A Meta-analysis of Perceptual Pseudoneglect reveals the Functional Anatomy of Perceptual Judgements

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Abstract

Major evidence for a right-hemisphere dominance of the brain in spatial and/or attentional tasks comes from lesion studies in patients with spatial neglect. However, the neuroanatomy of the different forms of neglect remains a matter of debate, and it remains unclear how dysfunctions in neglect relate to intact processes. In the healthy brain, perceptual pseudoneglect is the equivalent of neglect as observed in paradigms such as the line bisection task. Therefore, the current study investigated the intact functional anatomy of perceptual pseudoneglect using a meta-analysis to compensate for some of the limitations of individual imaging studies. We collated the data from 24 articles that tested 952 participants with a range of paradigms (landmark task, line bisection, grating-scales task, and number line task) obtaining 337 foci. Using Activation Likelihood Estimation (ALE) we identified a right-hemisphere biased network of cortical areas, including superior and intraparietal regions, the intraoccipital sulcus together with other occipital regions, as well as inferior frontal areas that were associated with perceptual pseudoneglect in partial agreement with lesion studies in patients with neglect. The present results are consistent with a framework of neural computations that explains the neural and behavioural asymmetries of perceptual pseudoneglect as due the need for to an integrated representation of spatial information during perceptual judgments.

Introduction

Spatial neglect is a set of spatial cognitive deficits that have been summarized as inabilities to report, respond, or orient to stimuli contralateral to the side of a brain damage (e.g., Heilman et al., 1993). Neglect is more commonly observed after right than left brain lesions, and thus it is an important indicator for a right-hemisphere dominance of the neural mechanisms underlying visual attention and spatial awareness. As such neglect has garnered significant interest in the literature. Yet, several questions remain unresolved. Crucially, it is unclear how neglect symptoms map onto brain damage.

A recent meta-analysis of lesion studies in neglect patients collated a list of best-practice criteria for lesion-symptom mapping (Moore et al., 2023; also see Bates et al., 2003; de Haan and Karnath, 2018; Sperber and Karnath, 2017; Thiebaut de Schotten et al., 2014) showing that none of the relevant studies attained a perfect score. What is more, depending on the degree to which studies adhered to the criteria, different patterns of functional neuroanatomy emerged with varying core lesions in the supramarginal gyrus, the superior longitudinal fasciculus, the insular cortex, or the postcentral gyrus. Furthermore, the analysis found substantial differences in functional anatomy between different types of neglect as well as in acute vs. chronic neglect. Also consistent with the heterogeneity of neglect, lesion patterns have been found to vary as a function of diagnostic tests (Molenberghs et al., 2012).

To complicate matters functional deficits and brain plasticity after brain lesions interact in a complex and difficult-to-observe manner (Pascual-Leone et al., 2005). For example, extinction, a deficit akin to neglect that affects contralesional stimuli presented together with competing ipsilesional stimuli, does not occur immediately after simulated brain lesions induced

by inhibitory continuous theta-burst stimulation (Vesia et al., 2015). Instead, the authors found extinction to arise several minutes after stimulation, arguably resulting from short-term plasticity due to interactions between the two hemispheres. Interhemispheric interactions also seem to play an essential role in neglect in general (Koch et al., 2008; also see Corbetta & Shulman, 2011) as well as in related asymmetries in the intact brain (Le et al., 2015). This suggests that behavioural impairments and the site of damage do not necessarily relate to one another in a straight-forward manner, contrary to one of the central assumptions of lesion studies (Caramazza, 1984).

Given these inherent challenges of lesion studies, a comprehensive picture of the functional anatomy of neglect calls for comparisons between research in patients with imaging studies in healthy participants to estimate to which extent lesion patterns in neglect agree with the anatomy of intact processes that can be assumed to be equivalent to spatial neglect. One such set of functions involve perceptual judgements about visuo-spatial features of horizontal lines or bars such as length (e.g., Harvey & Milner, 1995), luminance (Mattingley et al., 1994), or spatial frequency (Niemeier et al., 2007). These tasks have been shown to yield comparable visual field differences in the intact brain called perceptual pseudoneglect (Chen et al., 2020) or attentional bias (Bultitude et al., 2006; McCourt et al., 2005; Singh et al., 2011). Furthermore, the differences seem to reflect approximately complementary, although much less severe, asymmetries compared to deficits found in neglect patients (Bowers & Heilman, 1980; McCourt & Jewell, 1999) when performing line length judgements in the manual line bisection task that is commonly used in clinical assessments (e.g., Jewell & McCourt, 2000).

Line bisection and other perceptual judgment tasks have been employed in several imaging studies with a variety of designs. However, most of these studies used simple contrasts with only one experimental and one control condition (see Table 1) thereby bearing a greater risk

of false positive and false negative errors in the identification of relevant brain areas. This is particularly an issue for perceptual judgment paradigms given that they permit test participants to use a variety of tasks strategies.

A better approach is to design a control condition with physically identical stimuli that are used with different task instructions (e.g., Revill et al., 2011). However, as possible limitation of the approach brain areas, although critical for some task A, might activate more in some task B so that subtracting task B activity from task A activity removes an essential area from the results. This has been shown, e.g., for areas such as the frontal eye fields that are critical for saccade generation and yet activate more during reach tasks (Filimon et al., 2009).

A third approach then is to use more complex experimental designs for better experimental control. Benwell et al. (2014) used a factorial design for an EEG experiment with landmark tasks with long and short lines and with a control task that required bisections to be detected. To our knowledge a factorial design has not been used in an fMRI experiment on the attentional bias. Chen et al. (2020) used partial-least squares to model a cognitive vector based on four tasks that were incrementally more likely to involve brain regions to do with the attentional bias. However, not all perceptual judgment paradigms lend themselves to such a set of tasks. The arguably simplest way to attain better control would be a conjunction analysis where multiple contrasts of experimental and control tasks are looked at together such that confounds of one contrast are compensated for by other contrasts (Price & Friston, 1997). To our knowledge to date no pseudoneglect study has used conjunction analysis.

However, it can be assumed that, similar to a conjunction analysis, a meta-analysis collating multiple contrasts from different paradigms would discard some of the suspected false positive and false negative errors of the included studies. Therefore, the aim of the present study

was to conduct a meta-analysis of perceptual pseudoneglect to improve overall validity. Furthermore, the question was whether the resulting functional neuroanatomy would be mirrored in patients exhibiting line bisection deficits after lesions along the intraparietal and intraoccipital sulci (IPS and IOS), medial occipital cortex and anterior portions of the middle frontal gyrus (MFG; see meta-analysis in Molenberghs et al., 2012).

Materials and Methods

To ensure a comprehensive article list was obtained, imaging studies using perceptual judgments to measure attentional bias / pseudoneglect published on or prior to March 15, 2023 were obtained by searching the PubMed (https://pubmed.ncbi.nlm.nih.gov/), PsycInfo (https://www.apa.org/pubs/databases/psycinfo), and Web of Science (https://www.webofknowledge.com/) databases using the following keyword search: "(line bisection OR landmark task OR pseudoneglect OR greyscales task OR grayscales task OR grating-scales task) AND (fMRI OR PET)." Reference lists were also checked to avoid missing relevant articles. A repetition of the search on November 29, 2023, yielded no additional relevant publications.

Articles were selected according to the following inclusion criteria: 1) studies were published in English, 2) participants were healthy, neurotypical adults (18-65 years old), 3) studies assessed attentional biases using either horizontal line bisection, landmark, greyscales, or gratingscales tasks, 4) fMRI or PET was used to assess neural activity (one study using SPECT was included as well; additional searches revealed that no other relevant study used this method), and 5) Montreal Neurological Institute (MNI) or Talairach standardized coordinates of activation

were provided. The exclusion criteria were as follows: 1) participants with a history of brain damage or other clinical populations, 2) clinical or drug related interventions, 3) studies on children (< 18 years old) or seniors (65+ years old), and 4) meta-analyses or literature reviews as evidenced based on inspecting the articles' titles or content. Additionally, we only included those contrasts that compared task activation to a control or baseline condition. Using these criteria, we selected 24 articles consisting of 952 subjects and 337 foci of activation to be included in this meta-analysis. An inter-rater agreement of $r = 0.93$ was obtained between the authors' selections of studies to be included. Any discrepancy was then resolved through closer inspection of the articles in question. Figure 1 details our literature search and selection process.

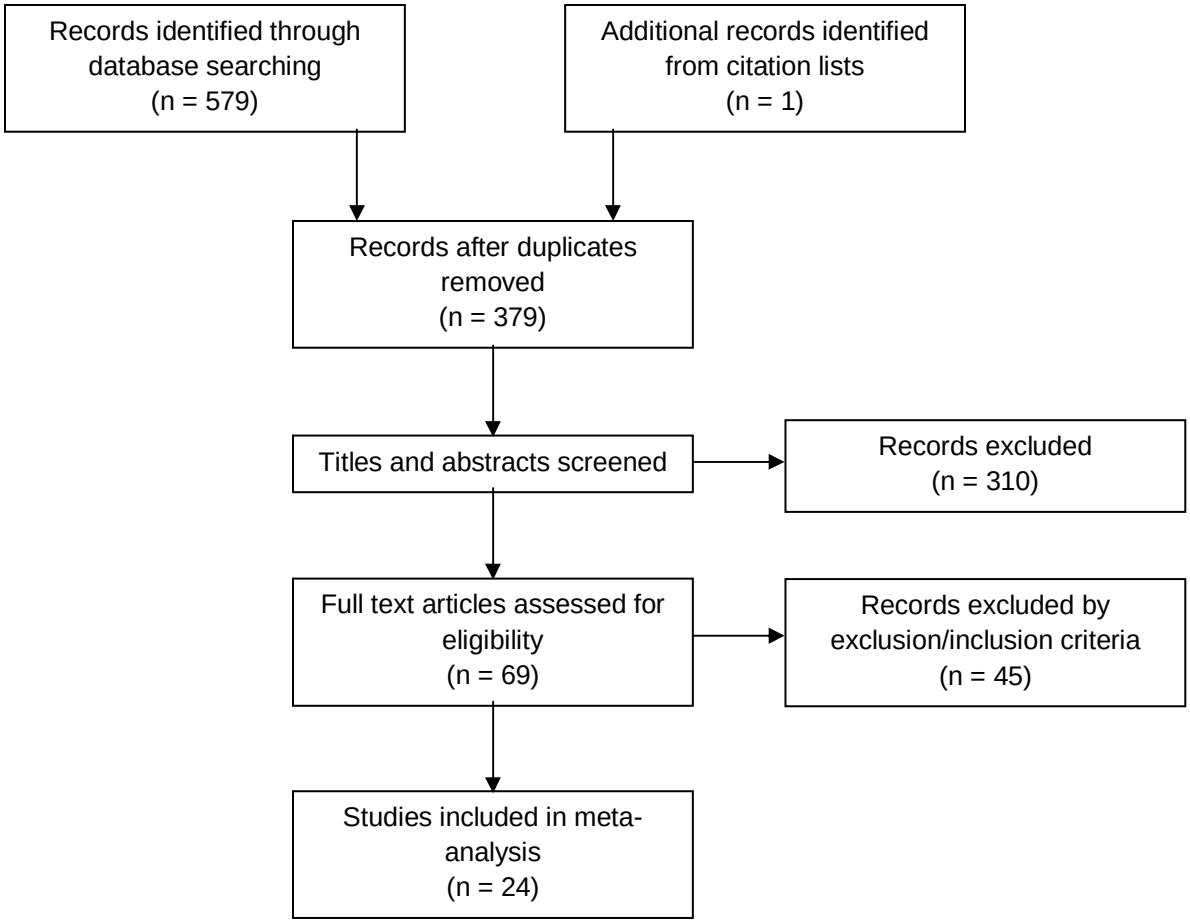

Figure 1. Outline of the literature search process.

Upon finalizing the list of studies, we converted all coordinates of activation reported in Talairach standardized space to MNI space using the mni2tal transform (https://bioimagesuiteweb.github.io/webapp/mni2tal.html). These data were then submitted to an omnibus meta-analysis (24 articles consisting of 952 subjects and 337 foci). Next, we categorized studies based on the paradigms used to assess pseudoneglect to allow for comparison among tasks. These included: landmark tasks, physical line bisection tasks, and number line bisection tasks. The meta-analysis for the Landmark task included 16 studies involving 810 subjects and 173 foci. Here, we selected contrasts that employed baseline/control conditions. The meta-analysis for the Line Bisection task included 6 studies involving 94 subjects and 44 foci.

Lastly, the exploratory meta-analysis for the Number Line task included 2 studies of 58 subjects and 52 foci. Multiple contrasts from a single experiment were pooled together to avoid greater weight being given to multiple analyses with the same set of participants (Müller et al., 2018). A complete list of studies and their attributes can be found in Table 1.

For each meta-analysis, data were analyzed using the Activation Likelihood Estimation (ALE) method outlined in Brainmap GingerALE Version 3 (http://brainmap.org/ale/). The algorithm accounts for spatial uncertainty by treating individual foci as centers of 3D Gaussian probability distributions with a width that depends on the sample size of the respective study. Summing over the Gaussians then results in a probability distribution that is superimposed with a grey matter mask. Next, a permutation procedure computes nonparametrically a null-distribution of random spatial association between experiments to identify statistically significant convergence of activation foci. Here, we employed a cluster level approach with a cluster-level family-wise error set at 0.01 and an uncorrected P value of 0.05. Threshold permutations were set at 1000, as per recommendations outlined in Eickhoff et al., 2012. Results of the ALE analyses were visualized using MRIcron (http://www.cabiatl.com/mricro/mricron/) and BrainNet Viewer (https://www.nitrc.org/projects/bnv/; Xia et al., 2013).

Table 1. Studies included in the meta-analysis.

Publication	N	Contrast	Foci	Analysis
Badzakova-Trajkov et al. (2010)	84	LM > Bisector Detection	7	Omnibus; Landmark
Badzakova-Trajkov et al. (2011)	199	LM > Bisector Detection	9	Omnibus; Landmark
Cai et al. (2013)	31	LM > Bisector Detection (includes L and R language dominance)	19	Omnibus; Landmark
Cavezian et al. (2011)	9	LM w/ greyscles > Bisector Detection	27	Omnibus; Landmark
		LB w/ greyscales > Saccade Task	14	Omnibus; Line Bisection

Chen et al. (2020)	21	Latent variable modelling a continuum of the grating-scales task/high spatial frequency vs. low spatial frequency vs. frame condition vs. fixation	21	Omnibus
Cicek et al. (2009)	11	LM > Bisector Detection	6	Omnibus; Landmark
		LB > Move cursor to edge	3	Omnibus; Line Bisection
Fink et al. (2000a)	12	LM > Bisector Detection	7	Omnibus; Landmark
Fink et al. (2000b)	12	LM > Bisector Detection	5	Omnibus; Landmark
Fink et al. (2001)	11	LMV + LM > Bisector Detection	13	Omnibus
Fink et al. (2002)	12	LM + LL > Instructions	12	Omnibus
Fink et al. (2003)	12	LM (eye movements) > Bisector Detection	9	Omnibus; Landmark
Flöel et al. (2005)	7	LM > Overlapping waveform line detection	26	Omnibus; Landmark
Hurwitz et al. (2011)	16	DB > Saccade task	3	Omnibus; Line Bisection
Liu et al. (2019)	34	Number LB > Number Recognition Task	37	Omnibus; Number Line
		LB > Dot Position Recognition Task	11	Omnibus; Line Bisection
Marshall et al. (1997)*	9	LM > Line Flicker Task	1	Omnibus; Landmark
Plewan et al. (2012)	24	LM Mueller Lyer > Rest	5	Omnibus; Landmark
Revill et al. (2011)	26	LM > Rest	15	Omnibus; Landmark
		LM > search task	13	Omnibus
Sahan et al. (2019)	24	Number LB > Shape Recognition Task (Encoding & Decision-Making Phases)	26	Omnibus; Number Line
Schuster et al. (2017)	15	LM (Version C) > Bisector Detection (Session 1 & 2)	31	Omnibus; Landmark
Weidner et al. (2007)	15	LM Mueller Lyer > Luminance Detection	2	Omnibus; Landmark
Weiss et al. (2000)	12	Near + Far LB > Pointing Task	6	Omnibus; Line Bisection
Weiss et al. (2003)	12	Near + Far LM > Near + Far LB	16	Omnibus
		Near + Far LB > Near + Far LM	7	Omnibus; Line Bisection
Zago et al. (2016)	293	LM > Saccade Task	11	Omnibus; Landmark
Zago et al. (2017)	51	LM > Saccade Task	10	Omnibus; Landmark

LM: Landmark task; LB: Line Bisection task; LMV: Vertical Landmark Task; LL: Line Length Task; DB: Dynamic Bisection Task. *The study employed SPECT.

Results

The functional anatomy of the perceptual attentional bias: omnibus analysis

Figure 2 shows the results of the omnibus meta-analysis, including all 24 studies. Significant overlap in activation was found in posterior regions, including the anterior and posterior intraparietal sulcus (IPS), superior parietal lobule (SPL), and intraoccipital sulcus (IOS), reaching into superior and middle occipital lobe, as well as medial occipital lobe around the calcarine fissure. In frontal regions overlap was found for the precentral sulcus at the level of the inferior frontal cortex (IFC) and the anterior insula. Notably, there was no significant overlap within the frontal eye fields (FEF) or the cerebellum. All regions showed stronger or exclusive activation in the right compared to the left hemisphere.

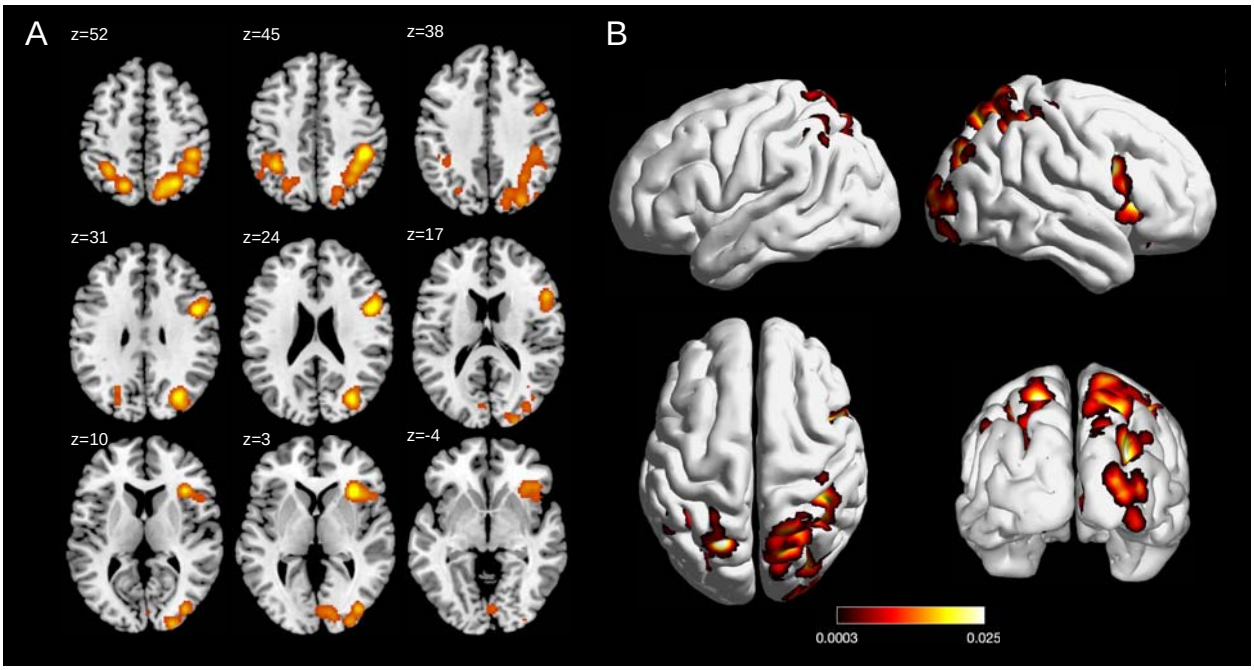

Figure 2. Results of the omnibus meta-analysis. A. Horizontal slices. B. Lateral, dorsal, and posterior views.

Influence of task on the cortical network of the perceptual attentional bias

Perceptual forms of attentional biases have been captured with several different kinds of tasks, although not all these tasks have been frequently used in imaging studies such that more commonly used paradigms have a stronger influence on our omnibus results. To examine the effect of task on brain activation we re-analyzed the data for specific tasks, respectively. Figure 3A shows significant overlap for studies using the landmark task. The resulting cortical network is quite similar to that found with the omnibus analysis. In addition, significant overlap emerged for the right premotor cortex at the level of the superior frontal sulcus (arguably the FEF) and for the right dorsolateral prefrontal (DLPF) cortex above and around the inferior frontal sulcus. Furthermore, lateral extrastriate cortex activated in both hemispheres. A remarkably similar network (although with more bilateral IOS activation and less extrastriate involvement) was

identified in the only existing study that used another purely perceptual paradigm, the grating-scales task (Chen et al., 2019; Fig. 3B).

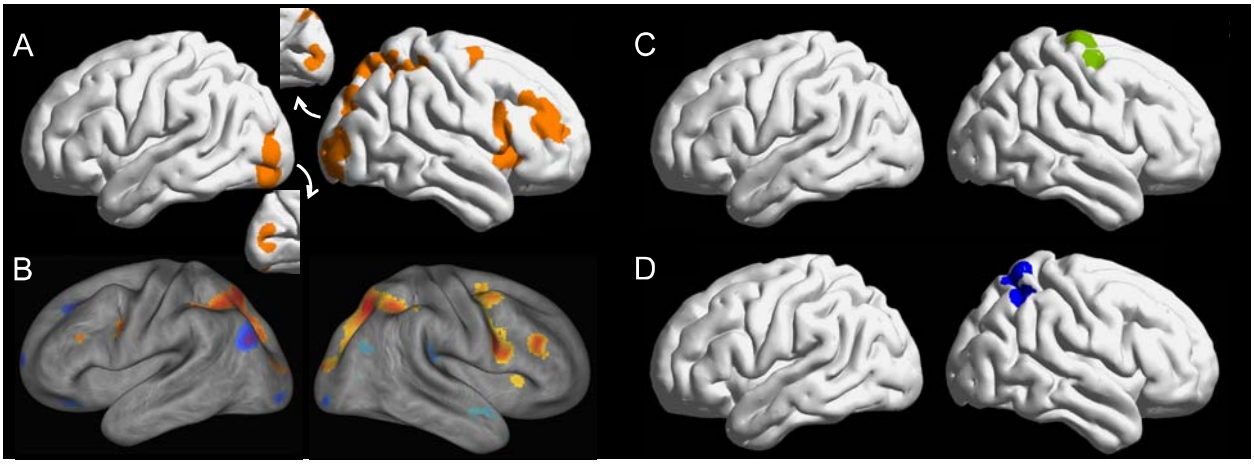

Figure 3. Task-specific analyses. A. Meta-analysis of the landmark task data. B. Partial-least square analysis of the grating-scales task (Chen et al., 2020). C. Meta-analysis of the line bisection data. D. Meta-analysis of the mental number line data.

In addition, to examine the influence of action and visual imagery we conducted two exploratory meta-analyses for the line bisection task and the mental number line task, respectively. For the former we observed significant overlap in the region around the frontal eye fields. For the mental number line task, activity around the anterior IPS and the SPL was significant. Although these results are tentative given the small number of available studies and the high probability of false negative results, this suggests a relatively greater emphasis of frontal and parietal regions during more action- and mental imagery-based aspects of attentional bias tasks, respectively. Nevertheless, these regions overlap with the network identified for the landmark task. In sum, relatively similar networks activate regardless of attentional bias task.

Discussion

With the current meta-analysis, we intended to investigate the intact functional anatomy underlying pseudoneglect as observed in perceptual judgement tasks. Our aim was to attain a comprehensive picture of the neural network that is involved in complementary forms of spatial neglect after brain damage. We found that across several paradigms (landmark task, line bisection, grating-scales task, and number line task) significant right hemisphere-biased overlap emerged for posterior regions: the IPS, the SPL, and the IOS together with adjacent occipital regions and medial occipital lobe. Furthermore, we observed overlap in caudal IFC and the anterior insula of the right hemisphere. As we will argue these results add to our understanding of right-dominant functions of spatial attention and awareness as well as spatial neglect utilizing some of the methodological advantages of conjunction analyses where the risk of false positive and false negative findings is reduced by comparing multiple contrasts with one another (Price & Friston, 1997).

However, as a caveat it should be noted that meta-analyses can only approximate cognitive conjunction analyses. Specifically, in the present study we included far more studies using the landmark task than other paradigms. Such a bias in existing data could result in imbalanced results that would be avoided in a systematically planned conjunction analysis. Despite this imbalance we found that results for the latter type of studies alone were in good agreement with results from a multivariate study using the grating-scales task (Chen et al., 2020; Fig. 3A vs. B). In sum, we reason that the current data do serve as a reasonably accurate approximation of a conjunction analysis. Therefore, in the following paragraphs we will proceed

to comparing the current results with those of other methods to then propose a new framework of the neuro-computations underlying perceptual pseudoneglect.

The results of our meta-analysis are partially consistent with the lesion patterns in stroke patients exhibiting line bisection deficits, i.e., lesion sites in the IPS and IOS, and medial occipital cortex as reported in a meta-analysis by Molenberghs et al. (2012). In addition, these authors found that line bisection deficits are associated with anterior portions of the MFG. Here we found similar prefrontal activation when we examined activation associated with the landmark task, and there was prefrontal activation for the grating-scales task (Chen et al., 2020). The fact that the present omnibus meta-analysis did not yield significant overlap in MFG likely indicates that dorso-lateral prefrontal activation is subject to greater task-dependent variability and does not belong to the core regions of perceptual pseudoneglect.

As another difference, Molenbergh et al. (2012), unlike the current study, found no evidence for SPL, IFC and anterior insula to be associated with line bisection deficits. This could indicate that these areas merely coactive in imaging studies without playing a critical role in perceptual judgments. On the other hand, it is possible that lesion studies overlook critical areas, either because these studies are administratively challenging and, thus, often have to deal with methodological imperfections (Moore et al., 2023), or because areas that are critically involved in perceptual judgments in the intact brain are rapidly substituted after lesions (e.g., Pascual-Leone et al., 2005). E.g., some evidence suggests that such neural plasticity starts to play out within minutes of a brain damage (Vesia et al., 2015) which would be outside the temporal scope of lesions studies, potentially resulting in false negative errors. Indeed, at least for right SPL (more specifically, retinotopic area SPL1) it has been shown that transcranial magnetic

stimulation impacts perceptual judgments (Szczepanski & Kastner, 2013), consistent with the present results.

In sum, we can argue that the current findings offer a largely valid view of the areas that are critically involved in perceptual judgments. Furthermore, this activation pattern can be approximately matched to source localization results from an electroencephalography (EEG) study: Le et al. (2015) observed that activation differences between grating-scales conditions that either do or do not capture pseudoneglect first emerge within roughly bilateral parieto-occipital cortex starting some 74 to 148 ms after stimulus onset and again from 210 to 242 ms, stretching across late stages of the visually evoked P1 component and past the P2, respectively. These sources of activation might be associated with IOS in both hemispheres for the grating-scales task (Fig. 3B) but could involve other visual areas in other tasks (e.g., lateral occipital cortex in the landmark task, Fig. 3A). From 242 to 280 ms then Le et al. (2015) observed clearly right lateralized activation over right posterior cortex (n.b., Lee et al., 2015, located the source in the temporo-parietal junction, probably due to imprecise EEG source localization). Based on the current results we believe that this signal originates from right IPS and SPL. The same regions are co-active together with additional sources in interior frontal regions, arguably IFC and anterior insula, from 280 to 340 ms before activation becomes confined to those frontal regions from 340 to 394 ms (Lee et al., 2015).

This putative temporo-spatial pattern suggests a network that first activates posterior portions of the dorsal attention network before involving anterior portions of the ventral attentional network (Corbetta & Shulman, 2002; Vossel et al., 2014). As such it could be viewed as consistent with the activation-orientation hypothesis of pseudoneglect (Bultitude & Aimola Davies, 2006; Reuter-Lorenz et al., 1990) according to which a right hemisphere dominance for

perceptual judgment tasks leads to greater activation of the right brain which then causes attention to orient to the left visual field (although see Chen et al. 2014; Chen et al. 2019; Karnath et al., 1998). Even so, it remains unclear what the right-hemisphere dominance entails and what causes leftward oriented attention to lead to biased perceptual judgments. Instead, here we suggest a more detailed framework informed by the current results.

A framework for perceptual judgments and pseudoneglect

Considering the functional network observed in the current study together with the EEG data obtained for the grating-scales task (Le et al., 2015) we tentatively propose the following neuro-computational steps that might underlie perceptual pseudoneglect. What is crucial in this context, we argue that these steps should follow a process of perceptual decision making given the fact that perceptual pseudoneglect is based on perceptual judgments:

1. Visual analysis. Perceptual judgment tasks trigger visual analysis of the stimulus material in approximately bilaterally activated striate and extrastriate areas.

2. Integration and magnitude estimation. Next, retinotopic areas in IPS and SPL activate especially in the right hemisphere (presumably after interhemispheric competition; Le et al., 2015). Importantly, right IPS and SPL areas are known to respond not only to the contralateral visual half field but also to larger portions of the ipsilateral half field (Sheremata & Silver, 2015). As such they would be suitable to form integrated representations of the stimulus (although with imperfect isometry of the left and right visual field) as a whole while preserving its topography.

2a. Feedback. It appears reasonable to assume that these parietal representations yield activation in striate and extrastriata areas thereby utilizing their high spatial resolution (e.g., Williams et al., 2008; Chambers et al., 2013; Monaco et al., 2017).

3. Magnitude comparison. The integrated representation of the stimulus then serves to compute magnitudes of the task-relevant feature of the stimulus (length of landmark stimuli, luminance of greyscales, spatial frequency of grating-scales etc.; Walsh, 2003) and to compare that magnitude for the two sides of the stimulus along its horizontal extent within IPS and SPL in the right hemisphere.

4. Perceptual decision and response implementation. Finally, a perceptual decision about the left vs. the right side of the stimulus is made involving the anterior insula, given that IFC and insula are associated with forming an action-oriented representation in preparation of a response (e.g., Demanet et al., 2016; Myers et al., 2017).

Although this framework is merely provisional requiring further investigation, it is consistent with perceptual judgment processes. As such we argue that the framework can explain multiple central properties of perceptual pseudoneglect. For one, stimulus analysis in visual areas contributing to perceptual pseudoneglect (step 1) is consistent with the recent finding that visual stimuli impoverished by pixel noise yield stronger biases in a variety of perceptual judgment tasks (Chen et al., 2019; Chen & Niemeier, 2014), perhaps due to stronger activation of earlier visual, in particular parvocellular processes (Niemeier et al., 2008) at the expense of higher-order visual information (e.g., Kayser et al., 2003; Murray et al., 2002). Next, we argue that forming integrated representations of visual stimuli in right parietal cortex (step 2) is the core reason for right-biased brain activation in perceptual judgment tasks and that within these areas a more detailed or salient representation of the contralateral visual field then leads to right-biased

behavioural biases (step 3). The fact that these parietal areas are also involved in attentional cueing paradigms (Corbetta & Shulman, 2002) further explains why attentional cues interact with perceptual pseudoneglect (Bultitude et al., 2006; McCourt et al., 2005; Singh et al., 2011). Finally, feedback as proposed to occur as step 2a might also occur in judgment tasks that involve imagery such as mental number line tasks.

In conclusion, in the present study we used a meta-analysis to identify the functional network involved in perceptual pseudoneglect to reduce the risk of false positive and false negative errors of previous imaging studies. Given the resulting set of brain areas matched against EEG data for their temporal activation pattern we propose a new framework of neuro-computational steps that explain pseudoneglect as the result of interhemispheric integration afforded by perceptual judgments that, as a consequence, results in asymmetric brain activation and biased attention rather than attentional biases causing asymmetric judgments. This framework and intact functional anatomy of perceptual pseudoneglect sheds new light on perceptual forms of spatial neglect after brain damage.

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