as potential meanings for ‘kiki’’ and ‘bouba’, but these are likely only one potential class of meanings among many and these pseudowords may map to other visual dimensions as well (but see Knoerferle et al., 2017; Tzeng et al., 2017).

with activity related to multisensory integration, e.g. in the superior temporal sulcus (STS) when audiovisual synchrony (Beauchamp, 2005a,b; van Atteveldt et al., 2007; Stevenson et al., 2010; Marchant et al., 2012; Noesselt et al., 2012; Erickson et al., 2014) or audiovisual identity (Sestieri et al., 2006; Erickson et al., 2014) are manipulated, or in regions such as the intraparietal sulcus (IPS) when audiovisual spatial congruency is manipulated (Sestieri et al., 2006).

Sensory features can often be characterized along polar dimensions of magnitude where one end is 'more than' the other (Smith & Sera, 1992) and stimuli in different modalities might be associated by virtue of their common position along a magnitude dimension. Such crossmodal magnitude relations have been proposed to underpin some crossmodal correspondences (Lourenco & Longo, 2011; Spence, 2011; Sidhu & Pexman, 2018). Spence (2011) referred to this second possibility as a "structural" mechanism emerging as a consequence of modality-independent neural coding mechanisms, e.g. the neural coding of stimulus magnitude in neuronal firing rates across multiple sensory modalities. Such a mechanism might explain, for instance, the correspondence between loudness and brightness (e.g., Stevens & Marks, 1965). Both visuospatial attributes of shapes (e.g., size, spatial frequency) and acoustic-phonetic attributes of linguistic segments (e.g., sonority, formant frequencies) could thus be encoded by a domain-general magnitude system (Dehaene et al., 2003; Walsh, 2003; Lourenco & Longo, 2011) in which different attributes might become associated by virtue of occupying similar positions along magnitude dimensions. Thus, in sound-symbolic language, magnitude representations may serve to link the sound structure of spoken language with object shapes (which can vary along dimensions of pointedness, roundedness, or other shape attributes). That judgments of the sounds of language vary systematically along such dimensions is supported by findings that pseudowords with varying collections of phonetic features are readily placed along continua of pointedness and roundedness (McCormick et al., 2015), and that ratings transition from rounded to pointed with increasing vocal roughness, as indexed by a number of acoustic parameters (Lacey et al., 2020). Crossmodal linkage of such pseudoword ratings to visual shape attributes is suggested by the ability to linearly match pseudowords varying in phonetic features with novel objects of varying size (Thompson & Estes, 2011), by correlations of dissimilarity matrices between auditory ratings of pseudowords and visual ratings of shapes as pointed or rounded

(Lacey et al., 2020) and by demonstrations of the systematic relationship of sound-symbolic associations to phonetic (Knoeferle et al., 2017) or acoustic (Lacey et al., 2020) features of sounds and to radial frequency patterns (Chen et al., 2016) or global indices of shape (Lacey et al., 2020). Based on this line of thinking, activity related to sound symbolism might be expected in the cortex lining the intraparietal sulcus (IPS), a region involved in processing both numerical and non-numerical (e.g., luminance) magnitude (Sathian et al., 1999; Eger et al., 2003; Walsh, 2003; Pinel et al., 2004; Piazza et al., 2004, 2007; Sokolowski et al., 2017).

The third possible mechanism for crossmodal correspondences proposed by Spence (2011) is semantic mediation. By this account, an unfamiliar word or pseudoword could be associated with a particular meaning by virtue of its similarity to other words. In the present context, it is pertinent that crossmodal sound-symbolic associations exist in natural language, for example, ‘balloon’ and ‘spike’ for rounded and pointed shapes (Sučević et al., 2015; Blasi et al., 2016), in addition to those already referred to for pseudowords. Familiar words such as these have established semantic, as well as sound-symbolic, associations. Although pseudowords lack established semantic associations, by definition, when people attempt to match pseudowords with shapes they might also rely in part on semantic associations between the pseudowords and phonologically close real words in order to assign meaning. For example, in assigning ‘maluma’ to a rounded shape (Köhler, 1929, 1947), they might invoke real words with similar phonological content (for example, ‘balloon’). This semantic mediation account predicts that pseudoword-shape associations might activate regions of the left hemisphere language network.

Sidhu & Pexman (2018) discussed five potential explanations for crossmodal correspondences. Their report was published after data acquisition for the present study had been completed; thus, their proposals did not directly influence our study design. However, three of their proposals are, in part, approximate matches to the mechanisms suggested by Spence (2011), and outlined above. The other two ideas they put forward, shared low- or high-level properties across modalities, and species-general mechanisms, did not appear to us to have been directly testable in the framework of the current study, even if their work had been available to us earlier. Hence, it bears emphasis that the design of our study was aimed at obtaining evidence in support of one or more of the mechanisms proposed by Spence (2011). The design of our study was also open to

the possibility of alternative mechanisms not considered by Spence (2011) or Sidhu & Pexman (2018).

There have been relatively few studies of the neural basis of sound symbolism, each with some limitations. Some studies employed a variety of sound-symbolic words and referent types (Ković et al., 2010; Revill et al., 2014; Sučević et al., 2015; Lockwood et al., 2016), which may obscure differences between mechanisms for different sound-symbolic effects (Sidhu & Pexman, 2018). Earlier fMRI studies did not attempt to distinguish between potential mechanisms (Revill et al., 2014; Peiffer-Smadja & Cohen, 2019); whereas EEG studies (Ković et al., 2010; Sučević et al., 2015; Lockwood et al., 2016), while providing excellent temporal information, may not have sufficient spatial resolution to identify the anatomical sources of activity in the brain.

Furthermore, few studies have examined individual differences in crossmodal correspondences. We addressed this by administering the Object-Spatial Imagery & Verbal Questionnaire (OSIVQ: Blazhenkova & Kozhevnikov, 2009). We hypothesized that individuals with a preference for verbal processing might be more adept at assigning potential meanings to pseudowords. Additionally, object imagers might be more apt to visualize the shapes associated with pseudowords since such individuals typically integrate multiple sources of information about an object, compared to the more schematic representations of spatial imagers (Blazhenkova & Kozhevnikov, 2009; Lacey et al., 2011). These hypotheses would be supported by finding correlations between task performance and/or neural activity with the verbal sub-scale of the OSIVQ and/or with preferences for object, rather than spatial, imagery.

In the present study, we used fMRI to investigate cerebral cortical localization of differential activations for congruent vs. incongruent sound-symbolic crossmodal correspondences between auditory pseudowords and visual shapes. It is not clear, *a priori*, whether greater activity would be found during the congruent or incongruent audiovisual condition. Peiffer-Smadja & Cohen (2019) reported foci showing activation during the incongruent relative to the congruent condition using implicit matching, whereas a preliminary report of another study from our group, using explicit matching, found effects favoring both congruent and incongruent conditions (Barany et al., 2021). Thus, we were interested in regions that were more responsive to either

audiovisual congruency or incongruency of sound-symbolic stimuli. We chose to rely on implicit correspondences by presenting audiovisual pseudoword-shape pairs, asking participants to discriminate either the auditory pseudowords or the visual shapes. This task was independent of the pseudoword-shape correspondence, but allowed us to obtain behavioral measures on each trial, in contrast to the study of Peiffer-Smadja & Cohen (2019), which required behavioral responses only to occasional targets. In order to test the relevance of the proposed mechanisms outlined above, we conducted three independent task contrasts in the same individuals, reflecting language processing, magnitude estimation, and multisensory integration. We hypothesized that a potential role for one of these mechanisms would be supported by finding cortical activations common to one of these independent task contrasts and the sound-symbolic (in)congruency between pseudowords and shapes. On the other hand, cortical activations lacking overlap with one of the independent task contrasts would suggest the operation of alternative mechanisms.

MATERIALS & METHODS

Participants

Twenty participants took part in this study, but one was excluded for excessive movement in the scanner (> 1.5mm), leaving a final sample of 19 (9 male, 10 female; mean age 25 years, 1 month). All participants were right-handed based on the validated subset of the Edinburgh handedness inventory (Raczkowski et al., 1974) and reported normal hearing and normal, or corrected-to-normal, vision. All participants gave informed consent and were compensated for their time. All procedures were approved by the Emory University Institutional Review Board.

Procedures

General

Five participants took part in the pseudoword-shape scans first, and then underwent three scans to test potential mechanisms underlying the pseudoword-shape correspondence. The remaining participants had already undergone the mechanism-testing scans approximately four months earlier as part of a separate study and thus completed the pseudoword-shape scans after these scans. After completing the required scan sessions, all participants performed a behavioral task to determine the strength of their crossmodal pseudoword-shape correspondence. All experiments were presented via Presentation software (Neurobehavioral Systems Inc., Albany

CA), which allowed synchronization of scan acquisition with experiments and also recorded responses and response times (RTs). After the final scan session, participants also completed the OSIVQ (Blazhenkova & Kozhevnikov, 2009).

Pseudoword-shape fMRI task

We created two auditory and two visual stimuli (pseudowords and novel two-dimensional outline shapes respectively). The auditory pseudowords were “lohmoh” (rounded) and “keekay” (pointed). The pseudowords were digitally recorded in a female voice using Audacity v2.0.1 (Audacity Team, 2012), with a SHURE 5115D microphone and an EMU 0202 USB external sound card, at a 44.1kHz sampling rate. The recordings were then processed in Sound Studio (Felt Tip Inc., NY), using standard tools and default settings, edited into separate files, amplitude-normalized, and down-sampled to a 22.05kHz sampling rate (standard for analyses of speech). Stimulus duration was 533ms for “keekay” and 600ms for “lohmoh”. The visual stimuli were gray outline shapes on a black background (Figure 1a), each subtending approximately 1° of visual angle and presented at the center of the screen for 500ms. The selected stimuli lay near the ends of independent rounded and pointed dimensions in each modality based on empirical ratings (pseudowords: McCormick et al., 2015; visual shapes: McCormick, 2015, unpublished data), i.e., the chosen rounded pseudowords and shapes were rated towards the high end of the rounded dimension and the low end of the pointed dimension, and vice versa for the chosen pointed stimuli. These stimuli were presented concurrently in audiovisual pairs (Figure 1a) that were either congruent (“keekay”/pointed shape or “lohmoh”/rounded shape) or incongruent (“keekay”/rounded shape or “lohmoh”/pointed shape) with respect to the crossmodal pseudoword-shape (sound-symbolic) correspondence. A mirror angled over the head coil enabled participants to see the visual stimuli projected onto a screen placed in the rear magnet aperture. Auditory stimuli were presented via scanner-compatible headphones.

There were four runs, each consisting of 8 task blocks (4 congruent and 4 incongruent, each block containing 10 word-shape stimuli with a 3s interval between the onset of successive stimuli), each lasting 30s and alternating with 9 rest blocks, each lasting 16s; total run duration was 384s. Pseudoword-shape pairs were pseudorandomly interleaved (no more than three trials in a row of the same pairing, no more than two blocks in a row of the same condition). In two of

the runs, participants attended to auditory stimuli; in the other two runs, they attended to visual stimuli; the order of attended modality was counterbalanced across participants, who performed a 2AFC task in the attended modality. Participants pressed one of two buttons on a hand-held response box when they heard either “keekay” or “lohmoh” (attend auditory condition) or saw either the rounded or pointed shape (attend visual condition). The right index and middle fingers were used to indicate responses, counterbalanced between subjects across modalities and across rounded and pointed stimuli. Note that this task differs from that used by Peiffer-Smadja & Cohen (2019) in which participants had to detect rare occurrences of visual crosses and auditory beeps rather than respond to the pseudowords and shapes, which were processed incidentally. As Peiffer-Smadja & Cohen (2019) note, the need to focus on these rare target stimuli may have modulated the processing of pseudowords and shapes, whereas in the present study, the in-scannr behavioral task involved distinguishing between stimuli in the attended modality and the effect of the unattended modality was implicit.

Independent localization tasks to test potential mechanisms

The order of these tasks was fixed, progressing from the one perceived as most difficult to the easiest: participants completed the magnitude estimation task first, then the temporal synchrony task, and finally the language task. Each of these tasks comprised two runs with a fixed stimulus order; the order of runs was counterbalanced across participants. These tasks were completed in a single session for most participants. As outlined in the Introduction, we chose these tasks to broadly reflect the three potential mechanisms underlying crossmodal correspondences proposed by Spence (2011): structural, e.g., driven by intensity or magnitude; statistical, i.e., features that regularly co-occur in the world and thus might lend themselves to multisensory integration; and semantic, i.e. driven by linguistic factors. In order to test the mechanisms proposed by Spence (2011), we chose localization tasks from the literature on language processing (Fedorenko et al., 2010), multisensory integration (e.g., Beauchamp, 2005a,b; van Atteveldt et al., 2007; Stevenson et al., 2010; Marchant et al., 2012; Noesselt et al., 2012; Erickson et al., 2014), and magnitude processing (Lourenco et al. 2012) as described below. A number of different task contrasts could potentially be designed to test each mechanism; thus it would be difficult to test all possibilities in a single study. We made choices from the literature that seemed reasonable *a priori*, with the thinking that the results of the present study should help to refine such choices in future work

(see Discussion) and with the goal of avoiding potential confounds. For example, in the multisensory task, we avoided audiovisual speech (e.g., van Atteveldt et al., 2007; Stevenson et al., 2010; Noesselt et al., 2012; Erickson et al., 2014) and familiar environmental sounds and images (e.g., Hein et al., 2007; Noppeney et al., 2008) because these would likely also involve semantic processing which we wished to test separately from multisensory integration. Additionally, we should note that we used the framework of Spence (2011) as a starting point for a tractable set of potential mechanisms rather than an exhaustive list.

Language task

In this task, adapted from Fedorenko et al. (2010), we contrasted complete semantically and syntactically intact sentences with sequences of pseudowords (examples are provided in Figure 1b) to identify brain regions processing word- and sentence-level meaning (Fedorenko et al., 2010, 2011; Bedny et al., 2011). The aim of this task contrast was to reveal potential overlaps between the processing of meaning in natural language and the artificial pseudowords we used; for the pseudowords, meaning is implied by the correspondence of their sounds with the visual shapes, as is the case in the extensive literature on sound-symbolic crossmodal correspondences. The complete sentences and pseudoword sequences each contained 12 words, each word/pseudoword being presented visually for 450ms for a total stimulus duration of 5.4s, followed by a 600ms inter-stimulus interval (ISI) during which participants were visually prompted to press a button. There were two runs, each consisting of 16 task blocks (8 of each type, each block containing 3 stimuli) of 18s duration and alternating with 17 rest blocks of 12s duration; total run duration was 492s. We expected the contrast of complete sentences > pseudowords to reveal regions mediating both semantic and syntactic processing (Fedorenko et al., 2010, 2011; Bedny et al., 2011), i.e., a largely left hemisphere network comprising the inferior frontal gyrus (IFG), angular gyrus (AG), and extensive sectors of the temporal lobe including the superior temporal sulcus (STS).

Multisensory integration

Among a number of possible tasks that could be used to test multisensory integration, we chose one that is sensitive to the synchrony of auditory and visual stimuli, as used in many studies of audiovisual integration (e.g., Beauchamp, 2005a,b; van Atteveldt et al., 2007; Stevenson et al.,

2010; Marchant et al., 2012; Noesselt et al., 2012; Erickson et al., 2014). As noted above, we attempted to avoid semantic connotations of the stimuli used in this task, such as speech or environmental sounds, with the goal of investigating non-linguistic audiovisual integration. The auditory stimulus was an 810Hz tone of 800ms duration with a 20ms on/off ramp. The visual stimulus was a gray circle (RGB values 240, 240, 240) subtending approximately 1° of visual angle and presented centrally for 800ms. In synchronous trials, auditory and visual stimuli were presented simultaneously for 800ms followed by a 3200ms ISI, while asynchronous trials contained stimuli offset by an intervening blank interval of 200ms followed by a 2200ms ISI (Figure 1c). Half the asynchronous trials presented the auditory stimulus first and half the visual stimulus first. There were two runs, each consisting of 12 active 16s-blocks (6 of each type, each block containing 4 trials) and alternating with 13 rest blocks each lasting 14s; total run duration was 374s. Participants had to press a button whenever an oddball stimulus (e.g., Crottaz-Herbette & Menon, 2006), either a square or a burst of white noise, occurred; two oddballs of each type occurred in each run, one in a synchronous block and one in an asynchronous block. The contrast between synchronous and asynchronous trials was used to identify brain regions sensitive to audiovisual synchrony; we anticipated that this contrast would activate superior temporal cortex (Beauchamp, 2005a,b; van Atteveldt et al., 2007; Stevenson et al., 2010; Marchant et al., 2012; Noesselt et al., 2012; Erickson et al., 2014).

Magnitude estimation

In order to identify brain regions sensitive to magnitude, we used a modified form of the estimation task from Lourenco et al. (2012). In each trial of this task, participants were asked to estimate whether there were more black or white elements in a visual array of small rectangles. For a control task, we modified these arrays so that one item was a triangle and participants indicated whether the triangle was black or white, thus the response – black or white – was the same for both the magnitude and the control tasks (Figure 1d). The aim of this task contrast was to isolate processing in a domain-general magnitude system, which may be relevant to assessing the magnitude along dimensions such as roundedness or pointedness. There were two runs, each containing 12 active 16s-blocks (6 of each type, each block containing 4 stimuli displayed for 1s with a 3s ISI) and alternating with 13 rest blocks each lasting 14s; total run duration was 374s. The contrast of magnitude estimation > control was used to identify those regions sensitive to

magnitude, which we expected would be primarily in posterior parietal cortex, particularly the IPS (Sathian et al., 1999; Eger et al., 2003; Walsh, 2003; Pinel et al., 2004; Piazza et al., 2004, 2007; Lourenco & Longo, 2011; Sokolowski et al., 2017).

Post-scan behavioral testing

As a final step, we tested whether participants reliably demonstrated the crossmodal pseudoword-shape correspondence using the implicit association test (IAT: Greenwald et al., 1998; Parise & Spence, 2012; Lacey et al., 2016). Originally devised as a test of social attitudes (Greenwald et al., 1998), the IAT has been successfully used to test the very different associations involved in crossmodal correspondences, including sound-symbolic ones (Peiffer-Smadja & Cohen, 2019; Parise & Spence, 2012; Lacey et al., 2016). The underlying principle is the same: response times (RTs) are faster if the stimuli assigned to a particular response key are congruent and slower if they are incongruent (Greenwald et al., 1998; Parise & Spence, 2012). The advantage of the IAT for testing crossmodal correspondences is that presenting each stimulus in isolation eliminates the confound of selective attention effects potentially causing slower RTs for incongruent pairings (Parise & Spence, 2012).

The auditory and visual stimuli were the same as for the imaging experiment except that rounded and pointed pseudowords and shapes were presented in isolation (note that the absolute size of the visual shapes was altered so that they subtended 1° of visual angle in both the IAT and fMRI experimental set-ups). The IAT was presented via Presentation software which also recorded RTs. Participants were instructed to associate pairs of stimuli with one of two response keys (the ‘left’ and ‘right’ arrow keys on a normal US ‘QWERTY’ keyboard). The pairs always consisted of one auditory and one visual stimulus and, in separate blocks of trials, were either congruent or incongruent. A trial consisted either of an auditory presentation (either “keekay” or “lohmoh”) or a visual presentation (either the rounded or the pointed shape) and participants were asked to respond as quickly as possible.

There were four runs, each comprising 96 trials divided into two blocks of 48 (totaling 384 trials across runs). The response key associations were congruent in one block and incongruent in the other; there were different associations between keys and responses in each block (see below)

and block order was counterbalanced across runs, thus avoiding order effects. Each block was preceded by an instruction screen describing the response key associations to be used, and by 12 practice trials (not included in the analysis) with on-screen feedback as to accuracy (for the practice trials only). For two runs, the congruent pairs were “keekay”/pointed shape (to be associated with the left arrow key) and “lohmoh”/rounded shape (associated with the right arrow key) while the incongruent pairs were “keekay”/rounded shape (left arrow key) and “lohmoh”/pointed shape (right arrow key). On the other two runs, the left/right key associations were reversed. Half the trials were auditory (either “keekay” or “lohmoh”) and half were visual (either the rounded or the pointed shape), split equally into congruent and incongruent blocks and occurring in pseudorandom order within each block. Trials consisted of a blank 1000ms followed by either a visual or an auditory stimulus. Visual stimulus duration was 1000ms and auditory stimulus duration was the length of the pseudoword (533ms for “keekay” and 600ms for “lohmoh”). Trials were terminated either by the participant pressing a response key or automatically 3500ms after stimulus onset if no response was made. On all trials, response keys did not become active until 300ms after stimulus onset so that auditory trials could not be terminated early by rapid or accidental responses. RTs were measured from stimulus onset. The length of each active block thus varied between participants but was a maximum of 330s.

Participants also completed the OSIVQ (Blazhenkova & Kozhevnikov, 2009), with the goal of examining the relationship between sound symbolism and individual differences in preferences for processing based on verbal, visual object imagery or visuospatial imagery. Such preferences have been argued to reflect fundamental styles of cognitive processing that vary between individuals and can predict abilities in many, seemingly unrelated, domains. In order to test the relationship to object or spatial imagery preference, which tend to oppose each other, we calculated the OSdiff score: the spatial score is subtracted from the object score of the OSIVQ to give a single scale on which positive/negative scores indicate a relative preference for object/spatial imagery respectively (Lacey et al., 2011, 2014, 2017; Occelli et al., 2014). The relationship to verbal preference was tested using the verbal score from the OSIVQ.

Image acquisition

MR scans were performed on a 3 Tesla Siemens Trio TIM whole body scanner (Siemens Medical Solutions, Malvern, PA), using a 12-channel head coil. T2*-weighted functional images were acquired using a single-shot, gradient-recalled, echoplanar imaging (EPI) sequence for blood oxygenation level-dependent (BOLD) contrast. For all functional scans, 34 axial slices of 3.1mm thickness were acquired using the following parameters: repetition time (TR) 2000ms, echo time (TE) 30ms, field of view (FOV) 200mm, flip angle (FA) 90°, in-plane resolution 3.125×3.125mm, and in-plane matrix 64×64. High-resolution 3D anatomic images were acquired using an MPRAGE sequence (TR 2300ms, TE 3.02ms, inversion time 1100ms, FA 8°) comprising 176 sagittal slices of 1mm thickness (FOV 256mm, in-plane resolution 1×1mm, in-plane matrix 256×256). Once magnetic stabilization was achieved in each run, the scanner triggered the computer running Presentation software so that the sequence of experimental trials was synchronized with scan acquisition.

Image processing and analysis

Image processing and analysis was performed using BrainVoyager QX v2.8.4 (Brain Innovation, Maastricht, Netherlands). Each participant's functional runs were real-time motion-corrected utilizing Siemens 3D-PACE (prospective acquisition motion correction). Functional images were preprocessed employing cubic spline interpolation for slice scan time correction, trilinear-sinc interpolation for intra-session alignment of functional volumes, and high-pass temporal filtering to 2 cycles per run to remove slow drifts in the data without affecting task-related effects. Anatomic 3D images were processed, co-registered with the functional data, and transformed into Talairach space (Talairach & Tournoux, 1988). Talairach-normalized anatomic data sets from multiple scan sessions were averaged for each individual, to minimize noise and maximize spatial resolution.

For group analyses, the Talairach-transformed data were spatially smoothed with an isotropic Gaussian kernel (full-width half-maximum 4mm). The 4mm filter is within the 3-6mm range recommended to reduce the possibility of blurring together activations that are in fact anatomically and/or functionally distinct (White et al., 2001), and the ratio of the smoothing kernel to the spatial resolution of the functional images (1.33) matches that of studies in which larger smoothing kernels were used (Mikl et al., 2008). Runs were percent signal change

normalized (i.e., the mean signal value for each voxel's time course was transformed to a value of 100, so that the individual values fluctuated around that mean as percent signal deviations).

For display of group activations, we created a group average brain. We first selected a representative (target) Talairach-normalized brain from the 19-participant group. We then individually aligned the 18 remaining participants' Talairach-normalized brains to this target (co-registration to match the gyral and sulcal pattern, followed by sinc interpolation). These 18 aligned brains were then averaged. This 18-subject average brain was then averaged with the target brain, creating a single Talairach template, with 1mm isotropic resolution, which was used to display the activations for the 19-subject group. This group average brain was displayed using the real-time volume rendering option in BrainVoyager QX. For statistical analysis, the 19-subject Talairach template was manually segmented in order to create a group average cortical 'mask' file with 3mm spatial resolution, equivalent to the spatial resolution of the functional data files.

Statistical analyses of group data used general linear models (GLMs) treating participant as a random factor (so that the degrees of freedom equal n-1, i.e. 18), followed by pairwise contrasts. This analysis allows generalization to untested individuals. Correction for multiple comparisons within a cortical mask (corrected $p < .05$) was achieved by imposing a threshold for the volume of clusters comprising contiguous voxels that passed a voxel-wise threshold of $p < 0.001$, using a 3D extension (implemented in BrainVoyager QX) of the 2D Monte Carlo simulation procedure described by Forman et al. (1995). This stringent voxel-wise threshold is recommended to avoid potential problems of false positives and also permits more accurate spatial localization of activation clusters than is possible with more lenient thresholds (Woo et al., 2014; Eklund et al., 2016). Activations were localized with respect to 3D cortical anatomy with the help of an MRI atlas (Duvernoy, 1999).

In reporting activations, we do not provide 'hotspot' or 't_{max}' coordinates (i.e. the voxel with the largest t-value) because the statistical significance of specific voxels is not tested against other voxels within the activation (Woo et al., 2014). Instead, we provide the 'center of gravity' (CoG) coordinates since these orient the reader to the anatomical location but are statistically neutral.

Where an activation spans several anatomical locations, we provide an extended description (see Table 1). Likewise, in order to compare the present results to previous studies, we have not computed the Euclidean distance between sets of coordinates since, in most cases, this would involve comparing t_{max} to CoG and therefore we would not be comparing like to like. Instead, we plotted the coordinates reported in previous studies onto our data in order to assess whether these fell within the activations we found here, such that we could reasonably say that there was some degree of overlap in the activations.

RESULTS

Behavioral

In-scanner tasks

Pseudoword-shape task

Two-way (congruency, modality) repeated-measures ANOVA (RM-ANOVA) showed that mean (±sem) accuracy was not significantly different between the 'attend auditory' (97.4±0.7%) and 'attend visual' conditions (97.6±0.6%: $F_{1, 18} = .05$, $p = .8$), nor between congruent (97.7±0.5%) and incongruent (97.3±0.6%) trials ($F_{1, 18} = .9$, $p = .3$). There was a significant interaction between the attended modality and congruency ($F_{1,18} = 9.6$, $p = .006$); this was due to greater accuracy for congruent compared to incongruent trials in the 'attend auditory' condition (98.2% vs 96.5%; $t_{18} = 2.6$, $p = .018$) but not the 'attend visual' condition (97.1% vs 98%; $t_{18} = -1.9$ $p = .06$: note that we are only concerned with these two comparisons, thus Bonferroni-corrected alpha = .025). We also performed non-parametric tests on the accuracy data since the 'ceiling' effects in all conditions indicate that the data were likely not normally distributed: these confirmed the result of the RM-ANOVA.

Analysis of RTs excluded trials for which there was no response (.6% of all trials) or an incorrect response (2.5% of responses), and further excluded trials for which the RT was more than ± 2.5 standard deviations from the individual participant mean (2.6% of correct response trials). RM-ANOVA showed that RTs were faster for the 'attend visual' (474±21ms) compared to the 'attend auditory' condition (527±23ms: $F_{1,18} = 21.3$, $p < .001$) and for congruent (489±21ms) compared to incongruent trials (513±22ms: $F_{1,18} = 18.7$, $p < .001$). There was a significant interaction between the attended modality and congruency ($F_{1,18} = 9.2$, $p < .007$) in which both auditory

(545ms) and visual (480ms) incongruent RTs were slower than congruent RTs in the same modality (auditory 509ms, $t_{18} = -4.0$, $p = .001$; visual 469ms, t_{18}, $p = .009$) but the absolute difference was greater for auditory than visual RTs (36ms vs 11ms).

Note that, despite the highly repetitive nature of the pseudoword and shape stimuli, it is unlikely that participants stopped paying attention to them given the high accuracy rates (> 97% in all conditions) and the fact that responses were made on 99.4% of trials. In addition, the mean auditory RTs (527ms overall, and 509ms vs. 545ms for congruent vs incongruent trials) suggest that participants often responded before the auditory stimulus was complete (duration = 533ms vs 600ms for 'keekay' vs. 'lomo'). This was likely unavoidable given that participants only had to identify which of the two, highly repeated, pseudowords they heard; but the first syllable of each pseudoword, either 'kee-' or 'lo-', also respects the class of the entire word, either pointed or rounded respectively. Thus, we do not believe that the results are affected by such rapid responses since our analyses reveal that while being scanned, participants still exhibited significant behavioral congruency effects related to sound symbolism, more prominently in the attend-auditory than the attend-visual condition.

Independent localization tasks

In the language task, participants were equally accurate in responding to the visual cue at the end of each sentence (mean ± sem: 98.4±1.0%) or pseudoword string (97.7±1.1%; $t_{18} = .9$, $p =.4$). Because of the low number of oddball trials (four for each participant) in the multisensory task, we conducted a non-parametric Wilcoxon test, which showed no significant difference between detection of synchronous (90.1±3.9%) and asynchronous (85.5±5.5%) oddballs ($Z = -1.4$, $p = .2$). For the magnitude task, there was no significant difference in accuracy between the magnitude estimation (92.2±2.0%) and control (96.4±1.3%) tasks ($t_{18} = -1.8$, $p = .1$) although RTs were significantly faster for the control task (900±45ms) compared to the magnitude task (991±53ms; $t_{18} = 3.4$, $p < .01$). These analyses allow us to infer that participants paid attention to the stimuli used in the independent localization tasks.

<u>Post-scan pseudoword-shape IAT</u>

An RM-ANOVA with factors of modality (auditory pseudowords, visual shapes) and response key association (congruent, incongruent) showed that accuracy was higher for the auditory pseudowords (95.8±0.8%) compared to the visual shapes (91.9±0.8%: $F_{1,18} = 31.8$, $p < .001$) and when response key associations were congruent (95.3±0.7%) compared to incongruent (92.4±1.2%: $F_{1,18} = 5.7$, $p = .03$). The modality x response key association interaction was not significant ($F_{1,18} < .01$, $p = .9$).

Analysis of RTs excluded trials for which there was no response or which failed to log (.7% of all trials), or incorrect responses (6.2% of responses), and further excluded trials for which the RT was more than ± 2.5 standard deviations from the individual participant mean (2.7% of correct response trials). RM-ANOVA showed that RTs were faster for the visual (606±19ms) compared to the auditory (702±21ms) stimuli ($F_{1,18} = 31.15$, $p < .001$) and when the response key associations were congruent (580±18ms) compared to incongruent (728±22ms: $F_{1,18} = 64.5$, $p < .001$). The modality x response key association interaction was not significant ($F_{1,18} = .5$, $p = .5$).

These analyses provide converging evidence, using a different approach from that employed during scanning, that participants experienced sound-symbolic congruency effects with the stimuli that were used.

Imaging

Pseudoword-shape task

To test for regions involved in processing the sound-symbolic word-shape correspondence, we tested for voxels showing differential activation for congruent and incongruent trials (C > I or I > C), i.e., congruency or incongruency effects, respectively. These analyses were performed independently for the attend-auditory and attend-visual runs. Within the group average cortical mask, at a voxel-wise threshold of $p < .001$, there were no activations that survived correction for multiple comparisons in the ‘attend visual’ condition, either for the C > I contrast or its reverse, the I > C contrast.

However, in the ‘attend auditory’ condition, while there was no effect favoring the congruent over the incongruent condition, several regions showed greater activation for incongruent,

compared to congruent, trials (the I > C contrast) within the cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 5 voxels). These regions included bilateral foci in the anterior IPS (aIPS) extending on the left into the mid-IPS and the SMG, and activations in the right SMG extending into the postcentral sulcus, in the left SPG and the left MFG (Table 1; Figure 2). Representative time-course curves for the I > C contrast in these regions are displayed in Figure 6A. These show greater activation for incongruent compared to congruent trials in all regions except for the left SPG region in which there was differential *de*activation. Since it is not clear how to interpret differential deactivations, we do not consider this SPG focus further. The neural incongruency effects were associated with a behavioral congruency effect in the 'attend auditory' condition in which responses to congruent trials were faster and more accurate than those to incongruent trials; this is consistent with the processing of incongruent trials being more effortful. The absence of a neural (in)congruency effect in the 'attend visual' condition is consonant with the absence of a congruency effect for accuracy data in this condition; although there was a congruency effect for RTs, this effect was significantly smaller in the 'attend visual' condition compared to the 'attend auditory' condition (see above).

<u>Independent localization tasks</u>

Language

As expected, the contrast of complete sentences > pseudowords within the group average cortical mask described in the Methods section (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 9 voxels) revealed large activations bilaterally along the STS, extending into parts of the superior temporal gyrus (STG); this activation extended more posteriorly on the left than the right. Additional activations were noted on the left precentrally and in the middle occipital gyrus (Table 2a; Figure 3). Thus, the language task broadly replicated the previously reported language network (Fedorenko et al., 2010, 2011).

Although not part of the original design of the present study, the contrast of pseudowords > sentences may reflect the greater role of phonological processing in reading strings of pseudowords compared to normal intact sentences (Fedorenko et al., 2010). Given that our auditory stimuli were pseudowords, we were interested in also examining this reverse contrast. The contrast of pseudowords > sentences within the cortical mask (voxel-wise threshold p <

.001, cluster-corrected $p < .05$, cluster threshold 9 voxels) revealed large, bilateral frontoparietal activations: in and around the superior frontal sulcus (SFS) extending all the way into the IFG on the right, and in the AG extending into the supramarginal gyrus (SMG) on the left and the IPS on the right. Smaller activations were also found along the medial surface of the left hemisphere in frontal and posterior cingulate cortex and in the parieto-occipital fissure (POF) (Table 2b; Figure 3). Consistent with a phonological basis, the left IFG activation on this contrast is close to an IFG focus showing greater activity for visually presented pseudowords relative to concrete words (Binder et al., 2005), a contrast similar to that used here. Additionally, the left SMG activation on this contrast is at a site reported to be involved in phonological processing for visually presented words (Price et al., 1997; Wilson et al., 2011). However, reading pseudowords is also more effortful than reading complete sentences, perhaps due to mapping unfamiliar orthographic representations to phonological representations. Therefore, another possibility is that some or all of the activations on this contrast might reflect this additional effort, particularly since many of the activations (principally those in the frontal cortex bilaterally) were also found in regions identified as part of the frontoparietal domain-general, 'multiple demand' system (Duncan, 2013; Fedorenko et al., 2013). We return to this point in the Discussion.

Multisensory synchrony

The contrast of synchronous > asynchronous within the cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 8 voxels) revealed bilateral activations in the anterior calcarine sulcus extending through the POF to the cuneus; in the left hemisphere, this activation further encompassed foci in the lingual and posterior cingulate gyri (Table 2c; Figure 4). The reverse contrast, asynchronous > synchronous, resulted in two right hemisphere activations, one in inferior parietal cortex extending across the SMG and AG and into the IPS, and one in the IFG (Table 2d; Figure 4). While some previous studies have shown greater activation for synchronous compared to asynchronous audiovisual stimuli, others have shown the reverse, and in some cases preference for synchrony and asynchrony occurred at foci in proximity to each other (e.g. Stevenson et al., 2010). The regions most consistently reported as being sensitive to synchrony in previous studies were in the STS and/or STG – we did not observe activations in these regions on the multisensory synchrony task here, perhaps reflecting differences in stimuli and tasks (see Discussion). However, the right IFG area that was more

active for asynchronous than synchronous stimuli in the present study was close to a region identified on the meta-analysis of Erickson et al. (2014) as exhibiting a preference for audiovisual stimuli characterized by either content incongruency or asynchrony.

Magnitude estimation

The contrast of magnitude estimation > control within the cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 7 voxels) showed exclusively right hemisphere activity in the SMG, the SPG extending into the IPS, and the middle occipital gyrus (MOG) extending through the intra-occipital sulcus (IOS) to the superior occipital gyrus (SOG: Table 2e; Figure 5). These loci are consistent with activations reported in previous studies of magnitude processing (Eger et al., 2003; Pinel et al., 2004; Piazza et al., 2004, 2007) and a recent meta-analysis (Sokolowski et al., 2017). The right MOG region is close to foci previously implicated in subitizing (Sathian et al., 1999) or that showed adaptation to magnitude (Piazza et al., 2007) while the right SPG-IPS region is close to a region involved in counting visual objects (Sathian et al., 1999).

Overlap of incongruency effect with independent localization task contrasts

Our approach to distinguishing between the competing potential mechanisms examined here was to look for overlap between areas showing pseudoword-shape (in)congruency effects and areas revealed by the independent language, magnitude, and multisensory tasks. Note that we assessed such overlap at voxel-wise thresholds of $p < .001$ for the activations being compared. Overlaps at this strict threshold, avoiding potential false positives and allowing more accurate spatial localization than at more liberal thresholds (Woo et al., 2014; Eklund et al., 2016), would provide support for candidate mechanisms. However, the presence of an overlap does not guarantee that the same process underlies both tasks at that locus nor that the same neuronal populations are activated; moreover, note that absence of overlaps would not allow such mechanisms to be definitively ruled *out*. The evidence of overlaps should be regarded as indicative and supportive of further research into the functional roles of those loci.

None of the regions showing sensitivity to the pseudoword-shape correspondence overlapped or were contiguous with (i.e. shared a common edge or vertex) any area revealed by the language

contrasts of sentences > pseudowords or the multisensory contrast of synchronous > asynchronous (Figure 7). Instead, regions showing pseudoword-shape incongruency effects showed overlaps and contiguities with the control conditions from the language and multisensory tasks, i.e. when the primary contrasts for these conditions were reversed (see notes to Table 1; Figure 7). The contrast of pseudowords > complete sentences from the language task revealed overlap with incongruency effects in the left MFG and SMG. Comparing the BOLD signal time-courses for these regions (Figure 6A & B) suggests that the left SMG region may be the more relevant of the two since it showed greater activation on the reverse contrasts. By contrast, the left MFG showed different response patterns in the sound-symbolic and language tasks: while there was greater activation for incongruent than congruent trials in the former task, it barely responded to pseudowords while deactivating to the sentence trials in the language task.

Although the pseudoword condition likely involves processing the phonological form of the pseudowords rather than the semantic or syntactic aspects of natural language (Fedorenko et al., 2010), the pseudowords > sentences contrast may have limitations as a formal test for phonological processing (see Discussion). Therefore, we also conducted a region-of-interest (ROI) analysis in which we created bilateral SMG ROIs, chosen because they were shown to be functionally involved in phonological processing using transcranial magnetic stimulation (TMS; Hartwigsen et al., 2010). The ROIs consisted of cubes of 15mm side, centered on coordinates from Hartwigsen et al. (2010; Talairach coordinates -45, -37, 42; 45, -36, 42; MNI coordinates were transformed into Talairach space using the online tool provided by Lacadie et al., 2008). Although the SMG was part of the inferior parietal cluster of sound-symbolic incongruency-related activations in both hemispheres, the ROI approach allows a more specific test of the relationship to phonology. The contrast of incongruent > congruent in the ‘attend auditory’ condition was significant in both left ($t_{18} = 3.6$, $p = .002$) and right ($t_{18} = 3.9$, $p = .001$) SMG ROIs. For completeness, there were no significant effects in either ROI in the ‘attend visual’ condition (left: $t_{18} = 1.1$, $p = .3$; right: $t_{18} = .8$, $p = .5$), matching the absence of activations within the cortical mask.

In the multisensory task, the contrast of asynchronous > synchronous showed overlaps with the right aIPS and SMG incongruency regions (see notes to Table 1; Figure 7). BOLD signal time-

courses for these regions showed that both exhibited similar response patterns for the sound-symbolic and multisensory synchrony tasks: greater activation for incongruent and asynchronous trials, respectively, relative to the corresponding comparison conditions (Figure 6A & C). Since the multisensory task did not reveal the STS activity that was expected on the basis of previous studies (Beauchamp, 2005a,b; van Atteveldt et al., 2007; Stevenson et al., 2010; Marchant et al., 2012; Noesselt et al., 2012; Erickson et al., 2014), we also carried out an ROI analysis in bilateral STS ROIs, chosen because they were sensitive to audiovisual integration of non-speech stimuli (tools and musical instruments and their associated sounds) and were also behaviorally relevant in that activation profiles predicted task performance (Werner & Noppeney, 2010). These ROIs, which were also used in a prior study from our group on the pitch-elevation crossmodal correspondence (McCormick et al., 2018), comprised cubes of 15mm side, centered on coordinates from Werner & Noppeney (2010; Talairach coordinates -57, -41, 14; 52, -33, 9; MNI coordinates were transformed into Talairach space as above). However, the contrast of incongruent > congruent was not significant in these ROIs, either in the 'attend auditory' condition (left: $t_{18} = .3$, $p = .8$; right: $t_{18} = .4$, $p = .7$) or the 'attend visual' condition (left: $t_{18} = 1.6$, $p = .1$; right: $t_{18} = 1.2$, $p = .2$).

Finally, in the magnitude task, the main magnitude estimation > control contrast overlapped with the right SMG incongruency region and was also contiguous with the right aIPS incongruency region (see notes to Table 1; Figure 7). The BOLD signal time-course for the right SMG region showed similar response patterns for the sound-symbolic and magnitude tasks: greater activation for incongruent and magnitude estimation trials, respectively, relative to the corresponding comparison conditions (Figure 6A & D).

Correlation analyses

Finally, we tested whether pseudoword-shape activation magnitudes correlated, across participants, with the magnitude of individual congruency effects derived from in-scanner RTs. The congruency effect computation used the formula $(RT_i – RT_c) / (RT_i + RT_c)$, where RT_i and RT_c represent RT for incongruent and congruent trials, respectively. We also tested for correlations with scores on the verbal sub-scale of the OSIVQ (Blazhenkova & Kozhevnikov, 2009) and with individual preferences for object compared to spatial imagery by reference to the

OSdiff score (see Methods). To avoid circularity, we conducted these correlation tests in the whole brain, i.e. independently of the activations, and in a similarly stringent manner, by setting a strict voxel-wise threshold of $p < 0.001$ within the cortical mask before applying cluster correction (corrected $p < 0.05$).

In the 'attend visual' condition, activation magnitudes for the C > I contrast were negatively correlated with the magnitude of the in-scanner RT congruency effects at a focus in the left SMG (Table 3a; Figure 8); this focus overlapped with the left SMG focus in the language control task. Additionally, a single voxel in the right SFS, contiguous with right SFS activation on the language control task (Table 3b; Figure 8), had a C > I activation magnitude that was positively correlated with verbal scores from the OSIVQ.

In the 'attend auditory' condition, several foci showed strong positive correlations between activation magnitudes for the I > C contrast and the magnitude of the in-scanner RT congruency effects (Table 3c; Figure 8), overlapping with the 'attend auditory' incongruency region in the left aIPS/SMG and close to the left mid-IPS incongruency region. Among the regions identified on the independent localization tasks, correlation foci were contiguous with pseudoword > sentence activations in the right precuneus and the left AG, IPS, and SMG, and close to the language control activation in the right IFS/IFG. A single correlation focus was close to the right SPG activation from the magnitude task. There were also foci at which the magnitude of the BOLD incongruency effect (I > C contrast) was positively correlated with preference for visual object imagery (Table 3d; Figure 8), i.e., magnitudes increased with increasing preference for object relative to spatial imagery. These correlated regions were primarily in the left precuneus, and visual cortical areas: the IOS, the posterior calcarine sulcus extending into the lingual gyrus, and the right MOG.

DISCUSSION

Comparison of present study with prior studies

To our knowledge, the present study is the first attempt to investigate in a principled way the neural mechanisms *by* which sound-symbolic associations are processed, as opposed to merely the neural loci *at* which they are processed. Previous studies employed a range of sound-

symbolic words and pseudowords (Ković et al., 2010; Revill et al., 2014; Sučević et al., 2015; Lockwood et al., 2016, Peiffer-Smadja & Cohen, 2019), the processing of which may rely on various mechanisms depending on the particular sound-symbolic relation (Sidhu & Pexman, 2018). Here, we concentrated on a specific kind of association, that between auditory pseudowords and visual shapes, investigating the effect of manipulating the congruency of this sound-symbolic correspondence. We compared the resulting neocortical activations to the results of functional contrasts designed to reflect potential underlying mechanisms, employing fMRI which offers greater anatomical resolution than the EEG paradigms of some prior studies (e.g., Ković et al., 2010; Sučević et al., 2015; Lockwood et al., 2016). As noted above, our findings are intended to serve as a spur to further research.

Relationship of incongruency effects to independent functional contrasts

Semantic and phonological processes

The regions identified on the language task showed no overlap at all with the observed activations due to incongruent, compared to congruent, pairings of auditory pseudowords and visual shapes. Thus, of the *a priori* explanations considered in the Introduction, the possibility of semantic mediation, i.e. correspondence between meanings that might be implicit in the pseudowords (e.g., by reference to relevant words with similar phonological content) and the shapes that are associated, appears least likely. However, the incongruency-related region in the left SMG and MFG overlapped with sites more active for pseudowords than complete sentences in the language task. In addition, foci demonstrating correlations of neural incongruency effects with in-scanner RT incongruency effects during the ‘attend auditory’ condition, in the right precuneus and right inferior frontal cortex, were adjacent to or near areas with a preference for pseudowords over sentences.

The premise of sound symbolism is that the sound structure of words mimics or relates to some aspect of what they represent, either explicitly and within-modally as in onomatopoeia (Catricalà & Guidi, 2015; Schmidtke et al., 2014) or by analogy as for ideophones or mimetics (Akita & Tsujimura, 2016; Kita, 1997) – for example, the repetitive sound of the Japanese mimetic term ‘kirakira’ may be considered analogous to flickering light. It is thus interesting that we found left-lateralized regions in the SMG and MFG that were common to both the pseudoword-shape

incongruency effect and the pseudoword condition of the language task, even though the former were presented auditorily and the latter were presented visually. Given that reading pseudowords likely depends on phonological processing (Fedorenko et al., 2010) whereas reading sentences also involves syntactic and semantic processing, this suggests that phonological processes may underlie this overlap. Both the left and right SMG are involved in phonological processing (Hartwigsen et al., 2010; Oberhuber et al., 2016), and the left SMG focus has previously been implicated in the phonological processing of visually presented words (Price et al., 1997; Wilson et al., 2011). In order to test the phonology hypothesis further, we conducted an ROI analysis of bilateral SMG foci derived from an earlier study (Hartwigsen et al., 2010), i.e., independently of our findings. This ROI analysis showed incongruency effects in bilateral SMG in the 'attend auditory', but not visual, condition. Based on these findings, we suggest that phonological processing could contribute to the pseudoword-shape correspondence. Since the phonological mechanism was not originally hypothesized, and thus the language task was not designed to test this mechanism, we cannot currently rule out alternative explanations, so this idea requires further investigation.

There are many aspects to phonology, e.g., syllable structure, stress, and prosody, and while the pseudowords > sentences contrast may reflect phonological processing, it likely involves multiple elements that need to be disentangled. Although several studies suggest that consonants contribute more than vowels to associations with pointed and rounded shapes (e.g., Nielsen & Rendall, 2011; Ozturk et al., 2013; Fort et al., 2015; but see Styles & Gawne, 2017) and that pointed/rounded shapes are associated with plosive/sonorant consonants (Monaghan et al., 2012; Fort et al., 2015), further work is required to investigate the relative contributions of different phonological and/or phonetic features to particular sound-symbolic associations (e.g. Knoeferle et al., 2017; McCormick et al., 2015). Finally, it should be noted that reading pseudowords involves mapping unfamiliar orthographic patterns[2] to phonological representations and may thus require more effort than reading complete sentences (Shechter & Share, 2020). Therefore, the overlaps with the activations related to sound symbolism may reflect involvement of the

[2] 'Unfamiliar' in the sense that, while the orthography is obviously known, the particular patterns do not constitute known words.

domain-general multiple demand system (Duncan, 2013; Fedorenko et al., 2013), rather than, or in addition to, phonological processes (see below).

The finding that brain regions active during processing of sound-symbolic pseudowords are distinct from the canonical language system (Fedorenko et al., 2010, 2011; Bedny et al., 2011) may offer a potential route for rehabilitation after language impairment, for example in stroke patients. To the extent that sound-symbolic and classical language systems involved in structure and meaning are dissociated, either channel could be exploited to tap into meaningful representations if the other channel showed a deficit. In the same way that hearing a tool sound can remind patients with apraxia how to use that tool (Worthington, 2016), intensive exposure to sound-symbolic words might provide a route back to normal language. In fact, there is preliminary evidence to suggest that patients with aphasia process sound-symbolic words better than more arbitrary word-meaning mappings (Meteyard et al., 2015). This possibility should be explored in further research.

Multisensory and magnitude estimation processes

As described in the Results, the multisensory task did not show activity in superior temporal cortex, the region most commonly activated in prior studies employing audiovisual (a)synchrony to demonstrate multisensory integration. Most previous studies employed audiovisual speech (van Atteveldt et al., 2007; Stevenson et al., 2010; Noesselt et al., 2012; Erickson et al., 2014) or combinations of familiar environmental sounds and images (e.g., Hein et al., 2007; Noppeney et al., 2008). Since both these stimulus types would be expected to trigger semantic processing, we avoided them given that semantic mediation might have been, *a priori*, a potential explanation for the correspondence between spoken pseudowords and visual shapes (although an EEG study suggests similar multisensory integration effects for both speech and non-speech stimuli [Stekelenburg & Vroomen, 2007]).

Additionally, asynchronous audiovisual stimuli are more likely to be perceived as synchronous if the visual element precedes the auditory element (V-A) compared to the reverse (A-V) (Bhat et al., 2015). Since there were equal numbers of V-A and A-V trials in the asynchronous condition, its effectiveness may have been reduced, if some of the V-A trials were actually perceived as

synchronous. In order to compensate for this and to test the multisensory integration hypothesis independently of the multisensory synchrony task, we conducted a further ROI analysis of foci in the STS, a classical multisensory region, derived from a previous study involving non-verbal, but semantically related, stimuli (Werner & Noppeney, 2010), but this showed no significant sound-symbolic effects in either of the attended modalities. Nonetheless, pseudoword-shape incongruency-related activations in the right aIPS and SMG overlapped with areas active during the asynchronous condition of the multisensory task. The right aIPS incongruency site is close to several IPS foci activated during processing of audiovisual spatial congruency (Sestieri et al., 2006). The IPS portions of our parietal incongruency regions also overlap with regions implicated in multisensory attention during difficult tasks (Regenbogen et al., 2018). This may be relevant to the contention that the brain is trying harder to integrate these inputs when they are incongruent (Noppeney, 2012: see also Section 4.3 below). The left MFG incongruency region likely overlaps with a region in inferior frontal cortex responding to audiovisual incongruency for familiar environmental stimuli (Hein et al., 2007) and incongruency between visual primes and auditory targets, whether environmental sounds or spoken words (Noppeney et al., 2008). Since the relevant effects were evoked by multiple types of stimulus incongruency, either of content or of timing, the most plausible explanation for these overlaps is the attention-driven effects cited above, perhaps due to unsuccessful attempts to integrate the audiovisual stimuli. It should be noted that multisensory integration can depend not only on temporal co-occurrence, as in the current synchrony task, but also on other types of congruency, such as spatial co-location (Spence, 2013). However, whether spatial co-location is important for integration may be modality- and task-dependent, being less important for some audiovisual (e.g., Regan & Spekreisje, 1977) than visuotactile tasks (e.g., Sambo & Forster, 2009), perhaps especially if, as here, the task is simply to identify the stimulus (Spence, 2013). As noted by Spence (2013, footnote b), auditory stimuli presented via headphones and visual stimuli presented on a screen are different spatial locations and it may be difficult to determine the role of spatial matching in such a set-up. However, participants were both faster and more accurate for congruent than incongruent trials in the ‘attend auditory’ condition, indicating that the spatially different sources of auditory pseudowords and visual shapes had little effect (in the ‘attend visual’ condition, participants were faster, but not significantly differentially accurate, for congruent trials).

In the present study, the right SMG incongruency region overlapped with activation during magnitude estimation and was contiguous with the right aIPS magnitude-sensitive region. The IPS is a classical locus for magnitude processing (Sathian et al., 1999; Eger et al., 2003; Pinel et al., 2004; Piazza et al., 2004, 2007; Sokolowski et al., 2017) while the SMG is among regions showing adaptation to magnitude (Piazza et al., 2007) or involved in detecting changes in numerosity (Piazza et al., 2004). Additionally, part of the right POF-precuneus region, whose activation magnitude correlated with RTs during attention to auditory stimuli in the scanner, was close to the right SPG activation evoked by magnitude estimation in the independent localization contrast – this region has been implicated in counting visual objects (Sathian et al., 1999). The two pseudowords used in this experiment were drawn, like the shapes, from a much larger set which were empirically rated as sounding more or less rounded or pointed (McCormick et al., 2015), it follows that participants had no problem in applying magnitude estimation (of roundedness or pointedness) to pseudowords. As noted earlier, sensory features often relate to polar dimensions of magnitude where one end is 'more than' the other (Smith & Sera, 1992), for example brighter vs. darker or louder vs. quieter, and a contrast targeting such sensory dimensions may have been relevant to the dimensions of pointedness and roundedness. We expected that magnitude processing would be reflected in congruent and incongruent trials because congruent trials involve stimuli occupying similar positions on a continuum whilst incongruent trials involve stimuli occupying different positions. It remains possible that the incongruency effects do indeed reflect magnitude processing because there are different magnitudes involved. However, the role of magnitude processing might become clearer in a parametric setting, using a range of pseudowords and shapes and thus sampling at multiple intervals along the rounded/pointed continuum (whilst accepting that the continuum might not be consistently mapped across individuals). Despite extensive overlap between brain regions involved in processing number- and sensory-based magnitude (Pinel et al., 2004), caution is indicated by recent challenges to the idea of a domain-general magnitude system (Anobile et al., 2018; Pitt & Casasanto, 2018; but see Holmes et al., 2019) which has been posited as a mechanism for crossmodal correspondences (Lourenco & Longo, 2011; Spence, 2011; Sidhu & Pexman, 2018). Additionally, while we cannot rule out magnitude estimation as a possible mechanism for the observed sound-symbolic incongruency effects, the regions of overlap between the magnitude estimation task and the incongruency effects are also implicated in

multisensory attentional processes, which may ultimately turn out to be a more important mechanism (see below).

Incongruency effects and attention

No brain regions showed congruency effects in either attended modality in the present study, which was also the case in the study of Peiffer-Smadja & Cohen (2019). However, when participants were attending to the auditory pseudowords, several neocortical regions showed greater activity for incongruent, compared to congruent, pairings with visual shapes. These areas were more widespread than the dorsolateral prefrontal regions found by Peiffer-Smadja & Cohen (2019), who used a task requiring only occasional responses (see below). We did not find incongruency effects when participants attended to the visual shapes, consistent with a behavioral congruency effect being absent in the 'attend visual' runs when accuracy was the dependent measure, and being significantly smaller in the 'attend visual' than the 'attend auditory' runs when RT was the dependent measure. These differences as a function of the attended modality may stem from greater unfamiliarity of auditory pseudowords relative to two-dimensional visual shapes. Alternatively, they might reflect timing differences in processing pseudowords compared to visual shapes, since the pseudowords unfold over time, whereas the visual shapes are in evidence from the start of each trial. Consequently, there may be more of an incongruency effect in the 'attend auditory' condition because the concurrent visual stimulus could trigger particular representations immediately, whereas in the 'attend visual' condition, the concurrent pseudoword may still be playing as the participant prepares a response to the visual stimulus.

The regions demonstrating activations attributable to incongruency were in various parts of parietal cortex bilaterally, and in the left MFG. The left MFG activation likely overlapped with an extensive zone of frontal cortical sensitivity to pseudoword-shape incongruency in the study of Peiffer-Smadja & Cohen (2019), although this was associated with greater deactivation for congruent than incongruent stimuli in that study. Furthermore, since the task in that study was to detect rare occurences of visual crosses and auditory beeps, the sound-symbolic pseudoword and shape stimuli were actually irrelevant to the main detection task; thus the frontal deactivation to mismatched pseudoword-shape pairs may have arisen because these were a distraction from the

explicit detection task (Peiffer-Smadja & Cohen, 2019). In the present study, however, participants had to process the pseudowords and shapes in order to respond and so the finding of greater cortical activity for incongruent compared to congruent pseudoword-shape pairs may seem puzzling at first glance. One view of congruency manipulations as a test of multisensory integration is that multiple sensory inputs are available to brain regions involved in integration, and that such regions respond more to congruent than incongruent multisensory inputs (Noppeney, 2012). However, Noppeney (2012) also argued that the brain might attempt, unsuccessfully, to integrate incongruent multisensory inputs. If so, regions involved in multisensory integration might, as here, show greater activity for incongruent than congruent stimuli. In a preliminary report from our group, another study using an explicit matching task found that a left precentral focus exhibited greater activity for incongruent than congruent stimuli, whereas a focus in the right caudate nucleus showed the opposite preference (Barany et al., 2021).

An incongruency effect of the type reported here might be enhanced when, as in the present study, participants selectively attend to one modality while ignoring the other (Noppeney, 2012). For example, when participants attended auditory targets after passively viewing visual primes, greater activity was elicited in several cortical areas (including one that likely overlaps with our left MFG incongruency region) when primes and targets were incongruent compared to congruent (Noppeney et al., 2008). Our left MFG incongruency region likely overlapped with a focus displaying greater activity for audiovisual stimuli that were familiar but semantically incongruent, compared to unfamiliar arbitrary pairings of abstract images and sounds (Hein et al., 2007). This region also corresponds to part of the domain-general ‘multiple demand’ attentional system described by Duncan (2013). In the ‘attend auditory’ incongruent condition, then, what may be happening is that the brain attempts to integrate a stimulus pair but instead detects a mismatch between a rounded pseudoword and a pointed shape or vice versa. On this reasoning, the basis of the observed incongruency-related activations might be greater attentional demand, rather than multisensory integration, during discrimination of (unfamiliar) auditory pseudowords in the presence of incongruent, compared to congruent, visual shapes. Consistent with this, the incongruency region in the right SMG is close to a focus exhibiting a preference for novel over familiar stimuli across auditory, visual, and tactile modalities (Downar et al., 2002),

and to one in which activation was stronger for unfamiliar abstract audiovisual stimuli compared to familiar, but semantically incongruent, audiovisual stimuli (Hein et al., 2007). Furthermore, the incongruency regions found here in bilateral aIPS and left SPG correspond to regions active during top-down attentional processing when visual targets were cued by semantically incongruent audiovisual stimuli (Mastroberardino et al., 2015), and to bilateral IPS foci (both of which overlap with our incongruency regions) shown to mediate audiovisual interaction during difficult processing of degraded stimuli (Regenbogen et al., 2018). This attentional explanation is especially likely for the subset of incongruency regions, comprising foci in the left IPS/SMG, that also exhibited correlations between the magnitudes of these neural incongruency effects and the corresponding RT congruency effects during scanning. We acknowledge that these considerations are subject to the limitations of reverse inference, although the limitations tend to be mitigated by our use of task-related reverse inference (Hutzler et al., 2014; McCormick et al., 2018). We suggest that the role of multisensory attention in relation to sound-symbolic crossmodal correspondences merits further research.

Relationship to visual imagery

Across participants, increasing preference for object as opposed to spatial imagery was strongly positively correlated with activation magnitudes for the incongruent > congruent contrast in the ‘attend auditory’ condition. Many of these correlated regions were in visual cortex (in the left IOS, posterior calcarine sulcus/lingual gyrus, and the right MOG), and one was in the left precuneus. This may reflect a greater tendency for object imagers to visualize shapes when associating these with pseudowords. The precuneus (Cavanna & Trimble, 2006), calcarine sulcus, lingual gyrus and MOG (Ganis et al., 2004) are all involved in visual imagery. Another possibility is that, since object imagers tend to integrate structural properties like shape with surface properties like texture (Lacey et al., 2011), the phonetic properties of the pseudowords, for example whether or not consonants are voiced or vowels are rounded, are more strongly bound to the visualized pointed and rounded shapes in these individuals. Interestingly, in contrast to the relatively widespread correlations with imagery preferences, there was little evidence that preference for verbal processing was connected to sound-symbolic associations since correlation of activation magnitudes with OSIVQ verbal scores was limited to a single voxel in the right SFS. Further work is required to investigate the potential for individual differences since these

might underlie the ability to either guess the meaning of sound-symbolic words in unknown foreign languages (Kunihira, 1971), or to learn such associations (Nygaard et al., 2009; Revill et al., 2018).

Conclusions

This study is the first to systematically examine the neural mechanisms underlying the sound-symbolic crossmodal correspondence between auditory pseudowords and visual shapes. We used independent contrasts and ROI analyses to test a number of *a priori* hypotheses for the neural basis of these correspondences. Overall, evidence for semantic mediation was lacking while that for multisensory integration and magnitude estimation was weak, at best. Albeit via task-based reverse inference, multisensory attention emerged as an important potential mechanism, as we also proposed previously for the crossmodal pitch-elevation correspondence (McCormick et al., 2018); we also found evidence consistent with phonological processing as an underlying explanation though this requires more rigorous testing. While this study addressed a tractable set of candidate mechanisms drawn from Spence (2011) and relevant to Sidhu & Pexman (2018), other possibilities remain to be explored, for example the neural basis of the sensorimotor hypothesis proposed by Ramachandran & Hubbard (2001). Nonetheless, our findings provide a basis for further research which should seek converging evidence using other methods (for example, multivariate analyses, repetition suppression, or transcranial magnetic stimulation) and should also address the relative weights of these different processes. Further, we observed several regions in visual cortex in which activation magnitudes scaled with individual preference for object imagery, thus suggesting a basis for individual differences in processing sound-symbolic associations to be followed up in future research. An important goal for research into crossmodal correspondences in general, as well as sound symbolism in particular, will be to distinguish the roles of high-level cognitive processes, such as phonology and attention, from those of lower-level sensory and perceptual processes.

Abbreviations

Directional: a, anterior; front, frontal; i, inferior; lat, lateral; m, mid; med, medial; p, posterior; s, superior; v, ventral.

Anatomical: AG, angular gyrus; AOS, anterior occipital sulcus; calcS, calcarine sulcus; CeS, central sulcus; cingG, cingulate gyrus; cingS, cingulate sulcus; collatS, collateral sulcus; FG, fusiform gyrus; fo, frontal operculum; InfOS, inferior occipital sulcus; Ins, insula; IOG, inferior occipital gyrus; IOS, intra-occipital sulcus; IPS, intraparietal sulcus; ITG, inferior temporal gyrus; ITS, inferior temporal sulcus; LG, lingual gyrus; MFG, middle frontal gyrus; MOG, middle occipital gyrus; OrbG, orbital gyrus; poCG, post central gyrus; po, pars opercularis; poCS, post central sulcus; POF, parieto-occipital fissure; preCS, precentral sulcus; preCG, precentral gyrus; precun, precuneus; preSMA, presupplementary motor area; pt, pars triangularis; SFG, superior frontal gyrus; SFS, superior frontal sulcus; SMG, supramarginal gyrus; SOG, superior occipital gyrus; SPG, superior parietal gyrus; STS, superior temporal sulcus. All other abbreviations are as in the main text.

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AUTHOR CONTRIBUTIONS

KM, KS, LCN and SL designed the experiment; KM created stimuli; KM and RS performed the research and analyzed data; KM, SL, KS and LCN wrote the paper.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Table 1 Incongruency effects: pseudoword-shape incongruency-related activations in the 'attend auditory' condition within the cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$ cluster threshold 5 voxels); x,y,z, Talairach coordinates for centers of gravity.

Region	**x**	**y**	**z**
R aIPS[1]	33	-40	42
R SMG – poCS[1,2]	45	-38	45
L SPG	-16	-61	58
L mid IPS - SMG – aIPS[3]	-36	-47	44
L MFG[3]	-42	30	28

[1] Overlaps with the asynchronous R aIPS and SMG in Table 1d.

[2] Overlaps with the R SMG and contiguous with the R aIPS magnitude foci in Table 1e.

[3] Overlaps with the semantic control L SMG and MFG in Table 1b.

Table 2 Activations on independent localization tasks: semantic (a,b), multisensory integration (c,d), and magnitude (e); all within cortical mask, voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster thresholds = semantic, 9 voxels; multisensory integration, 8 voxels; magnitude, 7 voxels; x,y,z Talairach coordinates for centers of gravity.

	Region	**x**	**y**	**z**
(a) Sentences > pseudowords	R a STG - a STS - mid STS - p STS	49	-6	-8
	L preCG – preCS - MFG	-44	-5	48
	L MOG	-40	-69	21
	L a STG - a STS - mid STS - p STS - p STG	-51	-19	-3
(b) Pseudowords > sentences	R SFG - SFS - MFG	29	19	47
	R SFS - SFG - MFG - IFS - IFG	32	49	15
	R med SFG	8	33	31
	R p cingS - p cingG	4	-31	36
	R precun - POF	11	-62	29
	R AG – mid IPS	46	-57	35
	L med SFG	-2	31	32
	L p cingS - p cingG	-4	-29	35
	L MFG - SFS	-31	28	38
	L IFS - IFG - lat OrbG - a OrbG	-31	48	8
	L SMG - AG	-44	-52	41
	L SPG - IPS - POF	-12	-68	31
	L MOG - InfOS	-36	-79	-3
(c) Synchronous > asynchronous	R a calcS - POF - cuneus	2	-60	15
	L a calcS - POF - cuneus - LG -p cingG	-4	-58	15
(d) Asynchronous > synchronous	R SMG – a IPS – mid IPS - AG	38	-47	42
	R IFG	53	11	16

(e) Magnitude > control	R SMG	42	-40	47
	R SPG - av IPS	18	-63	42
	R MOG - IOS - SOG	25	-86	8

Table 3 Correlations within cortical mask (r-map threshold p < .001, cluster-corrected p < .05 (except (b), FDR corrected q < .05), cluster thresholds = (a, c) 5 voxels, (d) 4 voxels; x,y,z, Talairach coordinates for centers of gravity.

Region	**x**	**y**	**z**	**Mean r**
(a) Attend visual (C > I) – RT congruency effect				
L SMG[1]	-50	-45	35	-.72
(b) Attend visual (C > I) – OSIVQ verbal score				
R SFS[2]	27	8	49	.70
(c) Attend auditory (I > C) – RT congruency effect				
R preSMA	3	5	52	.73
R POF – precun[3]	12	-66	37	.73
R IFS - IFG	32	12	28	.72
R a Ins - fo	34	25	7	.74
L preSMA	-6	5	47	.72
L pIPS - midIPS – AG[4]	-27	-57	41	.73
L aIPS – SMG[5]	-35	-45	36	.71
(d) Attend auditory (I > C) – OSdiff score				
R MOG	44	-61	3	.73
L SMA	-5	-5	63	.71
L precun	-6	-57	52	.74
L IOS	-22	-79	20	.74
L p calcS - LG	-10	-84	-6	.72

[1] Overlaps with the semantic control L SMG in Table 1b.

[2] Contiguous with the semantic control R SFS/MFG in Table 1b.

[3] Contiguous with the semantic control R precun – POF in Table 1b.

[4] Contiguous with the semantic control L AG/IPS in Table 1b.

[5] Overlaps with the incongruency effect L a IPS/SMG in Table 2 and contiguous with the semantic control L SMG in Table 1b.

FIGURE LEGENDS

Figure 1 Example stimuli for (a) the sound-symbolic word-shape correspondence task and the independent localization tasks: (b) semantic, (c) multisensory integration, (d) magnitude.

Figure 2 Sound-symbolic incongruency effects: pseudoword-shape incongruency-related activations in the attend auditory condition (Table 1).

Figure 3 Language task effects within cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 9 voxels). Contrast of sentences > pseudowords (orange) reveals semantic network (Table 2a); pseudowords > sentences (olive) (Table 2b).

Figure 4 Multisensory synchrony task effects within cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 8 voxels). Contrast of synchronous > asynchronous (turquoise) reveals putative integration network (Table 2c); asynchronous > synchronous (yellow: Table 2d).

Figure 5 Magnitude task effects within cortical mask (voxel-wise threshold $p < .001$, cluster-corrected $p < .05$, cluster threshold 7 voxels). Contrast of magnitude estimation > control reveals magnitude network (Table 2e).

Figure 6 Representative time-course curves for regions showing sound-symbolic incongruency effects in (A) the incongruent > congruent contrast and (B-D) contrasts from the independent contrasts with which they shared an overlap zone.

Figure 7 Sound-symbolic incongruency effects (blue) in relation to functional contrasts for semantics (orange), pseudowords > sentences (olive), multisensory integration (turquoise), and magnitude processing (green). Circles indicate areas of overlap or contiguity between incongruency effects and independent functional contrasts (see notes to Table 1).

Figure 8 Cortical regions showing correlations between activation magnitudes for the C > I contrast in the ‘attend visual’ condition and the magnitude of the RT congruency effect (brown: Table 3a) and scores on the verbal sub-scale of the OSIVQ (blue-gray: Table 3b); and between activation magnitudes for the I > C contrast in the ‘attend auditory condition and the magnitude of the RT congruency effect (red: Table 3c) and OSdiff scores (magenta: Table 3d) – higher OSdiff scores indicate stronger preference for object, rather than spatial, imagery. See notes to Table 3 for relationships to pseudoword-shape incongruency regions and independent functional contrasts.

Figure 1

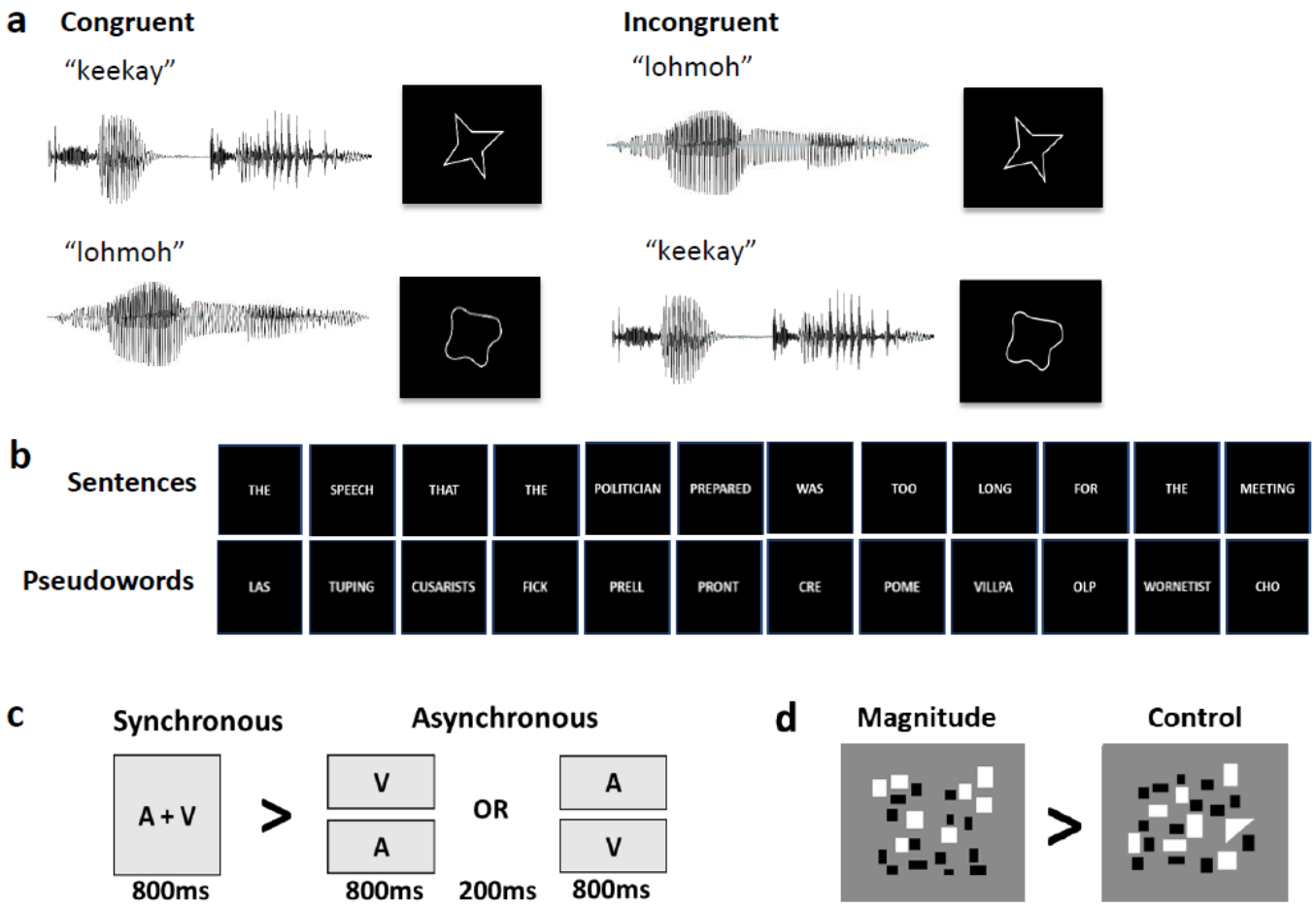
a
Congruent
"keekay"
"lohmoh"
Incongruent
"lohmoh"
"keekay"
b
Sentences
THE
SPEECH
THAT
THE
POLITICIAN
PREPARED
WAS
TOO
LONG
FOR
THE
MEETING
Pseudowords
LAS
TUPING
CUSARISTS
FICK
PRELL
PRONT
CRE
POME
VILLPA
OLP
WORNETIST
CHO
c
Synchronous
Asynchronous
A + V
800ms
>
V
A
800ms
OR
200ms
A
V
800ms
d
Magnitude
Control
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Figure 2

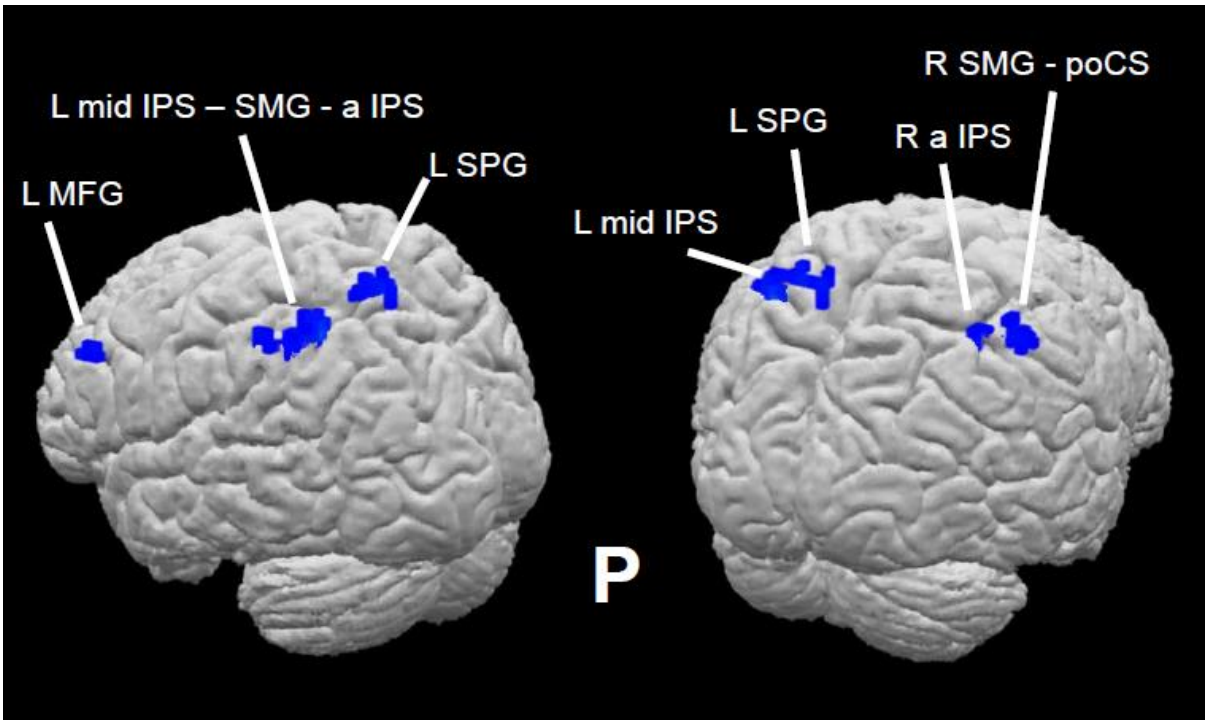


Figure 3

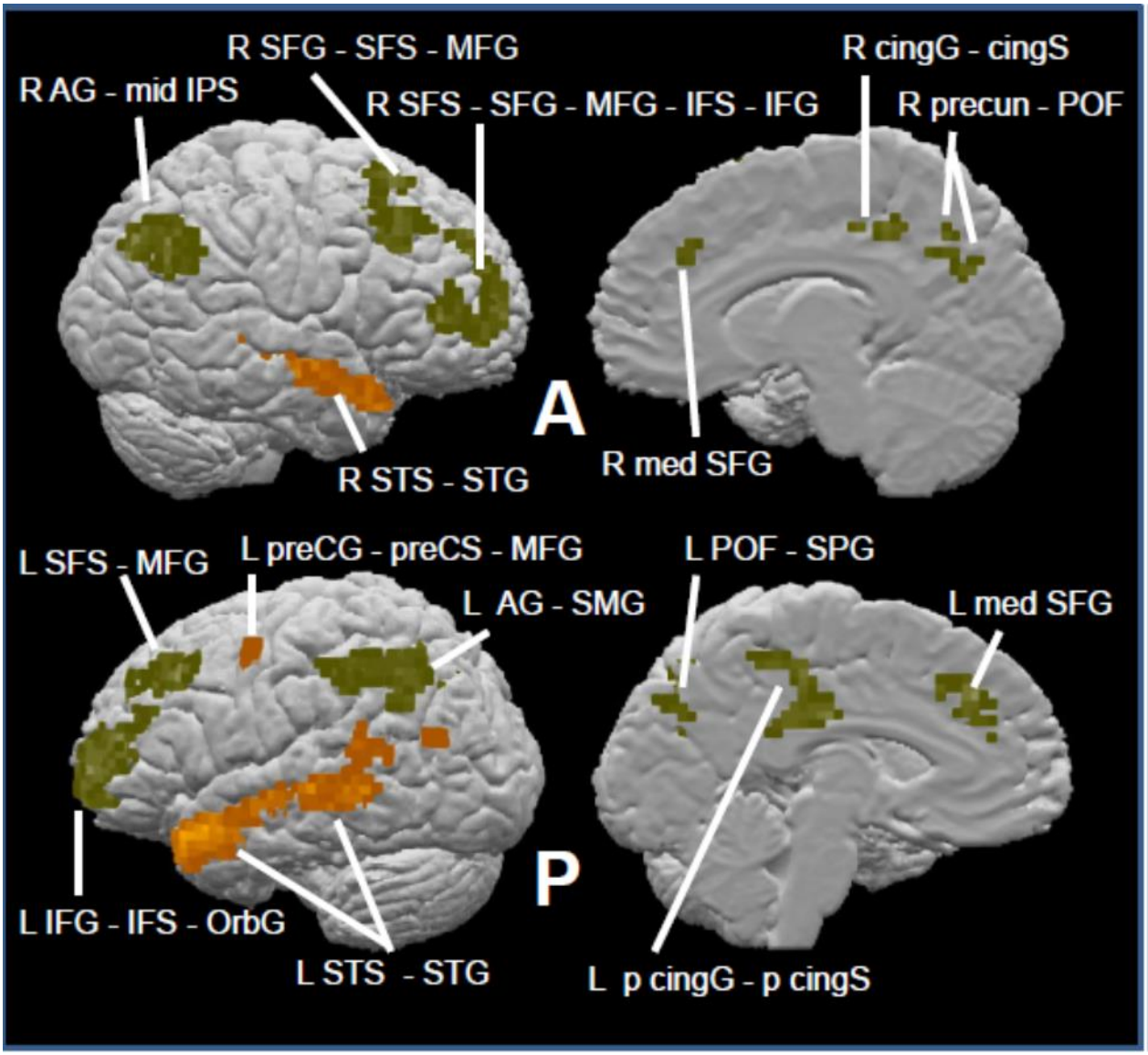

R SFG - SFS - MFG
R AG - mid IPS
R SFS - SFG - MFG - IFS - IFG
R cingG - cingS
R precun - POF
A
R STS - STG
R med SFG
L SFS - MFG
L preCG - preCS - MFG
L AG - SMG
L POF - SPG
L med SFG
P
L IFG - IFS - OrbG
L STS - STG
L p cingG - p cingS

Figure 4

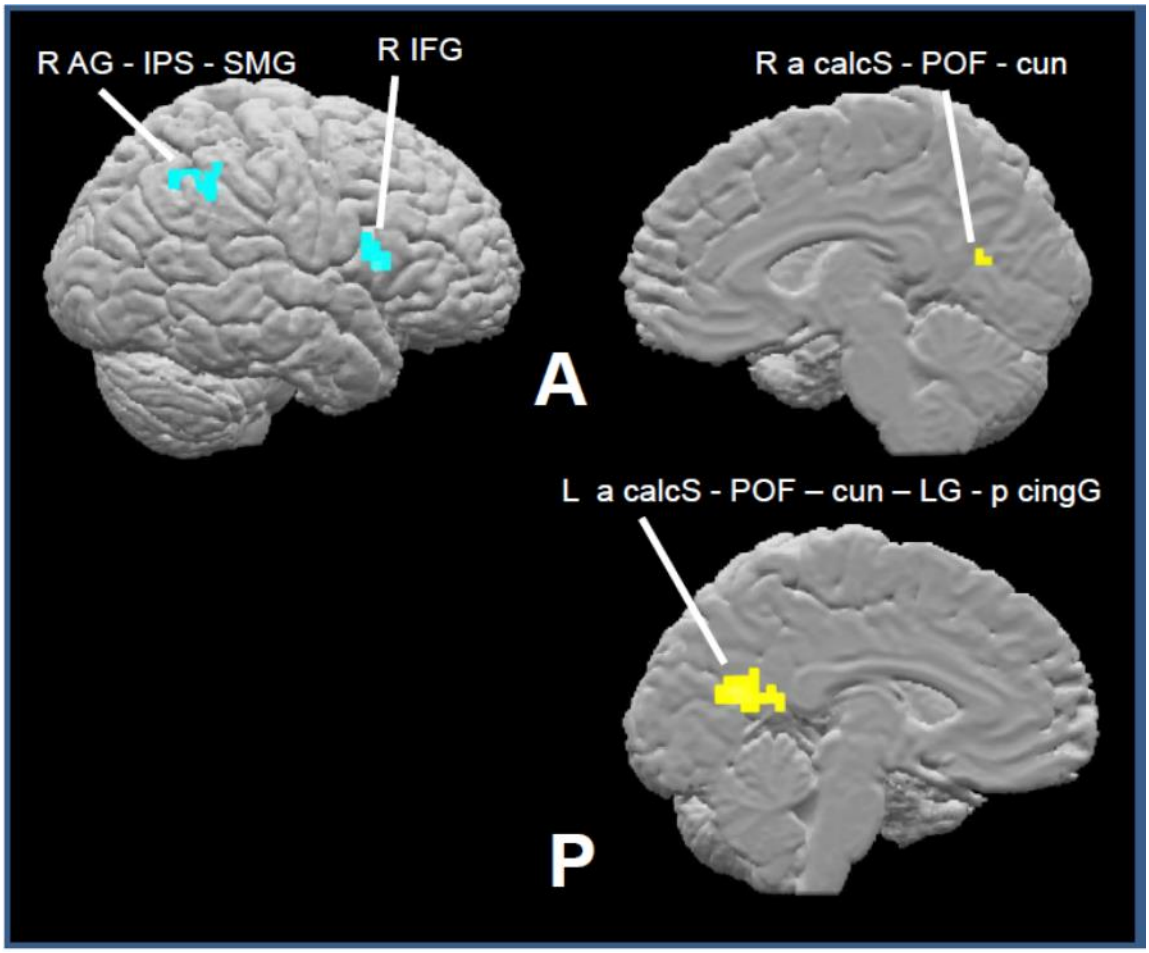


Figure 5

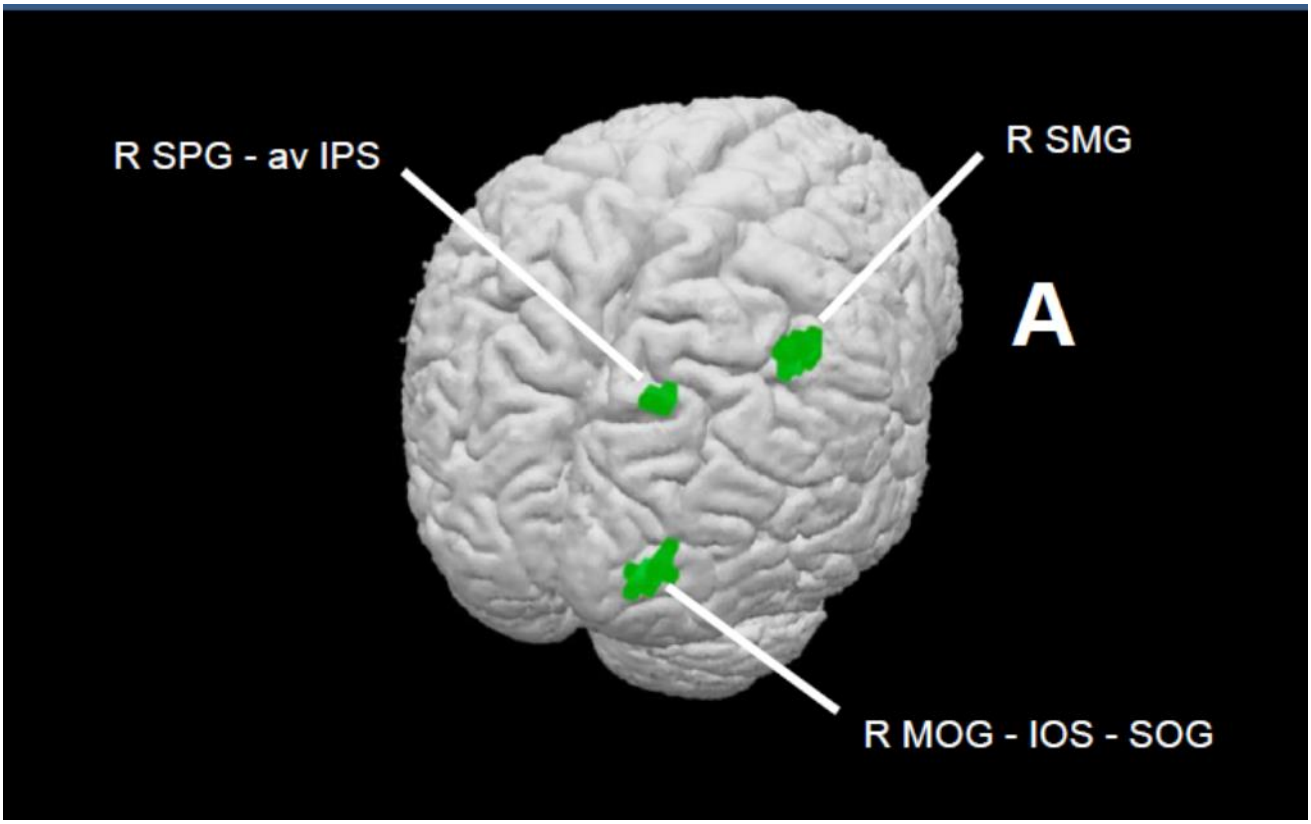


Figure 6

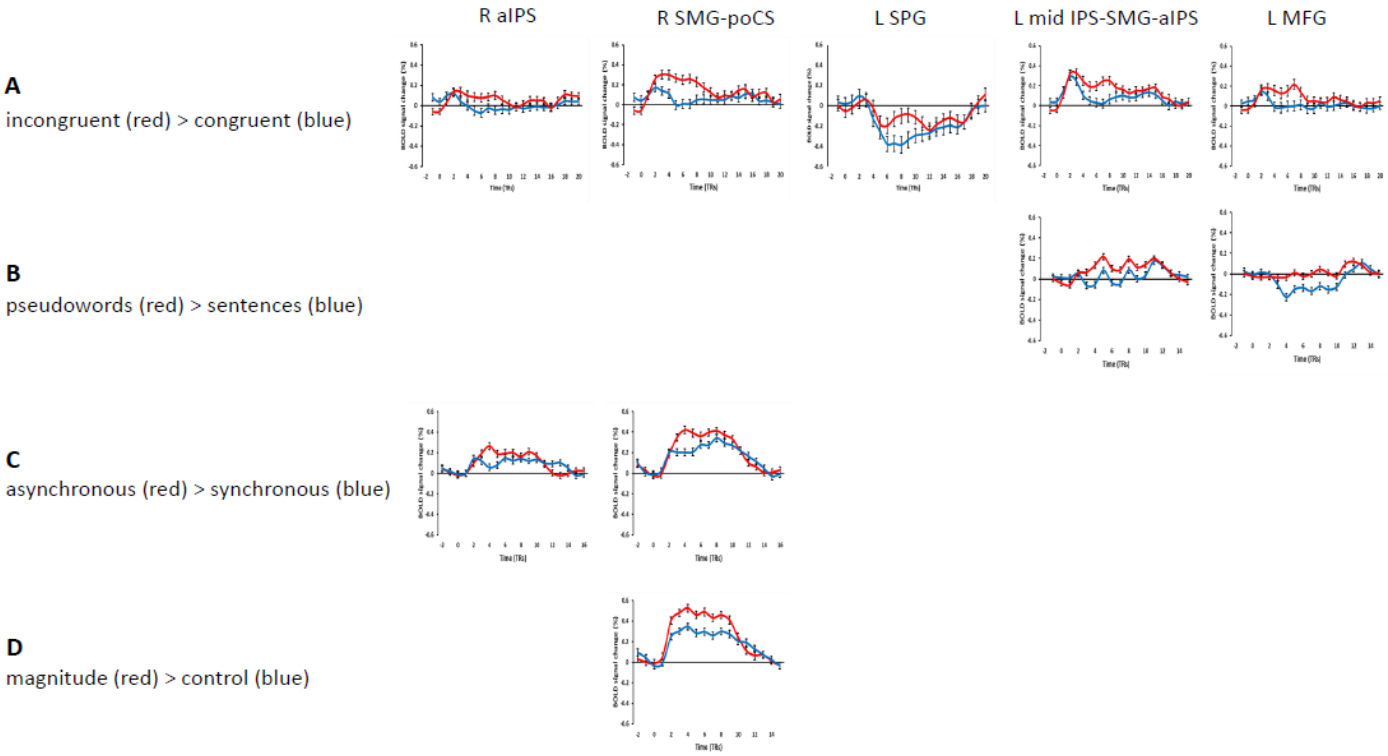

R aIPS
R SMG-poCS
L SPG
L mid IPS-SMG-aIPS
L MFG
A
incongruent (red) > congruent (blue)
B
pseudowords (red) > sentences (blue)
C
asynchronous (red) > synchronous (blue)
D
magnitude (red) > control (blue)

Figure 7

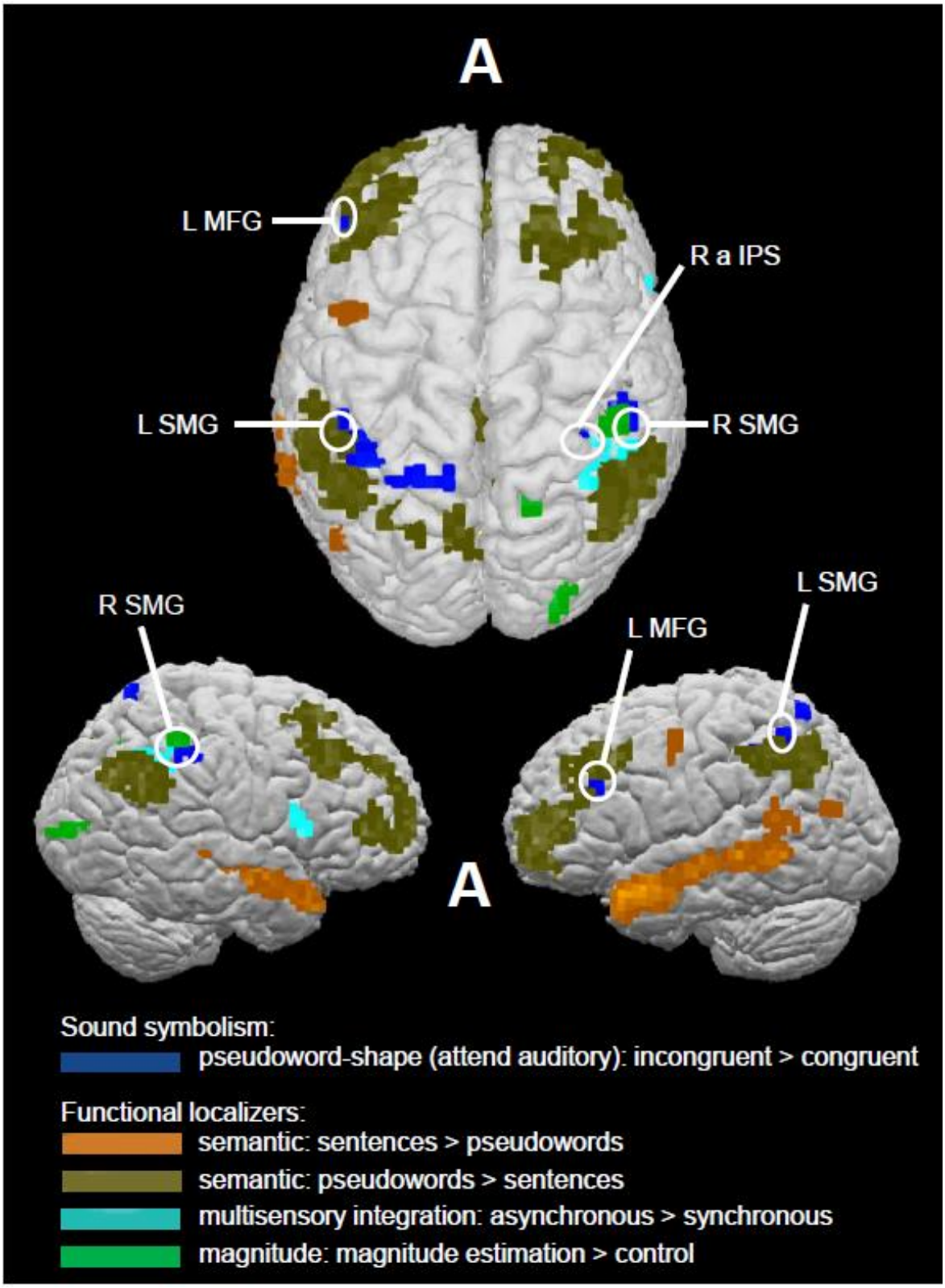
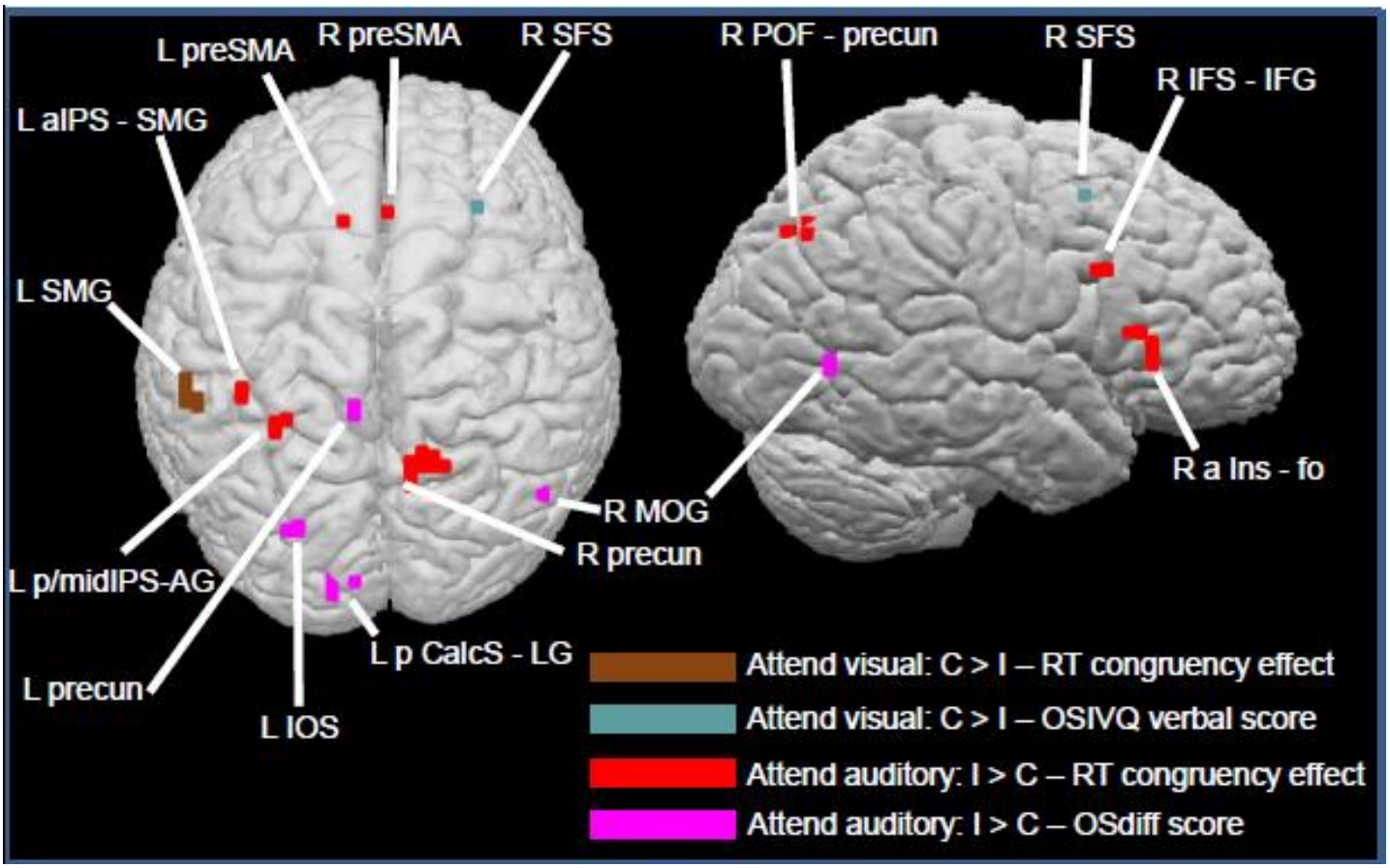

A
L MFG
R a IPS
L SMG
R SMG
R SMG
L SMG
L MFG
A
Sound symbolism:
pseudoword-shape (attend auditory): incongruent > congruent
Functional localizers:
semantic: sentences > pseudowords
semantic: pseudowords > sentences
multisensory integration: asynchronous > synchronous
magnitude: magnitude estimation > control

Figure 8


L preSMA
R preSMA
R SFS
R POF - precun
R SFS
R IFS - IFG
L aIPS - SMG
L SMG
R a Ins - fo
R MOG
R precun
L p/midIPS-AG
L p CalcS - LG
L precun
L IOS
Attend visual: C > I – RT congruency effect
Attend visual: C > I – OSIVQ verbal score
Attend auditory: I > C – RT congruency effect
Attend auditory: I > C – OSdiff score