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1 **Descriptive and functional anatomy of the Heschl Gyrus: historical review, manual labelling and current**
2 **perspectives**

3 Original article

4

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25 **Keywords:**

26 Heschl Gyrus, Primary Auditory Cortex, Temporal Lobe, Auditory System

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Abstract

Purpose

The Heschl Gyrus (HG), which includes the Primary Auditory Cortex (PAC), lies on the upper surface of the superior temporal gyrus (T1). It has been the subject of growing interest in the fields of neuroscience over the last decade. Given the considerable interhemispheric and interindividual variability of its morphology, manual labelling remains the gold standard for its radio-anatomical study. The aim of this study was to revisit the original work of Richard L. Heschl, to provide a broad overview of the available anatomical knowledge and to propose a manually labelled 3D digital model.

Methods

We reviewed existing works on the HG, from Heschl’s original publication of 1878, Dejerine neuroanatomical atlas of 1895 to the most recent digital atlases (Julich-Brain Cytoarchitectonic Atlas, the Human Connectome Project). Our segmentation work was based on data from the BigBrain Project and used the MRICron 2019 software.

Results

The original publication by Heschl has been translated into French and English. We propose a correspondence of previous nomenclatures with the most recent ones, including the Terminologia Neuroanatomica. Finally, despite the notable anatomical variability of the HG, clear and coherent segmentation criteria allowed us to generate a 3D digital model of the HG.

Discussion and Conclusion

Heschl’s work is still relevant and could impulse further anatomical and functional studies. The segmentation criteria could serve as a reference for manual labelling of the HG. Furthermore, a thorough, and historically based understanding of the morphological, microstructural and functional characteristics of the HG could be useful for manual segmentation.

1 **Introduction**

2

3 The Heschl Gyrus (HG), which includes the Primary Auditory Cortex (PAC), lies on the upper surface of the
4 superior temporal gyrus (T1). It has been the subject of growing interest in the fields of neuroscience,
5 neuroradiology, psychology and psychiatry over the last decade. Given the considerable interhemispheric and
6 interindividual variability of its morphology, manual labelling remains the gold standard for its radio-anatomical
7 study.

8 Due to the vast body of literature devoted to this structure, originating from various disciplines, dating back to
9 1878 and Richard L. Heschl's *princeps* article, it is not easy to encompass all the knowledge related to this
10 structure. Moreover, the macroanatomical descriptions of the HG are sometimes heterogenous and do not always
11 use the latest rigorous official neuroanatomical terminology, constituting a potential confounding factor in studies
12 relying on manual segmentation.

13 The aim of this study was to clarify its morphology and functional connectivity, to revisit the original work of
14 Richard L. Heschl, to provide a broad overview of the available knowledge related this structure, to propose
15 coherent and reliable segmentation criteria and a 3D manually labelled digital model.

16

17 **Biography**

18 Richard Ladislaus Heschl (1824 – 1881) received his medical doctorate in 1849 from the University of Vienna,
19 where he trained under the surgeons Franz Schuh (1804 – 1865) and Joseph Wattmann (1789 – 1866). The
20 following year he became the first assistant to the pathologist Carl von Rokitansky (1804-1878) at the same
21 university. He then pursued his career across the Austrian Empire, which became Austria-Hungary in 1867, being
22 appointed professor of anatomy in Olmütz in 1854, professor of pathological anatomy in Krakow in 1855, in Graz
23 in 1863 and finally in Vienna in 1875 as successor to Rokitansky. He died of pulmonary consumption (most likely
24 tuberculosis) in Vienna on May the 26th 1881, aged 56 years old [18] (**Fig. 1**).

25 As Amédée Dechambre stated in his “Encyclopedic Dictionary of Medical Sciences” of 1888, Heschl left behind
26 “une foule d’articles et de mémoires dans des recueils périodiques” (a series of articles and memoirs in periodicals),
27 many tomes, including the “Compendium of general and special pathological anatomy” of 1855, the “Sections-

1 Technik” of 1859, and his “On the anterior transverse temporal gyrus” of 1878 that described the gyrus named
2 after him [10, 19]. He also founded a pathological anatomy museum in Graz.



3

4 **Fig. 1** Portrait photography of Richard L. Heschl in Graz, October 2nd, 1872, at the age of 48 (courtesy of A.
5 Guédon).

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1 **Materials and methods**

2

3 **Recent and historical literature**

4 A literature review was conducted in databases such as Pubmed, Google Scholar, Web of Science using keywords
5 such as "Heschl Gyrus", "Primary Auditory Cortex", "Temporal Lobe", "Auditory System". We also used different
6 historical (Brodmann, Von Economo and Koskinas) and recent digital anatomical atlases (Julich-Brain
7 Cytoarchitectonic Atlas, Human Connectome Project's multimodal cortical parcellation 1.0).

8 Richard L. Heschl's historical description [19] is available on Google Book (<https://books.google.fr/>). An English
9 translation has been recently published [20]. We have done our own translation of the whole article into French
10 and of the most salient passages (the anatomical description of the HG) into English.

11

12 **Imaging**

13 The radiological illustrations are from the Neuroradiology Department of Lariboisière Hospital, AP-HP, Paris with
14 a three-dimensional T1 gradient echo sequence (MPRAGE) on a 3T MRI (Siemens Skyra, Siemens Healthineers,
15 Germany) and a 3D CT angiogram performed with a biplane angiography system (Artis Zee, Siemens
16 Healthineers, Germany).

17

18 **Portrait photography**

19 Théophile Le Comte, member of the Malacological Society of Belgium, naturalist living in Lessines, gathered in
20 1872/73, a beautiful album regrouping the European naturalists of which an unpublished photograph of Richard
21 Ladislaus Heschl dating from 1872.

22

23 **Manual labelling**

24 The BigBrain Project, devised by the Montreal Neurological Institute and the German Forschungszentrum Jülich
25 (<https://bigbrain.loris.ca/main.php>), provides a high-resolution 3D digital model of the human brain. It is based

1 on a total of 7404 coronal brain sections of a 65-year-old woman that have been stained according to the Merker
2 method and then digitalized [3].

3 For the present study, using MRICron 2019 software (available at nitrc.org), the left HG on 100 consecutive
4 sections of the 400 μ m reconstruction (full16_400um_2009b_sym.nii) were manually labelled. The 3D
5 reconstruction was performed using Mango version 4.1 software (<http://rii.uthscsa.edu/mango/>).

6

7 **Atlases**

8 The Julich-Brain Atlas [4] relies on histological sections of 23 post-mortem brains. Those tissues were fixed in
9 formalin, MR-imaged, embedded in paraffin, serially cut, stained, digitized, and registered to stereotaxic reference
10 coordinate spaces (the MNI Colin 27 and / or the MNI ICBM 152). The Human Connectome Project Multi-Modal
11 Parcellation [40] relies on topographic, myelin, cortical thickness, connectivity, and functional maps.

12

13 **Results**

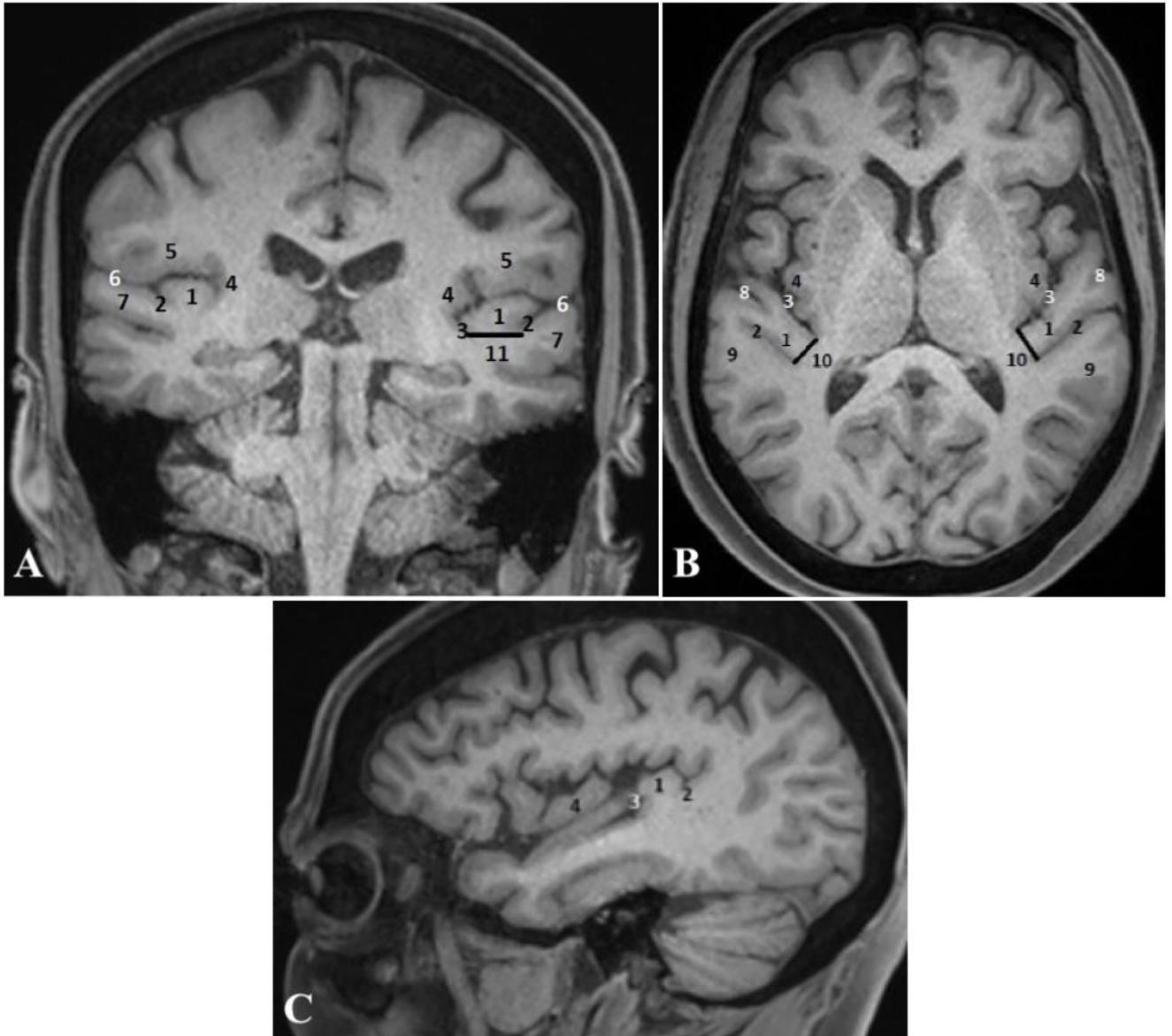
14

15 **Anatomy of the Heschl Gyrus (HG)**

16 Following the terminology of the 2017 version of the Terminologia Neuroanatomica (TNA) [15], most recent
17 works [5, 9, 29] describe Heschl's Gyrus/Gyri (HG), or "transverse temporal gyri", as a circumvolution that
18 originates from the depth of the lateral sulcus (of Sylvius) in the retro-insular region, that extends forwards,
19 downwards and laterally along the upper surface of the superior temporal gyrus (T1) towards its lateral bulge. As
20 described by Ten Donkelhaar et al. [13], the HG separates the Planum polare (PP) anteriorly from the Planum
21 temporale (PT) posteriorly on the upper surface of T1. In the left cerebral hemisphere, dominant for language, the
22 PT includes Wernicke's area that is involved in the comprehension of written and spoken language. Nevertheless,
23 both MRI and postmortem studies show that there are considerable interhemispheric, and interindividual variations
24 in this transverse temporal gyrus [1].

25 In accordance with TNA 2017, the anteromedial limit of the HG is defined by the anterior transverse temporal
26 sulcus (ATTS) that unites with the circular sulcus of the insula (of Reil). The posterolateral limit is determined by
27 the posterior transverse temporal sulcus (PTTS) (also known as Heschl's sulcus), which lies almost parallel to the

1 ATTS. HG's posteromedial border is formed by a line drawn from the medial ends of the PTTS and the ATTS,
 2 while its anterolateral edge is limited by the visible ending of the circumvolution [1]. Finally, the inferior boundary
 3 of the HG is formed by a line joining the bases of the anterior and posterior TTS (**Fig. 2**).



4
 5 **Fig. 2** Anatomy of the Heschl Gyrus. **A:** Coronal 3D T1 MPRAGE MRI section; **B:** Axial section; **C:** Sagittal
 6 section. **1:** Heschl's Gyrus (HG); **2:** posterior temporal transverse sulcus (PTTS) (also known as Heschl's sulcus);
 7 **3:** anterior temporal transverse sulcus (ATTS); **4:** Insula; **5:** Frontoparietal region; **6:** lateral sulcus (of Sylvius);
 8 **7:** superior temporal gyrus (T1); **8:** intermediate temporal transverse sulcus (ITTS) (of Beck); **9:** Planum
 9 Temporale (PT); **10:** posteromedial boundary; **11:** inferior boundary

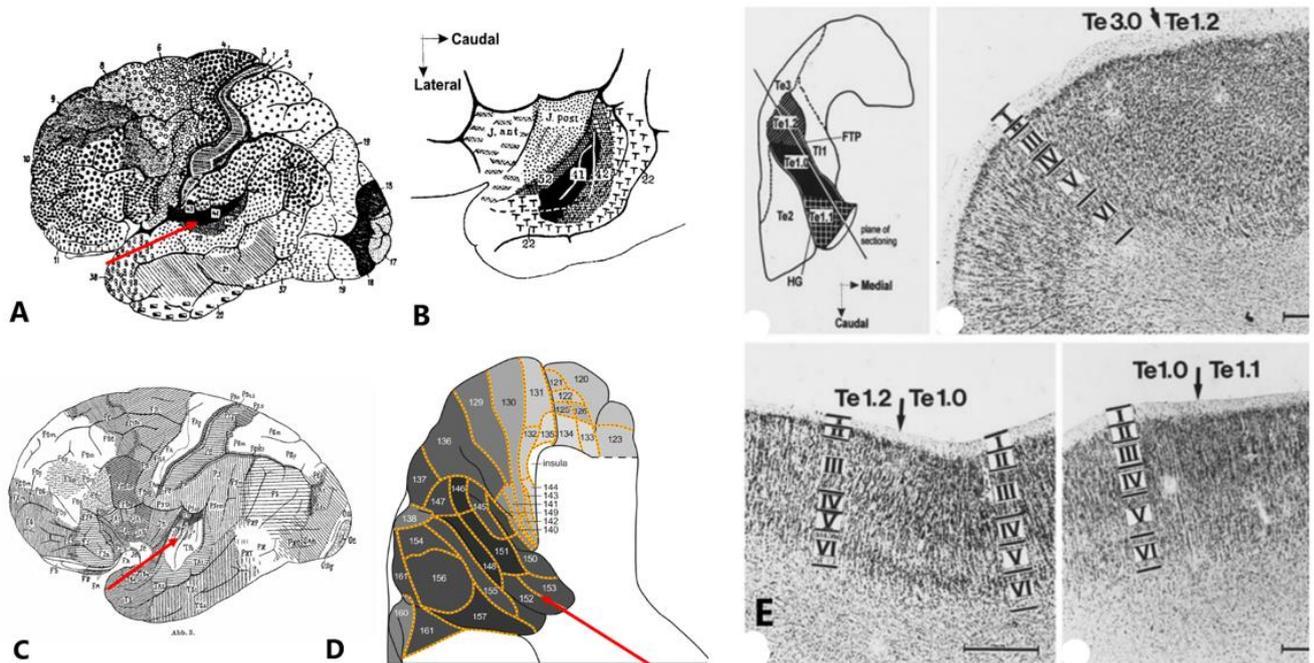
10
 11 Owing to the considerable anatomical variations, an intermediate transverse temporal sulcus (ITTS) (of Beck) has
 12 been described when this sulcus' length is comparable to those of the anterior and posterior TTS. The ITTS is
 13 parallel, between the ATTS and PTTS, in about 40% of the cerebral hemispheres of healthy living subjects [25].

1 The ITTS separates 2, 3, 4 and up to 5 gyri, with the frequency of the gyrification pattern decreasing with increasing
2 number of gyri, a 5-gyri pattern being extremely rare [5]. In the case of a duplication, the TNA 2017 defines an
3 anterior transverse temporal gyrus and a posterior transverse temporal gyrus.

4 On sagittal or coronal planes, the HG has been described as having an omega shape; alternatively shaped as a
5 mushroom, a heart, a bow tie or a two separate Ss [1]. With regard to what is the minimal length of the ITTS when
6 there are two HGs, the most consensual view in the literature is of an ITTS with a length of at least half of the HG,
7 a trait associated with a depth comparable to those of the TTS [30]; a shorter ITTS is commonly associated with a
8 reduced depth.

9 From a microanatomical perspective, the main structure of interest embodied in the HG is the primary auditory
10 cortex (PAC), initially described by Alfred Walter Campbell (1868 – 1937) in 1905 as an “auditory-sensory area”.
11 This area is also commonly known as Area 41, or “Area temporalis transversa interna” according to Korbinian
12 Brodmann (1868 – 1918) in 1909 [7], or as Area Te1 after Morosan et al. [26] (**Table 1** and **Fig. 3**).

13



14

15 **Fig. 3** The Primary Auditory Cortex included in the Heschl Gyrus represented in several atlases, from 1909 to
16 nowadays. **A** and **B**: Area 41 from Brodmann (1909) [7] reproduced with permission from Elsevier (Morosan,
17 2001) [26] **C**: Areas Tc and Td from Von Economo and Koskinas (1925) [14] reproduced with permission from
18 Elsevier (Scholtens LH, 2018) [33] **D**: Areas 145 to 157 from Nieuwenhuys (2017) [28] reproduced with
19 permission from Springer Nature **E**: Areas Te1.2, Te1.0, Te1.1 from Morosan (2001) [26] reproduced with
20 permission from Elsevier

21

1

2 The grey matter of the neocortex is traditionally described as a superposition of six layers, numbered from the
3 surface (I) to the depth (VI). Histological investigations make it possible to characterise, at the cellular and
4 molecular levels, specific areas of the neopallium linked to particular functions. Thus, the synthesis of cyto-,
5 myelo-, chemo-, and receptor-architectonic studies gives us an overview of the main microstructural characteristics
6 of the PAC: a koniocortex surrounded by pro- and para-koniocortices, a high density of granular cells, small
7 pyramidal cells in layer III, a well-developed and highly myelinated layer IV, a low cell density in layer V, a strong
8 expression of acetylcholine esterase in the neuropile and a high concentration of cholinergic muscarinic M2
9 receptors [1, 5] (**Fig. 3E**).

10 The inclusion of the PAC in the HG is widely understood. In the case of a duplication of the HG, the PAC most
11 commonly tends to occupy the anterior HG [1]. However, macroanatomical landmarks do not seem able to
12 delineate with high accuracy the PAC. For instance, the PAC has been described as extending beyond the PTTS.
13 The lack of consistent correspondence between the macroanatomical landmarks of the HG and the
14 microanatomical features of the PAC should be considered in the light of the considerable interhemispheric, and
15 interindividual variations for each of these structures, and the significant heterogeneity of the methods and
16 techniques used in the literature [26, 32]. Indeed, descriptions of HG are based on anatomical, morphological and
17 radiological studies, whereas the PAC is identified using cyto-architectonical approaches, connectivity and
18 functional imaging techniques.

19 Based on historical data from Oskar Vogt (1870 - 1959) - Cécile Vogt-Mugnier (1875 - 1962) laboratory and from
20 studies by Adolf Hopf (1923 - 2011), Nieuwenhuys et al. (2017) have recently published a high precision
21 myeloarchitectonic map of the human neocortex (180 areas). This describes the PAC as covering the anterior and
22 posterior HGs, and defines 13 densely myelinated areas (145 to 157) with a core of high density located on the
23 medial third of the anterior gyrus (146, 148 and 151) [28] (**Fig. 3D**).

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1 **Table 1** Main microanatomical descriptions of the PAC included in the HG, from the early 20th century to
 2 nowadays.

3

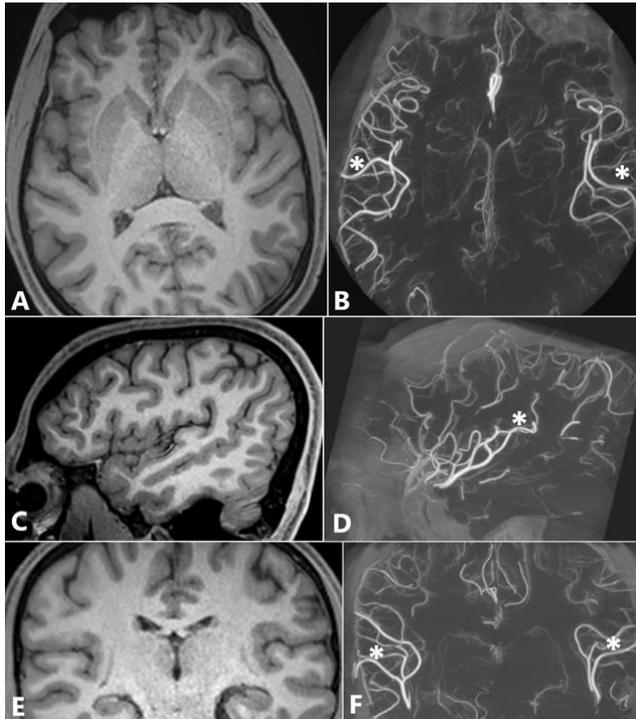
Authors	Heschl (1878) [19]	Dejerine (1895) [11]	Brodmann (1909) [7]	Von Economo (1925) [14]	Morosan (2001) [26]	Nieuwenhuys (2017) [28]
PAC/HG	Not described	Not described	BA41 (1 area)	Tc et Td (2 areas)	Te1.0, Te1.1, Te1.2 (3 areas)	145 à 157 (13 areas)
Total number of cortical areas			52	107		180

4

5

6 **Vasculature of the HG**

7 The lateral fissure (of Sylvian) contains the trunk and major branches of the middle cerebral artery. The artery
 8 appears distinctly in angiography as the “sylvian triangle” in the lateral projection (Schlesinger, 1953). The deep
 9 vascular plane is constituted by all the vessels running on the insula and the deep part of the HG (retro-insular
 10 region of Broca). The postero-inferior limit of this triangle is curved slightly upward by the HG. There is a
 11 succession of repeating loops at the level of the upper edge of the insula that describes a straight line. The last loop
 12 of the superior insular line warrants further attention. It adheres to the deepest part of the HG and is thus already
 13 retro-insular. At the intermediate or opercular plane, the inferior, or temporal, operculum carries the arteries
 14 destined for the temporal and temporoparietal regions. In the middle is the transverse bulge of the HG, passing
 15 obliquely forward from the deep plane (level of the insula) to the free edge of the superior temporal gyrus. The
 16 characteristic loops along the convexity of the HG indicate the site of the transverse sulcus and are discernible on
 17 an arteriogram. One of these arteries, or a finer branch, often runs in the transverse sulcus for a greater or lesser
 18 distance towards the surface, highlighting its antero-posterior obliquity [34] (**Fig. 4**).



1

2 **Fig. 4** Arterial vasculature of the Heschl Gyrus. **A, C, E:** Axial, right parasagittal and coronal 3D T1 MPRAGE
 3 MRI sections showing Heschl's gyri along the upper surface of the superior temporal gyri (T1), the left Heschl
 4 gyrus is partially duplicated. **B, D, F:** 3D CT angiogram of the two internal carotid arteries showing the
 5 vascularisation of Heschl's gyri (*) with the characteristic loops.

6

7

8 **English and French translation of Richard L. Heschl's 1878 article**

9 Anatomical description of the HG by Richard L. Heschl [19] :

10 *Translator's note: there are no bolded sections in the original article, they have been used to indicate key points.*

11 “[...]”

12 After opening the Sylvian fissure and removing the meninges, three surfaces can be observed. A superior
 13 surface – the inferior surface of the operculum (*translator's note: most likely the operculum frontale/parietale*)
 14 with its transverse gyri, - the lateral surface of the Insula, ample and prominent, showing 5 to 7 convolutions; and
 15 an inferior surface which corresponds to the superior surface of the left temporal lobe. The latter usually presents
 16 a triangular shape with curved edges; the lateral edge is convex towards the outside, corresponding to the superior
 17 surface of the superior temporal gyrus (inferior bank of the Sylvian fissure); the medial edge surrounds the Insula

1 at mid-length, forming a short and protruding circular arc; and the posterior edge, shorter than the two others,
2 connects the two posterior ends of the two previous ones and its curvature varies from one brain to another.

3 After exposing the triangular surface described above, whose most acute angle points anteriorly, **one**
4 **promptly notices that one or more gyri lay on the posterior half and expand transversely from the antero-**
5 **lateral part to the posterior-medial part of the surface. The anterior convolution is always found, but very**
6 **often one can also observe a second and often a third, sometimes even a fourth or a fifth convolution,** either
7 deploying like a fan or lying in a more parallel manner on the upper surface of the temporal lobe.

8 The first convolution (or anterior transverse temporal gyrus) emerges from the middle of the lateral edge of the
9 superior surface of the temporal lobe, namely from the first temporal gyrus (T_1 according to Ecker); it is the longest
10 of these gyri, merging quite often with the second transverse temporal gyrus. It ends either on its own or merging
11 with the second, in the most posterior angle of the Sylvian fissure, about 1 cm from the entrance of the inferior
12 horn (*Translator's note: cornu temporale or cornu inferius*) while the other convolutions end more laterally.

13 [...]

14 I termed these gyri as a whole, lying on the superior surface of the temporal lobe, (superior) transverse
15 temporal gyri. **Regarding the most anterior of these 3 to 4 gyri, which is always found, although its shape**
16 **may vary, I refer to it as T^1 .**

17 I have looked for it in no less than 1087 documented brains, and in hundreds of others, not less explicitly
18 described and have found it every single time as a well-characterised gyrus of consistent shape. **Its length varies**
19 **with the depth of the Sylvian fissure: its height ranges from 4 to 12 mm, its thickness is usually 12 to 15 mm.**
20 Sometimes the gyrus lies as anteriorly as posteriorly, and sometimes only posteriorly. **It is delimited from the**
21 **superior surface of the temporal lobe by a 6 to 8 mm deep sulcus, in such way that it rises with a 3 to 4 mm**
22 **wide foot and overlaps it, showing a mushroom shape (on an axial section)."**

23

24 The French translation is unpublished to the best of our knowledge, see **Supplementary material 1.**

25

26

27

1 **Segmentation criteria**

2 To ensure the reliability of the manual segmentation of the HG, it seems essential to us, on the basis of Heschl's
3 *princeps* article, our study of the literature, and our subjective experience, to follow two principles from which we
4 can deduce the correct order of identification of the relevant sulci, lobes, plana and gyri.

5

- 6 - Principle 1: Larger structures should be identified first
- 7 - Principle 2: Sulci should be identified before lobes, plana and gyri

8

9 In his 1878 article, Heschl first describes the dissecting instruments, methods, and steps to be followed to identify
10 the HG. He proceeds from the largest to the smallest structures and explains that first the brain must be separated
11 from the cerebellum, then both hemispheres, the meninges removed, the lateral sulcus opened, the fronto-parietal
12 operculum, the Insula, T1, the circular sulcus of the Insula identified. Also, Heschl argued for the importance of
13 the study of gyri and sulci in describing the anatomy of the brain and its embryological development: "Each
14 circumvolution inevitably matches two sulci, and each sulcus two circumvolutions." [19].

15

16 From these two principles, we can now deduce the steps for achieving a reliable segmentation of the HG (**Table**
17 **2**).

18 The widest and most constant sulcus to be identified first is the lateral sulcus, separating the temporal lobe and its
19 superior aspect, the superior temporal gyrus, from the frontal and parietal lobes. Next, the circular sulcus of the
20 Insula defines the Insula and the medial border of T1. At this stage, there is no decisive argument as to whether
21 we should identify the ATTS or the PTTS first. However, Heschl mentions in his paper: "a very deep posterior
22 sulcus is always found, with which the first temporal sulcus (*Translator's note: ATTS*) merges directly (fissura
23 parallela, t¹ according to Ecker), and ends in the crevices, the most medial and posterior faces of the Sylvian
24 fissure." Dejerine describes it as "deep temporal sulcus" [11] (**Table 3**). We therefore choose to identify the PTTS,
25 also called Heschl's sulcus [15], before the ATTS. As the Planum temporale, Planum polare and HG/HGs are
26 clearly visible to us, we then look for one or more ITTS. Finally, we identify the inferior border (which is not a
27 sulcus but an artificial border) to complete the segmentation of the HG.

28

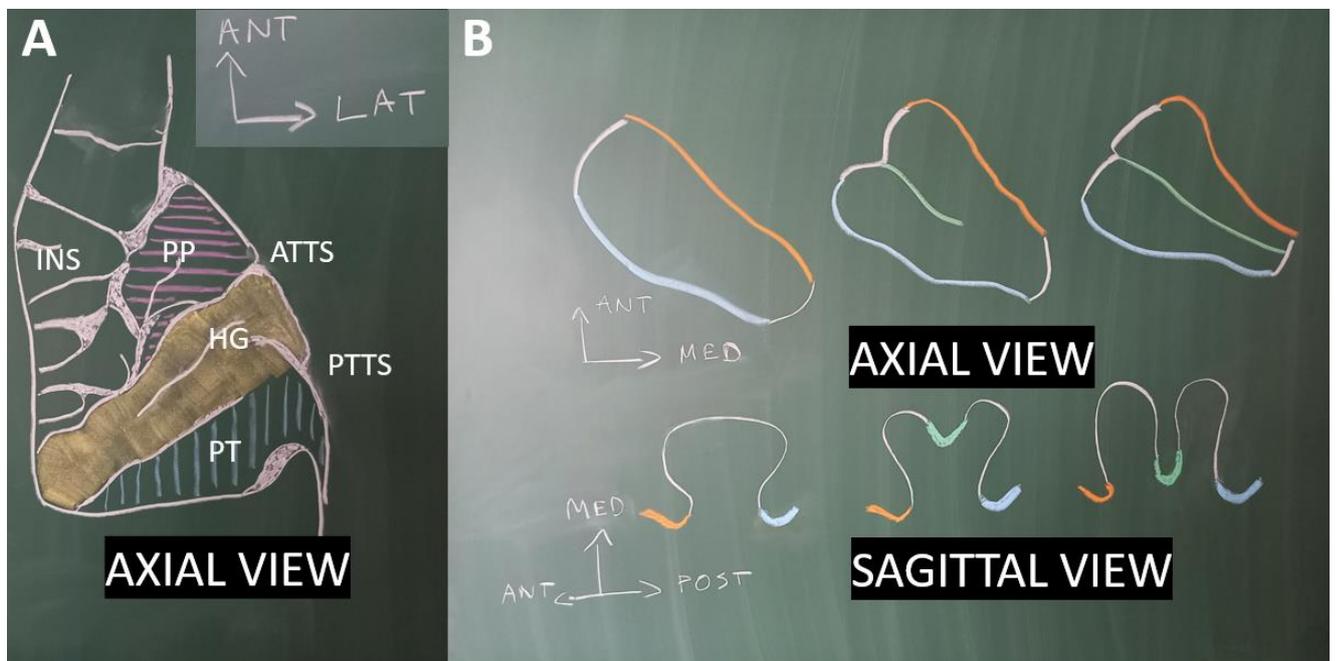
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2 **Table 2** Manual labelling of the Heschl Gyrus: a step-by-step methodology

Steps	Sulci	Lobes, Plana and Gyri
1	Lateral sulcus	Allowing to identify the Superior temporal gyrus
2	Circular sulcus of the insula	Allowing to identify the Superior temporal gyrus and the Insula
3	Posterior temporal transverse sulcus (Also known as Heschl's Sulcus)	Allowing to identify the Planum Temporale and the HG (or posterior HG , if applicable)
4	Anterior temporal transverse sulcus	Allowing to identify the Planum Polare and the HG (or anterior HG , if applicable)
5	Intermediate temporal transverse sulcus (sulci)	Allowing to determine the gyrification pattern its length should be compared with that of the ATTS and PTTS
6	Inferior and posteromedial boundaries (Between the depth of the ATTS and the PTTS)	Allowing the completion of the segmentation of the HG

3

4 The 6 steps described in **Table 2** should be applied to the coronal, axial and sagittal digital views. In addition, as
5 manual segmentation requires good hand-eye coordination, preparatory drawings on the blackboard with chalk
6 can be very useful (**Fig. 5**).



7

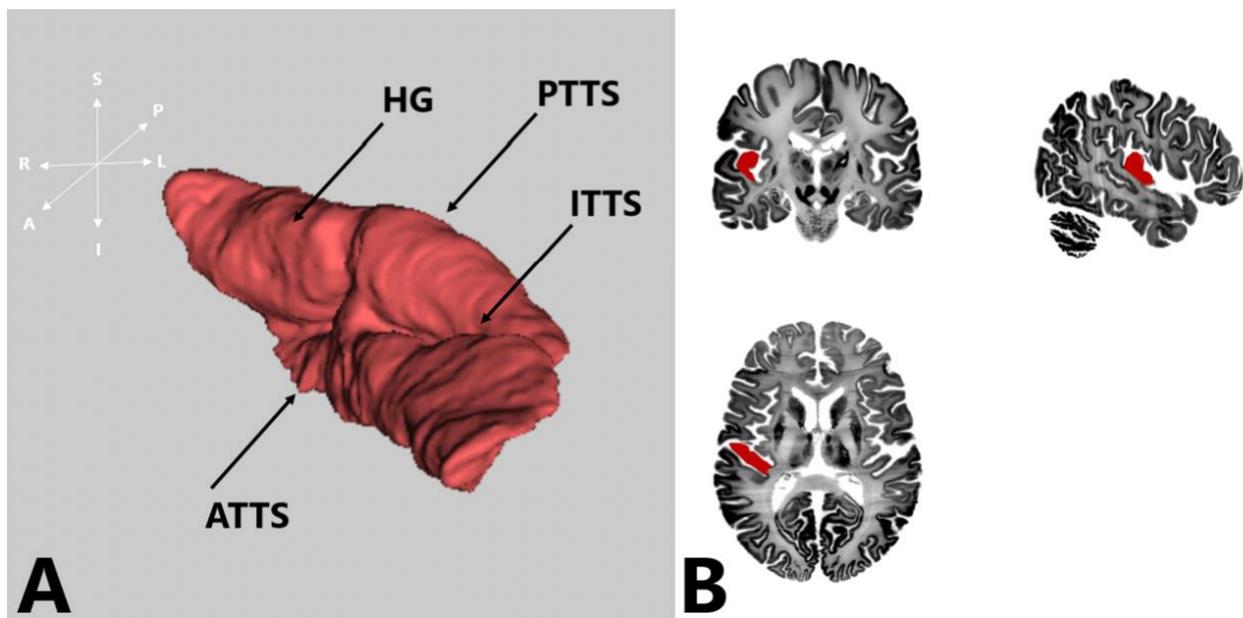
8 **Fig. 5** Preparatory drawing on the blackboard with chalk. **A:** Topographic superior view of the upper surface of
9 the right T1. PT: Planum temporale; HG: Heschl Gyrus; PP: Planum polare; INS: Insula; ATTS: Anterior temporal
10 transverse sulcus; PTTS: Posterior temporal transverse sulcus (also known as Heschl's sulcus) **B:** Single HG,
11 partial and complete duplication (right hemisphere). Red: ATTS; Blue: PTTS; Green: ITTS. ATTS: Anterior

1 temporal transverse sulcus; ITTS: Intermediate temporal transverse sulcus (of Beck); PTTS: Posterior temporal
2 transverse sulcus (also known as Heschl's sulcus)

3

4 **3D digital model of the HG and terminology**

5 We generated a 3D digital model of the HG based upon the BigBrain Project data with manual labelling of this
6 structure. As shown in **Fig. 6A**, the length of the ITTS is 30% of the length of the HG. *De facto*, we cannot describe
7 two separate HGs but instead a single HG with a partial duplication at its anterolateral third (also defined as
8 common stem duplication). Moreover, the ITTS is not as deep as the ATTS and the PTTS (**Figs. 6A and B**).



9

10 **Fig. 6** Manual labelling and 3D modelisation of the left HG from the BigBrain Dejerine Digital Atlas [31]. **A:** The
11 left HG from the BigBrain Dejerine Digital Atlas. **B:** Manual labelling of the HG using MRIcron 2019. Data were
12 used with permission from the BigBrain Project [3].

13

14

15 The proposed manual labelling of the HG will be included in a 3D digital atlas of the Human Brain [31] based on
16 the work of Jules Dejerine and Augusta Dejerine-Klumpke. Indeed, the two eminent French neurologists published
17 in 1895 the first volume of a major work in the field of neuroanatomy, « Anatomie des centres nerveux » [11] in
18 which they describe the « Circonvolutions temporales transverses de Heschl » (Transverse temporal Gyri of
19 Heschl). This “Digital Dejerine Atlas” is a collaborative work of the Trans-European Pedagogic Anatomical
20 Research Group (TEPARG, <https://teparg.com/>), it will be in accordance with the latest international anatomical

1 terminology of the Terminologia Anatomica (TA, 1998) and of the Terminologia Neuroanatomica (TNA, 2017)
 2 [15] (Table 3).

3

4 **Table 3** Terminology used for the description of the HG, Heschl (1878), Dejerine (1895) and TNA (2017)

Heschl (1878) [19]	Dejerine (1895) [11]	TNA (2017) Latin and English [15]
vordere quere Schläfenwindung	Circonvolutions temporales transverses de Heschl / plis de passage temporo-pariétaux / région rétro-insulaire de Broca (Tp)	(2062) Gyri temporales transversi – Transverse temporal gyri
sylvische Spalte	Scissure de Sylvius	(2003) Sulcus lateralis – Lateral sulcus
Insel von Reil	Insula	(2074) Insula - Insula
Klappdeckel		(2043) Operculum parietale – Parietal operculum <i>(most likely)</i>
erste Schläfenwindung (T ₁ nach Ecker)	première circonvolution temporale (T ₁)	(2057) Gyrus temporalis superior - Superior temporal gyrus
		(2067) Sulcus temporalis transversus anterior – Anterior transverse temporal sulcus
		(2068) Sulcus temporalis transversus intermedius – Intermediate transverse temporal sulcus
tiefe Furche	Sillon temporal profond (tp)	(2069) Sulcus temporalis transversus posterior – Posterior transverse temporal sulcus
	Circonvolution de l'enceinte de l'Insula	(2079) Sulcus circularis insulae – Circular sulcus of the insula

5

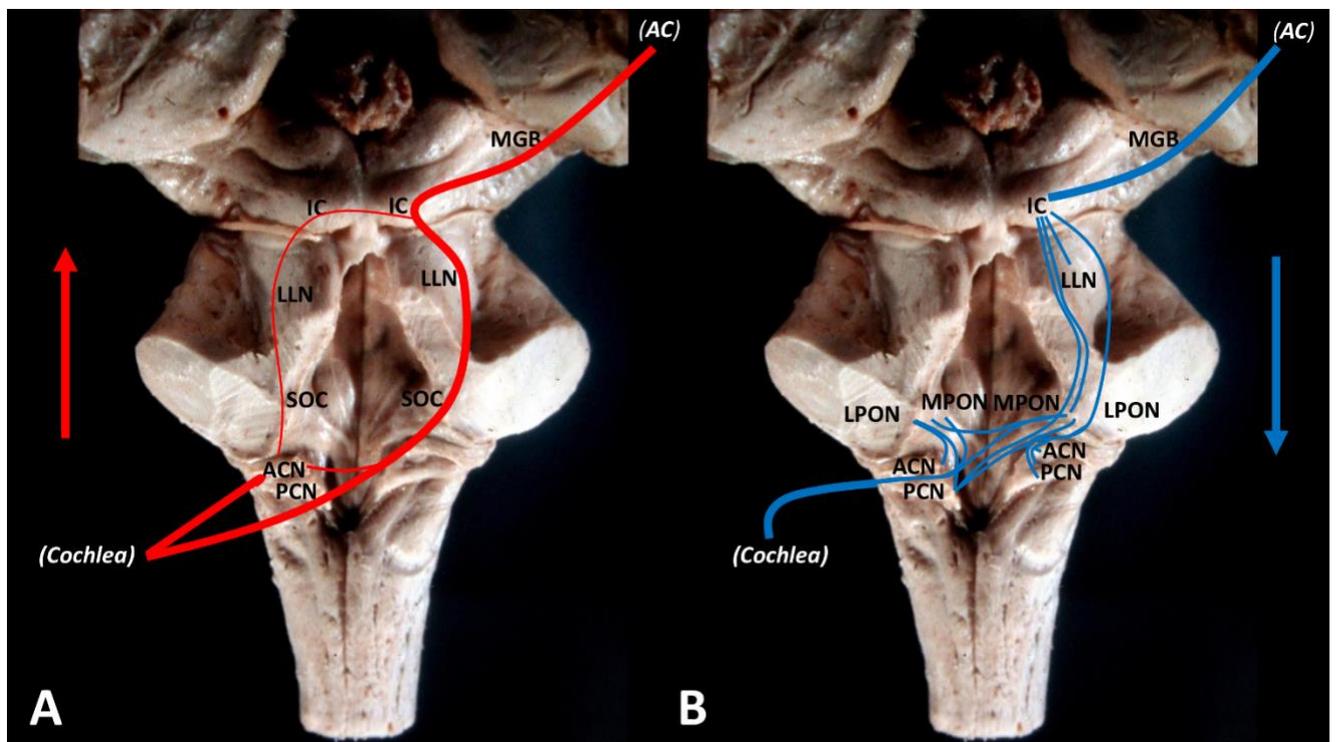
6

7 **Functional anatomy of the PAC included in the HG**

8 The ascending pathway of the auditory system involves a multi-synaptic network. It starts in the cochlea, diverges
 9 as it reaches the anterior and posterior cochlear nuclei, then projects bilaterally with a contralateral dominance as
 10 it continues through the superior olivary complexes and the nuclei of the lateral lemnisci. From the lemnisci, the

1 pathway merges at the contralateral inferior colliculus. Subsequently, the pathway projects to the contralateral
2 auditory cortex through the medial geniculate body (**Fig. 7A**).

3 The descending pathway shows even greater complexity. It is also characterised by contralateral dominance, but
4 not all projections cross the middle line. A direct pathway from the auditory cortex to the medial geniculate body
5 and the inferior colliculus has been described. It then diverges, projecting ipsilaterally to the nucleus of the lateral
6 lemniscus, the posterior cochlear nucleus and the medial periolivary nucleus, and contralaterally to the posterior
7 cochlear nucleus. Axons of neurons of the medial periolivary nuclei and the lateral periolivary nuclei on both sides
8 then reach the anterior and posterior cochlear nuclei. The contralateral cochlea is connected to the contralateral
9 medial and lateral periolivary nuclei, and to the ipsilateral medial periolivary nucleus [5] (**Fig. 7B**).



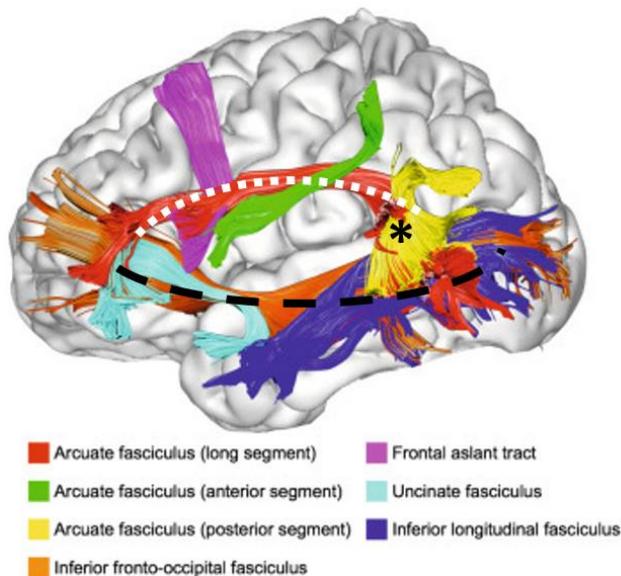
10

11 **Fig. 7** Ascending (A) and descending (B) pathways of the auditory system on a posterior view of the brain stem
12 (without the cerebellum). (Courtesy of the Anatomy Laboratory of Paris Cité University). ACN=anterior cochlear
13 nucleus; PCN=posterior cochlear nucleus; SOC=superior olivary complex; LLN=lateral lemniscus nucleus;
14 IC=inferior colliculus; MGB=medial geniculate body; LPON=lateral periolivary nucleus; MPON=medial
15 periolivary nucleus; AC=auditory cortex

16

17 The physical organisation of the PAC neurons is described in terms of their response to sound frequency.
18 According to this tonotopic organization, cells at the anterior end tend to be more responsive to low tones
19 (corresponding to the apex of the cochlea) and those at the posterior end to high tones (corresponding to the base
20 of the cochlea) [16].

1 While understanding the cortico-cortical connections of the PAC still requires further investigations, especially in
 2 humans, strong connections with both the anterior and posterior superior temporal gyri have been implicated,
 3 relying both on serial and parallel processing [5]. As part of the auditory cortex, the PAC has also been termed
 4 BA41 (Brodmann area 41) or A1 or “core area”. PAC is also related to the secondary auditory cortex (termed
 5 BA42 (Brodmann area 42) (**Figs. 3 A and B**) or A2 or “belt area”) and to the more lateral parabelt area [16]. Short
 6 and long-range connections pass beyond the temporal lobe to reach parietal and frontal regions and also the PAC
 7 of the opposite hemisphere. Recent tractography reconstruction has shown that auditory processing pathways can
 8 be visualised *in vivo* and information from the HG appears to be projected to the inferior parietal and posterior
 9 frontal gyri through the arcuate fasciculus. A ventral pathway also passes information “from posterior to more
 10 anterior temporal and frontal area through the longitudinal fasciculus, the uncinate fasciculus, and the inferior
 11 fronto-occipital fasciculus” [24] (**Fig. 8**).



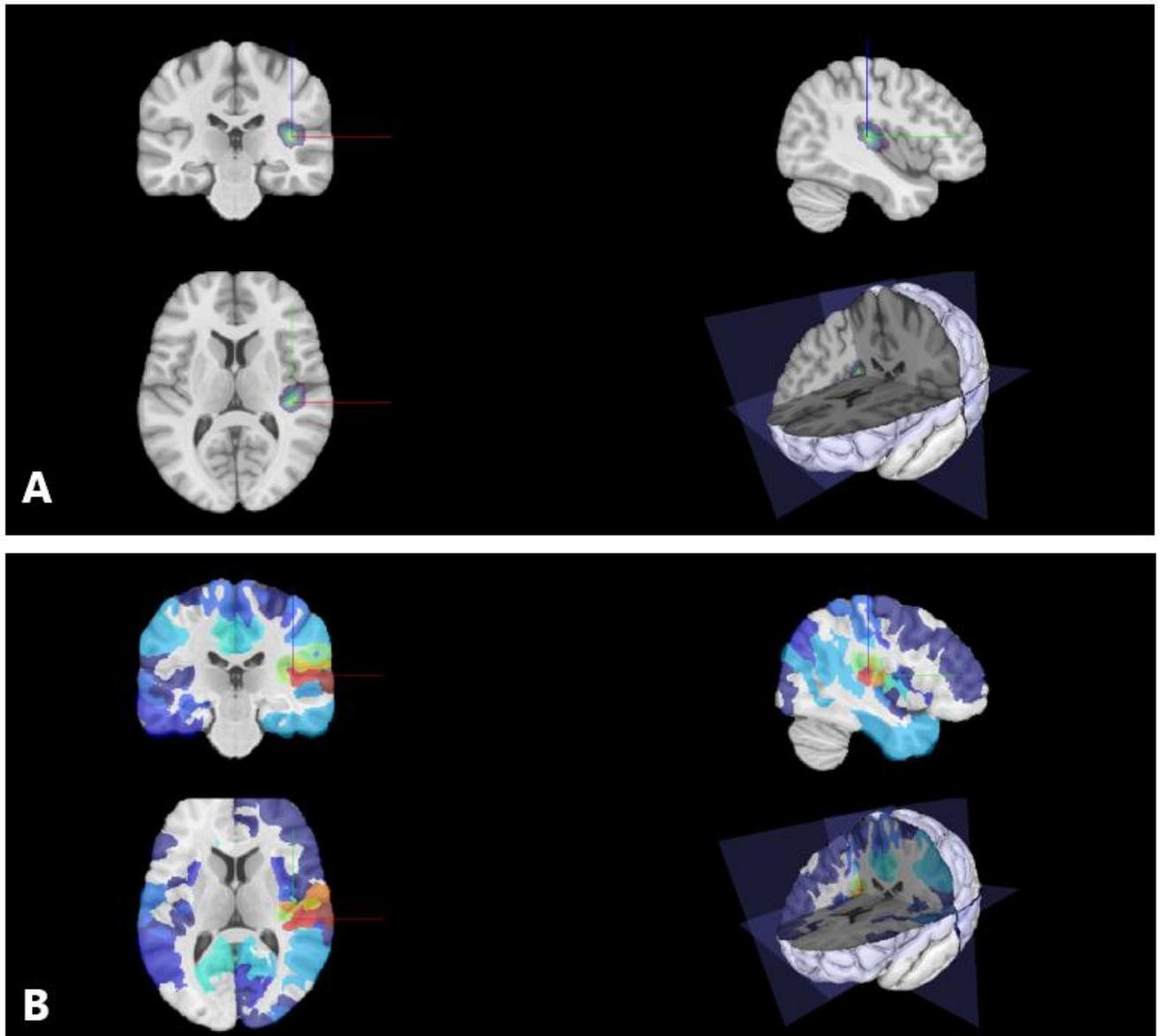
13 **Fig. 8** In vivo tractography reconstruction of the auditory processing pathways from Maffei (2015) [24]. White
 14 dots: arcuate fasciculus; Black dots: ventral pathway; Black star: the Heschl Gyrus

15

16

17 Providing reliable and accurate neuroanatomical atlases nowadays faces considerable challenges because of
 18 discrepancies arising from the variety of techniques employed to study the brain, including morphological, cyto-
 19 and myelo-architectonical investigations and study of functional and cortico-cortical connections. Various
 20 descriptions of HG and PAC could be overcome using a multi-modal parcellation approach that merges multiple
 21 deterministic and probabilistic maps.

1 In this perspective, the Julich-Brain by Amunts et al. [4] is a cytoarchitectonic whole brain parcellation atlas
2 containing probabilistic maps of cortical areas (**Fig. 9A**). The Julich Brain Atlas also proposes connectivity data
3 from the “1000 brains study” by Caspers et al. [8], thus allowing to visualize an estimation of the connection
4 strength from each region to all other areas (**Fig. 9B**).



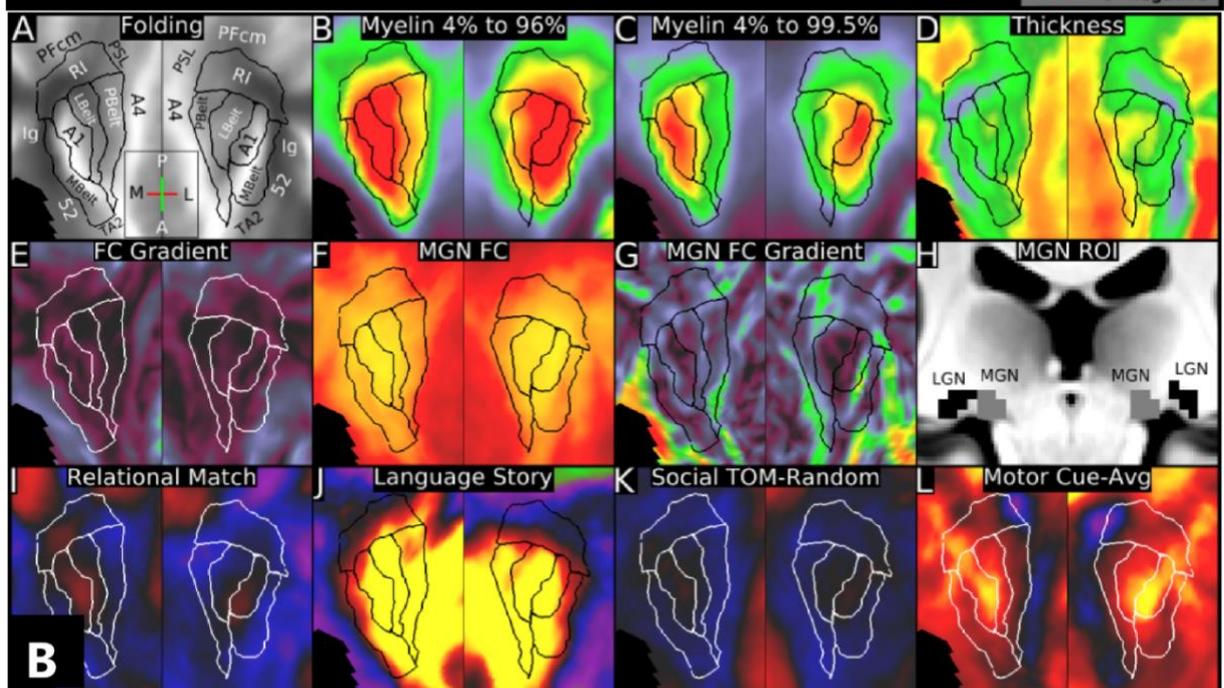
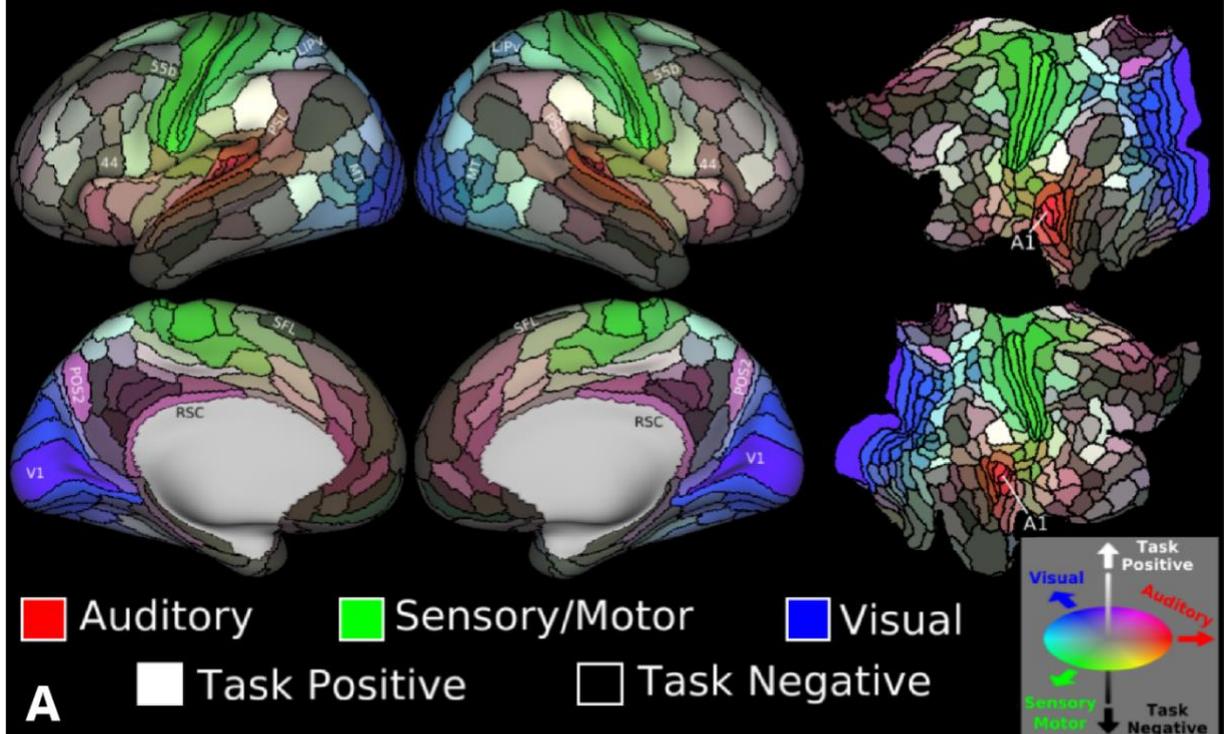
5
6 **Fig. 9** Cytoarchitectonic parcellation and connectivity data from the Julich Brain Atlas. **A:** Area Te1.1 right from
7 Amunts (2021) [4]. **B:** Connectivity profile of Area Te1.1 right (red=high, deep blue=low) from Caspers (2021)
8 [8]. Views from the *siibra-explorer* website: (<https://atlases.ebrains.eu/viewer/>)

9

10

- 1 Another well worth noting work is the population-based 180-areas multi-modal parcellation by Glasser et al. [17]
- 2 that is based upon the Human Connectome Project (Human Connectome Project Multi-Modal Parcellation version
- 3 1.0) (**Figs. 10A and B**).

The HCP's Multi-modal Cortical Parcellation (HCP_MMP1.0)



1

2

1

2 **Fig. 10** The Primary Auditory Cortex in the Human Connectome Project’s multimodal cortical parcellation
3 (version 1.0). **A:** The HCP’s multi-modal parcellation, version 1.0 (HCP_MMP1.0). The Primary Auditory Cortex,
4 Area A1 is represented in red. **B:** Multi-modal information used to parcellate the early auditory areas on flattened
5 surfaces. **A)** early auditory areas; **B)** and **C)** myelin maps; **D)** cortical thickness; **E)** functional connectivity
6 gradients; **F)** connectivity map; **G)** gradient of this map; **I), J), K),** and **L)** relational match, language story, social
7 tom-random and motor cue-avg task contrasts (<https://balsa.wustl.edu/RV3p>) [17] [40]

8

9

10 Given the fast-growing body of neuroimaging data, Yarkoni et al. [43] propose a large scale, high quality,
11 automated meta-analysis approach based upon the functional magnetic resonance imaging literature and available
12 online at neurosynth.org (**Fig. 11**).



13

14 **Fig. 11** Representation of the Heschl Gyrus from Neurosynth.org. This representation is based upon an automated
15 meta-analysis of all the functional magnetic resonance imaging studies in the Neurosynth database whose abstracts
16 include the term “Heschl Gyrus” at least once (85 studies for the HG)
17 (<https://neurosynth.org/analyses/terms/heschl%20gyrus/>) (Yarkoni et al. 2011) [43]

18

19 Finally, Dalboni da Rocha et al. [9] issued a specific and efficient automated segmentation tool dedicated to the
20 HG, TASH, built upon the FreeSurfer software. It allows to process imaging data from large series of subjects
21 (n=181) with satisfactory accuracy (assessed by good Pearson’s correlation scores) and within a shorter time, as
22 compared with the gold standard, manual labelling.

23

1 **Discussion**

2

3 In our study, we examined the morphology, microstructure and functional connectivity of the HG and its included
4 PAC, providing a broad overview of the available knowledge about this structure. We have revisited the original
5 work of Richard L. Heschl, presenting an unpublished French translation. We proposed segmentation criteria and
6 a manually labelled 3D digital model. We illustrated the challenges that modern neuroanatomical atlases face due
7 to the considerable development of neuroimaging and probabilistic approaches in the last decade and how this
8 relates to the HG.

9

10 **Comparative anatomy and an evolutionary perspective**

11 Despite the complexity of language and speech in humans, the structure of the PAC (BA41) for non-human
12 primates is similar to that in humans [22]. From a microanatomical perspective, these similarities include the
13 properties of sensory area, there being a high density of granular cells in layers III and IV of the cortex, a strong
14 expression of acetylcholinesterase, parvalbumin, cytochrome C oxidase, and a significant thalamic input [21]. It
15 has been suggested that structural differences in the PAC of humans are primarily quantitative in nature and could
16 relate to the way language diverged from the communication abilities of earlier primates. This change could be -
17 concomitantly with the increase in brain volume- alongside more complex communicative and social interactions.
18 A further consideration is the strong involvement of BA47 (the orbital area of the prefrontal cortex) in language
19 processing. The human prefrontal cortex is involved in the processing of syntax, relying on a different connectivity
20 of the ventral pathways for complex sounds processing (including Broca's area or BA 44/45) compared with non-
21 humans. However, there is great similarity in the extreme capsule (a long bidirectional association pathway
22 involved in language), as demonstrated between humans and macaques.

23 Differences in humans with respect to the anatomical and functional interhemispheric variability and the language
24 and speech related cortical areas of the left hemisphere could be related to levels of linguistic skills. Differences
25 in auditory processing among species have also been described. For instance, the auditory cortex of the rhesus
26 macaque has been shown to show species-specific vocalisations and to respond more to based-passed noises (BPN)
27 than to pure tone [36]. With regard to the areas associated with the PAC (core area), namely the belt, parabelt and
28 lateral belt areas, the degree of similarity between humans and non-human primates appears to be very high. Hence,
29 differences seem to concern high levels of auditory processing rather than the structure of the PAC [21].

1

2 **Clinical considerations**

3 It has been shown that the HG is linked to acoustic processing [41] and the morphology and size of the HG have
4 been linked to linguistic and musical abilities. Some authors have even considered the HG provides
5 neuroanatomical markers for these abilities [38, 42]. It has been reported that duplication of the HG in the right
6 cerebral hemisphere is correlated to higher scores in foreign languages and musicality tests.

7 In terms of language skills, bilinguals have larger HGs and multiple HGs in the right hemisphere and increased
8 grey matter volumes are correlated to language aptitude in children and teenagers [37]. Dyslexia has been linked
9 to a large duplication of the left HG [23]. Moreover the anatomy of the HG appears to be related to handedness
10 and its gyrification pattern to speech-listening hemispheric lateralization [39].

11 In terms of musicality, an increased volume in the right cerebral hemisphere is linked to the ability to identify each
12 sound by its name/frequency (“absolute pitch”) [42]. Multiple HGs, or an increased grey matter volume for this
13 structure, have also been more frequently identified in both professional and amateur musicians than in non-
14 musicians [6]. The morphology of HG has additionally been linked to musical instrument preference and multiple
15 HGs, and an increased volume in the left hemisphere, have been found in patients with hypermusia associated with
16 Williams Syndrome (microdeletion 7q11.23).

17 In deaf persons, the volume of the HG is not modified, although the grey/white matter ratio increases in favour of
18 grey matter. A reduction of the volume of the HG has also been correlated with tinnitus and, in the rare case of a
19 bilateral infarct of the HG, a cortical deafness can be observed [27]. Indeed, the ascending pathway of the auditory
20 system projects bilaterally to the primary auditory cortical areas, thus explaining why a unilateral acute cerebral
21 ischemia does not result in deafness, whereas an infarct of Broca’s area (BA 44/45) is more reliably associated
22 with aphasia.

23 Concerning psychiatric disorders, several studies have linked the morphology of the HG to auditory hallucinations
24 in patients with schizophrenia or schizophrenia spectrum disorders, one of the most recent being described by
25 Takahashi et al. [35]. Furthermore, the white and grey matter volumes in female patients suffering from this
26 psychiatric disorder seem inversely correlated to the symptom’s severity [12] but, regarding the grey matter, this
27 result is also found in male patients. Paradoxically, auditory hallucinations in patients with schizophrenia could
28 cause, over time, an increase in HG volume.

29 Beyond the above anatomical, functional, and pathological considerations, a major point to be elucidated is the
30 part played by neural plasticity in converting the subject’s experiences and the part of innate genetic factors.

1 Eventually, further histological and molecular studies are required to understand the mechanisms connecting
2 descriptive anatomy, pathology and linguistic or musical abilities [44].

3

4 **Strengths and limitations**

5 Our study has several strengths. The literature review we propose is comprehensive, including historical sources
6 than are often cited but not discussed in detail in most studies. Given the diverse backgrounds of the authors, we
7 provide an overview of knowledge about the HG that merges perspectives from different relevant fields, including
8 neuroradiology, psychiatry, medical anatomy, neuroscience, cognitive science, literature, and music.

9 Nevertheless, our study also has several limitations. The segmentation criteria are mainly based on subjective
10 experience, pedagogical tradition, and a review of the literature. The 3D digital model we propose has not been
11 evaluated by an independent panel and the criteria have not been tested in a prospective, single-blind, comparative
12 cohort study. They have a low level of evidence by current methodological standards. Such an experiment could
13 be conducted with first, second and third year medical students in European countries, for example, although
14 establishing standardised conditions and achieving statistical significance may be difficult due to the number of
15 participants required. By comparison, Dalboni da Rocha et al [9] in the TASH study use a single expert to set the
16 gold standard (manually labelled segmentation) to compare and validate their automated segmentation method.

17

18 **Perspectives**

19 There is no doubt that new technological breakthroughs in the fields of functional neuroimaging, probabilistic
20 neuroimaging data processing, and high-performance computing in a broad sense will both challenge and expand
21 our current knowledge of the HG. As discussed by Amunts et al [2], the construction of reliable digital twins of
22 the brain may be the next important and disruptive step in achieving clinically relevant applications.

23

24 **Conclusion**

25

26 We were able, by means of a thorough review of the literature, to define clear, coherent and reliable criteria for
27 manual labelling of the HG. These criteria could be used as groundwork to ensure the coherence of the various

1 studies devoted to the HG, and to establish, and validate automated segmentation methods. Richard L. Heschl's
2 work is still relevant today and could impulse further anatomical and functional studies in neurosciences.

3

4 **Declarations:**

5 **Ethical Approval**

6 Not applicable.

7 **Competing interests**

8 The authors have no conflicts of interest to declare.

9 **Author's contributions**

10 DH: Project development, Data collection or management, Data analysis, Manuscript writing/editing

11 IB: Data collection or management, Data analysis, Manuscript writing/editing

12 BM: Data analysis, Manuscript writing/editing

13 VF: Data collection or management, Data analysis, Manuscript writing/editing

14 OP: Data analysis, Manuscript writing/editing

15 AG: Project development, Data collection or management, Data analysis, Manuscript writing/editing

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18 **Availability of data and materials**

19 All data are available on request from the corresponding author.

20

21

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19 **Acknowledgements**

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28 the NIH Blueprint for Neuroscience Research; and by the McDonnell Center for Systems Neuroscience at
29 Washington University.

30 Figure 11 is reproduced with permission from Neurosynth

1

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3 "naturhistorisches Museum" in Vienna. We thank Petra Greeff, Eduard Winter and Gerald Höfler for their
4 valuable help.

5

6

7

8 **Supplementary Information**

9 Below is the link to the electronic supplementary material.

10