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Hearing it right:

Evidence of hemispheric lateralization in auditory imagery

Giulia Prete*, Daniele Marzoli, Alfredo Brancucci & Luca Tommasi

Department of Psychological Science, Health and Territory, 'G. d'Annunzio' University of Chieti-Pescara, Italy

* Corresponding author:

Giulia Prete

Department of Psychological Science, Health and Territory, University of Chieti

BLOCCO A, Via dei Vestini 29

I-66013 Chieti, Italy

e-mail: giulia.prete@unich.it

Tel.: +39 871 3554216

Fax: +39 871 35542163

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.

Keywords: Auditory imagery; Hemispheric asymmetry; Right ear advantage (REA); Auditory hallucinations.

Running title: Right ear bias in auditory imagery

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 & Bhagat, 2015), whereas the proposed right-hemispheric superiority for non-speech sound processing still remains more controversial (i.e., Brancucci, D'Anselmo, Martello & Tommasi, 2008; Brancucci et al., 2012; Fischer et al., 2009; Lewis, Phinney, Brefczynski-Lewis & DeYoe, 2006; Okamoto, Stracke, Draganova & Pantev, 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, Volkmann, Jäncke & Freund, 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 & 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, Nordby, Rimol & Hugdahl, 2005; Hirnstein, Westerhausen, Korsnes, & Hugdahl, 2013), as well as ecological observation (Marzoli & 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, Løberg, Specht, et al., 2008, 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, Hugdahl, & Green, 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, Løberg & Nygård, 2009; Hugdahl et al., 2003; Lennox, Park, Medley, Morris & Jones, 2000; Løberg, Jørgensen & Hugdahl, 2004). Moreover, besides the role of the temporal cortex in the genesis of auditory hallucinations, many other cerebral areas seem to be involved in different aspects of hallucinatory experience (Jones & Fernyhough, 2007; Rapp & Steinhäuser, 2013; Stephane, 2013; van de Ven & 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 & Linden, 2013). Daalman and colleagues (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 and colleagues (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, Macrae, Green and Kelly (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 and colleagues (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 and colleagues (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, Bartsch, & Gutschalk, 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 and colleagues (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, Silbersweig, Murray et al., 1996; McGuire, Silbersweig, Wright et al., 1996; Shergill et al., 2001; Shergill, Bullmore, Simmons, Murray & McGuire, 2000; Smith, Wilson & Reisberg, 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).

2. Materials and method

2.1. General procedure

A total sample of 400 right-handed participants were involved in the study (19 to 36 years old), divided in 8 single-trial Experiments (50 participants each). All of them were approached individually by a female experimenter, mainly at the Chieti University campus, making sure that the immediate surroundings were silent enough and that there was a chair on which the participant could sit.

The general procedure was similar in all experiments, and it was composed of three phases. In the first phase, the participant was approached by the experimenter and she/he was invited to take part in a short imagery task. There were not strict criteria in the selection of potential participants, except that both females and males had to be recruited in similar numbers, and that their age was between 18 and 30 years. Then, the participant was asked whether she/he suffered or had suffered of hearing problems, and only participants without previous or current hearing deficits were selected to take part in the test.

In the second phase, the participant was asked to sit, and to place her/his hands palm-down on the knees, without crossing either legs nor arms. The experimenter, standing behind the participant, instructed her/him to wear sound-attenuating headphones - used to allow participants to focus on the instructions and to not be distracted by possible environmental noises - and to close the eyes. Then, specific instructions were verbally read to the participant, ensuring that she/he could hear the experimenter's voice (the experimenter taking care to speak loudly enough to be heard by the participant). In the instructions, participants were asked to imagine hearing something at only one ear, but without specifying what kind of input had to be imagined (e.g., their own voice or another person's voice). The experimenter slowly repeated twice the specific instructions, and then she asked the participant whether she/he was able to clearly imagine the content as required. Once the participant stated that she/he had a vivid image consistent with the instructions, the experimenter asked her/him to open the eyes, and then she formulated the experimental question, namely at which ear the content had been heard. Participants who had difficulty in imagining the stimulus, or in imaging the stimulus at only one ear, were excluded from the study (3 participants were excluded for these reasons). The participant was then asked to briefly describe the content of the imagery.

In the last phase, the participant was asked to complete the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985), according to which the handedness score ranges from –100 (totally left handed) to +100 (totally right handed). The test was administered at the end of the procedure, in order to avoid a possible influence of the test on the lateralized response of participants. Among the 21 items in the inventory, 12 are referred to the laterality preference for the use of arms/hands, 3 for legs/feet, 3 for eyes, and 3 for ears. For each item, participants had to express their laterality preference according to 5 values: absolutely left (value -2), preferentially left (value -1), no preference (value 0), preferentially right (value +1), absolutely right (value +2). Besides the overall laterality index calculated considering all the items (using the formula [(Right preference – Left preference) / (Right preference + Left preference) × 100]), for each participants an ear laterality index was calculated considering the 3 items concerning ear preference (by means of the same formula). Moreover, in order to quantify the ear preference, the ear laterality index was compared with the no preference score (value 0) by means of exact t-tests. Porac, Coren, Steiger and Duncan (1980), by means of factor analytic techniques, have shown that human laterality preference is multidimensional, finding three independent factors representing limb (both arms and legs), eye, and ear preference, without difference among age and sex. Thus we did not expect differences in ear preference between left-handers and right-handers, because handedness laterality should be independent of ear laterality (see Porac et al., 1980), however we decided to test a group as homogeneous as possible, so only right-handed participants were involved in the experiments.

Each participant performed a single trial, taking part only in one experiment, as in previous studies in which a similar imagery procedure was used (Marzoli, Menditto, Lucafò & Tommasi, 2013; Marzoli, Mitaritonna, Moretto, Carluccio & Tommasi, 2011; Marzoli, Palumbo et al., 2011,), with the aim to avoid any possibility that repeated trials could be influenced by the first response. The entire procedure was carried out in accordance with the principles of the Declaration of Helsinki and lasted about 5 minutes for each participant.

For each Experiment the frequency of “Left Ear” (LE) and “Right Ear” (RE) responses were collected and compared by means of Chi-square tests. The desired sample size was calculated considering an alpha power of .05 and a power goal of .80. Based on a pilot study we estimated a population proportion of RE response of 0.7 (70% estimated RE responses) and a null proportion of 0.5 (random distribution of LE and RE responses). Starting from these values, the required sample size for each experiment was 46 participants, considering a two-tailed test. In order to obtain reliable results, each experiment was administered to 50 participants.

3. Results

3.1. Experiment 1

Experiment 1 was aimed at investigating the possible presence of a side preference in imagining a voice. The sample of 50 participants was composed of 37 females and 13 males, with an overall laterality quotient of 86.76 (± 2.45) and an ear laterality quotient of 54 (± 8.71; $t_{(49)}$ = 6.265, $p < .001$). The instructions were the Italian version of: “*Keeping your eyes closed, imagine hearing a voice at one ear*”. The voice was imagined as heard at the LE by 10 participants and at the RE by the remaining 40 participants (Figure 1). The asymmetry was statistically significant ($X_{(1)}$ = 18, $p < .001$, Cohen’s $d = 1.5$, $\eta^2 = .36$), providing evidence of a right ear bias in auditory imagery for voices.

********** FIGURE 1 ABOUT HERE **********

3.2. Experiment 2

Experiment 2 was aimed at investigating the potential side preference in imagining a non-specific sound. The sample of 50 participants was composed of 42 females and 8 males, with an overall laterality quotient of 87.49 (± 2.72) and an ear laterality quotient of 46 (± 7.63; $t_{(49)}$ = 6.09, $p < .001$). The instructions were the Italian version of: “*Keeping your eyes closed, imagine hearing a* *sound at one ear*". The sound was imagined as heard at the LE by 13 participants and at the RE by the remaining 37 participants (Figure 1). The asymmetry was statistically significant ($X_{(1)} = 11.52$, $p < .001$, Cohen's $d = 1.09$, $\eta^2 = .23$), confirming the right ear bias in auditory imagery for a non-specific sound input.

3.3. Experiment 3

Experiment 3 was aimed at clarifying the result of Experiment 1, starting from the differentiation between voices heard "inside" and "outside" the head. Specifically, because in Experiment 1 participants were asked to imagine a voice "at" one ear, possibly evoking an "external" source, Experiment 3 was aimed at investigating the side preference in imagining a voice from "inside" the head. To this aim, the instructions were the Italian version of: "*Keeping your eyes closed, imagine hearing a voice in one ear*". The sample of 50 participants was composed of 25 females and 25 males, with an overall laterality quotient of 87.22 (± 2.21) and an ear laterality quotient of 23.33 (± 10.68; $t_{(49)} = 2.209$, $p = .032$). The voice was imagined as heard in the LE by 17 participants and in the RE by 33 participants (Figure 1). The asymmetry was statistically significant ($X_{(1)} = 5.12$, $p = .024$, Cohen's $d = 0.67$, $\eta^2 = .10$), confirming the right ear bias in auditory imagery for voices. Finally, the frequencies of RE responses in Experiments 1 and 3 were compared by means of a chi-square test, showing that there was no statistical difference between the lateral bias concerning voices imagined as heard "in" and "at" one ear ($X_{(1)} = 0.67$, $p = .412$).

3.4. Experiment 4

Experiment 4 was aimed at clarifying the result of Experiment 2, in which participants were asked to imagine a sound "at" one ear. In Experiment 4, aiming at investigating the laterality in imagining a sound from "inside" the head, the instructions were the Italian version of: "*Keeping your eyes closed, imagine hearing a sound in one ear*". The sample of 50 participants was composed of 25 females and 25 males, with an overall laterality quotient of 89.64 (± 2.75) and an ear laterality quotient of 30 (± 8.62; $t_{(49)} = 3.516$, $p < .001$). The sound was imagined as heard in the LE by 16 participants and in the RE by 34 participants (Figure 1). The right ear bias was confirmed again, since the asymmetry was statistically significant ($X_{(1)} = 6.48$, $p = .011$, Cohen's $d = 0.77$, $\eta^2 = .13$). The frequencies of RE responses in Experiments 2 and 4 were compared by means of a chi-square test, showing that there was no statistical difference between the lateral bias concerning sounds imagined as heard "in" and "at" one ear ($X_{(1)} = 0.35$, $p = .553$).

3.5. Experiment 5

Starting from the right ear bias found in the first 4 experiments, Experiment 5 was aimed at investigating the possible effect of the presence of an "agent" in the process of generating an external mental image of a voice input. The sample of 50 participants was composed of 28 females and 22 males, with an overall laterality quotient of 82.54 (± 3.34) and an ear laterality quotient of 52.67 (± 8.28; $t_{(49)} = 6.424$, $p < .001$). The instructions were the Italian version of: "*Keeping your eyes closed, imagine that someone is saying something to you at one ear*". The voice was imagined as heard at the LE by 18 participants and at the RE by the remaining 32 participants (Figure 1). Also in this case, the result confirmed a significant right ear bias ($X_{(1)} = 3.92$, $p = .047$, Cohen's $d = 0.58$, $\eta^2 = .08$).

3.6. Experiment 6

Experiment 6 was aimed at better disentangling the possible effect of the mere presence and the directed movement of an imagined agent, on the lateral preference in imagining a voice. The sample of 50 participants was composed of 29 females and 21 males, with an overall laterality quotient of 85.85 (± 2.6) and an ear laterality quotient of 46.67 (± 8.82; $t_{(49)} = 5.346$, $p < .001$). The instructions were the Italian version of: "*Keeping your eyes closed, imagine a person who stands in front of you. Now imagine that this person approaches and says something to you at one ear*". In this case, 25 participants reported to have imagined the voice at the LE and 25 participants at the RE ($X_{(1)} = 0$, $p = 1$), thus showing no asymmetry (Figure 1).

3.7. Experiment 7

Results of Experiments 1 to 4 showed a strong right ear advantage during auditory imagery; Experiment 5 confirmed a significant bias even including an agent in the imagined scene, but Experiment 6, in which the responses were influenced by the movement of the agent, showed no asymmetry. In this latter case, in fact, participants were asked to report at which ear the imagined agent had spoken, but firstly they were asked to imagine the agent who approached them: the response of participants was thus determined by such movement, so that if the agent moved toward the listener's right side, the listener should report having heard something in her/his right ear. Thus, with the aim to investigate the role of the "agent" also in a first person's perspective in the imagined interaction, Experiment 7 investigated the lateral preference in saying something at someone else's ear (the participant becoming the "speaker" of the imagined interaction). The sample of 50 participants was composed of 39 females and 11 males, with an overall laterality quotient of 83.21 (± 2.54) and an ear laterality quotient of 37 (± 8.46; $t_{(49)} = 4.418$, $p < .001$). The instructions were the Italian version of: "*Keeping your eyes closed, imagine a person who stands in front of you. Now imagine saying something at one ear of this person*". Participants were asked to report at which ear of the person they had imagined to speak. The action was imagined as directed towards the person's LE by 27 participants, and to the person's RE by the remaining 23 participants (Figure 1). The analysis was not significant ($X_{(1)} = 0.32$, $p = .57$), confirming the result of Experiment 6: the interaction with another person - implying one's own directed movement toward someone else - did not yield any asymmetry.

3.8. Experiment 8

Experiment 8 was aimed at clarifying the possible existence of a lateralized bias in the imagined interaction between two persons, avoiding to focus the attention of participants on the imagined movement, and trying to focus specifically on listening. The sample of 50 participants was composed of 39 females and 11 males, with an overall laterality quotient of 77.04 (± 3.5) and an ear laterality quotient of 32.87 (± 8.94; $t_{(49)} = 3.712$, $p < .001$). The instructions were the Italian version of: "*Keeping your eyes closed, imagine a person who stands in front of you. This person is whispering something. Now imagine moving one ear to the person's mouth in order to hear what the person is saying*". The action was imagined as carried out involving the LE by 18 participants and the RE by the remaining 32 participants (Figure 1). The asymmetry was statistically significant ($X_{(1)} = 3.92$, $p = .047$, Cohen's $d = 0.58$, $\eta^2 = .08$), confirming the right ear advantage in auditory imagery for listening to voices.

3.9. Effects of imagined content

In all Experiments, participants were required to describe the content of the imagery in order to be sure that they had imagined the content specified in the instructions (i.e., sounds in Experiments 2 and 4, voices in the other Experiments). A qualitative inspection of these data revealed that in the experiments involving non-specific sounds (Experiments 2 and 4), 24% of the 100 participants reported to have imagined hearing a whistle, 10% musical instruments,16% environmental noises, 10% a clicking sound, whereas the response of the other 40% of participants did not fit any of these categories. A chi-squared test was used to compare the "human source sounds" (whistle and musical instruments) with the "natural sounds" (environmental noises and clicking sounds), and the result showed that there was no difference between these two categories, considering both Experiments 2 and 4 together ($X_{(1)} = 1.06$, $p = .302$), and separately (Experiment 2: $X_{(1)} = 0.714$, $p = .398$; Experiment 4: $X_{(1)} = 0.36$, $p = .548$). In the remaining experiments, in which participants were asked to imagine a voice, 48% of the 300 participants reported the sex of the imagined voice. Among these participants, 49.48% reported to have imagined a female voice and

50.52% a male voice, thus showing no preference according to the sex of the heard voice ($X_{(1)}$ = 0.02, p = .885). Moreover, the group in which a female voice was imagined was composed of 57.89% female participants (42.11% males), whereas the group in which a male voice was imagined was composed of 62.89% female participants (37.11% males). A 2×2 Chi-square test was used to investigate the possible interaction between the sex of the participants and the sex of the imagined voice, and the result was not significant ($X_{(1)}$ = 0.50, p = .479). As regards the emotional content of the imagined voices, the majority of participants reported a neutral message (for instance "hello", or "how are you?") and only 8.5% of the 300 participants reported a message with an unequivocal emotional content. Specifically, among these participants, 94.12% imagined a positive content (i.e., "I love you") and only 5.88% imagined a negative content (i.e., "I am worried"), showing a clear prevalence of positive content ($X_{(1)}$ = 26.47, p < .001, Cohen's d = 3.75, η^2 = .78), even if it should be remembered that the majority of participants reported to have imagined a neutral content (91.5%).

4. Discussion

The first aim of the study was to document a preference for imagining sounds in the right ear in the absence of acoustic stimulation. To our knowledge, this is the first time in which an ear preference was systematically investigated in a paradigm requiring pure mental imagery of auditory content: the REA effect extends beyond the domain of auditory perception, to that of auditory imagery. This result allows us to conclude that the imagery paradigm could be considered as a valid tool for the investigation of hemispheric asymmetries, at least in the auditory domain. Moreover, the present results could also be viewed as in line with the model proposed by Hugdahl (2009), concerning the causal role of left-hemispheric linguistic areas in the genesis of auditory hallucinations. Importantly, we showed that the bias is due to the auditory component of imagery, as it disappeared in those conditions in which the attention of participants was shifted from the imagery of listening to the imagery of approaching towards one ear for speaking (acted either by the participant or by the imagined person).

In the first four experiments we found a strong asymmetry in favor of the right ear. We manipulated the internal/external source of the imagined input by means of a specific linguistic change, namely the preposition used in the instructions (i.e., hearing something "at" or "in" one ear). In this regard, it is difficult to clearly state that this linguistic manipulation was effective in modulating the internal/external source of the imagined stimulus, but we started from the assumption that the preposition "at" could have conveyed a sense of direction (from outside the head), whereas the preposition "in" could have conveyed a sense of internal presence (inside the head). Notably, we expected to find a right ear preference in Experiments 1 and 3, in which participants were asked to imagine a voice, but we expected to find a left ear advantage in Experiments 2 and 4, in which participants were asked to imagine an unspecified sound. Nevertheless, we found a strong right ear preference in all these conditions, possibly corresponding to a left-hemispheric superiority for both verbal and non-verbal imagery. Importantly, in the non-verbal conditions, we did not require participants to imagine a specific content, so that the heterogeneity of the imagined sounds (i.e., musical instruments, natural sounds, tools, melodies, and so on) might have influenced the results. In this regard, in fact, it is useful to highlight that hemispheric asymmetry for non-verbal stimuli appears somewhat unclear, some studies supporting a clear right-hemispheric superiority, others showing less asymmetric results (e.g., Boucher & Bryden 1997; Brancucci & San Martini, 1999, 2003; Brancucci et al., 2008, 2012), or the opposite pattern (Noonan & Axelrod, 1981).

After confirming the right ear preference by means of the imagery paradigm, the second aim of the present study was to exclude some of the possible confounding effects underlying this bias. In order to obtain clearer results, only right-handed participants were recruited for the study, in order to avoid further confounding effects possibly due to the potentially different cerebral lateralization in linguistic processing in left-handers. However, this choice could cast the doubt that the bias we found reflected a mere motor asymmetry. To this aim, in Experiments 5 to 8 we investigated the possible role of movement of the imaged sound source in determining the ear asymmetry. The results showed that stressing the simple presence of another person in the role of source did not abolish the effect (i.e., Experiment 5), but – importantly – when the attention of participants was specifically (and voluntarily) focused on movements aimed at speaking rather than at listening, the bias disappeared (i.e., Experiments 6 and 7), to resurface when one's own movement was functional to listening (Experiment 8). This evidence allow us to be confident about the auditory nature of the bias: in the two experiments in which participants were explicitly required to imagine a person in front of them, and then that the person moved towards them or that they moved towards the person, the asymmetry completely disappeared.

A phenomenon bearing resemblance to auditory imagery is that of auditory hallucinations (Hubbard, 2010, 2013a). Neuroimaging results have shown asymmetric patterns of brain activity during vocal and non-vocal hallucinations. For instance, in an fMRI study involving both schizophrenic patients and healthy controls, Raij and Riekki (2012) asked participants to imagine a voice, and compared the brain activity during imagery with that recorded during verbal hallucinations: they found that speech-related fronto-temporal areas were similarly involved in both conditions and that the only difference concerned the supplementary motor area, less activated during hallucinations, mainly in the left hemisphere. Similar results had also been found in non-clinical "voice hearers" (Linden et al., 2010). A Diffusion Tensor Imaging (DTI) study (Steinmann, Leicht & Mulert, 2014) revealed a higher fractional anisotropy in the inter-hemispheric fibers in schizophrenic patients with auditory hallucinations than in patients without hallucinations. Importantly, a number of studies have revealed that the cerebral correlates of auditory hallucinations mainly consist in an abnormal activity of the auditory cortex (mostly in left-hemispheric linguistic-related areas), as well as in other regions, such as the anterior cingulate gyrus (see Diederen, Van Lutterveld & Sommer, 2012 for a review). All these findings are in agreement with the results of the present study, that show – at a behavioral level – the left-hemispheric advantage in imaging a voice.

The results of the present study confirmed a left-hemispheric superiority also for non-verbal stimuli, even if either a left- or right-hemispheric superiority could be expected in this case due to the opposite evidence found in different studies (e.g., Boucher & Bryden 1997; Brancucci & San Martini, 1999, 2003; Brancucci et al., 2008, 2012; Noonan & Axelrod, 1981). Accordingly, the direction of the possible cerebral asymmetry for non-verbal stimuli appears still unclear also in the clinical population: in schizophrenia patients, an abnormally increased alpha-band synchrony between left and right auditory areas was found during auditory hallucinations, together with an increased relative power in the left, but not in the right, auditory cortex (Sritharan et al., 2005). In a gamma band EEG synchronization study, Koenig, van Swam, Dierks and Hubl (2012) found that 40 Hz click-tones increased EEG activity in healthy controls and schizophrenic patients without verbal hallucinations, whereas a left-lateralized activity decrease was found in schizophrenic patients with verbal hallucinations. In another fMRI study, Zvyagintsev and colleagues (2010) found that the STG was bilaterally activated during auditory imagery and that visual imagery induced a deactivation of the STG, but they also found that STG activity in the left hemisphere was positively correlated with the vividness of the auditory images. However, Barta and colleagues (1990) found a correlation between the reduced volume of the left STG and the severity of auditory hallucination. Similarly, Hugdahl, Løberg, Specht, et al. (2008) confirmed a reduced density of grey matter in the left peri-Sylvian area in patients who suffered from hallucinations, as well as a strongly reduced REA, as measured by means of DL tests (Hugdahl et al., 2012; Hugdahl, Løberg, Jørgensen et al., 2008, for similar results see also Levitan, Ward & Catts, 1999).

5. Conclusions

The present study shows that auditory imagery could be a valid tool in the study of cerebral asymmetries, demonstrating a strong correspondence between auditory imagery and perceptual biases (REA effect). This conclusion opens up to a whole range of potential applications in the clinical field. Specifically, auditory imagery paradigms could be useful in the investigation of the relationships between imagery and hallucinations, providing a quick tool to link hemispheric imbalance to the genesis of hallucinatory experiences. Future studies could focus on the emotional content of auditory imagery, as well as on gender, age and other features of imagined voices, in order to investigate whether lateralization is modulated by such aspects in clinical and non-clinical samples.

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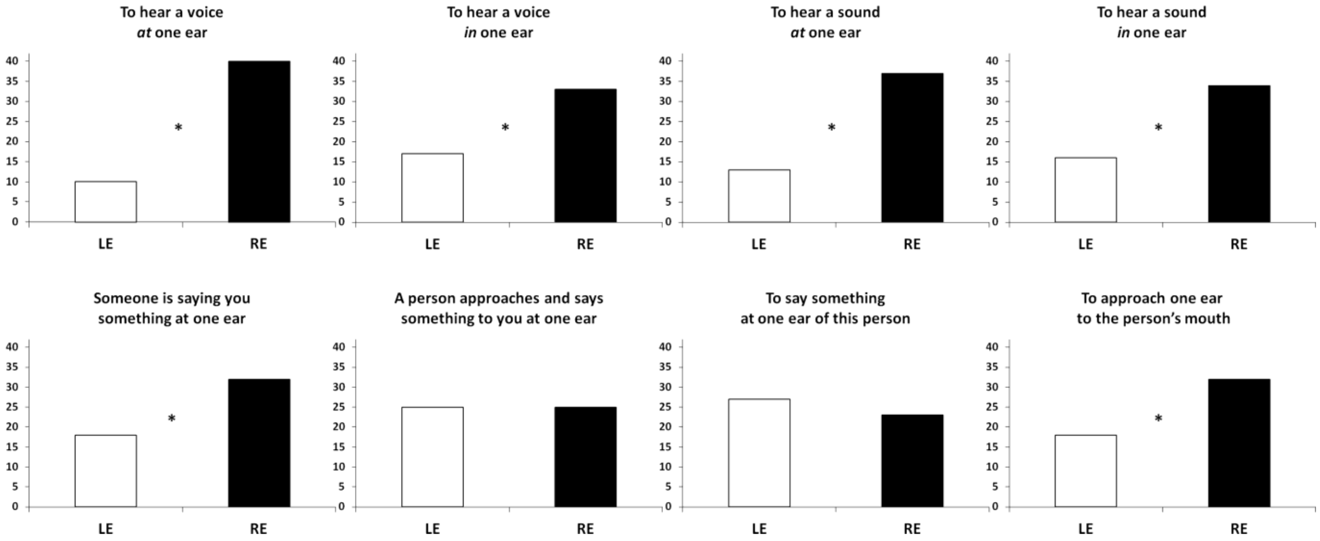
Figure caption

Fig. 1. Percentage of Left Ear (LE) and Right Ear (RE) responses in the 8 Experiments (50 right-handed participants each), in which it was asked (columns from left to right): "*Keeping your eyes closed, imagine* 1) *hearing a voice at one ear*; 2) *hearing a sound at one ear*; 3) *hearing a voice in one ear*; 4) *hearing a sound in one ear*; 5) *that someone is saying something to you at one ear*; 6) *a person who stands in front of you. Now imagine that this person approaches and says something to you at one ear*; 7) *a person who stands in front of you. Now imagine saying something at one ear of this person*; 8) *a person who stands in front of you. This person is whispering something. Now imagine moving one ear to the person's mouth, in order to hear what the person is saying*".

Asterisks show the significant comparisons.



To hear a voice
at one ear
To hear a voice
in one ear
To hear a sound
at one ear
To hear a sound
in one ear
Someone is saying you
something at one ear
A person approaches and says
something to you at one ear
To say something
at one ear of this person
To approach one ear
to the person's mouth
40
35
30
25
20
15
10
5
0
LE
RE
*