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Addressing long-standing controversies in conceptual knowledge representation in the temporal pole: A cross-modal paradigm

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Abstract

Conceptual knowledge allows us to comprehend the multisensory stimulation impinging on our senses. Its representation in the anterior temporal lobe is a subject of considerable debate, with the “enigmatic” temporal pole (TP) being at the center of that debate. The controversial models of the organization of knowledge representation in TP range from unilateral to fully unified bilateral representational systems.

To address the multitude of mutually exclusive options, we developed a novel cross-modal approach in a multifactorial brain imaging study of the blind, manipulating the modality (verbal vs pictorial) of both the reception source (reading text/verbal vs images/pictorial) and the expression (writing text/verbal vs drawing/pictorial) of conceptual knowledge. Furthermore, we also varied the level of familiarity. This study is the first to investigate the functional organization of (amodal) conceptual knowledge in TP in the blind, as well as, the first study of drawing based on the conceptual knowledge from memory of sentences delivered through Braille reading.

Through this paradigm, we were able to functionally identify two novel subdivisions of the temporal pole - the TPa, at the apex, and the TPdm - dorso-medially. Their response characteristics revealed a complex interplay of non-visual specializations within the temporal pole, with a diversity of excitatory/inhibitory inversions as a function of hemisphere, task-domain and familiarity, which motivate an expanded neurocognitive analysis of conceptual knowledge.

The interplay of inter-hemispheric specializations found here accounts for the variety of seemingly conflicting models in previous research for conceptual knowledge representation, reconciling them through the set of factors we have investigated: the two main knowledge domains (verbal and pictorial/sensory-motor) and the two main knowledge processing modes (receptive and expressive), including the level of familiarity as a modifier. Furthermore, the interplay of these factors allowed us to also reveal for the first time a system of complementary symmetries, asymmetries and unexpected anti-symmetries in the TP organization. Thus, taken together these results constitute a unifying explanation of the conflicting models in previous research on conceptual knowledge representation.

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Introduction

Conceptual knowledge allows us to comprehend the multisensory stimulation impinging on our senses; semantic representations allow us to both *generalize* and *express* knowledge appropriately over a wide variety of both *verbal* and *non-verbal* task domains. For example, knowledge can be expressed by naming and verbal definitions (i.e., verbally), as well as, by drawing and object use (nonverbally), (Lambon Ralph et al, 2009).

How is such conceptual knowledge represented in the brain? The vast interest in conceptual knowledge – both theoretical and clinical, particularly because of semantic dementia – led to the accumulation of a highly significant body of neuroimaging data, in spite of that, however, its neural representation is not well understood. Presently, there is considerable debate about its neural substrate. The anterior temporal lobe - and the "enigmatic" temporal pole (TP) in particular - are at the center of that debate (e.g., Olson et al., 2007). A recent large-scale meta-analysis (Grace et al., 2015) evaluated four most prominent theories: i) The "ATL hub-and-spoke" account proposes that the right and left ATLs represent conceptual knowledge in a unified manner as part of a bilateral, coupled system [thereby promoting robust representations: see Schapiro et al. (2013)]; ii) An extreme version of this account would predict no differences between the hemispheres; iii) A more nuanced position holds that graded hemispheric specialization emerges as a consequence of differential connectivity (Lambon Ralph et al. 2001; Binney et al. 2012; Schapiro et al. 2013); iv) Conversely, a greater degree of specialization between the right and left ATLs has been proposed as well, reflecting the modality of stimulus input (Gainotti 2007, 2013), the involvement of word retrieval or visual recognition in the task (Damasio et al. 2004), or the social content of the stimulus (Olson et al. 2007; Zahn et al. 2007).

Until recently, the TP has been considered both structurally and functionally homogeneous. However, it has now been demonstrated that the TP has rich cortical and subcortical connections (e.g., Fan et al., 2014). Because of its extensive connectivity with diverse modality-specific regions, the TP is ideal for forming *amodal semantic representations*, and it has been suggested as a key "amodal convergence hub". TP is capable of complex multisensory integration, but is also involved in various high-order cognitive functions, including semantic memory, high-level language processing, empathy, emotions, social and abstract semantic cognition, etc. When damaged, as in semantic dementia, a wide variety of semantically demanding tasks – *both receptive and expressive* – are affected. Thus, conceptual knowledge representations allow us not only to be the recipient of but to also express knowledge in a wide variety of domains; Furthermore, our semantic representations allow us to generalize knowledge across exemplars (Lambon Ralph and Patterson 2008).

Being so integral to our everyday lives, any impairments of semantic memory are extremely debilitating. That is why, the question of where in the brain conceptual knowledge is represented and what the underlying mechanisms are, is of key importance to neuroscience.

However, as seen above, the structural organization of knowledge representation is highly controversial, with proposed models ranging from a unilateral specialization (typically, leftlateralization) to a graded or fully unified bilateral TP representational system.

To address these mutually exclusive options, we have developed a novel *cross-modal approach* in a *multi-factorial brain imaging* study, comparing several modalities of reception and expression of conceptual knowledge through *Braille reading, Braille writing*, and *drawing,* including the level of *familiarity* as a modifier. Furthermore, we were able to achieve a *functional parcellation* of the temporal pole in the context of conceptual knowledge.

Methods

Experimental Design

A set of verbal descriptions of objects, faces and scenes were presented through tactile (Braille) text, to form comprehension-based non-visual memory in the blind reader, which was then expressed either through (i) memory-writing in Braille (***MemoryWritingFromBraille,*** BW) or ii) blind memory-drawing, also guided solely by the memory from the Braille reading (***MemoryDrawingFromBraille, MD***).

The blind ***MemoryDrawingFromBraille*** task wouldn't be possible without first employing our unique Cognitive-Kinesthetic Drawing Training (e.g., Likova, 2012, 2013) that allows us to achieve *rapid behavioral* and *brain plasticity* effects. Over only 5 sessions of 2 hr/day, blind participants learn to explore raised-line drawings so as to form precise and robust memory of the explored images, which subsequently guides the freehand drawing of these images without vision or any further tactile input (Likova, 2014, 2015). This training thus makes it possible for blind people to perform two different forms of drawing in the scanner, i) one based on pictorial-type reception (drawing guided by the pictorial memory of explored raised-line images; ***MemoryDrawingFromPictorial***), and ii) another one based on verbal-type reception (memory from Braille-reading guiding the drawing hand; ***MemoryDrawingFromBraille).***

The experimental design for functional Magnetic Resonance Imaging (fMRI) during the *Braille-involving tasks* was as in Likova et al (2016). Each sample of Braille text was used in two sequential scans. In the first scan, after it was read (***Braille reading, BR***), it was followed by two repetitions of Braille writing from memory (***BW1*** and ***BW2***) reproducing the description as understood and memorized from the preceding Braille-reading. In the second scan, the Braille reading was followed by two repetitions of expressing the memory through non-visual drawing (***MD1*** and ***MD2***). The tasks (20 sec each), were interleaved with 20 sec baseline/rest periods (rest).

Figure 1 illustrates the experimental tasks (left panel), the experimental sequence in the Braille involving tasks (upper right panel), and our custom MR-compatible lectern that makes it possible to run these complex non-visual tasks, each involving a precise motor control component (bottom right panel).

The fMRI experimental design for the blind memory-drawing, guided by the *pictorial memory* of the explored raised-line images, ***MemoryDrawingFromPictorial***, was as in Likova (2012). The drawing (20 sec) followed a 20 sec of exploration and memorization of presented raised-line images. The two tasks were separated by a 20 sec rest period, and followed by a 20 sec control task (***Scribble***).

General Methods

Equipment

Braille conditions: Braille writing was accomplished via the use of a standard slate and stylus system, as in Likova et al. (2016). The slate consisted of two pieces of plastic held together by a hinge, designed to hold the paper on which the participant wrote. The lower piece was solid with slight indentations for each of the 6 raised dots within each 2×3 Braille cell, and the upper piece had rectangular slots corresponding to each Braille cell. The stylus was a blunted aluminum point with a plastic handle.

To use this slate-and-stylus system, a sheet of paper was placed within the slate, and the stylus was used to puncture dots within each Braille cell outlined by the slate to create the desired characters. In the scanner, the MRI-compatible slate and stylus were positioned on top of our custom MRI-compatible lectern (Likova, 2012), providing both for haptic exploration of the Braille text during reading, and for Braille writing on a slate resting a two-slot (reading/writing) plexiglass table extending across the participant's lap. Auditory cues were presented through Resonance Technologies earphones (Resonance Technologies, Salem, MA).

Drawing conditions: The custom drawing lectern was used for the drawing conditions as well. In the case of raised-line pictorial stimulus, each stimulus was positioned in the left slot of the lectern, where it was explored with left hand and memorized, then drawn with a stylus in the right slot exclusively with the right hand. When the Braille text was the stimulus, it was placed in the left slot, read with left hand and memorized, then drawn from memory in the right slot with the right hand.

Functional MRI Acquisition and Analyses—Data were collected on a Siemens Trio 3T magnet equipped with a 12-channel head coil. BOLD responses were obtained using an EPI acquisition (TR = 2 s, TE = 28 ms, flip angle = 80°, voxel size = 3.0 × 3.0 × 3.5) consisting of 35 axial slices extending across the whole brain. Pre-processing was conducted using FSL (Analysis Group, FMRIB, Oxford, UK) and included slice-time correction and twophase motion correction, consisting of both within-scan and between-scan 6-parameter rigid-body corrections. To facilitate segmentation and registration, a whole-brain high-resolution T1-weighted anatomical scan was also obtained for each participant (voxel size = 0.8 × 0.8 × 0.8 mm). White matter segmentation in this T1 scan was conducted using FreeSurfer (Martinos Center for Biomedical Imaging, Massachusetts General Hospital) and Gray matter was identified with the mrGray function in the mrVista software package (Stanford Vision and Imaging Science and Technology).

To obtain estimates of neural activation amplitudes for each task, a general linear model (GLM) was fit to the acquired BOLD data for each three-task sequence. The GLM model consisted of a 3 separate 20-s boxcar predictors representing the 3 task activations plus an auditory predictor consisting of sequence of 1-s impulses corresponding to the 6 auditory cues. Each predictor was convolved with an estimated hemodynamic response function (HRF) derived from the whole cortical manifold averaged over the most activated voxels by filtering the 3-cycle sequence at a high activation threshold, and a 4th-order polynomial to account for low-frequency baseline fluctuations. For each task, statistical parametric maps (SPMs) were generated based on the estimated activation amplitudes from the above GLM in each voxel that exceeded the noise threshold defined by the variability in the residual. Note that the first stimulus presentations or task performances were designated as '*unfamiliar*', while their repeats as '*familiar'*.

Results

Functional Parcellation of the Temporal Pole

The fMRI analyses revealed two adjacent functional subdivisions within TP (Figure 2). These subdivisions - the apex (TPa) and a dorso-medial region (TPdm) – were differentiated on the basis of their contrasting behavior as a function of the three experimental variable of task-domain, hemisphere and familiarity.

Task-Dependent Hemispheric Specialization

We will refer to tasks with ***same*** modality of *reception (i.e.,* input of the information to be memorized*)* and *expression* (output) as '*within-domain* tasks'. These are i) the ***MemoryWritingFromBraille***, which had 'verbal reception/verbal expression', and ii) the ***MemoryDrawingFromPictorial***, which had 'pictorial reception/pictorial expression'.

The ***MemoryDrawingFromBraille***, on the other hand, is a '*cross-domain* task' as it is of a ***mixed*** modality by having a verbal input but the pictorial expression.

Different patterns of interhemispheric relationships were revealed as a function of the modalities of *both* the reception and of the expression of that memorized information.

Temporal pole apex (TPa)

Remarkably, for *within-domain* tasks, each subdivision showed previously unreported interhemispheric anti-symmetries such as reciprocal inter-hemispheric suppression.

The *cross-domain* **MemoryDrawingFromBraille** task, however, showed symmetrical *bilateral* activation, implying transformation of the conceptual information from the receptive format into the format of the expressive domain (e.g., from verbal into pictorial), before the expressive performance itself. Granger causality analysis differentiated the respective source and target networks involved (not included here).

Familiarity restricted hemispheric specialization patterns in dorsomedial temporal pole (TPdm)

Although, analogous types of hemispheric specialization patterns were observed in TPdm, they were manifested in the phase of *familiarity* only, i.e., only after task repetition or training (Fig. 4).

Moreover, the TPdm subdivision manifested a remarkable inversion of the familiarity effect (increase instead of decrease with familiarity). This inversion effect was strongly expressed in the familiarity phase (BW2, MD2) of both tasks (see Figure 5). In the unfamiliar phase, TPdm was either not significantly activated or was even suppressed. In the *within*-domain verbal/verbal task of ***MemoryWritingFromBraille*** (Figure 5, A) this effect was exhibited in the *left* hemisphere, while it was *bilateral* in the *cross*-domain verbal/pictorial task of ***MemoryDrawingFromBraille*** (Figure 5, B).

Discussion & Conclusions

Taken together the results from our multimodal paradigm shed new light on the path towards an explanation of current contradictions in the field of conceptual knowledge representation in the temporal poles of the two hemispheres of the brain. Also, we were able to functionally identify two specialized subdivisions of the 'enigmatic' temporal pole: the TPa, at the apex, and the dorso-medial TPdm. Additionally, an unexpected novel form of profound *push-pull interactions* was revealed, acting both inter-hemispherically (left vs right hemisphere) and inter-regionally (TPa vs TPdm). We also note that this is the first study of drawing based on conceptual knowledge from memory of sentences delivered through Braille reading, as well as, the first study to investigate the functional organization of (amodal) conceptual knowledge in TP ***in the blind***.

Although, our results are generally in support of the third of the theoretical accounts reviewed above – that of a greater degree of specialization (GDS) between the right and left ATLs - their implications go beyond that account. The main proposals within GDS are restricted to either i) the modality of stimulus input (Gainotti 2007, 2013), ii) the involvement of word retrieval or visual recognition in the task (Damasio et al. 2004), or iii) the social content of the stimulus (Olson et al. 2007; Zahn et al. 2007).

To address these proposals, our multidimensional study has included not only a passive task (***BrailleReading***) but also three active expression tasks, such as ***MemoryWritingFromBraille, MemoryDrawingFromBraille*** and ***MemoryDrawingFromPictorial***. Moreover, we have varied the modality (verbal vs pictorial) of *both* the reception source (reading text/verbal vs images/pictorial), and of the expressive output (writing text/verbal vs drawing/pictorial). We have also manipulated the level of *familiarity*.

Task-domain and familiarity

As a whole, the results reveal a complex interplay of non-visual hemispheric specializations for conceptual knowledge representation and expression within the temporal pole. The two subdivisions exhibited a diversity of *excitatory/inhibitory inversions* as a function of brain hemisphere, task-domain and familiarity, providing data for an expanded neurocognitive analysis of conceptual knowledge. Both *direct* and *inverse* familiarity effects were observed.

The *same-modality* task of memory *writing* from Braille text *activated* the ***left*** temporal pole only, while – unexpectedly - it strongly *suppressed* the *right* temporal pole. We call this unobserved previously behavior ***'inter-hemispheric push-pull model'***.

In contrast, the *mixed* modality - or *cross-domain* - task of memory *drawing* from Braille text fully conformed to a ***bilateral*** temporal pole model for conceptual knowledge representation in both TPa and TPm subdivisions. It was, however, a subject to a strong TPa/TPdm push-pull interaction driven by familiarity.

The task of memory drawing from *pictorial* input activated the ***right*** temporal pole only.

These differences in temporal pole lateralization above suggest that the *left* hemisphere component of the bilateral drawing activation in the *cross-domain* Braille memory drawing derives from the *verbal* nature of the *receptive* phase when the memory was formed from reading Braille text, while its *right* component derives from the *pictorial* nature of the *expression* phase.

In summary, these data show that, in the verbal input or expression mode, the left TP is activated; pictorial input or expression involves the right TP, and a mixed form input/expression (verbal and pictorial) gives a bilateral TP activation.

Relevance to models of conceptual representation

Importantly, the interplay of inter-hemispheric specializations found here accounts for the variety of conflicting models in previous research for knowledge representation. The multitude of seemingly contradictory findings in the literature, can be reconciled and now logically explained as a function of the set of factors we have investigated: the two main knowledge domains (verbal and pictorial/sensory-motor), the two main knowledge processing modes (receptive/input and expressive), with the level of familiarity as a modifier. Furthermore, varying these factors allowed us to also reveal for the first time a system of complementary symmetries, asymmetries and unexpected anti-symmetries in the TP functional organization relative to the left vs right hemisphere, activation vs suppression, and cooperation vs competition. Thus, taken together these results delineate a unifying explanation of the conflicting models in previous research on conceptual knowledge representation.

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Author Biography

Dr. Likova is the Director of Brain Plasticity, Learning & Neurorehabilitation Lab at Smith-Kettlewell Eye Research Institute. Based on her background in magnetic physics, cognitive neuroscience science and computer science, she has brought together a collaborative team focusing on the enhancement of brain plasticity for the rehabilitation of blind and low vision individuals. Through her unique Cognitive-Kinesthetic training regimen of less than a week’s duration, her lab has been able to drive brain plasticity and achieve major enhancements in both spatial memory and fine spatiomotor skills. Dr. Likova is on the HVEI Organizing Committee.

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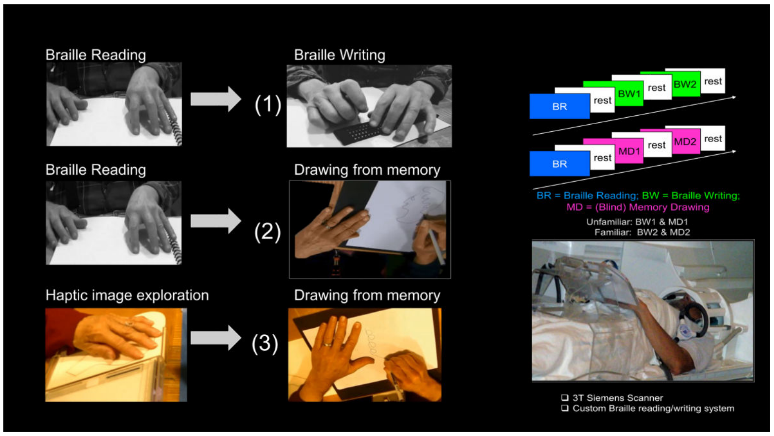


Figure 1. Experimental design:

Experimental tasks (**left panel**), the fMRI sequence in the Braille involving tasks (**upper right panel**), and our custom MR-compatible lectern that makes possible to run these complex non-visual tasks, each of which involves a precise motor control component (**bottom right panel**).

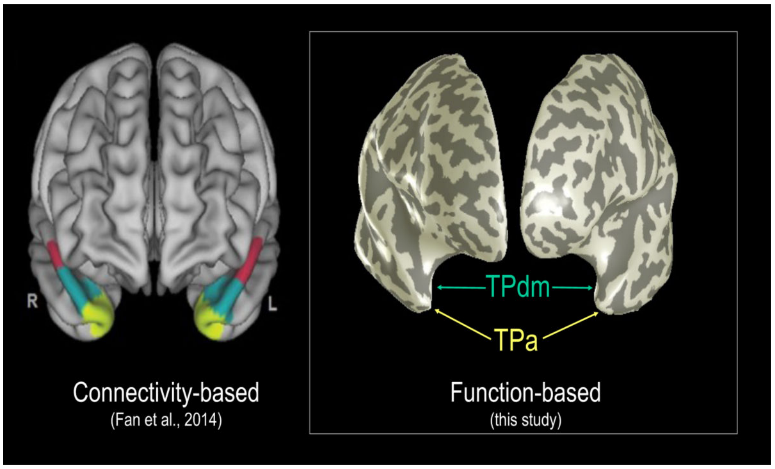
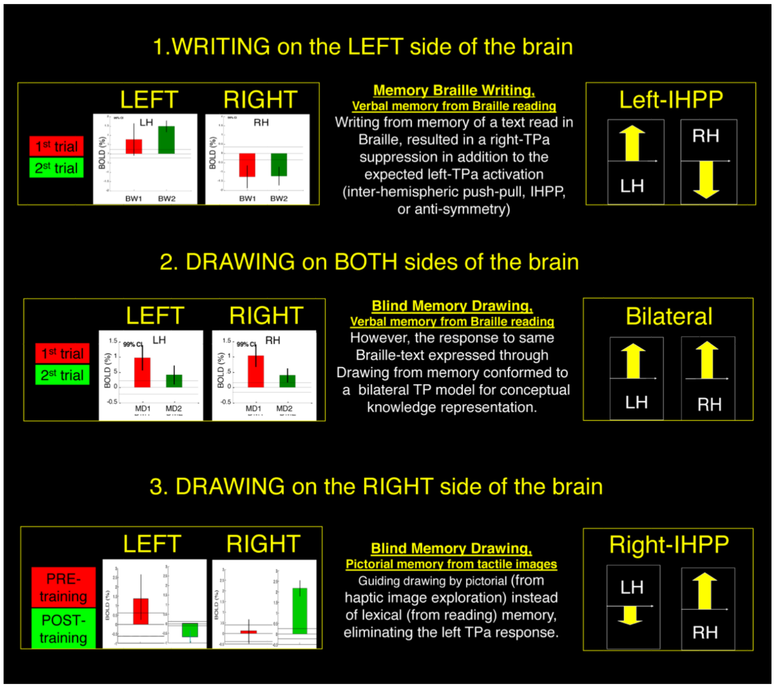


Figure 2.

Temporal pole parcellation. **Left panel:** Connectivity-based (Fan et al., 2014). **Right panel:** Function-based subdivisions (this study).



1.WRITING on the LEFT side of the brain

Memory Braille Writing,
Verbal memory from Braille reading
Writing from memory of a text read in Braille, resulted in a right-TPa suppression in addition to the expected left-TPa activation (inter-hemispheric push-pull, IHPP, or anti-symmetry)

2. DRAWING on BOTH sides of the brain

Blind Memory Drawing,
Verbal memory from Braille reading
However, the response to same Braille-text expressed through Drawing from memory conformed to a bilateral TP model for conceptual knowledge representation.

3. DRAWING on the RIGHT side of the brain

Blind Memory Drawing,
Pictorial memory from tactile images
Guiding drawing by pictorial (from haptic image exploration) instead of lexical (from reading) memory, eliminating the left TPa response.

Figure 3.

Temporal pole apex (TPa) responses: **1:** Comprehension of the Braille text expressed through the **MemoryWritingFromBraille** task produced neither bilateral nor left-hemisphere-only response, but a previously unobserved **interhemispheric push-pull (IHPP)** behavior with a strong left-lateralized response, combined with extensive contralateral suppression. **2:** Braille-text comprehension expressed through the blind **MemoryDrawingFromBraille** task fully conformed to the **bilateral** TP model for conceptual knowledge representation, both in the unfamiliar and in the familiar phase after repetition. Interestingly, the **familiarity effect** is manifested as a **reduction** (rather than enhancement) of the response, similarly to what we have already observed in the perirhinal cortex of the blind in the pictorial memory drawing task after the Likova Cognitive-Kinesthetic training (Cacciamani & Likova, 2016). **3:** Memory drawing guided by pictorial memory (from raised-line image exploration) eliminated the left, and conformed to the **right** TPa only.

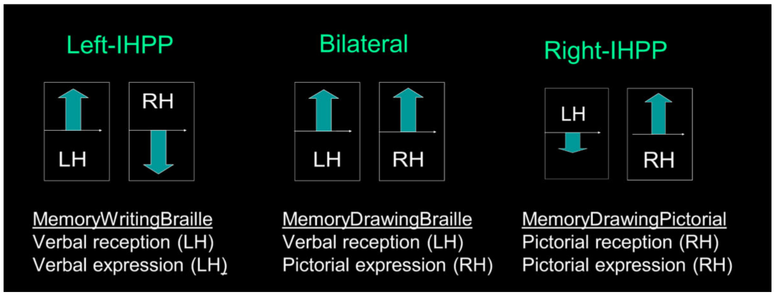


Figure 4.

Analogous types of hemispheric specialization patterns were observed in TPdm. TPdm was involved, however, in the **familiarity** phase only of each task.

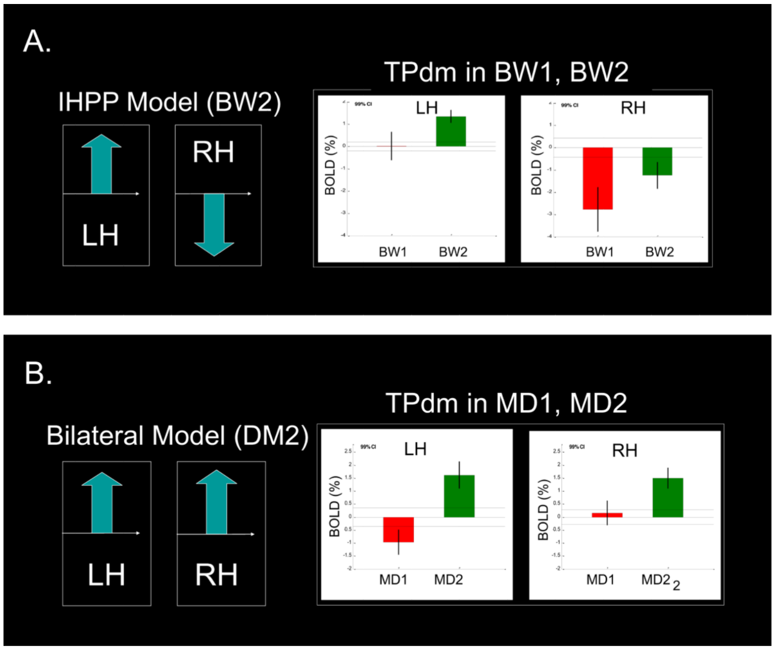


Figure 5. Inversed familiarity effect in the dorso-medial subdivision of the temporal pole (TPdm):

A familiarity effect, inversed in comparison with TPa (and PRC), i.e., an increase instead of a decrease with familiarity, was observed in both BW2 and MD2. The inversed effect was left-hemispheric in the MemoryWritingFromBraille (see **panel A**), while, it was bilateral in MemoryDrawingFromBraille (see **panel B**).

Table 1.

Hemispheric engagement as a function of the receptive/expressive modality combination.

	EXPRESSIVE MODALITY (Task)		
RECEPTIVE MODALITY (Stimulus Input)	**Verbal (Reading Braille)**	**Verbal/Motor (Memory Writing Braille)**	**Pictorial/Motor (Memory Drawing)**
Verbal (Braille Text)	**Left** TP	**Left** TP	**Left** TP + **Right** TP
Pictorial (Raised-line Images)	N/A	N/A	**Right** TP