



Research paper

Hearing it right: Evidence of hemispheric lateralization in auditory imagery

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ARTICLE INFO

Article history:

Received 21 July 2015

Received in revised form

26 November 2015

Accepted 2 December 2015

Available online 17 December 2015

Keywords:

Auditory imagery

Hemispheric asymmetry

Right ear advantage (REA)

Auditory hallucinations

ABSTRACT

An advantage of the right ear (REA) in auditory processing (especially for verbal content) has been firmly established in decades of behavioral, electrophysiological and neuroimaging research. The laterality of auditory imagery, however, has received little attention, despite its potential relevance for the understanding of auditory hallucinations and related phenomena. In Experiments 1–4 we find that right-handed participants required to imagine hearing a voice or a sound unilaterally show a strong population bias to localize the self-generated auditory image at their right ear, likely the result of left-hemispheric dominance in auditory processing. In Experiments 5–8 – by means of the same paradigm – it was also ascertained that the right-ear bias for hearing imagined voices depends just on auditory attention mechanisms, as biases due to other factors (i.e., lateralized movements) were controlled. These results, suggesting a central role of the left hemisphere in auditory imagery, demonstrate that brain asymmetries can drive strong lateral biases in mental imagery.

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1. Introduction

One aspect of cerebral lateralization that has received relatively more attention concerns hemispheric asymmetries for different categories of auditory stimuli: starting with Broca (1861), decades of research have shown a clear left-hemispheric advantage for speech (Bidelman and Bhagat, 2015), whereas the proposed right-hemispheric superiority for non-speech sound processing still remains more controversial (i.e., Brancucci et al., 2008; Brancucci et al., 2012; Fischer et al., 2009; Lewis et al., 2006; Okamoto et al., 2009). Evidence of hemispheric asymmetries in the auditory modality comes from both anatomical and functional investigations. Regarding anatomical substrates, it is well-known that the most asymmetric cerebral structure of the human brain belongs to the auditory cortex in the posterior portion of the superior temporal gyrus (STG), namely the *planum temporale* (PT), more extended in the left than in the right hemisphere, mainly in right-handers (i.e., Steinmetz et al., 1991). Moreover, this anatomical asymmetry directly leads to functional asymmetries (i.e., speech versus music sounds; spectral versus temporal processing, and so

on), confirmed by experimental results (i.e., Tervaniemi and Hugdahl, 2003; James et al., 2015).

The behavioral paradigm most used in the study of asymmetric auditory processing is the Dichotic Listening (DL) test, in which two different stimuli are simultaneously delivered in the two ears and the listener is asked to specify the item heard first or best (Kimura, 1967). By means of DL a large number of studies have shown the so-called Right Ear Advantage effect (REA; Kimura, 1961), which has been confirmed also by means of brain imaging and electrophysiological studies (i.e., Eichele et al., 2005; Hirmstein et al., 2013), as well as ecological observation (Marzoli and Tommasi, 2009).

The REA is so reliable a bias that its deviation is considered a marker of language impairments, such as dyslexia (see Beaton, 1997; for a review), and correlates with psychiatric conditions, such as auditory hallucinations (see Hugdahl, 2009; Hugdahl et al., 2008b; for reviews). Interestingly, contrasting results have been collected regarding the relationship among PT size, REA effect, and auditory hallucinations: if on one hand a number of morphometric studies have shown the connection between reduced STG area and the severity of schizophrenic symptoms (Modinos et al., 2013) as well as reduced REA (Løberg et al., 1999), on the other hand an increased activation of the STG has also been shown in schizophrenic patients during the experience of auditory hallucinations (Hugdahl et al., 2009; Hugdahl et al., 2003; Lennox et al., 2000; Løberg et al., 2004). Moreover, besides the role of the temporal

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cortex in the genesis of auditory hallucinations, many other cerebral areas seem to be involved in different aspects of hallucinatory experience (Jones and Fernyhough, 2007; Rapp and Steinhäuser, 2013; Stéphane, 2013; van de Ven and Linden, 2012).

Auditory hallucinations are specific symptoms of psychotic disorders (Larøi et al., 2012), mainly schizophrenia (70% of schizophrenic patients report hallucinatory experiences), but they are also relatively frequent in the non-clinical population (4–15%, Hill and Linden, 2013). Daalman et al. (2011) compared the performance of 101 non-clinical participants with frequent hallucinations with that of 101 matched participants without hallucinations, and they found a lower performance in executive functions and verbal abilities in participants who experienced auditory hallucinations. Verbal abilities of patients with hallucinations were taken into consideration also in the model proposed by Hugdahl (2009), who attributed their deficit in bottom-up perceptual processes to a failure of top-down control: according to this model, a failure of prefrontal and cingulate inhibition processes could be the cause of the hyper-activity of the temporal-linguistic cortex. In line with this view, in an fMRI study on healthy participants, Hunter et al. (2005) found a left-hemispheric temporal activity during silence, that also led to right-hemispheric activity by means of homotopic inter-hemispheric connections. The authors proposed that this “default mode” auditory pathway, activated without real stimulation, could constitute the neural basis of auditory hallucinations, mainly involving temporal areas in the left hemisphere. Similarly, Kraemer et al. (2005), by means of fMRI, showed that silent gaps during the listening of familiar songs induced a greater activation in the left auditory cortex, when compared to unknown songs: during the silent gaps, participants imagined a continuation of the familiar song presented, and the authors attributed the activity of these areas to such spontaneous auditory imagery.

A specific issue in the context of auditory hallucinations is the spatial localization of the imaged sound source, that is, if the sound source was imagined to be outside the body or if the sound was heard ‘in the head’. Hunter et al. (2003a) investigated the neural bases of experiencing inside- and outside-head “hallucination-like voices”, namely voices recorded with the same characteristics of the voices often listened by patients who experience auditory hallucination (male voices with a neutral emotional valence, uttering commands in the second person): they found that the left PT was crucially activated by outside-head voices, independently of the actual left or right provenance of hallucination-like stimuli. In line with these findings, in a behavioral study by the same group it was found that right-handed healthy participants showed a REA effect in distinguishing between the inside and the outside source of hallucination-like voices (Hunter et al., 2003b). In a recent survey on the phenomenological aspects of auditory hallucinations carried out on 198 psychiatric patients, McCarthy-Jones et al. (2014) confirmed in the clinical population the dichotomy introduced by Hunter and colleagues between the spatial source of hallucinations, described as heard coming from ‘inside’ or ‘outside’ the head, with 47% of patients reporting “internal”, 38% reporting “external”, and 15% reporting both internal and external localized hallucinations. Moreover, for voices/sounds heard as coming from inside the head, 46% of patients localized them “inside all over” and 23% “inside middle”; for voices/sounds heard as coming from outside the head, 38% of participants localized them “outside all around”, 29% “outside left”, and 22% “outside right”. The authors also found that 32% of patients reported hearing non-verbal sounds. Finally, one of the few lateralization studies on hallucinations dealt with two patients with right-sided temporal lobe epilepsy, who experienced hallucinations as left-lateralized (Hug et al., 2011).

The cerebral lateralization of auditory imagery and hallucinations probably depends on shared brain processes but its direction

is unclear. As pointed out by Hugdahl (2009), auditory hallucinations could depend on the hyper-activity of the left-hemispheric peri-Sylvian regions. Accordingly, when tested by means of a DL test, patients with hallucinations fail to show the REA effect, and this failure may be explained by the competition for the left-hemispheric linguistic access by both perceptual and hallucinatory inputs. On the other hand, however, Zatorre and Halpern (1993) found that patients with right temporal-lobe lesions performed significantly worse on both perceptual and imagery pitch discrimination tasks than either patients with left temporal-lobe lesions or normal controls, suggesting a right temporal lobe specialization for auditory imagery (for a comprehensive review, see Halpern, 2003). Shergill et al. (2001) asked healthy participants to perform two different tasks during fMRI: inner speech production and auditory verbal imagery. The authors found that inner speech activated left frontal and temporo-parietal areas, as well as the right cerebellum and supplementary motor cortex; the same areas were also bilaterally activated during verbal imagery, together with precentral and superior temporal gyri. In accordance with these results, a number of studies have shown a different pattern of cerebral activity related to “inner voice” (auditory images of a voice in third person, with articulatory information) and to “inner ear” (auditory images of one’s own voice, without kinesthetic information; e.g., McGuire et al., 1996a; b; Shergill et al., 2001; Shergill et al., 2000; Smith et al., 1995). However, the distinction between inner voice and inner ear has been recently doubted (for a deepened discussion see Hubbard, 2010, 2013b). Paradoxically, despite the amount of studies that have focused on cerebral activation during imagery/hallucinations, the behavioral lateralization of these phenomena has received little attention (see Hubbard, 2010). In the field of auditory perception the REA effect has been widely explored primarily by exploiting the DL, but a possible lateral bias for verbal and non-verbal auditory images remains largely unexplored.

In the present study we aimed at investigating the lateralization of verbal and non-verbal auditory imagery, focusing on both imagery experienced as originating inside the head or as produced by an object outside the body, and exploring possible confounding effects. To these aims, in a series of eight Experiments, we asked healthy participants to imagine a lateralized auditory input and to report in which ear the input had been experienced. Based upon the REA effect found with physical auditory inputs, we hypothesized a right ear bias. Moreover, we tried to disentangle the role of the auditory component of imagery from that of motor behaviors implied in communication, asking participants to imagine listening while being spoken to one ear, or to speak into one ear of another person, or to orient one ear to a whispering person. The hypothesis was that, if the expected bias in auditory imagery is exclusively centered on the auditory modality, this bias should be confirmed during imaginary listening, but it should disappear when the attention is shifted to other aspects, as the imaginary movement carried out to speak or to listen someone else’s voice. If these hypotheses are confirmed, two main conclusions could be drawn: from an applied point of view, the auditory imagery protocol could be considered as a novel, ecological, and easy-to-use tool to evaluate the hemispheric superiority in auditory processing; from a theoretical point of view, the REA effect expected in this task could be considered as a behavioral confirmation with healthy participants of Hugdahl’s model explaining the self-generated auditory inputs (in clinical and non-clinical “voice hearers”) as caused by an endogenous activity of the auditory areas, mainly involving the left hemisphere (Hugdahl, 2009).

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