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Regional topography of auditory and visual attention: An fMRI-based meta-analysis

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ABSTRACT

More than three decades of functional magnetic resonance imaging (fMRI) has gathered extensive evidence of auditory and visual attention effects in the human brain. However, a meta-analysis covering both modalities is lacking. The present activation likelihood estimation (ALE) based meta-analysis reports overlap and segregation of auditory vs. visual attention effects, further dividing those to effects of orienting vs. maintenance of attention, top-down controlled vs. bottom-up triggered attention, and attention to spatial vs. linguistic stimuli. Forty-three eligible auditory and 96 visual studies reporting a total of 1884 activation foci were found with PubMed and Scopus search. ALE meta-analysis revealed multimodal attention-related convergence zones with specific regional specialization in the dorsal and ventral parietal and frontal cortices and supplementary motor area / anterior cingulate cortex. Overall, visual attention was biased towards the dorsal attention network and auditory attention towards the ventral attention network. Midline posterior parietal cortex was associated with spatial attention in both modalities and language-related attention effects in the left inferior frontal and inferior temporal cortices were observed in the audition. In conclusion, the present study showcases the regional topography of attention effects in the brain, identifying brain areas dependent or independent of sensory modality, subprocess of attention, and type of stimulus. The proposed evidence-based multimodal model of attention can be used for interpreting future brain imaging findings as well as clinical observations.

1. Introduction

Imagine a world where humans would not be able to process incoming sensory information selectively. When surrounded by other people, such as in a lively party, following someone's speech would require extraordinary processing capacity if irrelevant information could not be ignored. Luckily, our brain effortlessly detects various *auditory* and *visual* cues from the overwhelming stimulus stream helping us to *orient attention* to a specific target, such as a certain speaker (Cherry, 1953). The ability to re-orient the focus of attention, and when necessary, voluntarily *maintain attention* to selected inputs while ignoring irrelevant information is crucial beyond social situations for all human-environment interaction (Näätänen, 1990, Posner and Petersen, 1990). Together, stimulus-driven or *bottom-up triggered* processes that exogenously guide our attention with a rather minimal voluntary effort and goal-directed or *top-down controlled* processes associated with control of attentional focus in an endogenous manner make it possible to manage especially information-rich and dynamically varying situations (Corbetta and Shulman, 2002). Abundant research has elucidated how the human brain employs cognitive processes described above to resolve the problem of selective attention. However, a comprehensive meta-analysis characterizing the functional architecture of subprocesses associated with attention in the human brain is currently lacking.

The mechanisms allowing selection of information for in-depth

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processing are tightly integrated to sensory systems, as well as higher-level cognitive processes involved in controlling our actions, decisions, and thoughts (Alho et al., 2024, Corbetta and Shulman, 2002, Posner and Petersen, 1990). A hierarchical organization where simple sensory features are integrated into more complex perceptual representations in separate routes processing spatial (‘where’) and semantic (‘what’) contents can be found in both auditory (Kaas and Hackett, 2000, Romanski et al., 1999) and visual (Ungerleider and Mishkin, 1982) systems. The dorsal pathways for spatial processing are tightly integrated with the motor system (‘how’) supporting besides sensory processing, for instance, hand-eye coordination, movements of the head and eyes, and motor control of speech (Goodale and Milner, 1992, Hickok and Poeppel, 2004). The auditory and visual ventral pathways for semantic processing, in turn, are strongly linked to the *language* system operating with semantic representations (Hickok and Poeppel, 2004, Rauschecker, 2011). While the dual pathway organization and related attention effects concern both auditory (Alain et al., 2001, Degerman et al., 2006, Zatorre et al., 1999) and visual (Corchs and Deco, 2004, Maunsell and Treue, 2006) systems, there is no consensus on the differences in attentional effects arising from sensory-level processing (e.g., Braga et al., 2013, Braga et al., 2017, Salmi et al., 2007a). More specifically, selective listening relying on transient spectrotemporal acoustic patterns (i.e., tonotopic coding; Fritz et al., 2007) may well pose differential requirements for attention than selective viewing supported by a stable and precise 3D representation of the world (i.e., visuospatial coding; Carrasco, 2011). Considering the importance of these two modalities in human cognition, it is surprising how little research has been devoted to the convergence and divergence of attention effects in audition and vision (Alho et al., 2024). The present meta-analysis pulls together the findings related to attention effects in auditory and visual tasks obtained with one of the most common neuroimaging methods, functional magnetic resonance imaging (fMRI) to clarify this issue.

Besides fMRI studies, a great deal of knowledge has been gained from reports where specific subfunctions of attention are compromised after a damage to a particular brain region. For instance, a lesion to *the temporoparietal junction* (TPJ) or to the posterior parts of *the ventral frontal cortex* (VFC), particularly in the right hemisphere, often results in unilateral hemispatial neglect. In this condition, stimuli in the visual (Bisiach and Luzzatti, 1978, Bisiach et al., 1981) or auditory (Heilman and Valenstein, 1972, Brozzoli et al., 2006) field opposite to the damage no longer capture one’s attention (Corbetta and Shulman, 2002). Damage to superior areas of *the posterior parietal cortex* (PPC), in turn, may lead to Balint’s syndrome compromising holistic visual experience, along with difficulties in voluntary directing of attention or control of eye movements (Moreaud, 2003). Two other key regions involved in controlling voluntary attention that are heavily connected with superior PPC areas, both through direct connections (Mesulam, 1981) as well as projections via the pulvinar nucleus (Bos and Benevento, 1975; LaBerge, 1995), are *the frontal eye field* (FEF) and *supplementary motor area / anterior cingulate cortex* (SMA/ACC). Areas encompassing TPJ/VFC and PPC/FEF named as *the ventral and dorsal attention networks*, respectively, are involved in bottom-up and top-down attention (Corbetta and Shulman, 2002). In many studies, the functional role of SMA/ACC in attention effects has been associated with voluntary intentions to act (e.g., Goldberg, 1985), but due to the multitude of tasks involving SMA/ACC, for instance, Petersen and Posner (2012) named this area as “the executive control system” in their well-known model of attention.

Several of the higher-level regions described above contain neurons responsive to auditory, visual and multimodal stimulation (Cohen et al., 2005; Lewis and Van Essen, 2000 Dec 4; Plakke and Romanski, 2014), but the information of exact multimodal convergence zones is limited as only a few of the fMRI studies reporting regional activations have directly compared auditory and visual attention (e.g., Finoia et al., 2015, Hein et al., 2007, Salmi et al., 2007a, Salo et al., 2017, Smith et al., 2010). The overlap and segregation between brain regions involved in various attention control processes in audition and vision would be difficult to examine at the level of single studies. However, a meta-analysis gathering comprehensive evidence of the neurofunctional architecture of attention effects could potentially disentangle the modality effects across various subfunctions of attention.

The goal of the present meta-analysis of auditory and visual attention was to first pool together the experimentally controlled studies examining regional fMRI activations for different types of attention effects. We hypothesized that besides attention effects in the *auditory and visual cortices* (AC and VC, respectively), visual attention effects are biased to the dorsal stream and auditory attention effects are biased to the ventral stream (Fig. 1). This hypothesis is based on distribution of the neurons responsive for auditory and visual stimulation (e.g., Cohen et al., 2005; Lewis and Van Essen, 2000 Dec 4; Plakke and Romanski, 2014), biases in the related anatomical pathways (e.g., Braga et al., 2017), as well as findings of the single fMRI studies including both auditory and visual tasks (e.g., Salmi et al., 2007a, Salo et al., 2017). Then we further divided auditory and visual attention effects into those involving orienting vs. maintenance of attention (Posner and Petersen, 1990, Näätänen, 1990) and top-down vs. bottom-up controlled attention (Corbetta and Shulman, 2002) following the popular models of attention. Orienting of attention and top-down attention were both expected to show prominent effects in the dorsal attention stream for both modalities, with the difference that top-down effects would be additionally highlighted in the respective sensory areas (attention-related ‘gain’ effects). Bottom-up attention and orienting of attention were assumed to show regional activations in the ventral stream (Corbetta and Shulman, 2002, Corbetta et al., 2008). Finally, we separated activations for spatial vs. linguistic stimuli, expecting to find a division based on the putative functional roles of the dorsal vs. ventral streams (Kaas and Hackett, 2000, Romanski et al., 1999, Ungerleider and Mishkin, 1982) and lateralization to the right (Reuter-Lorenz et al., 1990, Sosa et al., 2010) vs. left (Friedrici and Gierhan 2013, Hickok and Poeppel, 2004, Price, 2010) hemisphere in both modalities (see Fig. 1). To emphasize homogeneity of the studies and interpretability of the findings, we decided to compare spatial and linguistic attention to each other, instead of adding categories ‘non-spatial’ and ‘non-linguistic’ that would gather studies activating diverse areas and hence likely result to poor spatial convergence. Altogether, our study tested how well the existing evidence from regional fMRI studies fit to the popular models of visual (Corbetta and Shulman, 2002, Posner and Petersen, 1990) and auditory (Näätänen, 1990) attention, with a particular aim to delineate the multimodal convergence zones and modality-specific brain areas as well as specialization according to the types of attention effects.

2. Methods

2.1. Protocol and study selection

The protocol of this study followed ‘The Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA)’ guidelines, when possible (Liberati et al., 2009). Scopus and PubMed were used as the primary search engines. Keywords ”attention,” “auditory,” ”visual,” and ”fMRI” produced a total of 12,174 hits (Fig. 2). The numbers of potentially eligible studies are from the final search conducted in November 2024. From the studies found with the keywords above, we excluded those that were not conducted with fMRI, did not describe the task or stimuli clearly, or did not report whole-brain regional data with standard-space (Montreal Neurological Institute, MNI or Talairach) coordinates. Hence, we excluded, for instance, studies examining functional connectivity, using independent component analysis (ICA) or multivoxel pattern analysis (MVPA), in addition to various studies that did not include a contrast that was clearly related to an attentional effect, or reported activations in predefined regions of interest. Studies with ICA and MVPA were excluded from this meta-analysis to avoid methodological heterogeneity that would make the interpretation of the results less straightforward and possibly lead to unbalanced contrasts, as

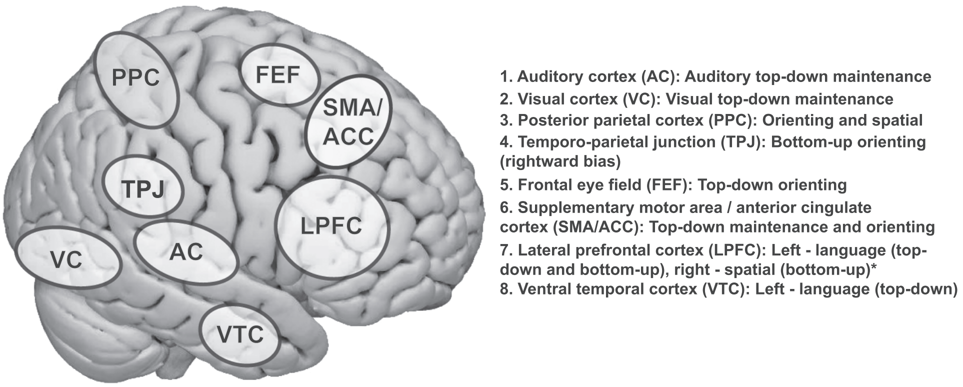

Fig. 1. A schematic illustration of the expected regional architecture of attention effects. *LPFC here includes both dorsolateral prefrontal cortex (DLPFC) and ventral prefrontal cortex (VFC).

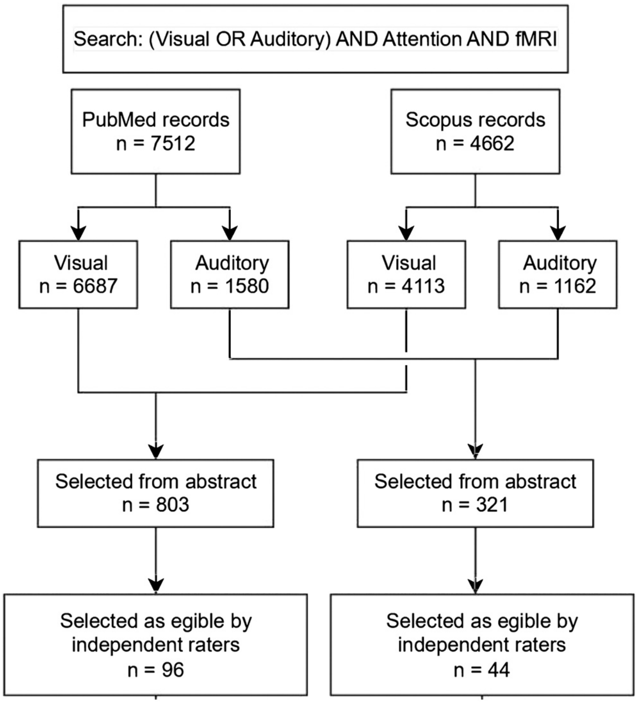

Fig. 2. A flow diagram of the search and selection process.

the coordinate data available for meta-analysis in such studies is still limited. To reduce the heterogeneity of the data, we also excluded data in children and clinical groups. At least two authors (BA, BP, SKa, SKä, and HR) went through each abstract identified in the search, and selected 1124 potentially eligible studies for further evaluation that was conducted by JS, PW, BA, and KA. In addition to PubMed and Scopus search, we went through other meta-analyses and review articles on auditory or visual attention to verify that all relevant studies were included. We requested the missing data from authors of the studies that were otherwise eligible but did not report MNI or Talairach coordinates. However, no additional data was acquired. At least two authors were involved in final selection, and all choices were carefully discussed in consensus meetings. In the review, authors also rated the level of experimental control in the design of the study (see Supplementary Table 1). Studies that compared two conditions that were different only with respect to the type of attention condition (e.g., orienting of attention vs. maintenance of attention or vice versa), i.e. had identical stimuli and motor responses, were labelled as “fully controlled”; studies that had stringent control but could have minor confounding factors (e.g., stimuli in the two conditions compared were not identical) were labelled as “partially controlled”; studies that had a clear attention effect and controlled task but compared that with a condition that could be clearly affected by a confound (e.g., baseline task did not require attention) were labelled to the “other” category. Due to the limited number of studies with fully controlled tasks, we used the related data only for validation purposes to examine the robustness of the main analyses.

Study selection and categorization followed the conceptual framework of well-known prior studies. The Posner’s paradigm represents a characteristic example of the auditory and visual orienting tasks, with both top-down (endogenous orienting condition) and bottom-up (exogeneous orienting condition) variants (for a review see Posner and Petersen 2012, Corbetta and Shulman, 2002). Similar features where attention is voluntarily directed from one type of task contents to another (top-down) or captured by a change in the external stimulus in a stimulus-driven manner (bottom-up) were considered also to categorize other studies relevant to this conceptual distinction. Orienting versus maintenance of attention, in turn, is studied for instance with the Rapid Serial Visual (or Auditory) Presentation tasks (RSVP, Yantis et al., 2002, Shomstein and Yantis, 2006, Esterman et al., 2009). Other tasks resembling RSVP in a sense that attention is either maintained in particular contents over prolonged time or shifted between different types of stimulus contents, also those with no linguistic (e.g., Salmi et al., 2007a, Salmi et al., 2009) or spatial (Alho et al., 2015) component were also considered in this categorization. Because spatiotopy represents the fundamental organization of the visual system, spatial location of the stimuli is very often the stimulus feature being manipulated to discover the attention effects, independent of the task design. For auditory attention, the relative number of linguistic tasks is larger due to the important role of speech in the auditory domain, but also manipulation of the spatial location has been incorporated into many of the common auditory experimental designs (such as Posner’s paradigm and RSVP).

The sample containing 63 contrasts (comparisons between two experimental conditions) from 43 auditory attention studies and 143 contrasts from 96 visual attention studies included 3D coordinates for a total 1884 activation foci (see Supplementary Table 1 for the studies). Auditory studies reported 607 activation foci and visual studies reported 1277 activation foci. Out of 63 contrasts extracted from auditory studies for the final analyses, 34 examined orienting of attention, 29 maintenance of attention, 47 top-down attention, and 11 bottom-up attention. Thirty-four auditory contrasts were related to spatial and 30 to linguistic attention (i.e., attention to auditory or visual linguistic stimuli). Out of the 143 contrasts extracted from visual studies, 105 examined orienting of attention, 35 maintenance of attention, 83 top-down attention, and 47 bottom-up attention. Among the visual attention studies, 95 contrasts were related to spatial attention and 17 to linguistic stimuli. For auditory attention, overlap between spatial and linguistic effects was observed in 15 contrasts (i.e. both spatial and linguistic components in the same contrast) in the first-level analysis that was separately conducted for the two categories. However, the overlapping studies were removed for the contrast analysis comparing the attention effects between spatial and linguistic tasks.

2.2. *Activation likelihood estimation*

GingerALE software (version 3.02, www.brainmap.org) was used to generate activation likelihood estimation (ALE) based convergence maps. The analysis was conducted with a revised random-effects algorithm (Eickhoff et al., 2009) with the non-additive within-experiment correction proposed by Turkeltaub and colleagues (2012). GingerALE models coordinate data as spatially smoothed 3D Gaussian probability distributions, capturing the uncertainty of the observed activations. Importantly, this uncertainty is not fixed: studies with larger sample sizes are assumed to provide more precise estimates of activation locations, and are therefore assigned narrower Gaussian distributions, whereas studies with smaller samples receive wider Gaussian distributions. This sample-size–dependent smoothing increases the anatomical realism of ALE maps by weighting findings according to the expected precision of their reported coordinates (Eickhoff et al., 2009). Probabilities of nearby foci are joint with a separate algorithm to avoid overweighting experiments that report cluster subpeaks (Turkeltaub et al., 2012).

ALE values were calculated by the voxel-wise union of the probabilities in the modeled activation maps. Finally, ALE maps were thresholded at family-wise error (FWE) corrected $p < 0.05$ (clusters defined through 5000 permutations at $p < 0.01$). Separate ALE maps were computed for all attention effects (auditory and visual), auditory attention effects, and visual attention effects. Moreover, we computed ALE maps within the attended modality for top-down and bottom-up attention, maintenance and orienting of attention, spatial and non-spatial attention, and verbal and non-verbal attention, as well as contrasts between each pair of attention effects at subfunction level. We included only categories with minimum 20 contrasts (see Eickhoff et al., 2016), which left categories Auditory Bottom-up and Visual Language out from the final analyses. GingerALE output data along with the full coordinate information is published together with the manuscript (Supplementary Data).

3. Results

3.1. *Overall attention effects in the auditory and visual system*

An analysis across all studies within a single modality showed that Auditory Attention elicits bilateral activity in AC, PPC, SMA/ACC and VTC, and unilateral activity in the right FEF, dorsolateral prefrontal cortex (DLPFC) and VFC (Fig. 3, see Supplementary Figure 1 for multi-slice images). For Visual Attention, bilateral activity is observed in VC, PPC, and SMA/ACC and unilateral activity in the right FEF, VFC, DLPFC and the cerebellum (Cb) (Fig. 3, see Supplementary Figure 1 for multi-slice images). To evaluate the robustness of these results, we conducted a further analysis including only the fully-controlled studies (see Supplementary Figure 2). These analyses revealed activations partially overlapping with the main analysis including all studies. However, due to the lesser number of studies the related results were considerably dependent on the statistical thresholding. Comparison between all auditory vs. all visual attention effects revealed bilateral activations restricted to AC, VTC, SMA/ACC and unilateral activations in the right TPJ and FEF (Fig. 3). Comparison between all visual vs. all auditory studies, in turn, showed activity besides widespread VC areas, also bilateral PPC, and right FEF and DLPFC (Fig. 3).

3.2. *Effects related to orienting and maintenance of attention*

Auditory Orienting revealed bilateral activity of AC, extending to TPJ and VTC, as well as PPC, SMA/ACC, and left FEF (Fig. 4, Supplementary Figure 3). Visual Orienting showed bilateral activity in widely distributed areas including PPC, TPJ, VFC, DLPFC, FEF and SMA/ACC, and in the right VC and Cb (Fig. 4, Supplementary Figure 3). Contrasting Auditory Orienting vs. Visual Orienting revealed higher activity for Auditory Orienting in AC, TPJ, and SMA/ACC (Fig. 4, Supplementary Figure 3) and higher activity for Visual Orienting in bilateral VC areas extending to the dorsal visual stream, PPC and FEF (Fig. 4).

Auditory Maintenance showed activation in AC with clusters extending to VTC and TPJ (Fig. 4). SMA/ACC was also activated for Auditory Maintenance. Visual Maintenance, in turn, showed activity in the left VC and dorsal visual stream areas covering widespread PPC regions bilaterally (Fig. 4). Visual Maintenance showed activity also in the right FEF, SMA/ACC, and the left Cb (see Supplementary Figure 3). Contrasting Auditory Maintenance vs. Visual Maintenance highlighted the role of AC and TPJ in the auditory modality and widespread VC and dorsal PPC areas in the visual modality (Fig. 4).

Contrasting Auditory Orienting vs. Auditory Maintenance revealed activations in the right TPJ for orienting and in AC, extending to VTC in the left hemisphere, for maintenance (Fig. 4). Contrasting Visual Orienting and Visual Maintenance revealed orienting-related activations in the superior midline PPC areas, and maintenance-related activations in the lateral PPC, VC, VFC, SMA/ACC, and Cb (Fig. 4, Supplementary Figure 3).

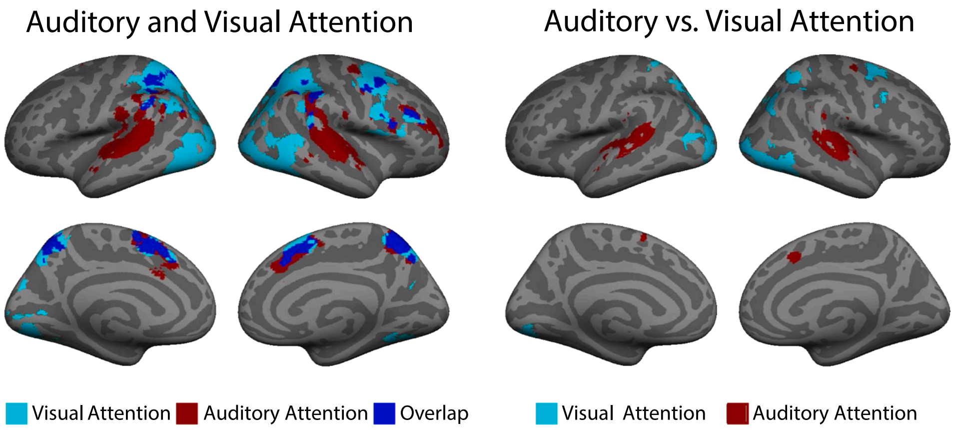

Fig. 3. ALE brain maps resulting from an analysis based on Auditory (n = 63) and Visual (n = 143) Attention and Auditory vs. Visual Attention aggregated across all studies. The brain maps are thresholded at FWE corrected $p < 0.05$. All images are displayed in neurological orientation (i.e., the left hemisphere is shown on the left and the right hemisphere on the right).

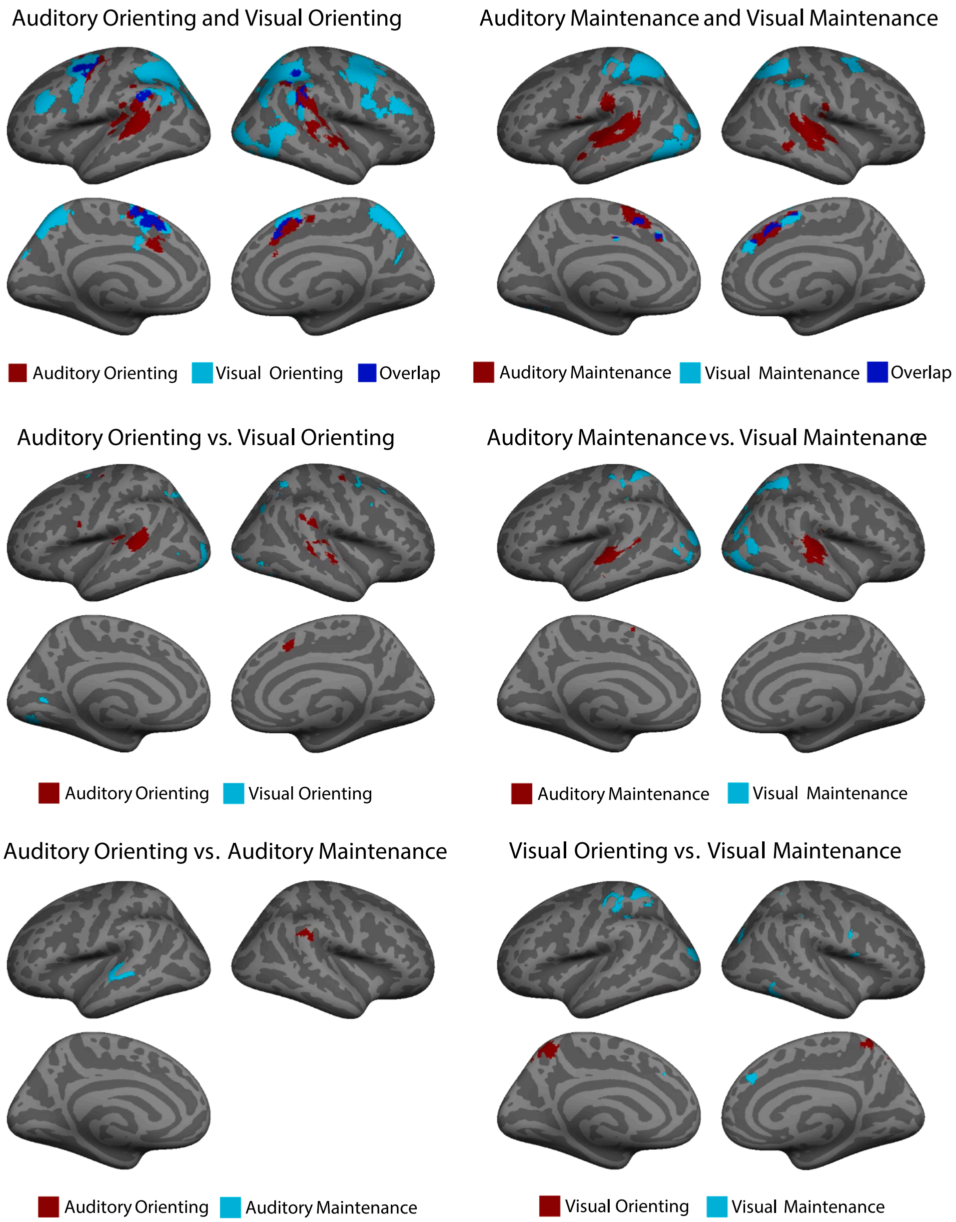

Fig. 4. ALE brain maps for main effects of Auditory Orienting (n = 34) and Visual Orienting (n = 105) and Auditory Maintenance (n = 29) and Visual Maintenance (n = 35) of Attention, as well as intermodal and intramodal contrasts (‘vs.’). The brain maps are thresholded at FWE corrected $p < 0.05$.

3.3. Effects related to top-down and bottom-up attention

Auditory Top-Down Attention elicited activity in AC, SMA/ACC, TPJ, VTC and inferior/superior PPC bilaterally, and in the left VFC and DLPFC (Fig. 5, see Supplementary Figure 4). Visual Top-Down Attention was coupled with bilateral activity in the posterior/dorsal PPC, and unilateral activity in the left VC and Cb (Fig. 5, see Supplementary Figure 4). Contrasting Auditory Top-Down vs. Visual Top-Down Attention showed bilateral activity in AC, SMA/ACC, and the inferior PPC areas including TPJ for auditory attention (Fig. 5) and in the dorsal visual stream extending to bilateral PPC, as well as the left VC for the visual attention (Fig. 5).

No consistent activations associated with Auditory Bottom-Up Attention. Visual Bottom-Up Attention, in turn, showed activation in VFC/DLPFC, TPJ, FEF and widespread PPC areas mostly lateralized to the right hemisphere (Fig. 5). Contrasting Visual Top-Down vs. Visual Bottom-Up Attention showed activity in the higher-level VC, the left Cb, dorsal visual stream including superior PPC, and left lateralized FEF for top-down attention and right lateralized TPJ and PPC activations for bottom-up attention (Fig. 5, see Supplementary Figure 4).

3.4. Attention effects in linguistic and spatial tasks

Auditory Spatial attention tasks showed bilateral activity in AC, TPJ and PPC bilaterally (Fig. 6). Visual Spatial attention tasks, in turn, activated distributed bilateral VC areas extending to the inferior and superior PPC, and the right FEF/DLPFC and Cb (Fig. 6, see Supplementary Figure 5). Contrasting Auditory Spatial vs. Visual Spatial tasks showed higher activity for auditory tasks in the left AC, VTC and TPJ, and higher activity for visual tasks in the posterior PPC areas and other areas of the dorsal visual stream including VC, and in the right FEF (Fig. 6, see Supplementary Figure 5).

Auditory Linguistic tasks showed consistent activity in the left AC, and the cluster extended to TPJ and VTC. In addition, activity in the left DLPFC/VFC was observed in Auditory Linguistic tasks (Fig. 6). Contrasting Auditory Spatial vs. Auditory Linguistic tasks elicited

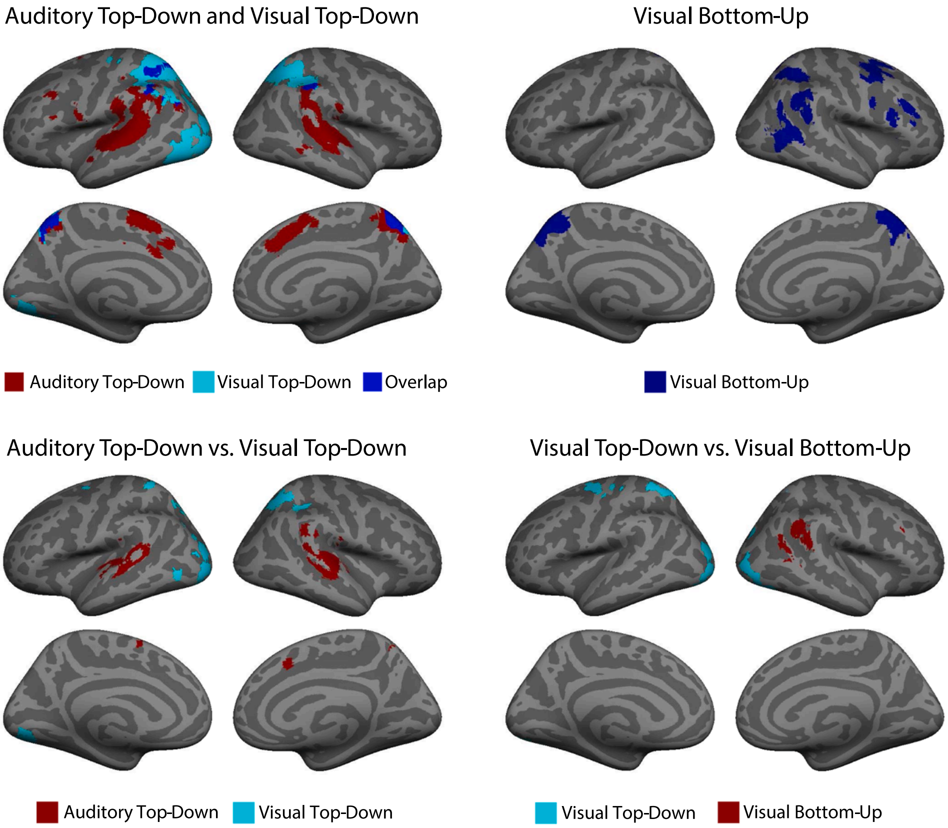

Fig. 5. ALE brain maps for Auditory Top-Down (n = 47) and Visual Top-Down (n = 83) and Visual Bottom-Up (n = 47) Attention as well as intermodal and intramodal contrast effects. The brain maps are thresholded at FWE-corrected $p < 0.05$.

activations in midline PPC and the left FEF for spatial tasks and in the left VFC/DLPFC for linguistic tasks (Fig. 6).

To compare the present results with other meta-analyses, we have also included analyses with family-wise error (FWE) corrected $p < 0.05$ with $p < 0.001$ as a threshold for defining the clusters (5000 permutations) in the Supplementary Figure 6.

4. Discussion

We performed a meta-analysis of fMRI studies covering subfunctions of auditory and visual attention. We addressed four main research questions below, each followed by a summary:

(1) *Which brain regions show auditory and visual attention effects overall*? As expected, widespread PPC and PFC areas, including SPL, TPJ, VFC/DLPFC and SMA/ACC showed attention effects in both auditory and visual tasks. Effects unique to auditory and visual attention across all tasks were observed mostly in the respective sensory cortices in the temporal and occipital lobe, but also in the dorsal attention network (PPC and FEF) for the visual tasks.

(2) *Which brain areas are activated when auditory or visual tasks require orienting or maintenance of attention*? In accordance with Posner and Petersen's (1990) model, evidence supporting that orienting of attention activates areas including PPC, TPJ and FEF/DLPFC was found (see also Shomstein and Yantis, 2006, Yantis et al., 2002). However, some additional brain areas (e.g., SMA/ACC) showed orienting-related effects as well, and besides sensory-specific cortical areas (AC or VC), maintenance of attention activated also TPJ, SMA/ACC and dorsal PPC (see also Serences and Yantis 2007). Hence, evidence for the orienting-related network suggested by Posner and Petersen was found in both sensory modalities. However, the functional specialization is not quite as clear cut as posited in the model.

(3) *What is the convergence and divergence of attention effects associated with top-down and bottom-up processes*? As expected, the effects of top-down attention were observed in PPC and PFC areas largely overlapping with those observed for orienting of attention. Evidence supporting Corbetta's and Shulman's (2002) model of dorsal (top-down) and ventral (bottom-up) attention networks was found only in vision, as the amount of auditory tasks examining bottom-up attention was limited. In the ventral attention network, visual bottom-up effects were lateralized to the right hemisphere.

(4) *How are brain activations separated by spatial vs. linguistic attention in the auditory and visual modalities?* Consistent with the dual pathway models, evidence for specialization of the dorsal attention stream for spatial attention was found in both modalities. Moreover, both in audition and vision, posterior and anterior bias was observed for spatial and linguistic tasks, respectively. Unexpectedly, however, attention effects in the language-related left inferior frontal and inferior temporal cortices were observed only in auditory tasks.

4.1. *Modality-specific and multimodal activations*

Historically, the models for brain mechanisms of attention have largely been based on findings related to visual attention and it is not obvious that auditory attention would involve the same neural systems (Alho et al., 2024, Näätänen, 1992, Alho et al., 2015). The present study provides the first comprehensive meta-analytical comparison of the two modalities and reveals that besides AC, auditory attention involves consistent activations also in the dorsal and ventral PPC, VTC, FEF, VFC/DLPFC, and SMA/ACC. Left-lateralized ventral PPC areas and VTC showing modality-specific auditory attention effects are crucial parts of the "linguistic brain" and critically involved, for instance, in speech understanding and production (Friederici, 2011). While the role of these functions in auditory attention is clearly undisputed (e.g., Davis and Johnsrude, 2007), the present pool of visual studies had too limited

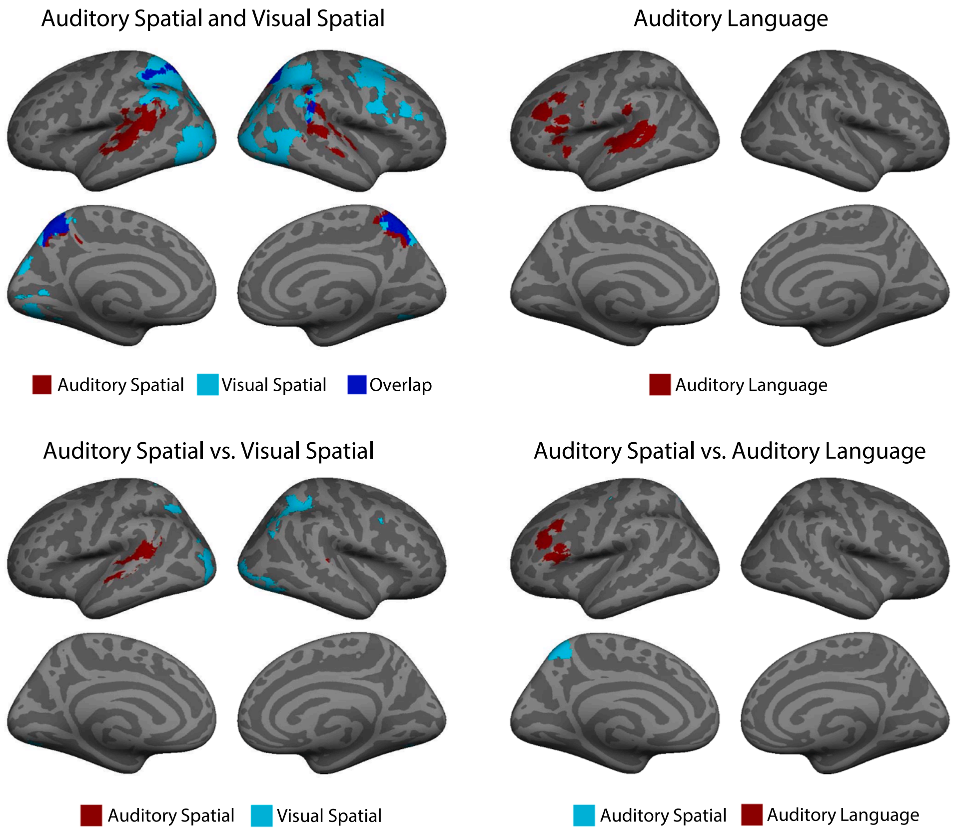

Fig. 6. ALE brain maps for Auditory Spatial (n = 34) and Visual Spatial (n = 95) and Auditory Linguistic (n = 30) attention tasks, as well as intermodal and intramodal contrast effects. The brain maps are thresholded at FWE-corrected $p < 0.05$.

amount of data to examine the role of visual linguistic attention effects in these areas. Nevertheless, our findings provide further evidence supporting the bias towards ventral PPC in the auditory system and dorsal PPC in the visual system (e.g., Fig. 6), which receives support from both neuroanatomical (Braga et al., 2017) as well as functional (Braga et al., 2013, Salmi et al., 2007a) studies.

Besides the distributed visual cortex areas in the occipital lobe, visual attention effects were also observed in the dorsal visual stream posterior to PPC areas showing auditory attention effects. The areas of the visual stream showing these effects match with the anatomical projections of the visual modality (Ungerleider and Mishkin, 1982) and the same is true for the auditory dorsal stream (Hickok and Poeppel, 2004, Rauschecker, 2011). The two modalities seem to converge mostly in SPL/IPS, and also in TPJ. However, consistent with the relatively larger proportion of neurons sensitive to visual than auditory stimulation in PPC (Cohen and Andersen, 2002) and FEF (Lanzilotto et al., 2013), our findings suggest that these areas are dominant in visual attention as compared with auditory attention. Indeed, a key functional role of FEF is related to controlling eye movements strongly coupled with visual attention (Paus, 1996). In summary, modality-specificity in attention effects appears to follow the general organization of the auditory and visual systems rather than being specific to attention.

Multimodal convergence zones, spanning across different types of attention effects, were found in the midline and lateral PPC, SMA/ACC, and the right TPJ and FEF. These observations largely match with the results of the individual studies that have included both auditory and visual attention tasks (Mayer et al., 2006; Mayer et al., 2009; Salmi et al., 2007b; Salmi et al., 2007a; Salmi et al., 2009; Salo et al., 2017). For instance, Esterman and colleagues (2009) have suggested that midline PPC areas, particularly the superior parietal lobule, are involved in any task that requires switching of the task contents, independent of the sensory modality. At the same time, the posterior-lateral PPC was more dependent on the modality and type of attention effect. Altogether, our findings showing both modality-specificity and multimodal convergence highlight the importance of considering modality as one factor in the models of attention.

4.2. *Orienting vs. maintenance of attention in audition and vision*

Although dissociating the attention effects according to moments when the focus of attention is shifted or kept constant is one of the simplest and widely used ways to specify subfunctions of attention, particularly in the auditory modality the number of studies that have conducted such a comparison is small. In agreement with those studies (e.g., Alho et al., 2015, Salmi et al., 2007a,b, Salmi et al., 2009, Shomstein and Yantis, 2006), our findings suggest that PPC and dorsal PFC are involved particularly in orienting of attention. For PPC, midline areas showed contributions to visual orienting and lateral PPC contributed also to auditory orienting and maintenance of attention in both modalities (Fig. 4). In the visual modality, activations of the sensory-specific cortex were observed only in the Maintenance vs. Orienting contrast where Maintenance activated sensory-specific areas more than Orienting. In the audition, no differences in the sensory-specific cortex activity were observed between Orienting and Maintenance. One could speculate that the differences between audition and vision could reflect differential demands for attentional selection at the level of sensory processing, which could be higher in the auditory domain where the stimuli are typically highly dynamic and short lasting. This further aligns with the speculation regarding the role and mechanisms of selective attention in the early visual areas (Carrasco, 2011).

Besides modality-specific sensory-cortex effects described above, also SMA/ACC activations were observed both in orienting and maintenance of attention tasks (Fig. 4). All in all, task specifics associated with SMA/ACC activations appear to be complex and without a careful analysis related to the task specifics it is better to keep the conclusions limited. Considering the attention model by Petersen and Posner (2012), the present results largely agree on the regional architecture associated with orienting attention. However, the current analysis is not suited, for instance, to further specify the functional contributions of SMA/ACC proposed to be involved in executive attention.

4.3. *Top-down vs. bottom-up attention in audition and vision*

The model of attention proposed by Corbetta and Shulman (2002) is largely based on visual spatial attention, even though decades of auditory research has separated between top-down and bottom-up processes as well (see, e.g., Alho et al., 2024). As we expected, empirical analysis of the extant literature clearly supported the involvement of all areas in the dorsal and ventral attention networks in top-down and bottom-up processing, but some characteristics in the observed activity patterns deserve further inspection. It should be noted that the present pool of studies is much broader than the one considered in the model of Corbetta and Shulman (2002) due to numerous related studies conducted during the last two decades. Moreover, it is experimentally quite challenging to fully separate between these two domains- since exogeneous orienting is typically coupled with endogenous orienting at least to some extent, and in most of the cases endogenous orienting is based on exogeneous trigger cue. Corbetta and Shulman (2002) also described the reciprocal interaction between different areas of the dorsal and ventral attention networks.

Other differences between auditory and visual top-down attention relate to the involvement of partially distinct dorsal PPC areas in the two modalities and the role of TPJ in auditory top-down attention. To our knowledge, the present results provide the most comprehensive imaging data supporting such organization for subprocesses of attention. As for several other contrasts, the functional specialization of SMA/ACC to auditory vs. visual attention does not obtain support from the existing literature and it is possible that the modality differences relate to specific task characteristics rather than the modality per se. The comparison between visual top-down and bottom-up attention replicated the model by Corbetta and Shulman (2002) accurately despite the vast diversity of experimental paradigms in this analysis. In summary, the original part of the Corbetta and Shulman model concerning visual attention is supported by the present literature. Unfortunately, the present data for auditory bottom-up attention did not allow testing whether this model can be further expanded to consider auditory attention.

4.4. *Attending to space and language in audition and vision*

Attention tasks are always built on certain stimulus characteristics, of which perhaps one of the most common is the distinction between spatial and linguistic tasks, which receives strong support also from other neuroimaging, neuroscience, and clinical neuropsychology literature outside the field of attention research (Kaas and Hackett, 2000, Romanski et al., 1999, Ungerleider and Mishkin, 1982). Due to the complex mix of paradigms, the existing literature makes it difficult to comprehensively examine interactions between stimulus representations and subcomponents of attention, but as seen in Fig. 6, the present data making a division between two common task types provides evidence that the type of stimulus does play a key role in attention effects, at least in audition. In addition to the division between spatial and linguistic attention tasks, there are various other potentially interesting categories (e.g., attention to animate vs. inanimate objects). Because the pool of available literature on attention effects associated with stimulus categories is limited, more detailed analysis of the effects of stimulus contents is better suited for future studies employing other methodologies. Heterogeneity of the studies may have also affected separate analyses conducted for the fully-controlled studies that were less robust and dependent on the statistical thresholding but still somewhat consistent with the main analyses.

As seen in Fig. 6, activations related to auditory and visual spatial attention show marked overlaps in superior parietal areas and temporoparietal junction areas. These overlaps suggest intermodal sharing of spatial attention mechanisms presumably due to intertwined development of auditory and visual spatial attention already in infancy (Neil et al., 2006). Often, auditory and visual spatial objects are coupled in real-world situations and related to the same phenomenon and overlap between the underlying neural mechanisms could potentially support integration of auditory and visual information.

4.5. *Implications of the present findings*

The present findings have direct clinical implications as attention deficits are commonly observed, not only as an outcome of brain lesions (e.g., Loetscher and Lincoln, 2013) but also in neurodevelopmental as well as neurodegenerative disorders (Sarrias-Arrabal et al., 2023). More specifically, Corbetta and Shulman (2002) model of visual attention separating between the dorsal and ventral attention networks directly links to unilateral hemispatial neglect (involuntary attention – ventral attention network) and Balint's syndrome (voluntary attention – the dorsal attention network). Expanding the model to the auditory domain could help understanding the mechanisms of auditory neglect (Gutschalk and Dykstra, 2015), and also shed light on the contribution of the dorsal attention network on auditory symptoms resulting from brain damage. While the number of studies reporting auditory bottom-up attention effects was limited, clear evidence was found that the ventral attention network does contribute to multiple aspects of auditory attention too. These two attention networks, along with the sensory areas, are also consistently reported to show aberrant activation in individuals with attention deficit hyperactivity disorder (ADHD, see Cortese et al., 2012). However, the neural underpinnings of ADHD symptoms associated with auditory modality (e.g., 'does not seem to listen when spoken to directly', 'has difficulty remaining focused during lectures or conversations') are still poorly understood. Despite the important role of auditory tasks such as listening to speech in our everyday life, the assessment methods for identifying related deficits are seldom available at the clinic. Our findings encourage considering auditory attention more carefully in the theoretical models of ADHD, and attention deficits in general, as well as in more practical aspects of the clinical assessment. Although the focus of clinical research has largely shifted from regional studies to connectivity studies, the present findings could well be applied in interpreting the functional or structural connectivity findings, and in designing new studies examining interactions between the "nodes" of the attention networks and related functional architecture.

4.6. *Limitations*

Typical to neuroimaging meta-analyses, the findings could be partially affected by the heterogeneity of the studies that comes from multiple different sources, including task designs and related experimental controls (Carrasco, 2011), as well as variability in signal properties (e.g., different scanners), preprocessing pipelines (Poldrack et al., 2017), and statistical procedures (e.g., thresholding), and resolution that is sometimes limited. For instance, registration errors could lead to activity in the visual cortex to 'spread' to the cerebellum and vice versa. In some contrasts, however, cerebellar activations were in the mid-posterior parts far from the visual cortex and at least in these cases there is reason to assume that the attention effects in the cerebellum are robust. Moreover, in several included studies, attention was not fully controlled (see Supplementary Table 1). Besides sensory-motor processes, limited control of attention may sometimes relate to differences in task difficulty. However, in some cases task difficulty is hard to control due to the qualitative differences between the conditions. For example, different cognitive processes (e.g., orienting and maintenance) may directly affect response times and significantly affect accuracy, and attention effects in tasks relying on different perceptual representations may not be fully comparable even if response times and accuracies in the tasks would be similar (e.g., one system could rely more on automatic and other on controlled processing). Overall, studies with stringent control of task difficulty represent a minority in the fMRI research of attention. Including only stringently controlled studies would have led into samples of studies too small for meta-analytical purposes. Due to the insufficient number of studies, there were also several types of attention effects that were not included (e.g., studies on audiovisual attention) or separately examined (e.g., studies on social attention, attention effects to biological vs. non-biological stimuli, negative attention effects) and for some of the included categories the amount of data was limited (e.g., auditory bottom-up attention and visual linguistic attention). It is important to note that the overlap between regions associated with auditory and visual attention does not indicate that these regions include neurons with multimodal responses per se. Instead, these effects could be explained by activity of interdigitated populations of modality-specific neurons. Audiovisual attention studies have contributed significantly to identifying supramodal control processes (e.g., Degerman et al., 2007, Salo et al., 2017, Wikman et al., 2021, Wikman et al., 2024). Unfortunately, the sparsity of audiovisual attention studies that fulfilled our inclusion criteria prevented us from adding such studies to the present analyses. However, we would like to highlight the importance of audiovisual attention as a topic for future scrutiny.

Like many of the previous neuroimaging meta-analyses, the present study was not preregistered. The present hypotheses and comparisons conducted with ALE, however, directly follow the main literature and were not affected by the authors' views, perhaps excluding highlighting the auditory literature. Furthermore, methodologically this field has strongly shifted towards functional connectivity studies and multivariate analysis methods. Studies with methods like ICA or MVPA were excluded from this meta-analysis to avoid methodological heterogeneity that would influence interpretation of the results and unbalanced contrasts, as the coordinate data available for a meta-analysis from such studies is still limited. Hopefully, the present findings will help to interpret also studies with more advanced methods (e.g., MVPA, ICA) and there are various further opportunities to use the published data, for instance, for functional connectivity mapping. Finally, in future studies it would be important to publish subject-specific maps, which were not available for the present study.

5. Conclusions

Regional fMRI studies examining attention effects have been conducted for some three decades (for early studies, see Pugh et al., 1996, Woodruff et al., 1996), yet a meta-analysis including both auditory and visual attention studies has been lacking. Our findings resulting from such meta-analysis generally agree with influential models of attention, but provide further evidence related to modality-specific regional specialization of multiple brain areas. The overlaps between various types of attention effects and most common stimulus effects would be difficult to delineate in single studies. Thus, meta-analytic approach provides a powerful method to expand the existing models reviewing selected individual studies. Contribution of this article relates particularly to the extending the discussions to the auditory domain, and description of the modality-specificity and modality-independence, which have been largely neglected in the previous literature.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2026.106698.

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