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A single case neuroimaging study of tickertape synesthesia

Fabien Hauw^{1,2}✉, Mohamed El Soudany¹, Charlotte Rosso^{1,3}, Jean Daunizeau¹ & Laurent Cohen^{1,2}

Reading acquisition is enabled by deep changes in the brain's visual system and language areas, and in the links subtending their collaboration. Disruption of those plastic processes commonly results in developmental dyslexia. However, atypical development of reading mechanisms may occasionally result in ticker-tape synesthesia (TTS), a condition described by Francis Galton in 1883 wherein individuals "see mentally in print every word that is uttered (...) as from a long imaginary strip of paper". While reading is the bottom-up translation of letters into speech, TTS may be viewed as its opposite, the top-down translation of speech into internally visualized letters. In a series of functional MRI experiments, we studied MK, a man with TTS. We showed that a set of left-hemispheric areas were more active in MK than in controls during the perception of normal than reversed speech, including frontoparietal areas involved in speech processing, and the Visual Word Form Area, an occipitotemporal region subtending orthography. Those areas were identical to those involved in reading, supporting the construal of TTS as upended reading. Using dynamic causal modeling, we further showed that, parallel to reading, TTS induced by spoken words and pseudowords relied on top-down flow of information along distinct lexical and phonological routes, involving the middle temporal and supramarginal gyri, respectively. Future studies of TTS should shed new light on the neurodevelopmental mechanisms of reading acquisition, their variability and their disorders.

Reading acquisition is enabled by deep functional and anatomical changes in the brain's visual system and language areas, and in the links that subtend their collaboration¹⁻⁴. Whenever those delicate plasticity processes are compromised, various sorts of developmental dyslexia may result^{5,6}.

However, atypical development of reading mechanisms may occasionally result in another condition, in some sense opposite to dyslexia, one which has not received sufficient scientific attention. The polymath Francis Galton noted in 1883 that "some few persons see mentally in print every word that is uttered and they read them off usually as from a long imaginary strip of paper, such as is unwound from telegraphic instruments"⁷. This unusual phenomenon, was dubbed by Galton ticker-tape synesthesia (TTS). TTS, once purely anecdotal, actually touches on the core of the brain mechanisms of normal and impaired reading. Indeed, while reading is the translation of visual letters into speech, TTS may be viewed as its exact opposite, i.e. the translation of speech into internally visualized letters, respectively the "inducer" and "concurrent" in synesthesia parlance^{8,9}.

More generally, synesthesia encompasses a range of subjective phenomena in which stimulation in one sensory or cognitive domain (the inducer) automatically triggers additional perceptions in one or several other unstimulated domains (the concurrent). For example, in grapheme-color synesthesia, one of the most studied synesthesia, digits and letters, printed or even imagined, are perceived as colored¹⁰.

During word reading, letters and their order are first identified in the Visual Word Form Area (VWFA), a reproducible sector of the left ventral occipitotemporal (VOT) cortex, whose lesion yields pure alexia^{1,11,12}. Orthographic information is then broadcast to language areas, giving access to the associated sounds (the "phonological route") and meaning (the "lexico-semantic route")¹³⁻¹⁵. Reciprocally to this "bottom-up" spread of information, brain imaging revealed that in literate individuals, language areas exert "top-down" influences upon orthographic representations. Thus, attended speech activates the VOT cortex including the VWFA¹⁶⁻¹⁸, and language areas send different top-down influences to the VWFA during the reading of real words and of pseudowords¹⁹. In this framework, as first hypothesized by Holm et al.⁸, TTS would reflect exceptionally powerful and automatic top-down influences from speech processing areas onto the VWFA.

This connectivity hypothesis of TTS is compatible with most neuroscientific theories of synesthesia, which all propose increased connectivity as a core mechanism⁹. According to the pruning theory²⁰, some connections

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present in children are not pruned and then are responsible for the persistence of atypical anatomical connections in adults. Alternative theories rather support atypical functional connectivity, particularly disinhibition of the links from inducer to concurrent²¹.

Using functional MRI (fMRI) in a man in whom TTS was triggered by both real words and pseudowords, we assessed the hypothesis that TTS would essentially upend the reading system to generate letters from sound.

We implemented this hypothesis as the following four specific predictions. (1) TTS should activate perisylvian language areas involved in speech processing and phonology-to-orthography translation, and VOT regions subtending orthography. (2) Regions involved in TTS should overlap with those involved in reading. (3) Assuming that TTS reflects intense top-down flow of information in the reading system, dynamic models should reveal an increased drive of the reading system by speech input. (4) Due to the overarching distinction between the lexical and phonological routes, top-down influences should follow different paths within the reading system depending on whether synesthesia is triggered by words or pseudowords.

Materials and methods

A case of tickertape synesthesia. MK was a 69 years old man, right-handed, native French speaker, a still active engineer and researcher in the field of radar technology, with no significant medical history. For as long as he could remember, when listening to speech, he had been simultaneously perceiving the words in their written form. About a year before the present study, while talking with friends, he accidentally discovered that this phenomenon was quite unusual. He knew about our scientific interest in reading from the media and contacted one of us out of curiosity. TTS was triggered by speech perception, irrespective of whether it was somebody else or MK himself speaking, of whether he could see the face of the speaker or not, of whether he was himself speaking overtly or covertly “in his head”.

During TTS, MK felt that he perceived distinctly each and every letter. Mental images of words did not occupy a well-defined position in external space, but were rather “in his head”; still they looked black, and could be in upper or lower case. Size was “normal, as when you’re reading”. He felt that he perceived about one word at a time. The illusion appeared immediately upon speech onset and persisted briefly after speech ended. TTS was unaffected by the voice, the gender, or the emotion of the speaker, nor by the content of the utterance. It occurred even with unattended speech, such as from neighbor travelers on a train. MK could not voluntarily inhibit TTS, and found parasitic speech quite disturbing when he was reading, although this may be a common nuisance. MK enjoyed listening to wordless music, which generated no TTS. He had no other associated type of synesthesia. His daughter and a niece were subject to the same phenomenon²².

Controls. We compared MK to two groups of healthy typical controls, whose data were collected in the context of other protocols unrelated to synesthesia. One group (G1) included 22 participants, aged 20–36 years (median 28 years, 10 men). The other group (G2) included 14 older controls, aged 51–75 years (median 64 years, 5 men). All participants were native French speakers, right-handed according to the Edinburgh Inventory²³, had no history of neurological or psychiatric disorders. The research was approved by the institutional review board of the Institut national de la santé et de la recherche médicale (protocols C10-50 and C13-41), and all participants provided informed written consent. All studies were carried out in accordance with the Declaration of Helsinki.

Experiment 1: normal and reversed speech perception. *Stimuli and procedure.* The Red Riding Hood story was recorded with a female voice, and a time-reversed version of the recording was derived by playing it backward. MK and group G1 received a pseudo-random alternation of 6 blocks of normal and 6 blocks of reversed speech (block duration 15 s), separated with silent rest periods, for a total of 5 min and 12 s. Group G2 received a slightly shorter version (4 normal and 5 reversed blocks, for a total of 4 min and 15 s). Participants were simply asked to pay attention to the story.

MRI acquisition. For MK and G1, multi-echo (ME) fMRI images²⁴ were acquired on a Siemens 3 T MAGNETOM Prisma scanner, with a 20-channel receive-only head coil: TR 1.3 s; multi-TE 15, 34.24, 53.48 ms; flip angle 68°; voxel size 3 × 3 × 3 mm; 48 slices. An anatomical T1-weighted image was acquired: TR 2.3 s; TE 2.76 ms; flip angle 9°; voxel size 1 × 1 × 1 mm). For G2, single-echo sequences were acquired on a Siemens 3 T MAGNETOM Verio scanner, with a 20-channel receive-only head coil: TR 3 s; TE 25 ms; flip angle 90°; voxel size 2 × 2 × 2.5 mm; 49 slices. An anatomical T1-weighted image was acquired: TR 2.3 s; TE 4.18 ms; flip angle 9°; voxel size 1 × 1 × 1 mm).

Preprocessing. For MK and G1, using `afni_proc.py`, all echo timeseries were slice-time corrected, motion correction was computed on the first echo and applied to all echos, and echo images were merged using `t2smmap.py` from the `meica.py` toolbox provided with AFNI: <http://afni.nimh.nih.gov/afni/>. Then, using SPM12 (Wellcome Institute of Imaging Neuroscience, London, UK) implemented in Matlab, functional time-series were co-registered to the anatomical volume, normalized, resampled to 3 mm cubic voxels, and spatially smoothed (6 mm FWHM). For G2, time-series were preprocessed only with SPM12, following the same steps: slice-timing, realignment, co-registration to the anatomy, normalization, resampling to 3 mm cubic voxels, smoothing (6 mm FWHM).

Regions of interest. In addition to the whole-brain approach, we restricted some analyses within two a priori defined regions of interest (ROI). First, we used a 8 mm radius sphere centered at the peak of the VWFA (MNI

–44 –50 –14), as identified in Dehaene et al.²⁵. Second, we created a ROI covering left-hemispheric language areas and VOT cortex (Supplementary Fig. S1), by merging the opercular and triangular parts of the inferior frontal gyrus, the supplementary motor area, the precentral, fusiform, inferior parietal, supramarginal, angular, superior and middle temporal, and inferior temporal gyri, as defined in the AAL 3 atlas²⁶.

Statistical analysis. One subject was excluded due to technical issues during acquisition. For single-subject analyses, we used a general linear model (GLM) including regressors for normal and reversed speech, convolved with the canonical SPM hemodynamic response function (HRF), plus 6 motion parameters, and high-pass filtering (128 s cutoff). For second-level analyses, we used two sample t-tests to assess differences between MK and control participants, with age as a covariate. We set both the first- and second-level voxel-wise cluster-forming threshold to $p < 0.001$, and the cluster-wise threshold to $p < 0.05$ corrected for multiple comparisons across the whole brain or within ROIs. In the text and in Tables, we provide Z-scores for contrasts of interest at peak activation voxels.

Experiment 2: visual localizer. *Stimuli and procedure.* Only MK participated in this experiment. He was presented with an alternation of blocks of pictures (8 s per block) and periods of rest (7.8 s per period). Each stimulation block included eight pictures from one of the following categories: printed words, numbers, faces, houses, tools, body parts. Each picture was displayed for 600 ms and followed by a 400 ms blank screen. During rest and inter-trials intervals, a black central fixation cross was presented to minimize eye-movements. The experiment included 10 s of initial rest, followed by 30 blocks of pictures (six for each category) and 30 periods of rest. Blocks were presented in pseudorandom order to maximize the variety of transitions between conditions while avoiding repetition of the same condition in successive blocks. Participants were asked to press a button with their right thumb whenever a picture was identical to the previous one, which was the case for 20% of stimuli (1–3 repetitions/block).

MRI acquisition, preprocessing, and statistical analysis. Functional images were acquired on a Siemens 3 T MAGNETOM Verio scanner equipped with a 64-channel receive-only head coil: TR 1022 ms; TE 25 ms; flip angle 62°; voxel size 2.5 × 2.5 × 3 mm; 45 slices. Preprocessing was the same as for single-echo data in Experiment 1. Statistical analysis and thresholding followed the same method as in Experiment 1, apart from the definition of regressors of interest: here we defined one regressor for each of the 5 categories of stimuli, plus a regressor for responses to targets.

Experiment 3: listening to words and pseudowords. *Stimuli and procedure.* MK and the G1 group of control subjects participated in this experiment. We generated a list of 64 words and 32 pseudowords matched in number of phonemes and syllables. Real words included 32 high- and 32 low-frequency words, whose activation pattern did not differ, and which were averaged in all analyzes. Stimuli were synthesized with a female French voice, and equated for maximum amplitude. Stimuli had a mean duration of 644 ms, with no difference between words and pseudowords.

Stimuli were organized in 48 mini-blocks of 8 stimuli each. Mini-blocks were grouped in 8 consecutive blocks, each composed of 2 mini-blocks of PW and 4 mini-blocks of words. The run started and ended with a 15 s silence, and an additional 15 s pause was present between blocks. The total duration was about 12 min. Subjects had to detect the occasional target pseudoword “tatatata”, pronounced by the same voice as stimuli.

MRI acquisition, preprocessing, and statistical analysis. Acquisition and preprocessing were the same as for multi-echo data in Experiment 1. Univariate analyses and thresholding followed the same method as in Experiment 1, apart from the definition of regressors of interest: here we defined regressors for low-frequency words, high-frequency words, pseudowords, targets and responses to targets. As controls were all younger than MK, an age regressor would have absorbed any difference between the two. Hence no age regressor was included in second-level analyses. Moreover, multivariate pattern analyses (MVPA) were conducted using The Decoding Toolbox²⁷, in order to decode words from pseudowords. To train and test the support vector machine, we performed 8 leave-one-block-out cross validation folds, across the 8 blocks of the experiment. Decoding was performed across the volume activated by the averaged words and pseudowords (voxelwise $p < 0.01$), using a 12 mm radius searchlight. Decoding performance around each voxel was quantified as the “area under the curve” (AUC) of signal-detection theory. In order to assess the significance of decoding accuracy in individual participants, we computed a permutation test, with a total of 128 permutations. We report voxels with better-than-chance decoding performance ($p < 0.05$), with moreover an ad-hoc minimum cluster size of 50 voxels.

Dynamic causal modelling (DCM). We performed deterministic DCM analysis on Experiments 1 and 3, using the DCM toolbox implemented in SPM12. First, a GLM was defined for each experiment, with one regressor modeling all auditory stimulations, plus a parametric modulator taking the value +1 or –1 for normal and reversed speech in Experiment 1, and the value +1 or –1 for words and pseudowords in Experiment 3. Time series were extracted from 4 ROIs identified in Experiments 1 to 3: (1) The mid superior temporal gyrus ROI (STGm) was defined as a 6 mm radius sphere centered on the activation peak of reversed speech > rest in controls in Experiment 1; (2) The supra-marginal gyrus ROI (SMG) was the cluster, identified in the contrast normal speech > reversed speech in MK > controls in Experiment 1; (3) The middle temporal ROI (MTG) was the cluster of effective lexicality decoding in MK in Experiment 3; (4) The VWFA was defined as a 6 mm radius sphere centered on the activation peak of words > faces and houses in MK in Experiment 2. The VWFA and STG

ROIs were defined as spheres because activation clusters were large and extended to adjacent irrelevant regions. We specified a set of a priori constraints on the connections between the 4 regions (defining possible model “families”), and on the modulations acting on those connections, as fully presented in the Results section. In MK, within those constraints, we successively identified for each experiment, (1) the most likely set of intrinsic connections between ROIs, and (2) the most likely pattern of modulation of those connections by experimental factors. In brief, we pooled models into model families, each of which shares the same intrinsic connectivity pattern. Within each family, different models then corresponded to different connectivity modulation patterns.

Significance statement. Some individuals, whenever they are hearing speech, see vividly in their mind’s eye the corresponding words in written form, as mental subtitles. This unusual condition, termed ticker-tape synesthesia (TTS), far from being purely anecdotal, actually touches on the core of the brain mechanisms of normal and impaired reading acquisition. Through 3 fMRI experiments, we provide an in-depth study of a single individual (MK) with ticker-tape synesthesia. A set of left-hemispheric regions were more activated in MK than in controls during speech vs reversed speech perception, including an occipitotemporal area specialized for orthographic representation, and the supra-marginal gyrus, involved in grapheme-phoneme conversion. We propose that TTS, a situation in some sense symmetrical to developmental dyslexia, reflects an inverted flow of information through the reading system, such that speech is automatically translated into internally visualized letters. Future studies of TTS should shed new light on the neurodevelopmental mechanisms of reading acquisition and of synesthesia.

Results

Experiment 1: the correlates of tickertape synesthesia during speech perception. We first scanned MK with fMRI while he was listening to continuous speech (the Red Riding Hood story), to time-reversed speech as a control for low-level auditory perception, and while he was at rest, and his activations were compared to neurotypical controls (see Methods). As expected, MK reported that listening to normal speech induced vivid synesthesia, while reversed speech did not generate orthographic imagery.

In controls, reversed speech minus rest activated the bilateral mid-superior temporal gyrus (STG), inferior frontal gyrus (IFG) and supplementary motor area (SMA), and the left precentral gyrus (Fig. 1 and Table S1). The contrast of normal minus reversed speech additionally activated the bilateral left-predominant IFG and superior temporal sulcus (STS) from the temporal pole to the angular gyrus (AG), the left precentral cortex, the bilateral SMA and precuneus, plus the VOT cortex along the lateral occipitotemporal sulcus anterior to MNI $Y = -62$ (Fig. 1 and Table S1).

We then compared MK to controls. In order to identify the functional correlates of TTS, we compared the contrast of normal minus reversed speech in MK relative to controls (Fig. 1 and Table 1). MK’s activation was stronger than in controls in a set of left-hemispheric regions: the IFG (MNI $-33\ 5\ 26$, $Z = 5.59$; MNI $-42\ 20\ 29$, $Z = 5.02$), the supramarginal gyrus (SMG; MNI $-48\ -43\ 32$; $Z = 6.47$), precuneus, the SMA, plus the fusiform gyrus close to the usual location of the VWFA (MNI $-42\ -46\ -10$; $Z = 4.25$, corrected within an anatomically defined VOT region of interest; see Methods). We did not find differences between MK and controls in low-level

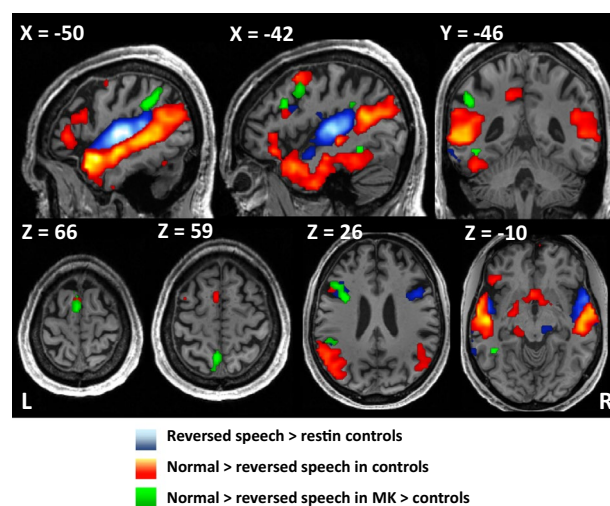


Figure 1. Experiment 1: Correlates of tickertape synesthesia (TTS) during speech perception. Activation in control participants by reversed speech minus rest (blue), and by normal minus reversed speech (hot colors). The latter included left-predominant perisylvian areas usually involved in speech comprehension, plus the left ventral occipitotemporal cortex. When listening to normal speech, MK was subject to TTS and showed a larger difference between normal and reversed speech than controls in the left SMG, IFG, VWFA, precuneus, and SMA (green). *TTS* tickertape synesthesia, *IFG* inferior frontal gyrus, *SMG* supra-marginal gyrus, *VWFA* visual word form area, *SMA* supplementary motor area.

Region (left hemisphere)	Contrast	Peak coordinates (MNI)	Z value	Cluster size	p value (cluster-level, FWE corrected)
SMG	MK > (G1 + G2)	-48 -43 32	6.47	61	0.005*
	MK > G1	-48 -43 32	6.11	56	0.027*
	MK > G2	-45 -40 29	5.3	75	<0.001*
IFG	MK > (G1 + G2)	-33 5 26	5.59	117	<0.001*
	MK > G1	-30 8 26	5.24	58	0.023*
	MK > G2	-33 8 26	4.45	158	<0.001*
IFG	MK > (G1 + G2)	-42 20 29	5.02		<0.001*
	MK > G1	-42 20 29	5.6	34	0.148
	MK > G2	-42 20 29	3.92	158	<0.001*
SMA	MK > (G1 + G2)	-3 -1 68	5.15	60	0.005*
	MK > G1	-12 2 71	4.48	45	0.062
	MK > G2	0 5 68	4.89	88	<0.001*
Precuneus	MK > (G1 + G2)	-3 -55 59	4.64	42	0.03*
	MK > G1	-3 -55 59	4	29	0.222
	MK > G2	-3 -52 62	4.65	232	<0.001*
VWFA	MK > (G1 + G2)	-42 -46 -10	4.22	8	0.005**
	MK > G1	-42 -49 -10	3.88	9	0.006**
	MK > G2	-42 -46 -10	3.62	3	0.013**

Table 1. Experiment 1: Regions more activated in MK than in controls when listening to normal > reversed speech. *Significant cluster-level P , with voxelwise $P < 0.001$ and clusterwise $P < 0.05$ corrected for multiple comparisons across the whole brain. **Significant cluster-level P , with voxelwise $P < 0.001$ and clusterwise $P < 0.05$ corrected for multiple comparisons within an a priori occipitotemporal region of interest (see Methods). The five main regions displayed are the regions where MK showed overactivation when compared to all controls for the contrast normal speech > reverse speech.

visual cortex. For brevity, we will refer to this set of regions as the TTS network in subsequent results. We defined an anatomical mask including all language areas and the left VOT cortex (see Methods). The TTS network was almost entirely included in those regions (Supplementary Fig. S1), in agreement with our first prediction.

In order to determine whether MK's over-activations were within the range of variation of control participants, we compared the contrast of normal minus reversed speech in each control subject minus all others. While 14 controls showed some significant differences from the group (excluding the cerebellum), those over-activations were randomly distributed all over the brain, with little overlap with the language and VOT masks (overlap range 0–58 voxels; mean = 11, as compared to MK's overlap of 232 voxels; Crawford t -test: $t(34) = 11.2$; $p < 0.001$).

The two control groups G1 and G2 were scanned on different magnets, and G1 controls were younger than MK. In order to make sure that the overall differences which we observed between MK and controls were not due to age and scanner differences, we compared separately MK > G1 and MK > G2, and found that the main differences were remarkably replicated across both analyses, using the same statistical thresholds as in the global comparison (Fig. S2). The MK > G1 comparison showed overactivation in the left SMG, IFG and VWFA. The MK > G2 comparison showed overactivation in the left SMG, IFG, SMA, precuneus and the VWFA (see Table 1). Moreover, we directly compared the two control groups. We found stronger activation for G1 > G2 in bilateral superior temporal sulci (STS), and stronger activation for G2 > G1 in the right prefrontal cortex (Fig. S3). Those regions had no overlap with the areas distinguishing MK from controls.

Finally, the opposite contrast of normal minus reversed speech in all controls minus MK showed no activations. Activation by reversed speech minus rest and by normal speech minus rest did not differ between MK and controls.

In summary, this experiment supported our first prediction by showing abnormally strong activation during TTS, both in perisylvian frontoparietal language areas (the IFG and SMG), and in the left VOT at the usual location of the VWFA.

Experiment 2: tickertape synesthesia as reverse reading. Beyond proposing that TTS should involve both the perisylvian and the VOT regions, we predicted that TTS-related activations should overlap with regions activated during word reading. Particularly, is the VOT component of the TTS network identical to the VWFA, as usually defined by word-specific visual activations? In order to delineate his reading network, MK was scanned while viewing images of words, faces, houses, tools, body parts, numbers, and during simple fixation (see Methods).

We first characterized the mosaic of VOT regions showing category preferences (Fig. 2 and Table S2). MK had a fully normal pattern of specialization, as documented in a host of previous studies^{28–30}. Subtractions of each of the 3 categories words, faces and houses minus the other 2 showed the left VWFA (MNI -45 -52 -10; $Z > 8$), the right fusiform face area (FFA), and the bilateral parahippocampal place area (PPA), respectively. Subtractions of tools and of body parts minus the previous 3 categories showed bilateral lateral occipital cortex (LOC) activations.

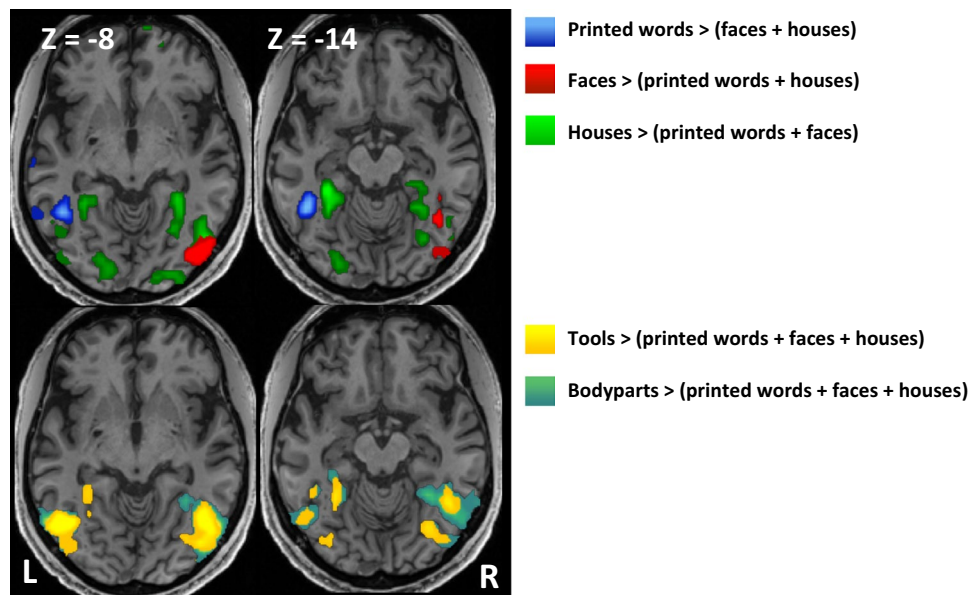


Figure 2. Experiment 2: Category-selective activations by visual objects. MK's VOT cortex showed a typical mosaic of category preference. Upper row : the VWFA for words (blue), the FFA and OFA for faces (red), the PPA for buildings (green). Bottom row : lateral occipital activations for tools (yellow) and body parts (blue-green). *VOT* ventral occipito-temporal, *VWFA* visual word form area, *FFA* fusiform face area, *OFA* occipital face area, *PPA* parahippocampal place area.

Crucially, the VOT area which was overactivated during TTS in Experiment 1 was identical to the VWFA defined here on the basis of visual stimulation (Fig. 3A, white arrow). Beyond the VWFA, this overlap extended to all components of the TTS network (SMG, IFG, precuneus and SMA), which were also significantly activated here during reading (Fig. 3A).

Finally, in order to further compare MK to controls while avoiding statistical double dipping³¹, we defined ROIs of the TTS network on the basis of the current experiment, and plotted data from Experiment 1. In a 10 mm radius sphere centered on peaks of MK's activation by words minus faces and houses, we computed the average activation by the contrast of normal > reversed speech from Experiment 1, across the 10% most activated voxels (Fig. 3B). In the SMG, IFG, precuneus and SMA, MK exceeded all of the 35 controls, with a significantly stronger activation (Crawford's *t*-tests: all *P*s ≤ 0.001). At the VWFA, 4 controls showed higher activation than MK, who was marginally stronger than the group of controls (*p* = 0.055).

In summary, we observed an extensive overlap of the activations related to TTS and to word reading, supporting our hypothesis that TTS resulted from an atypical operation of the cerebral reading system.

Experiment 3: tickertape synesthesia for words and pseudowords. The reading system is thought to associate a phonological route mapping orthography to sounds on the basis of statistical regularities, and a lexico-semantic route mapping orthography to the mental lexicon, including stored word sounds. Assuming that TTS resulted from the reverse operation of the reading system, how did those two routes contribute to TTS? MK's introspection was that TTS was triggered by both real words, which appeared in their correct orthography, and by pseudowords, which appeared in a plausible spelling, suggesting that both reading routes were feeding the TTS phenomenon. The left SMG appeared as an obvious candidate for phonological processing, considering its involvement in a broad variety of phonological tasks, particularly whenever phonology has to be interfaced with orthography, audiovisual language, or sensorimotor processing^{32–37}. The aim of Experiment 3 was to identify regions subtending lexical access from speech in MK, allowing us to then study their contribution to TTS. To this end, MK was scanned while he was presented with spoken words and with matched pseudowords. A group of controls were also scanned (see Methods).

As usual, both words and pseudowords triggered TTS. In MK, words and pseudowords activated essentially identical left-predominant fronto-temporo-parietal areas relative to rest. Those areas encompassed the entire TTS network, as identified in Experiment 1 (Supplementary Fig. S4). Unless stated otherwise, all further analyses of this experiment were restricted to the volume which was activated in MK by averaged words and pseudowords > rest (voxelwise *p* < 0.01). We then compared MK minus controls for the contrasts words > rest and pseudowords > rest. Both comparisons replicated the results of Experiment 1, revealing overactivation in MK's TTS network, including the IFG, SMG and SMA (Supplementary Fig. S5). The VWFA also was overactivated in MK for words > rest when correcting within the same a priori ROI as in Experiment 1.

We then compared activations by words and pseudowords, using univariate contrasts and multivariate pattern analysis (MVPA). The contrasts of words > pseudowords and pseudowords > words showed no significant

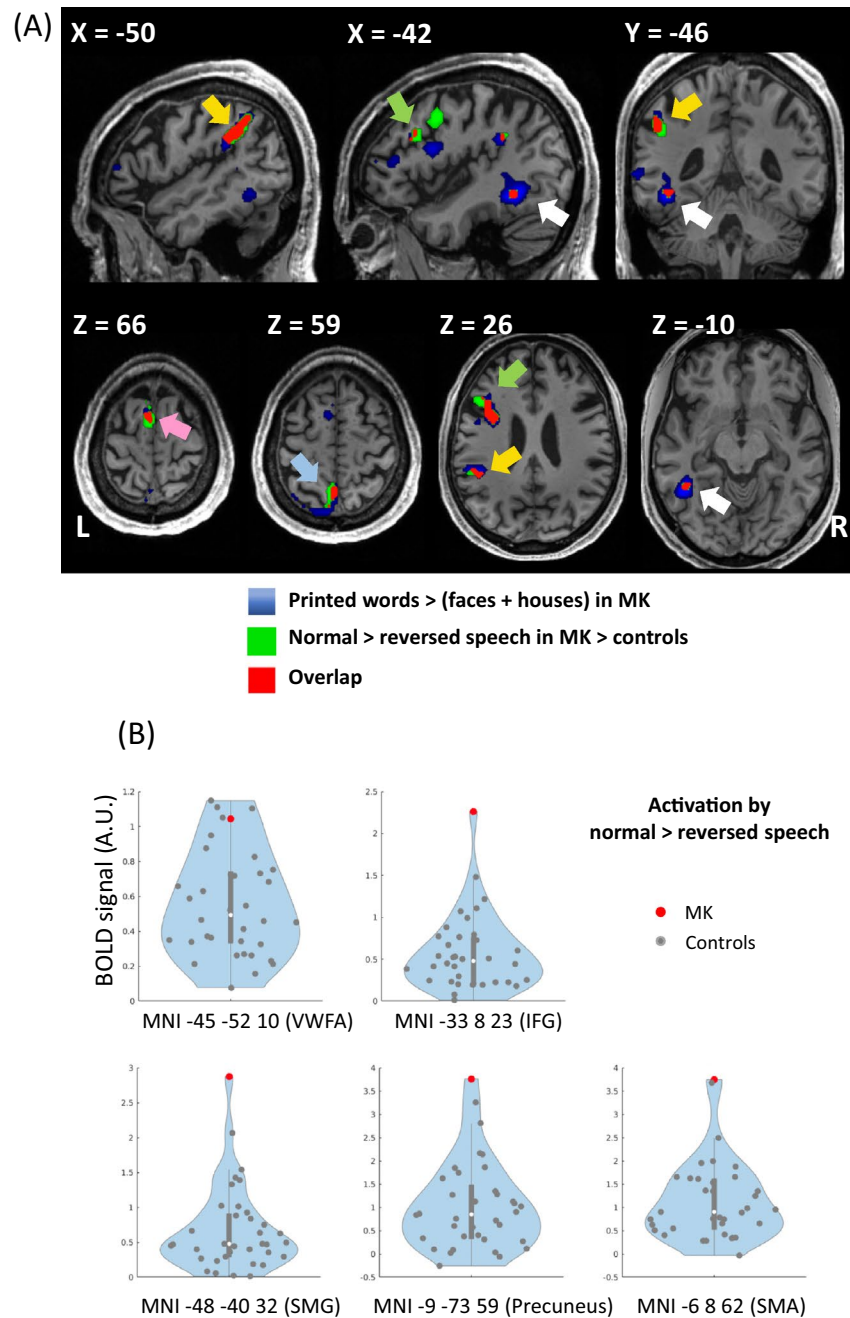


Figure 3. Experiments 1 and 2: Tickertape synesthesia (TTS) as inverted reading. **(A)** In MK, areas over-activated during TTS in Experiment 1 (green) and areas selectively activated by printed words in Experiment 2 (blue) showed perfect overlap (red), in the VWFA (white arrow), SMG (yellow arrow), IFG (green arrow), SMA (pink arrow) and precuneus (light blue arrow). **(B)** Plot of individual activation intensity for the contrast of normal > reversed speech (Experiment 1), in MK (red dots) and controls (grey dots), at the peaks of MK's word-selective activations as identified in Experiment 2. In the IFG, SMG, precuneus and SMA, MK exceeded all of the 35 controls. TTS tickertape synesthesia, VWFA visual word form area, IFG inferior frontal gyrus, SMG supra-marginal gyrus, SMA supplementary motor area.

effect of lexicality in MK. Controls showed stronger activation for pseudowords > words in bilateral superior temporal sulci and in bilateral inferior frontal gyri. MK did not differ from controls in either of those contrasts. Moreover, we compared activation by words and pseudowords in MK at the peak voxels of the 5 regions of the TTS network as identified in Experiment 1. MK had stronger activations for pseudowords > words in the precuneus ($p < 0.001$), and no difference in the other regions (all $P_s > 0.07$).

We then used an MVPA searchlight to decode activation by words vs. pseudowords. In MK, the bilateral left-predominant posterior middle temporal gyrus (MTG) and the VWFA (MNI - 48 - 46 - 19) distinguished words from pseudowords better than chance (Fig. 4). This pattern did not differ between MK and controls.

In summary, while univariate analyses showed no significant effect of lexicality in MK, MVPA showed effective decoding in the VWFA, and in posterior MTG areas. Neuropsychology and imaging studies have long involved the left posterior MTG in lexical processing^{36,38–41}, which makes it a sensible implementation of the lexical component of TTS. Having identified a set of candidate regions involved in all aspects of TTS, we are now in a position to investigate their functional interactions.

Dynamic causal modelling of ticker-tape synesthesia. The set of regions identified in Experiments 1–3 as associated to TTS generation belong to the usual cerebral reading network. This overlap was specifically demonstrated in Experiment 2 (Fig. 3A). In addition to a higher univariate activation level in those regions, we predicted that TTS should be associated with an atypical flow of information among them, featuring an increase in top-down influences. We assessed this prediction using DCM, a method whose aim is to estimate the functional coupling among brain regions, and the changes in this coupling that are associated with different experimental conditions. Alternative models of how observed time series were generated in the brain are compared using a Bayesian approach (see Methods)⁴².

We modeled the causal links among the core regions involved in TTS generation, based on the hypothesis that speech perception triggers interacting phonological and lexical processes, eventually generating a vivid orthographic image. This is equivalent to assuming, as proposed before, that TTS results from the top-down operation of a two-route reading system. We re-analyzed MK's data from Experiments 1 and 3 using dynamical causal modeling (DCM), in order to identify the best model among alternative candidates. We translated our specific hypotheses into a set of constraints on the space of candidate models.

Among the regions identified in Experiments 1–3, we selected as regions of interest the mid-STG, the SMG, the MTG, and the VWFA (see Methods). To define the space of possible models, we assumed (1) that the mid-STG is the input region for all auditory stimuli, and that it is unidirectionally connected to the SMG, the MTG, or both (3 possible configurations); (2) that the VWFA is the output region subtending orthographic representations, and that it receives unidirectional input from the SMG, the MTG, or both (3 possible configurations); (3) that the SMG and MTG are mutually connected. Combining the 3 input and the 3 output options resulted in 9 families of models (Supplementary Fig. S6)⁴³.

We then allowed some of the connections defining these families to be modulated by experimental factors. In Experiment 1, the connections from the mid-STG to the SMG and MTG could be modulated by the normal versus reversed speech factor. This is because this difference should only be relevant early in the flow of information, i.e. low-level acoustic stimuli should not propagate to high-level speech and language representations. In Experiment 3, all connections could be modulated by the real words vs pseudowords factor (Supplementary Fig. S6).

In summary, this resulted in 9 model families, including a total of 24 models for Experiment 1, and 256 models for Experiment 3.

For Experiment 1, the comparison of the 9 families selected a structure including all possible connections (posterior probability 0.86, Fig. 5A). The second-best family did not include the connection from the SMG to the VWFA (posterior probability 0.11). For Experiment 3 also, the model featuring all possible connections was the most accurate (posterior probability 0.99, Fig. 5B).

We then compared the models within the two winning families, in order to identify for each experiment the model with the most accurate pattern of modulation. In Experiment 1, the best model among 4 candidates had a posterior probability of 1. The connections from the STG to both the SMG and the MTG were significantly modulated, switching from strongly excitatory for normal speech to mildly inhibitory for reversed speech (Fig. 5A). Regarding non-modulated connections, on average across normal and reversed speech, the links from the MTG to the VWFA were excitatory, while reciprocal connections between the SMG and MTG and connection from SMG to the VWFA were slightly inhibitory.

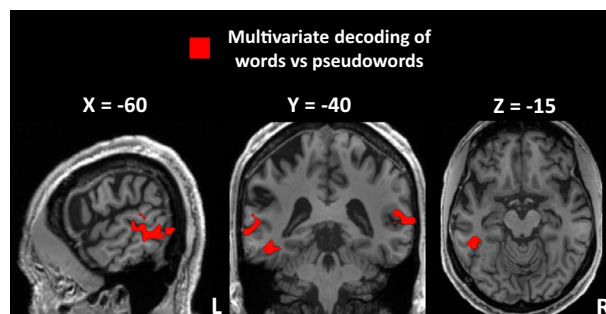


Figure 4. Experiment 3: Tickertape synesthesia (TTS) for words and pseudowords. MVPA discrimination between words and pseudowords in MK, showing effective decoding of lexical status in the left-predominant MTG and in the VWFA. MVPA multivariate-pattern analysis, MTG middle temporal gyrus, VWFA visual word form area.

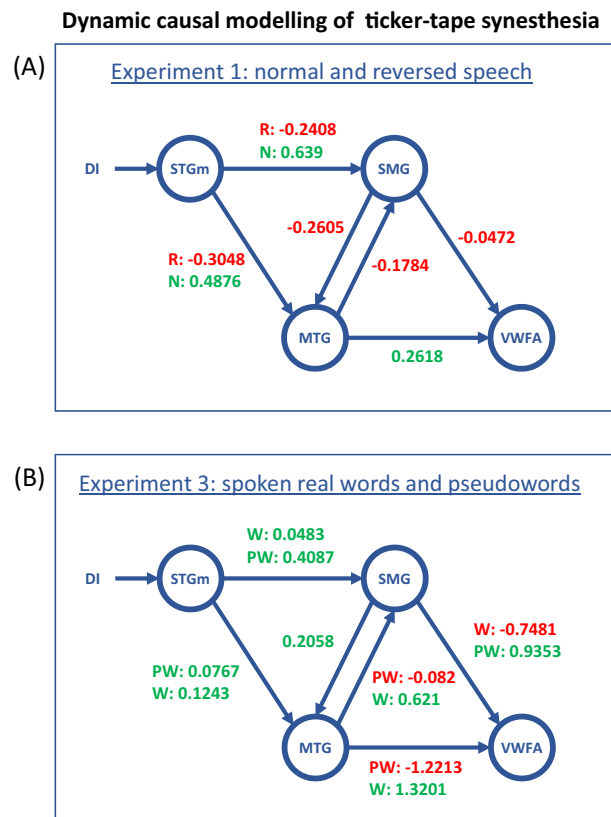


Figure 5. Dynamic causal modelling of ticker-tape synesthesia (TTS). Most likely models for MK's TTS-associated activations. The driving input (DI) corresponds to auditory stimulations entering the network through the STG. Blue arrows represent the intrinsic connections between the nodes. Values represent the strength of connections, which may be positive/excitatory (green) or negative/inhibitory (red). Two values are associated to connections significantly modulated by conditions, one value corresponding to each of the two experimental conditions. (A) In Experiment 1, normal speech (N) was driving the whole network down to the VWFA, while reversed speech (R) did not. (B) In Experiment 3, connections implementing the phonological route (STG-SMG and SMG-VWFA) were excitatory for pseudowords (PW) and inhibitory for real words (W). Conversely connections involved in the lexical route (MTG-VWFA and MTG-SMG) switched from inhibitory with pseudowords to excitatory with real words. *STG* superior temporal gyrus, *SMG* supra-marginal gyrus, *VWFA* visual word form area, *MTG* middle temporal gyrus.

In Experiment 3, the best model among 64 candidates had a posterior probability of 0.31 (Fig. 5B). Connections from the STG to both the SMG and MTG were excitatory for words and pseudowords. The connections implementing the phonological route, i.e. from the STG to the SMG and from the SMG to the VWFA, were both significantly modulated, both with an advantage for pseudowords over words. Particularly, the connection from the SMG to the VWFA switched from strongly excitatory for pseudowords to strongly inhibitory for words. Connections implementing the lexical route, i.e. from the STG to the MTG and from the MTG to both the VWFA and the SMG, were also modulated, all with an advantage for words over pseudowords. Particularly, the connection from the MTG to the VWFA switched from strongly excitatory for real words to strongly inhibitory for pseudowords. On average across words and pseudowords, the unmodulated connection (SMG to MTG) was excitatory (Fig. 5B). The second-best model had a posterior probability of 0.28. The modulations were the same as in the best model, minus the one from the STG to MTG. Modulations for words and pseudowords on other connections were similar. The third best model had a posterior probability of 0.20. It was also similar to the best one, with an additional modulation of the SMG-to-MTG connection. Connections of the phonological route, i.e. from STG to SMG and from SMG to MTG, still showed an advantage for pseudowords (excitatory) over words (inhibitory). Thus the second- and third-best models preserved the main features of the dual-route pattern of connection, supporting the stability of our findings.

Discussion

Summary of findings. The main outcome of Experiment 1, in which we presented normal and reversed speech, was that a set of areas were more active in MK than in controls during normal than reversed speech, that is whenever MK was subject to synesthesia. Supporting our first prediction, this “TTS network” included both frontoparietal areas involved in speech processing and the VWFA subtending orthography (Fig. 1).

In this experiment, one group of controls was not matched to MK in age, while the other group was scanned on a different device. It was therefore essential to determine whether the identification of the TTS network could not be confounded by differences in age or in scanning device. To this end, after delineating the TTS network by comparing MK versus all controls, we compared MK versus Group 1 and Group 2 separately. We observed a remarkable overlap between the outcome of both comparisons (Fig. S1), demonstrating that MK's activation peculiarities were uncontaminated by age or scanning device. Finally, we directly compared the two groups of controls, in order to determine whether potential differences would overlap with the TTS network. We only found minor differences, far remote from the TTS network, further confirming the robustness of our findings.

The differences which we found between the groups of controls were likely a correlate of aging (Fig. S2). Indeed, like in the present case, older age is associated with increased prefrontal activation in a variety of tasks, including language tasks⁴⁴, an increase that correlates with improved speech discrimination⁴⁵. Also like in the present case, older age is associated with weaker activation of auditory regions during speech perception^{46,47}.

In Experiment 2, we delineated MK's reading areas by comparing activation by written words minus other categories of visual items. The set of reading-specific areas turned out to be essentially identical to the TTS network from Experiment 1, thus backing our second prediction that TTS and reading should rely on the same pathways (Fig. 3). In Experiment 3, we refined our approach by presenting MK with spoken words and pseudowords. Both triggered TTS and activated the TTS network, although possibly with different underlying dynamics. This experiment allowed us to identify an MTG area involved in lexical reading, and presumably in the lexical component of TTS (Fig. 4). Finally, we developed a dynamic two-route model of information flow during TTS. In MK, we found that speech was driving the TTS network, while reversed speech, which does not trigger synesthesia, had an inhibitory effect (Fig. 5A). Moreover, functional connections implementing the phonological route were inhibitory when synesthesia was triggered by real words, while they were excitatory when synesthesia was triggered by pseudowords. The converse pattern prevailed for connections implementing the lexical route (Fig. 5B). This result fits our fourth prediction that, analogous to reading processes, top-down information should follow distinct paths depending on whether synesthesia was triggered by words or pseudowords.

We will first discuss the two major components of TTS generation: The VWFA and its role in orthographic imagery, and the perisylvian areas and their role in translating speech to orthography.

The VWFA and orthographic mental imagery. We hypothesized that the orthographic content of TTS is supported by the VWFA, because there is ample evidence from brain damage and imaging that the VWFA computes orthographic representations from visual input. Importantly, in the absence of written stimuli, the VWFA may also be activated from top-down by speech^{16–18}. We reasoned that such top-down effects may contribute to orthographic imagery, and that TTS may be seen as an exceptionally vivid and automatic form of such imagery, an ability possessed to some degree by all literate individuals^{8,48}. Supporting the role of the VWFA in orthographic imagery, at least some of the alexic patients with VWFA lesions lose this type of imagery^{49–52}. This fits with the present findings that the VWFA was involved in TTS: the VOT region which was over-activated during TTS, and the VWFA as defined by its preference for written words, were precisely identical.

In MK, TTS largely escaped voluntary control, while mental imagery is usually optional and effortful⁵³. However the degree of automaticity of orthographic imagery is variable across individuals, rather than distributed in an all-or-none manner between TTS and non-TTS individuals. Thus, Holm et al.⁸ asked participants from a general population to specify the extent of their control of word visualization. A small number of subjects qualified for TTS in the strictest sense, similar to MK, synesthesia being obligatory, and induced by other persons' speech, one's own speech, and when thinking verbally. Interestingly, a larger number of participants reported that word visualization was under some voluntary control, relevant to the issue of continuity between synesthesia and normal perception, a controversial issue in the field of synesthesia studies^{54,55}.

Considering the vividness and automaticity of mental imagery in MK, we may draw a parallel between TTS and the visual hallucinations that occur in schizophrenia, in Parkinson's disease and other neurological conditions, and in the Charles Bonnet syndrome. Although the mechanisms of such hallucinations are still elusive, they are often associated with overactivation of visual cortices, which show abnormal intrinsic and distant connectivity, supporting predominant top-down over bottom-up influences on visual experience^{56–60}.

From speech to orthography. *The superior temporal gyrus.* In the dynamical model of TTS, we treated the mid-STG cortex as a common auditory input region, because it was equally activated by both speech and reversed speech. Indeed the center of the STG region of interest (MNI – 48 – 16 5) belonged to the early auditory cortex, as defined architectonically, with a probability of 85% (areas TE 1.0 1.1 1.2)⁶¹. Further supporting the role of the mid-STG as the initial stage of TTS generation, DCM showed that it was significantly driving the SMG and MTG whenever MK was subject to synesthesia.

In MK, both externally perceived and inner-speech triggered synesthesia. This may result from the remarkable overlap of STG activation by external and by inner-speech^{62–64}, and also during auditory-verbal hallucinations in schizophrenia patients⁶⁵.

The supramarginal gyrus. Beyond the auditory entry point, the STG is a complex mosaic of modules computing various representations of speech and sounds^{33,66–68}. In continuity with the posterior STG, the SMG supports phonological representations at the interface with other modalities. This includes audio-motor mapping for speech production⁶⁹, phonological working memory^{70,71}, lip-reading and audiovisual language^{72–74}.

It is also critically involved in non-lexical reading, such that per-operative stimulation of the SMG disrupts selectively the reading of pseudowords but not of exception words^{75,76}. Similarly, transcranial stimulation of the SMG interferes with sound-oriented but not with meaning-oriented reading^{77,78}. Further supporting its role in

phoneme-grapheme correspondences, the SMG is more activated by pseudowords than real words, both during reading¹⁵ and during spelling⁷⁹. Graves and Binder⁸⁰ found that the left SMG showed a negative effect of bigram frequency, millimeters away from the current SMG peak, revealing sensitivity to the difficulty in binding phonemes and graphemes. Moreover Bouhali et al.⁸¹ found stronger functional connectivity of the SMG with the VWFA when reading aloud pseudowords than during lexical decision with words, that is whenever phonological demands were higher.

In MK, the role of the SMG in TTS may be to map perceived phonemes to illusory graphemes on the basis of statistical regularities, in interaction with the lexical route. One may putatively view the overactivation of the SMG in synesthesia as functionally symmetric to the hypoactivation observed repeatedly in developmental dyslexia, where phoneme-grapheme mapping is impaired^{5,82}.

The middle temporal gyrus. The posterior MTG is one of the most systematically activated regions during lexico-semantic tasks³⁸, and electrical stimulations cause transcortical sensory aphasia, that is an impairment of language comprehension with preserved phonological processing³⁹, in agreement with the consequences of focal lesions⁴¹. This region may be seen as a “convergence hub” for binding spread-out pieces of lexical knowledge⁸³, or similarly as a “semantic control” region^{40,84,85}.

During reading, the posterior MTG is also consistently activated when contrasting words minus pseudowords^{15,86}, supporting its involvement in the lexical reading route⁸⁷. However, lexicality interacts with task, such that MTG activation is mostly present during tasks with strong lexical demands, typically lexical decision relative to reading aloud⁸⁶. This may explain why in Experiment 3, where participants only had to detect an odd-ball meaningless signal, we found no univariate effect of lexicality. In the MTG, MVPA proved more sensitive for discriminating words from pseudowords, similar to previous findings^{88–90}.

This background made the MTG, as identified in MK during synesthesia, a sensible implementation of lexical processing within a simple model of TTS.

After discussing the putative roles of the VWFA and perisylvian areas in TTS, we now turn to the dynamic model of their interactions which we explored using DCM.

A simple dynamic model of TTS. Constraints on the model. When designing the DCM model of synesthesia, we selected a set of 4 areas of interest, admittedly a simplistic network, leaving aside the IFG, SMA and precuneus, although they were also over-activated in MK. This allowed us to restrict the space of possible models on the basis of strong a priori motivations, a methodological requirement of DCM⁹¹. The STG, SMG, MTG, and VWFA are essential components of auditory, phonological, lexical, and orthographic processing, respectively, and were all defined on the basis of their functional features during TTS. The 4 selected regions thus provided a sensible sampling of the lexical and phonological routes.

We reasoned that the IFG and SMA probably played no critical role in the generation of TTS. While the IFG is often activated by reading words and pseudowords^{81,92}, it is thought to control spoken phonological output, and should not contribute to the purely audio-visual phenomenon of TTS¹⁵. The SMA is also commonly activated during reading, and its primary language-related role is thought to be the control of speech output^{93,94}. Finally, the precuneus is a top-level hub in the hierarchy of brain areas, it intervenes in a variety of cognitive control processes, and its putative role in TTS is difficult to pinpoint from the current data^{95,96}. Still in a recent meta-analysis, Spagna et al.⁹⁷ proposed that activation of both the SMA and precuneus are associated with mental imagery, and their putative role in TTS may deserve further study.

In defining the space of possible models, we posited that the SMG and MTG, as implementing the phonological and lexical routes, should always have the possibility of influencing each other. There is a host of behavioral evidence of close interactions between the two routes. Thus, illustrating the automatic impact of phonology on lexical reading, during visual lexical decision, words are automatically parsed into phonologically defined syllables⁹⁸. In the same task, response to word targets is facilitated by pseudoword homophone primes (mayd MADE), as compared to control primes (mard MADE), revealing the computation of phonological codes and their impact on word reading⁹⁹. Conversely, showing the influence of lexical knowledge on phonological reading, pseudowords are pronounced faster when they are orthographically similar to a large number of real words¹⁰⁰. A point of interest in the context of TTS as “inverted reading”, not only the reading but also the spelling of pseudowords is also influenced by the existence and frequency of real word neighbors¹⁰¹.

At the brain level, close interactions between the SMG and posterior MTG are supported by their strong anatomical connections^{102–104} and their functional connectivity at rest^{104,105}.

Architecture and modulations of the TTS network. In Experiment 1, normal speech had a strong excitatory driving influence on the circuit, while reversed speech had a minor inhibitory effect. Moreover, in the most likely model family, words propagated from the STG to both the MTG and SMG, while only the latter further relayed information to the VWFA. In other terms, until they are assigned an orthographic form by the VWFA, perceived words mostly follow the lexical route through the MTG. The specific contribution of the MTG here may be to allow access to stored orthographic knowledge, possibly by performing semantic disambiguation of auditory words^{40,83–85}. Finally, the phonological route (SMG) only had a small inhibitory effect on the lexical route (MTG), suggesting that it did not play an important role in generating TTS for normal speech.

This interpretation is aligned with the DCM results of Experiment 3 which, in contrast to Experiment 1, included both normal speech (real words) and pseudowords. The most likely network included the same connections as in Experiment 1. When first neglecting inhibitory effects, Experiment 3 essentially recapitulates Experiment 1, in that real words reach the VWFA through the lexical route, i.e. through the MTG. In contrast, pseudowords drive the VWFA through the phonological route, i.e. through the SMG. The pattern of inhibitory

effects further suggests that the lexical route (MTG to VWFA) acts to lessen VWFA responses to pseudowords, whereas the phonological route (SMG to VWA) dampens VWFA responses to real words. This indicates that the two routes are somehow competing for access to the VWFA, eventually facilitating accurate orthographic coding of both words and pseudowords. Overall, these results support our fourth hypothesis that top-down influences should follow distinct lexical vs phonological paths depending on whether synesthesia is triggered by words or pseudowords.

In Experiment 3, we found only a weak excitatory effect of real words from the STG to the SMG, while in Experiment 1 the excitatory effect of normal speech was strong. As real words consist in normal speech, we may have expected a strong positive effect of words in Experiment 3 also. Leaving aside DCM reproducibility issues, this discrepancy may result from differences in task requirements: In Experiment 1, participants payed attention to a meaningful narration while in Experiment 3, they were encouraged to process words at a low level. Words lists carried no sentential meaning, and the target “tatata” could be best detected by paying attention to phonology. This may explain why words had a stronger influence in Experiment 1 than 3. Direct comparisons of words, pseudowords and low-level sounds with a constant task could clarify this issue.

Schematically, we construed TTS as an idiosyncratic operation of the reading system. We will now briefly discuss the alternative view of TTS as inner spelling.

TTS as inner spelling. We proposed that TTS resulted from intense top-down activation of the reading network, initially because MK reported a subjective experience of inner reading, with no active spelling-related feeling. Alternatively however, TTS could have been construed as an extreme form of inner spelling. In some sense MK was automatically “writing out in his head” the speech he was perceiving. Actually those two points of view are largely equivalent, as writing and spelling share core cognitive components and neural substrates^{106,107}. There is thus a shared set of perisylvian regions whose lesion yields both reading and spelling deficits¹⁰⁸.

Focusing on regions which are presumably involved in MK’s synesthesia, the left IFG and the VWFA are activated by both reading and spelling, show cross-task adaptation suggestive of shared orthographic representations^{106,109,110}, and are both sensitive to word frequency during spelling and reading^{80,107}. The left SMG, posterior MTG, precuneus and SMA are also activated during both reading and spelling^{79,107}. Moreover, the SMG plays a predominantly phonological role during spelling, as it does during reading and in TTS⁷⁹. Thus, TTS may reflect atypical functioning, during speech perception, of the single network which links sounds and letters during both reading and writing.

Ticker tape synesthesia and brain connectivity. Beyond TTS, atypical anatomical or functional connectivity is at the core of most theories of synesthesias⁹. Within this broad framework, theories differ along multiple dimensions: is there an increase in anatomical or in functional connections, are those disinhibited or structurally stronger²¹, do they link the inducer and concurrent regions directly or through higher-level cortices^{111,112}, do the same principles apply to all forms of synesthesias, etc.? For instance, in grapheme-color synesthesia, the most studied type of synesthesia, increased fractional anisotropy was detected in the fusiform and other regions¹¹³. Furthermore, differences in functional connectivity were found between synesthetes and controls¹¹⁴, and between subtypes of grapheme-color synesthetes¹¹². However the reproducibility of those findings across studies appears questionable¹¹⁵. Our DCM analysis clarifies the pattern of functional connectivity involved in TTS, but is not in a position to adjudicate between general theories of synesthesia.

Of particular interest is the idea that synesthesia “magnifies connections present in early life that are pruned and/or inhibited during development and that persist in muted form in all adults”²⁰. In this hypothesis, TTS would reflect the persistence of a transient state of stronger connection which would normally vanish after literacy acquisition. Indeed, in a longitudinal study of reading acquisition, Dehaene-Lambertz et al.² observed an increase in word-specific activation in parietal (MNI – 44 – 42 46) and frontal (MNI – 48 6 24) areas during the first year of alphabetization, only millimeters away from MK’s SMG and IFG overactivation peaks. These two regions later show a decrease in activation, and are thought to play a transient role in reading acquisition, specifically in binding phonemes and graphemes. One may thus speculate that long-term survival of a normally transient role of the SMG and IFG, contributes to the genesis of TTS.

Furthermore, it is also possible that TTS involves the persistence of processes linked to spelling rather than reading acquisition. Indeed effective mental imagery in children does not predict better reading acquisition, while it predicts spelling acquisition¹¹⁶. During spelling, it is necessary to generate and maintain an orthographic representation of the current word while serially writing or typing the component letters¹¹⁷. This orthographic working memory, or “graphemic buffer”, may involve strings of abstract letters, but also visual images of the current string, providing a target pattern and allowing for feedback control during the writing process. Visual control plays a limited role in expert writers¹¹⁸, but it is critical during handwriting learning¹¹⁹. Thus TTS might be construed as the persistence of an hyperactive graphemic buffer and its associated visual images. Indeed the maximum overlap of lesions yielding graphemic buffer impairments is millimeters away from MK’s SMG overactivation¹²⁰, while the VWFA would support mental images per se as discussed before.

As a final topic for speculation related to the developmental origins of TTS, one may mention the intriguing case of a man in whom TTS was associated with two other developmental conditions, chronic psychosis and an arachnoid cyst¹²¹.

Conclusion

Among the many kinds of synesthesia, as many as 88% involve language either as the “inducer” as in grapheme-color synesthesia, or as the “concurrent” as in perfect pitch^{122,123}. TTS stands out as the single form of synesthesia in which both the inducer and the concurrent are language representations. Specifically, TTS involves the same

orthographic and phonological representations which support reading and spelling. One may thus speculate that TTS results from an atypical developmental trajectory with enduring hyperconnectivity between speech and vision, a situation in some sense symmetrical to developmental dyslexia, in which defective connectivity was repeatedly observed^{124–126}.

At this stage, the present study being restricted to a single case, and in the absence of any previous data on the cerebral mechanisms of TTS, all general inferences should be cautious. Francis Galton⁷ noted that “the experiences differ in detail as to size and kind of type, colour of paper, and so forth, but are always the same in the same person”, pointing to the issue of individual variability. Beyond the perceptual features of TTS mentioned by Galton, synesthetes also differ in the level of control that they exert on TTS, and in the stimuli (external speech, inner speech, etc.) that trigger the phenomenon⁸. We predict that all cases of TTS should conform to the general pattern of “upended reading”, but expect that the exact pattern of visual activation, and the involvement of attention and control systems should vary substantially.

Further study of TTS may therefore shed light on the mechanisms of reading acquisition, their variability and their disorders. Among others, future studies should address resting-state and anatomical connectivity in TTS individuals, potential behavioral differences in oral and written language processing between TTS individuals and controls, associations with other synesthesias, variants and dissociations within TTS, and TTS-like phenomena in typical and dyslexic children learning to read.

Data availability

Data are available at <https://zenodo.org/record/6900980>.

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References

- Dehaene, S., Cohen, L., Morais, J. & Kolinsky, R. Illiterate to literate: Behavioural and cerebral changes induced by reading acquisition. *Nat. Rev. Neurosci.* **16**, 234–244 (2015).
- Dehaene-Lambertz, G., Monzalvo, K. & Dehaene, S. The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLOS Biol.* **16**, e2004103 (2018).
- López-Barroso, D. *et al.* Impact of literacy on the functional connectivity of vision and language related networks. *Neuroimage* **213**, 116722 (2020).
- de Thiebaut, S. M., Cohen, L., Amemiya, E., Braga, L. W. & Dehaene, S. Learning to read improves the structure of the arcuate fasciculus. *Cereb. Cortex* **24**, 989–995 (2014).
- D’Mello, A. M. & Gabrieli, J. D. E. Cognitive neuroscience of dyslexia. *Lang. Speech Hear. Serv. Sch.* **49**, 798–809 (2018).
- Friedmann, N., Coltheart, M. Types of developmental dyslexia. *Handb. Commun. Disord. Theor. Empir. Appl. Linguist. Perspect.* 1–37 (2016).
- Galton, F. *Inquiries into Human Faculty and its Development* (Macmillan, 1883).
- Holm, S., Eilertsen, T. & Price, M. C. How uncommon is tickertaping? Prevalence and characteristics of seeing the words you hear. *Cogn. Neurosci.* **6**, 89–99 (2015).
- Ward, J. & Simner, J. Synesthesia. In *Multisensory Perception* 283–300 (Elsevier, 2020). <https://doi.org/10.1016/B978-0-12-812492-5.00013-9>.
- Simner, J. & Bain, A. E. A longitudinal study of grapheme-color synesthesia in childhood: 6/7 years to 10/11 years. *Front. Hum. Neurosci.* **7**, 603 (2013).
- Cohen, L. *et al.* The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain* **123**, 291–307 (2000).
- Dejerine, J. Contribution à l’étude anatomo-pathologique et clinique des différentes variétés de cécité verbale. *Mém. Soc. Biol.* **4**, 61–90 (1892).
- Coltheart, M. Modeling reading: The dual-route approach. In *The Science of Reading: A Handbook* (eds Snowling, M. J. & Hulme, C.) 6–23 (Blackwell Publishing, 2012).
- Perry, C., Ziegler, J. C. & Zorzi, M. Nested incremental modeling in the development of computational theories: The CDP+ model of reading aloud. *Psychol. Rev.* **114**, 273–315 (2007).
- Taylor, J. S., Rastle, K. & Davis, M. H. Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. *Psychol. Bull.* **139**, 766–791 (2013).
- Cohen, L., Salondy, P., Pallier, C. & Dehaene, S. How does inattention affect written and spoken language processing? *Cortex* <https://doi.org/10.1016/j.cortex.2021.02.007> (2021).
- Ludersdorfer, P. *et al.* Left ventral occipitotemporal activation during orthographic and semantic processing of auditory words. *Neuroimage* **124**, 834–842 (2016).
- Yoncheva, Y. N., Zevin, J. D., Maurer, U. & McCandliss, B. D. Auditory selective attention to speech modulates activity in the visual word form area. *Cereb. Cortex* **20**, 622–632 (2010).
- Sharoh, D. *et al.* Laminar specific fMRI reveals directed interactions in distributed networks during language processing. *Proc. Natl. Acad. Sci.* **116**, 21185–21190 (2019).
- Spector, F. & Maurer, D. Synesthesia: A new approach to understanding the development of perception. *Dev. Psychol.* **45**, 175–189 (2009).
- Grossenbacher, P. G. & Lovelace, C. T. Mechanisms of synesthesia: Cognitive and physiological constraints. *Trends Cogn. Sci.* **5**, 36–41 (2001).
- Tilot, A. K. *et al.* Rare variants in axonogenesis genes connect three families with sound–color synesthesia. *Proc. Natl. Acad. Sci.* **115**, 3168–3173 (2018).
- Oldfield, R. C. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* **9**, 97–113 (1971).
- Posse, S. Multi-echo acquisition. *Neuroimage* **62**, 665–671 (2012).
- Dehaene, S. *et al.* How learning to read changes the cortical networks for vision and language. *Science* **330**, 1359–1364 (2010).
- Rolls, E. T., Huang, C.-C., Lin, C.-P., Feng, J. & Joliot, M. Automated anatomical labelling atlas 3. *Neuroimage* **206**, 116189 (2020).
- Hebart, M. N., Gørgen, K. & Haynes, J.-D. The decoding toolbox (TDT): A versatile software package for multivariate analyses of functional imaging data. *Front. Neuroinformatics* <https://doi.org/10.3389/fninf.2014.00088> (2015).
- Deen, B. *et al.* Organization of high-level visual cortex in human infants. *Nat. Commun.* **8**, 13995 (2017).
- Malach, R., Levy, I. & Hasson, U. The topography of high-order human object areas. *Trends Cogn. Sci.* **6**, 176–184 (2002).

30. Monzalvo, K., Fluss, J., Billard, C., Dehaene, S. & Dehaene-Lambertz, G. Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. *Neuroimage* **61**, 258–274 (2012).
31. Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F. & Baker, C. I. Circular analysis in systems neuroscience: the dangers of double dipping. *Nat. Neurosci.* **12**, 535 (2009).
32. Binder, J. R. Current controversies on Wernicke's area and its role in language. *Curr. Neurol. Neurosci. Rep.* **17**, 58 (2017).
33. DeWitt, I. & Rauschecker, J. P. Phoneme and word recognition in the auditory ventral stream. *Proc. Natl. Acad. Sci.* **109**, E505–E514 (2012).
34. Hickok, G. & Poeppel, D. Chapter 25 - Neural basis of speech perception. In *Neurobiology of Language* (eds Hickok, G. & Small, S. L.) 299–310 (Academic Press, 2016). <https://doi.org/10.1016/B978-0-12-407794-2.00025-0>.
35. Martin, A., Kronbichler, M. & Richlan, F. Dyslexic brain activation abnormalities in deep and shallow orthographies: A meta-analysis of 28 functional neuroimaging studies. *Hum. Brain Mapp.* **37**, 2676–2699. <https://doi.org/10.1002/hbm.23202> (2016).
36. Pillay, S. B., Stengel, B. C., Humphries, C., Book, D. S. & Binder, J. R. Cerebral localization of impaired phonological retrieval during rhyme judgment: Phonological retrieval. *Ann. Neurol.* **76**, 738–746 (2014).
37. Savill, N. J., Cornelissen, P., Pahor, A. & Jefferies, E. rTMS evidence for a dissociation in short-term memory for spoken words and nonwords. *Cortex* **112**, 5–22 (2019).
38. Binder, J. R., Desai, R. H., Graves, W. W. & Conant, L. L. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* **19**, 2767–2796 (2009).
39. Boatman, D. Transcortical sensory aphasia: Revisited and revised. *Brain* **123**, 1634–1642 (2000).
40. Davey, J. *et al.* Exploring the role of the posterior middle temporal gyrus in semantic cognition: Integration of anterior temporal lobe with executive processes. *Neuroimage* **137**, 165–177 (2016).
41. Hart, J. & Gordon, B. Delineation of single-word semantic comprehension deficits in aphasia, with anatomical correlation. *Ann. Neurol.* **27**, 226–231 (1990).
42. Friston, K. J., Harrison, L. & Penny, W. Dynamic causal modelling. *Neuroimage* **19**, 1273–1302 (2003).
43. Penny, W. D. *et al.* Comparing families of dynamic causal models. *PLOS Comput. Biol.* **6**, e1000709 (2010).
44. Davis, S. W., Zhuang, J., Wright, P. & Tyler, L. K. Age-related sensitivity to task-related modulation of language-processing networks. *Neuropsychologia* **63**, 107–115 (2014).
45. Du, Y., Buchsbaum, B. R., Grady, C. L. & Alain, C. Increased activity in frontal motor cortex compensates impaired speech perception in older adults. *Nat. Commun.* **7**, 12241 (2016).
46. Cardin, V. Effects of aging and adult-onset hearing loss on cortical auditory regions. *Front. Neurosci.* **10**, 199 (2016).
47. Tremblay, P., Dick, A. S. & Small, S. L. Functional and structural aging of the speech sensorimotor neural system: Functional magnetic resonance imaging evidence. *Neurobiol. Aging* **34**, 1935–1951 (2013).
48. Boursolone, C. *et al.* Presentation of an assessment battery for visual mental imagery and visual perception. *Rev. Neurol. (Paris)* **165**, 1045–1054 (2009).
49. Bartolomeo, P., Bachoud-Levi, A. C., Chokron, S. & Degos, J. D. Visually- and motor-based knowledge of letters: evidence from a pure alexic patient. *Neuropsychologia* **40**, 1363–1371 (2002).
50. Rosazza, C., Appollonio, I., Isella, V. & Shallice, T. Qualitatively different forms of pure alexia. *Cogn. Neuropsychol.* **24**, 393–418 (2007).
51. Sirigu, A. & Duhamel, J. R. Motor and visual imagery as two complementary but neurally dissociable mental processes. *J. Cogn. Neurosci.* **13**, 910–919 (2001).
52. Volpato, C., Bencini, G., Meneghello, F., Piron, L. & Semenza, C. Covert reading of letters in a case of global alexia. *Brain Lang.* **120**, 217–225 (2012).
53. Mazard, A. *et al.* Impact of fMRI acoustic noise on the functional anatomy of visual mental imagery. *J. Cogn. Neurosci.* **14**, 172–186 (2002).
54. Deroy, O. & Spence, C. Lessons of synaesthesia for consciousness: Learning from the exception, rather than the general. *Neuropsychologia* **88**, 49–57 (2016).
55. Martino, G. & Marks, L. E. Synesthesia: Strong and weak. *Curr. Dir. Psychol. Sci.* **10**, 61–65 (2001).
56. Amad, A. *et al.* The multimodal connectivity of the hippocampal complex in auditory and visual hallucinations. *Mol. Psychiatry* **19**, 184–191 (2014).
57. Dujardin, K. *et al.* What can we learn from fMRI capture of visual hallucinations in Parkinson's disease?. *Brain Imaging Behav.* **14**, 329–335 (2020).
58. ffytche, D. H. *et al.* The anatomy of conscious vision: An fMRI study of visual hallucinations. *Nat. Neurosci.* **1**, 738–742 (1998).
59. Hahamy, A., Wilf, M., Rosin, B., Behrmann, M. & Malach, R. How do the blind 'see'? The role of spontaneous brain activity in self-generated perception. *Brain* **144**, 340–353 (2021).
60. Waters, F. *et al.* Visual hallucinations in the psychosis spectrum and comparative information from neurodegenerative disorders and eye disease. *Schizophr. Bull.* **40**, S233–S245 (2014).
61. Morosan, P. *et al.* Human primary auditory cortex: cytoarchitectonic subdivisions and mapping into a spatial reference system. *Neuroimage* **13**, 684–701 (2001).
62. Alderson-Day, B. *et al.* The brain's conversation with itself: neural substrates of dialogic inner speech. *Soc. Cogn. Affect. Neurosci.* **11**, 110–120 (2016).
63. Alderson-Day, B. & Fernyhough, C. Inner speech: Development, cognitive functions, phenomenology, and neurobiology. *Psychol. Bull.* **141**, 931 (2015).
64. Shergill, S. S. *et al.* Modulation of activity in temporal cortex during generation of inner speech. *Hum. Brain Mapp.* **16**, 219–227 (2002).
65. Jardri, R., Pouchet, A., Pins, D. & Thomas, P. Cortical activations during auditory verbal hallucinations in schizophrenia: A coordinate-based meta-analysis. *Am. J. Psychiatry* **168**, 73–81 (2011).
66. Binder, J. R. The Wernicke area: Modern evidence and a reinterpretation. *Neurology* **85**, 2170–2175 (2015).
67. Scott, S. K. From speech and talkers to the social world: The neural processing of human spoken language. *Science* **366**, 58–62 (2019).
68. Yi, H. G., Leonard, M. K. & Chang, E. F. The encoding of speech sounds in the superior temporal gyrus. *Neuron* **102**, 1096–1110 (2019).
69. Hickok, G. & Poeppel, D. Neural basis of speech perception. In *Handbook of Clinical Neurology* Vol. 129 149–160 (Elsevier, 2015).
70. Buchsbaum, B. R., Olsen, R. K., Koch, P. & Berman, K. F. Human dorsal and ventral auditory streams subserve rehearsal-based and echoic processes during verbal working memory. *Neuron* **48**, 687–697 (2005).
71. Buchsbaum, B. R. & D'Esposito, M. The search for the phonological store: From loop to convolution. *J. Cogn. Neurosci.* **20**, 762–778 (2008).
72. Dick, A. S., Solodkin, A. & Small, S. L. Neural development of networks for audiovisual speech comprehension. *Brain Lang.* **114**, 101–114 (2010).
73. Hocking, J. & Price, C. J. The role of the posterior superior temporal sulcus in audiovisual processing. *Cereb. Cortex* **18**, 2439–2449 (2008).

74. Wright, T. M. Polysensory interactions along lateral temporal regions evoked by audiovisual speech. *Cereb. Cortex* **13**, 1034–1043 (2003).
75. Roux, F.-E. *et al.* Segregation of lexical and sub-lexical reading processes in the left perisylvian cortex. *PLoS ONE* **7**, e50665 (2012).
76. Simos, P. G. *et al.* Brain mechanisms for reading: The role of the superior temporal gyrus in word and pseudoword naming. *NeuroReport* **11**, 2443–2447 (2000).
77. Pattamadilok, C., Knierim, I. N., Kawabata Duncan, K. J. & Devlin, J. T. How does learning to read affect speech perception?. *J. Neurosci.* **30**, 8435–8444 (2010).
78. Sliwinska, M. W., James, A. & Devlin, J. T. Inferior parietal lobule contributions to visual word recognition. *J. Cogn. Neurosci.* **27**, 593–604 (2015).
79. DeMarco, A. T., Wilson, S. M., Rising, K., Rapcsak, S. Z. & Beeson, P. M. Neural substrates of sublexical processing for spelling. *Brain Lang.* **164**, 118–128 (2017).
80. Graves, W. W., Desai, R., Humphries, C., Seidenberg, M. S. & Binder, J. R. Neural systems for reading aloud: A multiparametric approach. *Cereb. Cortex* **20**, 1799–1815 (2010).
81. Bouhali, F., Bezagu, Z., Dehaene, S. & Cohen, L. A mesial-to-lateral dissociation for orthographic processing in the visual cortex. *Proc. Natl. Acad. Sci.* **116**, 21936–21946 (2019).
82. Kronbichler, M. *et al.* Evidence for a dysfunction of left posterior reading areas in German dyslexic readers. *Neuropsychologia* **44**, 1822–1832 (2006).
83. Patterson, K., Nestor, P. J. & Rogers, T. T. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* **8**, 976–987 (2007).
84. Davey, J. *et al.* Automatic and controlled semantic retrieval: TMS reveals distinct contributions of posterior middle temporal gyrus and angular gyrus. *J. Neurosci.* **35**, 15230–15239 (2015).
85. Jedidi, Z. *et al.* Incidental verbal semantic processing recruits the fronto-temporal semantic control network. *Cereb. Cortex* <https://doi.org/10.1093/cercor/bhab169> (2021).
86. McNorgan, C., Chabal, S., O’Young, D., Lukic, S. & Booth, J. R. Task dependent lexicality effects support interactive models of reading: A meta-analytic neuroimaging review. *Neuropsychologia* **67**, 148–158 (2015).
87. Binder, J. R. *et al.* Neural correlates of lexical access during visual word recognition. *J. Cogn. Neurosci.* **15**, 372–393 (2003).
88. Baeck, A., Kravitz, D., Baker, C. & de Op, B. H. P. Influence of lexical status and orthographic similarity on the multi-voxel response of the visual word form area. *Neuroimage* **111**, 321–328 (2015).
89. Fedorenko, E., Nieto-Castañon, A. & Kanwisher, N. Lexical and syntactic representations in the brain: An fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia* **50**, 499–513 (2012).
90. Mattheiss, S. R., Levinson, H. & Graves, W. W. Duality of function: Activation for meaningless nonwords and semantic codes in the same brain areas. *Cereb. Cortex* **28**, 2516–2524 (2018).
91. Stephan, K. E. *et al.* Ten simple rules for dynamic causal modeling. *Neuroimage* **49**, 3099–3109 (2010).
92. Heim, S. *et al.* The role of the left Brodmann’s areas 44 and 45 in reading words and pseudowords. *Cogn. Brain Res.* **25**, 982–993 (2005).
93. Alario, F.-X., Chainay, H., Lehericy, S. & Cohen, L. The role of the supplementary motor area (SMA) in word production. *Cogn. Brain Res.* **1076**, 129–143 (2006).
94. Hertrich, I., Dietrich, S. & Ackermann, H. The role of the supplementary motor area for speech and language processing. *Neurosci. Biobehav. Rev.* **68**, 602–610 (2016).
95. Cavanna, A. E. & Trimble, M. R. The precuneus: A review of its functional anatomy and behavioural correlates. *Brain* **129**, 564–583 (2006).
96. van den Heuvel, M. P. & Sporns, O. Network hubs in the human brain. *Trends Cogn. Sci.* **17**, 683–696 (2013).
97. Spagna, A., Hajhajate, D., Liu, J. & Bartolomeo, P. Visual mental imagery engages the left fusiform gyrus, but not the early visual cortex: A meta-analysis of neuroimaging evidence. *Neurosci. Biobehav. Rev.* **122**, 201–217 (2021).
98. Conrad, M., Grainger, J. & Jacobs, A. M. Phonology as the source of syllable frequency effects in visual word recognition: Evidence from French. *Mem. Cognit.* **35**, 974–983 (2007).
99. Grainger, J. & Holcomb, P. J. Neural constraints on a functional architecture for word recognition. In *The Neural Basis of Reading* (ed. Cornelissen, P.) (Oxford University Press, 2008).
100. Peereman, R. & Content, A. Neighborhood size effect in naming: Lexical activation or sublexical correspondences?. *J. Exp. Psychol. Learn. Mem. Cogn.* **21**, 409 (1995).
101. Tainturier, M.-J. Lexical neighborhood effects in pseudoword spelling. *Front. Psychol.* **4**, 862 (2013).
102. Caspers, S. *et al.* Probabilistic fibre tract analysis of cytoarchitectonically defined human inferior parietal lobule areas reveals similarities to macaques. *NeuroImage* **58**, 362–380. <https://doi.org/10.1016/j.neuroimage.2011.06.027> (2011).
103. Jung, J., Cloutman, L. L., Binney, R. J. & Ralph, M. A. L. The structural connectivity of higher order association cortices reflects human functional brain networks. *Cortex* **97**, 221–239 (2017).
104. Xu, J. *et al.* Tractography-based parcellation of the human middle temporal gyrus. *Sci. Rep.* **5**, 18883 (2016).
105. Turken, A. U. & Dronkers, N. F. The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front. Syst. Neurosci.* **5**, 1 (2011).
106. Purcell, J. J., Jiang, X. & Eden, G. F. Shared orthographic neuronal representations for spelling and reading. *Neuroimage* **147**, 554–567 (2017).
107. Rapp, B. & Dufor, O. The neurotopography of written word production: An fMRI investigation of the distribution of sensitivity to length and frequency. *J. Cogn. Neurosci.* **23**, 4067–4081 (2011).
108. Philipose, L. E. *et al.* Neural regions essential for reading and spelling of words and pseudowords. *Ann. Neurol.* **62**, 481–492 (2007).
109. Ellenblum, G., Purcell, J. J., Song, X. & Rapp, B. High-level integrative networks: A resting-state fMRI investigation of reading and spelling. *J. Cogn. Neurosci.* **31**, 961–977 (2019).
110. Purcell, J. J., Napoliello, E. M. & Eden, G. F. A combined fMRI study of typed spelling and reading. *Neuroimage* **55**, 750–762 (2011).
111. Hubbard, E. M., Brang, D. & Ramachandran, V. S. The cross-activation theory at 10. *J. Neuropsychol.* **5**, 152–177 (2011).
112. van Leeuwen, T. M., den Ouden, H. E. M. & Hagoort, P. Effective connectivity determines the nature of subjective experience in grapheme-color synesthesia. *J. Neurosci.* **31**, 9879–9884 (2011).
113. Rouw, R. & Scholte, H. S. Increased structural connectivity in grapheme-color synesthesia. *Nat. Neurosci.* **10**, 792–797 (2007).
114. Sinke, C. *et al.* Inside a synesthete’s head: A functional connectivity analysis with grapheme-color synesthetes. *Neuropsychologia* **50**, 3363–3369 (2012).
115. Hupé, J.-M. & Dojat, M. A critical review of the neuroimaging literature on synesthesia. *Front. Hum. Neurosci.* **9**, 103 (2015).
116. Guarnera, M., Pellerone, M., Commodari, E., Valenti, G. D. & Buccheri, S. L. Mental images and school learning: A longitudinal study on children. *Front. Psychol.* **10**, 2034 (2019).
117. Buchwald, A. & Rapp, B. Rethinking the graphemic buffer?. *Brain Lang.* **91**, 100–101 (2004).
118. Danna, J. & Velay, J.-L. Basic and supplementary sensory feedback in handwriting. *Front. Psychol.* **6**, 169 (2015).

119. Meulenbroek, R. G. & Van Galen, G. P. The acquisition of skilled handwriting: Discontinuous trends in kinematic variables. In *Advances in Psychology* Vol. 55 273–281 (Elsevier, 1988).
120. Rapp, B., Purcell, J., Hillis, A. E., Capasso, R. & Miceli, G. Neural bases of orthographic long-term memory and working memory in dysgraphia. *Brain* **139**, 588–604 (2016).
121. Bastiampillai, T., Dhillon, R. & Chui, C. W. ‘I saw the words right from your mouth’: An unusual case of synaesthesia. *Aust. N. Z. J. Psychiatry* **48**, 199–200 (2014).
122. Simner, J. Beyond perception: Synaesthesia as a psycholinguistic phenomenon. *Trends Cogn. Sci.* **11**, 23–29 (2007).
123. Simner, J. *et al.* Synaesthesia: The prevalence of atypical cross-modal experiences. *Perception* **35**, 1024–1033 (2006).
124. Cui, Z., Xia, Z., Su, M., Shu, H. & Gong, G. Disrupted white matter connectivity underlying developmental dyslexia: A machine learning approach: White matter disconnection in dyslexia. *Hum. Brain Mapp.* **37**, 1443–1458 (2016).
125. Schurz, M. *et al.* Resting-state and task-based functional brain connectivity in developmental dyslexia. *Cereb. Cortex* **25**, 3502–3514 (2015).
126. van der Mark, S. *et al.* The left occipitotemporal system in reading: disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. *Neuroimage* **54**, 2426–2436 (2011).

Author contributions

F.H. and L.C. designed the experiment, gathered the data prepared the figures and wrote the main manuscript. J.D. helped analyzing the data. M.E.S., C.R. helped gathering the data. All authors reviewed the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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