Common and distinct neural trends of allocentric and egocentric spatial coding: an ALE Meta-analysis

Abiot Y. Derbie [1,2], Bolton K.H. Chau [1], Clive H. Y. Wong [3], Li-dian Chen [4], Kin-hung Ting[5], Bess Y. H. Lam [1], Tatia M. C. Lee[3], Chetwyn C. H. Chan [1,5]

[1]Applied Cognitive Neuroscience Laboratory, Department of Rehabilitation Sciences, The Hong Kong Polytechnic University, Hong Kong, China
[2]Department of Psychology, Bahir Dar University, Bahir Dar, Ethiopia
[3]Neuropsychology Laboratory, Department of Psychology, The University of Hong Kong, Hong Kong, China
[4]Fujian University of Traditional Chinese Medicine, Fuzhou, China
[5]University Research Facility in Behavioral and Systems Neuroscience, The Hong Kong Polytechnic University, Hong Kong, China

Corresponding Author: Prof. Chetwyn Chan, PhD, Applied Cognitive Neuroscience Laboratory, Department of Rehabilitation Sciences, The Hong Kong Polytechnic University, Hong Kong. Tel: 852-2766-6727, E-mail: chetwyn.chan@polyu.edu.hk. https://orcid.org/0000-0003-0307-6337

_____

Abstract
The uniqueness of neural processes between allocentric and egocentric spatial coding has been controversial. The distinctive paradigms used in previous studies for manipulating spatial coding could have attributed for the inconsistent results. This study was aimed to generate converging evidence from previous functional brain imaging experiments for collating neural substrates associated with these two types of spatial coding. An additional aim was to test whether test-taking processes would have influenced the results. We obtained coordinate based functional neuroimaging data for 447 subjects and performed Activation Likelihood Estimation (ALE) meta-analysis. Among the 28 experiments, the results indicate two common clusters of convergence. They were the right precuneus and the right superior frontal gyrus, as parts of the parieto-frontal circuit. Between-type differences were in the parieto-occipital circuit, with allocentric showing convergence in the superior occipital gyrus (SOG) cluster compared with egocentric showing convergence in the middle occipital gyrus (MOG) cluster. Task-specific influences were only found in allocentric spatial coding. Spatial judgment-oriented tasks seem to increase the demands on manipulating spatial relationships among the visual objects, while spatial navigation tasks seem to increase the demands on maintaining object representations. Our findings address the theoretical controversies on spatial coding that both the allocentric and egocentric types are common in their processes mediated by the parieto-frontal network, while unique and additional processes in the allocentric type are mediated by the parieto-occipital network. The positive results on possible task-specific confound offer insights into the future design of spatial tasks for eliciting spatial coding processes.

Introduction

Spatial navigation is a complex cognitive process that relies heavily on how one dynamically selects and utilizes the external environment's cues. To enhance the signal-to-noise ratio in visuospatial attention, individuals need to use spatial strategies for selecting useful cues and ignoring less useful ones. The common strategies are allocentric and egocentric spatial coding; the former encodes objects relative to other visual cue(s) or object(s) in space, and the latter encodes objects relative to the viewer's bodily coordinates (Figure 1; Area C and Area D). Previous functional magnetic resonance imaging (fMRI) studies revealed inconsistent results (Table 1) on the activation of the neural substrates associated with these two types of spatial coding. The inconsistencies could have been due to differences in the nature of the paradigm and associated cognitive processes. This study was aimed at conducting a meta-analysis on the existing fMRI studies for addressing these discrepancies and hence gaining a better understanding of the neural mechanisms underlying allocentric and egocentric spatial coding.

Potential overlaps between egocentric and allocentric spatial coding

Dorsal and ventral attention networks are distinct anatomically and functionally (Corbetta & Shulman, 2002; Vossel, Geng, & Fink, 2014) and have been associated with the encoding of the object in egocentric and allocentric maps, respectively (Vossel et al., 2014). The association of the ventral attention network with allocentric spatial coding is that the network plays a key role in maintaining spatial relationships of objects in space (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). Key neural substrates of the ventral attention network are the temporoparietal junction (TPJ) (including the superior temporal gyrus, inferior parietal lobule, and lateral occipital regions) and the middle and inferior frontal gyrus (Corbetta, Patel, & Shulman, 2008; Kravitz et al., 2013; Vossel et al., 2014). These neural substrates are related to the processing of salient and behaviorally relevant stimuli, such as

identification of cued targets (Corbetta et al., 2008; Vossel et al., 2014) and memory-based identification of objects in space (Ptak, 2012). The TPJ plays a higher-level role in contextual visuospatial updating (Derbie et al., 2021; Geng & Vossel, 2013; Ptak, 2012) and reorienting of cued targets (Corbetta & Shulman, 2002; Posner, 1980). In contrast, key neural substrates of the dorsal attention network are the intraparietal sulcus (IPS), the superior parietal lobule (SPL), and the frontal eye field (FEF) (Corbetta et al., 2008; Kravitz et al., 2013). The SPL is associated with maintaining head-centered maps of somatosensory and visual spaces, the FEF with encoding spatial relationships, and the IPS with attentional selection (Kravitz et al., 2013; Ptak, 2012; Ptak & Schnider, 2010).

There is a major controversy in the role played by the dorsal attention network in spatial coding (Kravitz, Saleem, Baker, & Mishkin, 2011; Kravitz et al., 2013). Szczepanski, Pinsk, Douglas, Kastner, and Saalmann (2013) proposed that the dorsal attention network is involved in egocentric and allocentric types. Szczepanski et al. (2013) demonstrated that the dorsal attention network's inter-cortical connections vary with the types of reference frame required. In particular, the IPS2–FEF connectivity is associated with viewer-centered, i.e., egocentric, spatial coordinates. The SEF (supplementary eye field)–SPL1 connectivity is related to object-centered, i.e., allocentric, spatial coordinates (Szczepanski et al., 2013). Other studies share similar findings of the dorsal attention system's flexibility supporting both allocentric and egocentric spatial coding (Galati et al., 2000; Zaehle et al., 2007; Zanto & Gazzaley, 2013). Kravitz et al. (2011) proposed that the dorsal attention network is composed of three functionally distinctive sub-pathways subserving allocentric and egocentric spatial coding in different ways. Kravitz et al. (2011) further suggested that all these sub-pathways originate from the parieto-occipital circuits (involving SOG and the caudal parts of the IPL) visual information held in this region is encoded in an egocentric map. The three sub-pathways are the parieto-prefrontal (spatial working memory), parieto-

premotor (visual-guided behavior), and parieto-medial temporal (navigation) pathways. The differentiated roles of these sub-pathways possibly explain the dorsal attention network dual role in spatial coding. According to Kravitz et al., the parieto-premotor pathway is involved in encoding object in space for forming an egocentrically visuospatial map. The associated neural substrates with this sub-pathway are the IPS, precuneus, retrosplenial cortex (RSC), medial superior temporal gyrus, and the prefrontal cortex (Corbetta & Shulman, 2002, 2011; Galletti et al., 2001; Gamberini et al., 2009). In contrast, the parieto-medial temporal sub-pathway has been found to mediate allocentric spatial coding (Byrne, Becker, & Burgess, 2007; Crowe, Averbeck, & Chafee, 2008; Ekstrom, Arnold, & Iaria, 2014). Neural substrates associated with the parieto-medial sub-pathway are the caudal part of intraparietal lobule (area PG) (Chafee, Averbeck, & Crowe, 2007; Crowe et al., 2008), posterior cingulate cortex (Hashimoto, Tanaka, & Nakano, 2010), RSC (Vann, Aggleton, & Maguire, 2009), and the hippocampus and parahippocampal areas (Burgess, 2008; Burles, Slone, & Iaria, 2017). The hippocampus has been found to heavily involve in spatial navigation, particularly when the upcoming visual information requires to be maintained in an allocentric map (Burgess, 2008; Byrne et al., 2007). The hippocampus directly receives information from the caudal parts of the IPL (Kravitz et al., 2011) via the posterior cingulate cortex (PCC) and RSC (Bartsch et al., 2010; Rushworth, Behrens, & Johansen-Berg, 2006). The overlaps of the neural substrates between the parieto-premotor and parieto-medial sub-pathways support the notion that neural processes associated with egocentric spatial coding could be part of the neural processes in allocentric spatial coding (Galati et al., 2000; Kravitz et al., 2011; Zaehle et al., 2007).
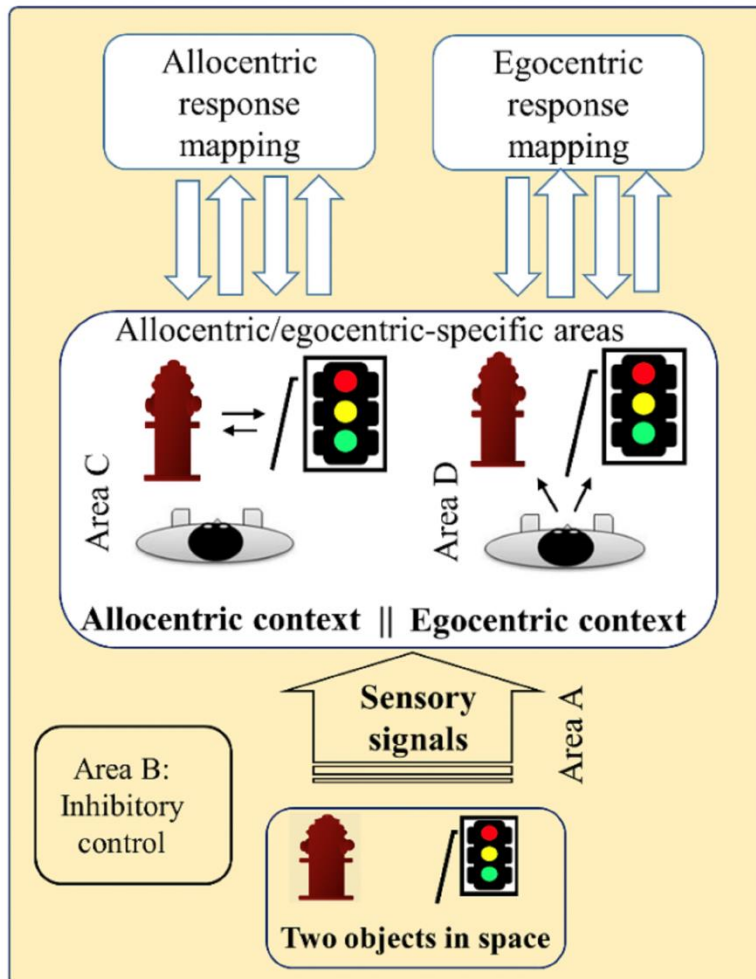
Figure 1. Schematic diagram depicting the cognitive processes of allocentric and egocentric spatial coding. Visuospatial information about the two objects in space (Area A) is attended to. Task-relevant signals inhibitory control (Area B) help to focus volitionally on the two objects in space. Depending on the task requirements, relevant signals are selected using inhibitory control (Area B). Allocentric spatial coding is characterized by the visuospatial information to be modulated by the coordinates of other objects in space (Area C). Egocentric spatial coding is characterized by the information to be encoded based on one's bodily coordinates (Area D).

Experimental paradigms as a confounding factor

The experimental paradigms used in previous studies on spatial coding can broadly be divided into spatial judgment (SJ) or spatial navigation (SN) tasks. A common feature of SJ tasks is that the target mapping operates mainly by sensorimotor interactions with little or no mental shifting (e.g.: Liu, Li, Su, & Chen, 2017). Such tasks require participants to indicate a left or right position with reference to the position of an object shown on screen or the midsagittal position of one's body. In contrast, SN tasks' common features are that the visual targets are embedded in a complex background and that map-like spatial layouts are required to generate visuospatial images for making responses (e.g.: Committeri et al., 2004). Compared with SJ tasks, SN tasks often require participants to maintain visuospatial images for relatively long periods, demanding additional attention and visuospatial working memory-guided during navigation (e.g.: Committeri et al., 2004; Zhang & Ekstrom, 2013). As expected, the processing of these two types of tasks would involve different task processes supported by different cognitive functions and demands. For instance, the cognitive demands of the SJ tasks predominantly consist of allotting visual attention at a location in space, whereas those of the SN tasks include mainly encoding, retrieval from working memory, top-down attention control, and visuospatial working memory (for critical review see: Filimon, 2015).

As the task-specific processes between the two spatial coding methods are different, these differences might have confounded previous studies' results and produced inconsistent findings. This study was therefore aimed at separating the tasks into the SJ and SN groups and compared their cortical convergence and effect sizes. The grouping of the studies based on the task designs would set controls on the task-specific processes and brain activations.

Hypotheses of the study

It was hypothesized that the dorsal attention network's involvement (i.e., FEF and SPL) would be common to both the egocentric and allocentric spatial coding. Egocentric spatial coding would be unique by the clusters of convergence in the superior occipital gyrus and the lateral/ventral intraparietal sulcus, precuneus, and RSC. Allocentric spatial coding, in contrast, would be unique by the clusters of convergence in the IPL, the medial temporal lobe, and perhaps the TPJ. To further test the notion that allocentric-related processes involve retrieval of spatial representations from visual working memory, which is not the case in egocentric spatial coding, we hypothesized that there would be differences in clusters of convergence within the ventral attention network, particularly in the medial temporal lobe (the hippocampus). It was anticipated that the studies adopting SJ tasks would be biased with clusters of convergence involving the superior occipital and parietal regions compared to the studies adopting SN tasks, which would be biased with clusters of convergence involving the MTL and parietal regions.

Method

The guidelines for neuroimaging meta-analysis (Muller et al., 2018; supplementary file 1) and the Preferred systematic Re-views and Meta-Analysis (PRISMA) (Moher, Liberati, Tetzlaff, Altman, & Group, 2009) were used in this section.

Searching strategies

Functional neuroimaging studies published between 2000 and 2020 (last updated October 2020) were searched from PubMed. The search strings, which produced 2295 results from PubMed, were as follows: "allocentric" OR "egocentric" OR "viewer-centered" OR "world-centered' OR "body-centered" OR "frame of reference" OR "spatial navigation" combined ("AND") with "fMRI" or "PET" or "SPECT".

Selection criteria

The inclusion criteria for selecting the articles were as follows: 1) articles were published in peer-reviewed journals; 2) Montreal Neurological Institute (MNI) or Talairach and Tournoux (1988) stereotaxic coordinates were provided; 3) task-related brain activations were elicited from tasks involving allocentric and/or egocentric spatial coding; 4) subjects were comprised of healthy young human adults; and 5) responses on the tasks were obtained by pressing keys on a keyboard or a joystick. Additional papers were included by tracing from the retrieved articles and other review articles. The data extraction procedures were done according to guidelines for ALE meta-analysis (Muller et al., 2018), and the checklist can be found in Supplementary Table 1.

The experiments included in this study were further classified into SJ (example: Galati et al., 2000) and SN (example: Committeri et al., 2004) task types. Characteristics of SJ tasks are: 1) encoding stimulus-based predominantly on external attention (Chun, Golomb, & Turk-Browne, 2011); 2) having no cue-target association (Corbetta & Shulman, 2002), 3) making responses according to the real-time stimulus presented on the screen (e.g., judging the location of a vertical line); and 4) involving low level of mental manipulation of stimulus before making responses. Characteristics of SN tasks are 1) encoding stimuli based predominantly on internal orienting (for the difference between internal and external attention see: Chun et al., 2011); 2) making responses according to the stimulus presented on-screen; 3) possibly involving the retrieval and/or maintaining of visuospatial representation.

Twenty-eight articles containing 34 experiments (number of subjects, n = 447) were identified (Figure 2 and Table 1). Among them, 22 experiments involving allocentric tasks (n = 352 with 252 foci) were grouped for conducting the meta-analysis 1 (allocentric, number of experiments, N = 22). The subsequent ten SJ experiments (1a, n = 136 with 68 foci) and eight SN experiments (1b, n = 157 with 125 foci) were grouped for task-specific meta-analysis.

Another 22 experiments involving egocentric tasks (n = 327 with 277 foci) were grouped for conducting the meta-analysis 2 (egocentric, N = 22), and the subsequent 12 SJ experiments (2a, n = 157 with 125 foci) and nine SN experiments (2b, n= 149 with 128 foci) were grouped for task-specific meta-analysis. Five experiments with four allocentric tasks and one egocentric task were excluded from the task-specific meta-analyses, as their tasks did not conform to SJ or SN types (Table 1 and Figure 2). In summary, four different ALE meta-analyses were performed: meta-analysis 1 (allocentric), meta-analysis 2 (egocentric), meta-analysis 1a (SJ) and 1b (SN) (task-specific allocentric), and meta-analysis 2a (SJ) and 2b (SN) (task-specific egocentric). Grön et al. (2000) reported significant gender effects on the performance in spatial navigation. However, previous studies in spatial coding did not reveal gender laterality in aSC or eSC tasks (e.g.: Barra, Laou, Poline, Lebihan, & Berthoz, 2012; Nori et al., 2018; Ruggiero, D'Errico, & Iachini, 2016). Together with the fact that the studies included in the current analysis did not use gender as a group variable, no attempt was made to explore the role of gender in this ALE meta-analysis.
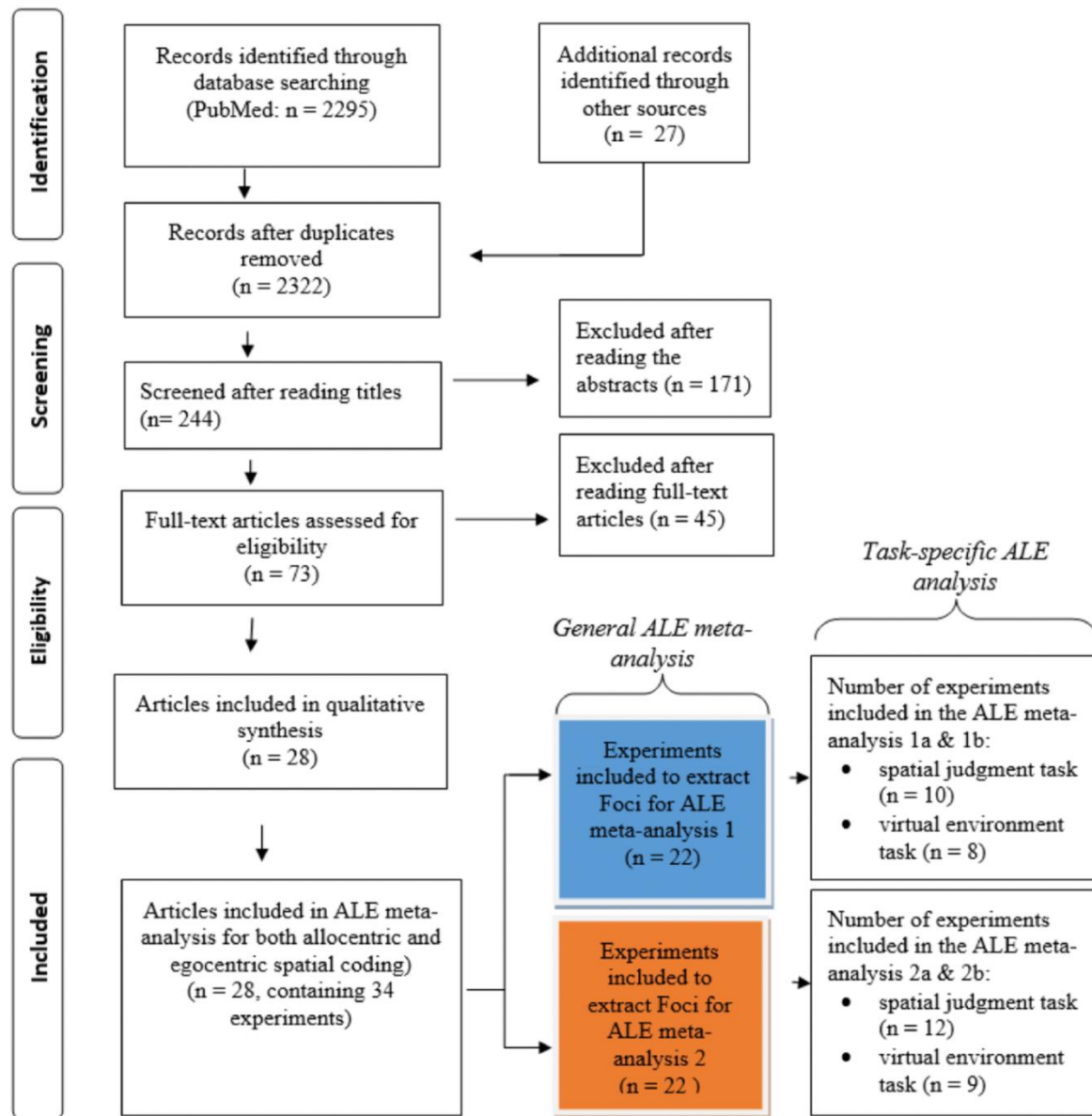
Figure 2. Study selection diagram of the present review and meta-analysis.

Table 1. List of the selected neuroimaging studies on allocentric and egocentric spatial coding types.

Study	N	Age	Imaging technique and design*	Contrasts	Modality	*Nature of the task	Key common and distinctive brain areas subserving aSC and eSC			N (Foci mined)	Meta-Analysis No.
							Common to both	Distinctive			
								Allocentric	Egocentric		
Barra et al. (2012)	26	18-29	fMRI-b	eSC > slanted aSC > slanted	Visual	SN	Cuneus, calcarine sulcus, OT, MOG, SPL, IPS	-	PHG, FusiFG precuneus, LG	aSC, 3 eSC, 15	1,2, 3b, 4b
Chen et al. (2014)	13	23-40	fMRI-e	eSC > control aSC > control	Visual Auditory	SJ	IFG, IPS, MFG, SMA, EC	ITG, calcarine, LG	SOG, IOG PMd	eSC, 3 aSC, 6	1,2, 3a, 4a
Chen et al. (2012)	19	24±3	fMRI-b	eSC > control aSC > control	Visual	SJ	SPL, MOG,	ITG	PreCG, PG	aSC, 6 eSC, 10	1,2, 3a, 4a
Committeri et al. (2004)	14	23-33	fMRI-b	eSC > control aSC > control	Visual	SN	SPL, IPS, PMd, SOG	ventrolateral occipital–temporal cortex	IFG, SFG	eSC, 17 aSC, 27	1,2, 3b, 4b
Creem, Downs, Snyder, Downs III, and Proffitt (2001)	10	NA	fMRI-b	eSC > control aSC > control	Visual	SJ	SPL, Precuneus, PMD, SFG, MFG	-	-	aSC, 10 eSC, 14	1,2, 3a, 4a
Creem-Regehr, Neil, and Yeh (2007)	17	20-26	fMRI-b	eSC > fixation	Visual	A/E-GR	NA	NA	LO, IPC, SPC, Hi, CRBL	eSC, 24	2
Fink et al. (2003)	12	19-36	fMRI-b	aSC > control	Visual	SJ	NA	VLPFC, LIPC, PO, EC, PMVr	NA	aSC, 9	1, 3a

Frings et al. (2006)	13	21-39	fMRI-b	aSC > control	Visual	SN	NA	PrCu, IT, IPC, SFG, SPC, IFG	NA	aSC, 27	1, 3b
Galati et al. (2000)	8	22-29	fMRI-b	eSC > control aSC > control	Visual	SJ	SPL, MTG, IPS, PrCu, PreCG, PMd, IFG, SFG, MTG, STG	-	mLG, fornix-Hi	aSC, 6 eSC, 24	1,2, 3a, 4a
Galati, Committeri, Sanes, and Pizzamiglio (2001)	10	24-29	fMRI-b	eSC > control	Visual	SJ	NA	NA	PPC, IPS, SFG, IFG, Pre-SMA, aSMG	eSC, 24	2,4a
Ganesh, van Schie, Cross, de Lange, and Wigboldus (2015)	23	23 (m)	fMRI-b	eSC > control	Visual	E-GR	NA	NA	TPJ	eSC, 2	2
Gomez, Cerles, Rousset, Le Bas, and Baciu (2013)	20	17-30	fMRI-b	eSC > control	Visual	SN	NA	NA	PrCu, ITG, MTG, PCC	eSC, 3	2, 4b
Gomez, Cerles, Rousset, Remy, and Baciu (2014)	18	17-30	fMRI-b	eSC > control aSC > control	Visual	SN	-	Cuneus	SFG, MFG, Hi	aSC, 12 eSC, 8	1,2, 3b, 4b
Gramann, Muller, Schonebeck, and Debus (2006)	10	22-34	EEG source reconstruction	eSC > control aSC > control	Visual	SN	OT	FusiFG, MTG	Cuneus, SOG, MOG, IFG,	aSC, 9 eSC, 11	1,2, 3b, 4b
Liu et al. (2017)	19	18-25	fMRI-b	eSC > control aSC > control	Visual	SJ	MOG, MFG,	PreCG	SPL	aSC, 5 eSC, 6	1,2, 3a, 4a

Neggers, Van der Lubbe, Ramsey, and Postma (2006)	12	22-29	fMRI-e, rapid)	eSC > control aSC > control	Visual	SJ	MFG	Caudate	STG, SPL, SOG	aSC, 2 eSC, 5	1,2, 3a, 4a
Parslow et al. (2004)	11	19-45	fMRI	eSC > rest aSC > rest	Visual	SN	ACC, PrCu, STG, PreCG, SFG	Hi, PHG	-	aSC, 24 eSC, 26	1,2, 3b, 4b
Saj et al. (2014)	16	25.7	fMRI		Visual	SJ				aSC, 6 eSC, 6	1,2, 3a, 4a
Schindler and Bartels (2013)	12	22-30	fMRI-b	eSC > control	Visual	SN	NA	NA	PrCu, IPS, IFG, PrG, IPL, SFG	eSC, 21	2, 4b
Shibata and Inui (2011)	18	26(m)	fMRI-b	aSC	Visual	A-GR	Pre-SMA, TPO, DLPFC, mSFG, IFG, IPS, PoG, PrCu	NA		aSC,14	1
Thaler and Goodale (2011)	14	NA	fMRI-b	aSC > target-directed	Visual	A-GR	PMd, IPS	NA		aSC, 5	1
Vallar et al. (1999)	7	21-24	fMRI-b	eSC > control	Visual	SJ	NA	NA	SOG, IPS, AG, PreCG, IFG	eSC, 7	2, 4a
Walter and Dassonville (2008)	16	18-32	fMRI-b	eSC > control	Visual	SJ	NA	NA	SPC, SOG, MTG, PreCG, MFG, aSMG	eSC, 11	2, 4a
Wegman et al. (2014)	47	23 (m)	fMRI-e	aSC > baseline	Visual	SN	PrCu, MOG, Hi, PHG, MFG, CN, SFG	NA		aSC, 22	1,3b
Weniger et al. (2010)	19		fMRI-b	eSC > Baseline	Visual	SN	NA	NA	PHG, OTG, RSC, POS, LG, MTG,	eSC, 17	2, 4b

									MOG, PoG, AI		
Werner (2005)	12	24 (m)	fMRI-b	eSC > control aSC > control	Visual	SJ	occipito-parietal	MTL, ACC, MPFC	-	aSC, 8 eSC, 6	1,2, 3a, 4a
Zaehle et al. (2007)	16	20-40	fMRI-b	eSC > control aSC > control	Auditory	SJ				aSC, 10 eSC, 9	1,2, 3a, 4a
Zhang and Ekstrom (2013)	15	NA	fMRI-b	aSC > control	Visual	SN	IFG, SPL, IPL, MOG, IOG, PHG, FG, AG, MFG, PrG, PrCu	NA	NA	aSC, 32	1,4b

Note: One selected study may have one or more experiment(s) in eSC and/or aSC. SN – Spatial Navigation, SJ –Spatial Judgment, A/E-GR - allocentric/egocentric guided reaching, LER - location encoding recognition, fMRI-b - functional magnetic resonance imaging with block design, fMRI-e - functional magnetic resonance imaging with an event-related deign. R/L - bilateral. OT-occipito-temporal, PHG- parahippocampal gyrus, RSC- retrosplenial cortex, OTG- occipito-temporal gyrus (fusiform gyrus), MOG- middle occipital gyrus, SPC- superior parietal cortex, ITG – inferior temporal gyrus, IFG – inferior frontal gyrus, MFG – middle frontal gyrus, SFG – superior frontal gyrus, IPC – inferior parietal cortex, PO – parietal-occipital, LOT – lateral occipito-temporal, MOT – middle occipito-temporal, PoG – postcentral gyrus, CRBL-cerebellum, LO – lateral occipital, Hi – hippocampus, PMVr - ventral premotor cortex, VLPFC - ventrolateral prefrontal cortex, LIPC – lateral inferior parietal cortex, EC - extrastriate cortex, PrCu – precuneus, Cu – cuneus, MO- middle occipital, PMC – premotor cortex, aSMG – supramarginal gyrus, TPJ – temporo- parietal junction, PCC – posterior cingulate cortex, PC – posterior commissure, CN – caudate nucleus, PMd – dorsal premotor area, AI – Anterior insula, POS – parieto-occipital sulcus, SPOC – superior parieto-occipital cortex, CF - calcarine fissure. NA- not applicable.

Activation likelihood estimate (ALE)

ALE is a coordinate-based meta-analysis method and software developed to pool and map common neural trends across different neuroimaging studies. The extracted coordinates were analyzed using the revised ALE algorithm (Eickhoff et al., 2009). The reported foci in each experiment were considered centers of 3D Gaussian probability distributions, capturing each focus's spatial uncertainty (Eickhoff et al., 2009). The probabilities of all the foci' distributions were then combined at voxel levels and used to create cluster maps (Turkeltaub et al., 2012). Last, using the ALE score, dissociation was made between random and true clusters of convergence (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). The analyses were carried out using GingerALE version 3.0.2 (Research Imaging Institute, UT Health Science Center, San Antonio). GingerALE offers conversion of coordinates based on Talairach space to the MNI space. The cluster-wise inference threshold method was used to map the clusters of convergence, producing results with higher specificity and sensitivity than the voxel-wise thresholding method (Eickhoff et al., 2012; Eickhoff et al., 2016). The clusters' locations were anatomically labelled with the SPM Anatomy Toolbox (Eickhoff et al., 2005).

Two general ALE analyses were performed on the foci derived from the selected articles for each allocentric (aSC) and egocentric (eSC) spatial coding types. Conjunction analyses, based on the thresholded z-maps and to be followed by a subsequent ALE analysis, were carried out to test whether the two spatial coding types elicited comparable clusters of convergence. Two contrasting meta-analyses were then conducted on the convergence results: [aSC > eSC] and [eSC > aSC]. Additional meta-analyses were performed to test the possible foci differentiation between the SJ and SN task types. All the derived ALE maps were thresholded at the cluster level $p < .05$, using family-wise error correction for multiple comparisons, and were based on a Monte Carlo simulation cluster-forming threshold of $p < .001$ on the voxel level (Eickhoff et al., 2012; Eickhoff et al., 2009). The ALE results

were visualized using MANGO (Research Imaging Institute, UT Health Science Center, San

Antonio). The "Colin27_T1_seg_MNI.nii" high resolution anatomical template (available at

www.brainmap.org/ale) was overlaid onto the visual images in the MNI space.

ALE Results

Meta-analysis 1 (aSC)

Three clusters of convergence were identified for the 22 experiments that employed

allocentric spatial coding. The significant clusters were in the right SOG ($z = 5.75$, $p < .001$),

the precuneus, including a portion of the left IPL ($z = 4.64$, $p < .001$), and the right superior

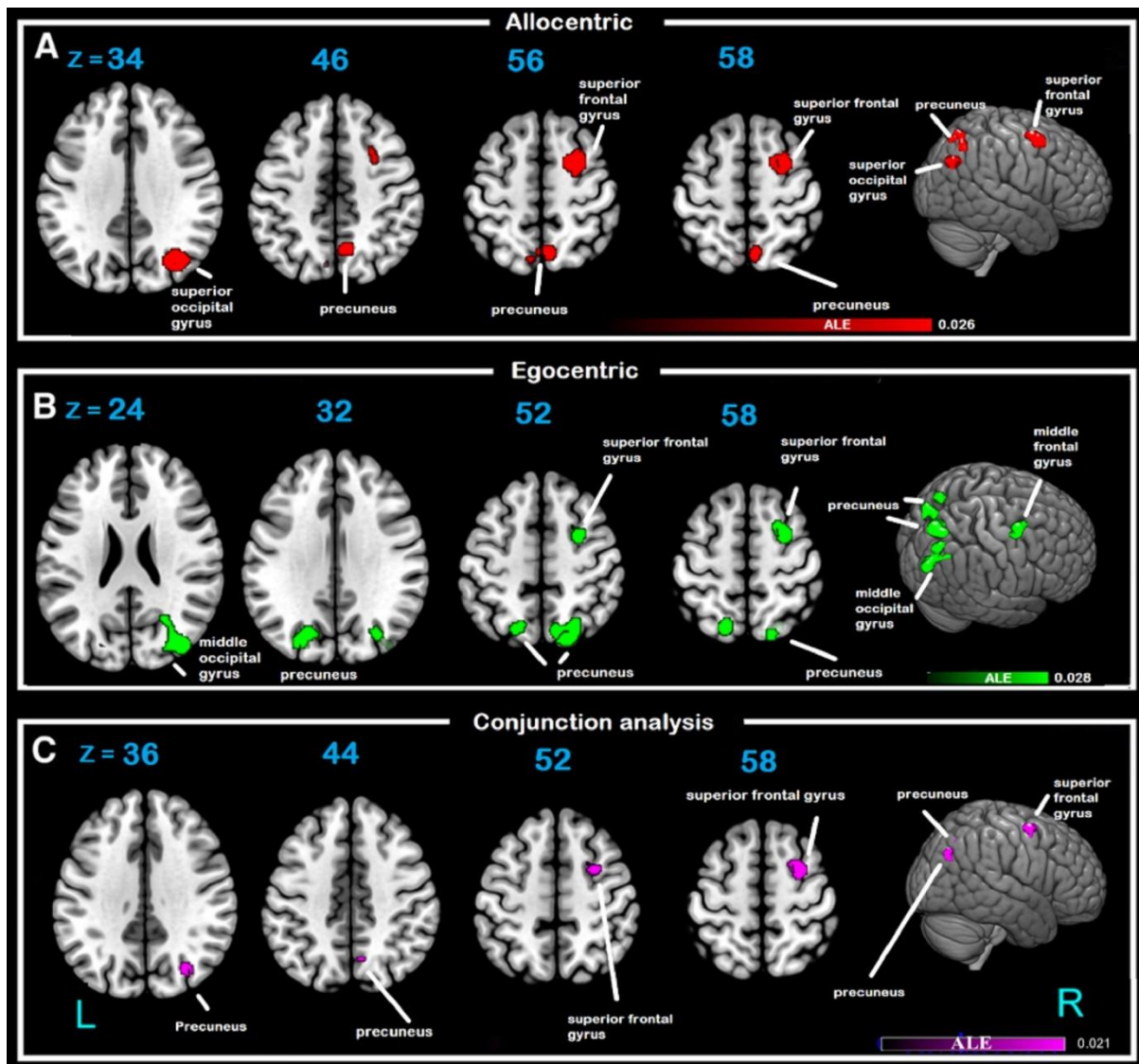frontal gyrus (SFG) ($z = 5.08$, $p < .001$) (Figure 3: Panel A and Table 2).

Figure 3. Brain regions showing task-related brain activations in allocentric spatial coding studies (meta-analysis 1; Panel A) and egocentric spatial coding studies (meta-analysis 2; Panel B). Panel C (conjunction analysis) shows common task-related brain activations appeared in both spatial coding studies. Color bar presents activation likelihood estimation (ALE) z-values.

Meta-analysis 2 (eSC)

Five clusters of convergence were identified for the 22 experiments that employed egocentric spatial coding. The significant clusters were in the right MOG, including a portion of the posterior cingulate cortex ($z = 6.0$, $p < .001$), the right and left precuneus (RH: $z = 6.04$, $p < .001$; LH: $z = 4.73$, $p < .001$), and the right medial frontal gyrus (MFG) ($z = 5.01$, $p < .001$) (Figure 3: Panel B and Table 2). The right middle occipital gyrus and a portion of the right posterior cingulate were two other areas of convergence for the egocentric spatial representations.

Contrast and conjunction analyses (aSC and eSC)

Two contrasting meta-analyses were conducted between the two spatial coding types [aSC > eSC] and [eSC > aSC] and no significant results were obtained. Conjunction analysis of aSC and eSC revealed two clusters of convergence with their main peaks located at the right precuneus and the right SFG (Figure 3: Panel C and Table 2).

Table 2 ALE results of cluster of convergence on conjunction analysis of allocentric and egocentric spatial coding types

Cluster	mm^3	Coordinates X	y	z	ALE value	P value	z-score	Hemi	BA	Anatomical Labeling
Meta-analysis 1: allocentric										
1	2264	22	4	56	0.022	<.001	5.08	R	6	Superior frontal gyrus
		28	8	54	0.020	<.001	4.88	R	6	Middle frontal gyrus
2	1952	36	-72	34	0.026	<.001	5.75	R	19	Superior occipital gyrus
		8	-60	46	0.019	<.001	4.64	R	7	Precuneus
3	1872	8	-60	46	0.019	<.001	4.64	R	7	Precuneus
		-6	-70	52	0.014	<.001	3.80	L	7	Precuneus
Meta-analysis 2: egocentric										
1	3656	38	-80	24	0.028	<.001	6.00	R	19	Middle occipital gyrus
		32	-72	40	0.022	<.001	5.03	R	19	Precuneus
		26	-62	22	0.014	<.001	3.73	R	31	Posterior cingulate cortex
2	2896	18	-74	52	0.028	<.001	6.04	R	7	Precuneus
3	1728	28	2	58	0.021	<.001	5.01	R	6	Superior frontal gyrus
		28	-2	50	0.017	<.001	4.31	R	6	Precentral gyrus
4	1448	-26	-78	32	0.020	<.001	4.73	L	31	Precuneus
5	1096	-16	-66	56	0.019	<.001	4.67	L	7	Precuneus
Conjunction Analysis										
1	1048	28	2	58	0.021	NA	NA	R	6	Superior frontal gyrus
2	616	32	-72	36	0.018	NA	NA	R	19	Precuneus
3	88	8	-64	44	0.013	NA	NA	R	7	Precuneus

Note: NA = not available. Conjunction analysis was based on intersection z-maps, which were thresholded and corrected for multiple comparison using FWE at p < .05. Thus p-value and z-score cannot be computed.

Meta-analysis 3a (SJ) and 3b (SN) (task-specific aSC)

The results of ALE for the SJ tasks (allocentric) revealed five clusters of convergence (Figure 4 and Table 3). Regions with significant convergence were in the right MFG (z = 4.06, p < .001), right precuneus (z = 4.09, p < .001), right fusiform gyrus (z = 4.60, p < .001),

and right IPL (z = 4.27, p < .001). Two clusters of convergence were revealed for the SN

counterpart, and the regions were in the right superior lateral occipital cortex (z = 4.57, p <

.001) and the right precuneus (z = 4.11, p < .001), which included a portion of the left
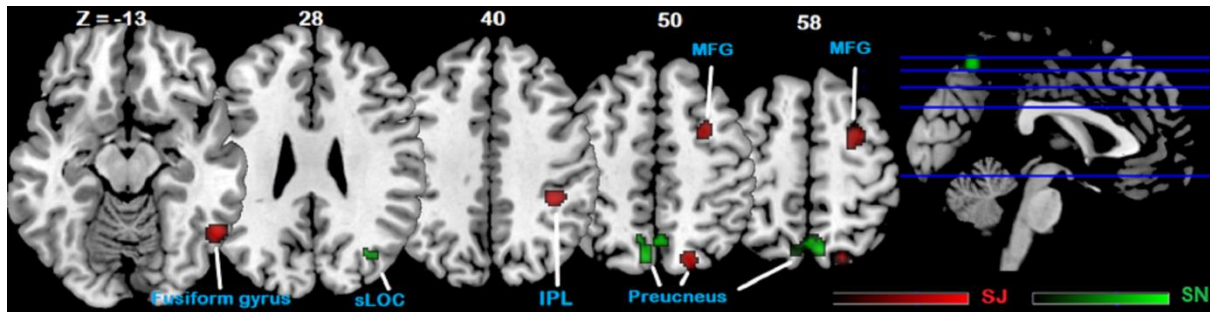
precuneus (z = 4.11, p < .001).

Figure 4. Results of ALE for the SJ (red) and SN (green) in allocentric spatial coding studies.

Color bar indicates the ALE values. Note: SJ = spatial judgment tasks. SN = Spatial

Navigation tasks. sLOC = superior lateral occipital cortex. IPL = inferior parietal lobule.

MFG = middle frontal gyrus.

Meta-analysis 4a (SJ) and 4b (SN) (task-specific eSC)

The results of ALE revealed two clusters of convergence for the SJ tasks. These

clusters were in the right MOG (z = 6.10, p < .001), precuneus (z = 5.82, p < 001), right MFG

(z = 5.57, p < .001), and partially right SFG (z = 5.04, p < .001). On the other hand, three

clusters of convergence were revealed for the SN tasks, which were in the right MOG (z =

4.38, p < .001) and bilateral precuneus (RH: z = 4.78, p < .001; LH: z = 4.84, p < .001)
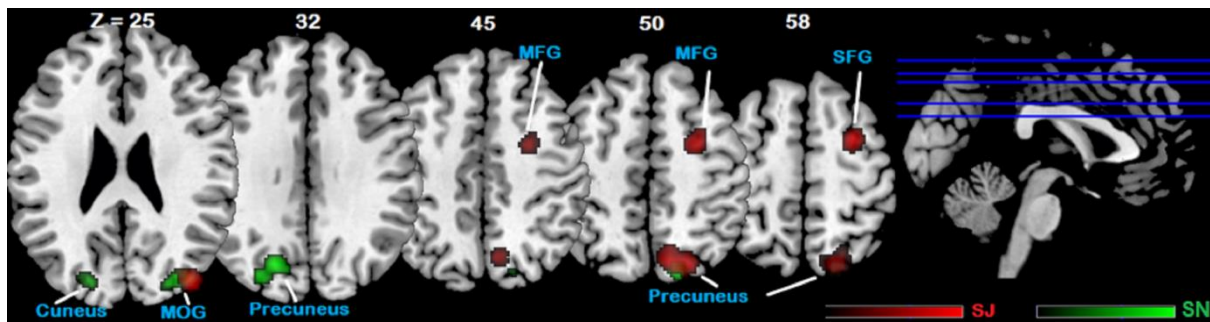
(Figure 5 and Table 3).

Figure 5. Results of ALE for the SJ (red) and SN (green) in egocentric spatial coding studies. Color bar indicates the ALE values. Note: SJ = spatial judgment tasks. SN = Spatial Navigation tasks. MOG = middle occipital gyrus. MFG = middle frontal gyrus. SFG = superior frontal gyrus.

Table 3 Task-specific (meta-analyses 3 and 4) related cluster of convergence in SJ versus SN of allocentric and egocentric spatial coding types

Cluster	mm^3	Coordinates			ALE value	*p value*	z score	hemi	BA	Anatomical Labeling
		x	y	Z						
Meta-analysis 3a (SJ) (for aSC)										
1	1096	30	4	48	0.011	<.001	4.06	R	6	Middle frontal gyrus
2	872	34	-72	34	0.011	<.001	4.09	R	19	Precuneus
3	840	54	-58	-12	0.013	<.001	4.60	R	37	Fusiform gyrus
4	712	40	-36	42	0.011	<.001	4.27	R	40	Inferior parietal lobule
5	680	20	-74	52	0.014	<.001	4.95	R	7	Precuneus
Meta-analysis 3b (SN) (for aSC)										
1	1472	6	-66	58	0.014	<.001	4.11	R	7	Precuneus
		2	-62	52	0.014	<.001	4.11	L	7	Precuneus
2	816	34	-70	32	0.016	<.001	4.57	R		Superior lateral occipital cortex
Meta-analysis 4a (SJ) (for eSC)										
1	2952	18	-72	54	0.021	<.001	5.82	R	7	Precuneus
2	2192	28	0	58	0.020	<.001	5.57	R	6	Middle frontal gyrus
		28	-2	50	0.017	<.001	5.04	R	6	Superior frontal gyrus
3	1376	40	-82	24	0.023	<.001	6.10	R	19	Middle occipital gyrus
Meta-analysis 4b (SN) (for eSC)										
1	1720	-18	-72	32	0.017	<.001	4.78	L	31	Precuneus
		-28	-80	32	0.013	<.001	4.16	L	19	Superior occipital gyrus
		-22	-80	28	0.012	<.001	3.90	L	18	Cuneus
2	976	36	-80	26	0.015	<.001	4.38	R	19	Middle occipital gyrus
		26	-84	24	0.010	<.001	3.54	R	18	Cuneus
3	728	18	-76	52	0.017	<.001	4.84	R	7	Precuneus

Allocentric spatial coding type was associated with the convergence in the right SFG

and SOG (Figure 6). In contrast, the egocentric spatial coding type appears to associate with

convergence in the right MFG and MOG. Convergence in the right precuneus seems to

associate with both spatial coding types. Substantial differences in convergence were

revealed between the SJ and SN tasks in each of the allocentric and egocentric types. Task-

specific allocentric spatial coding appears to demand the most diverse clusters of

convergence, including the right inferior parietal lobule (IPL), superior lateral occipital cortex

(sLOC), and right fusiform gyrus (FG).
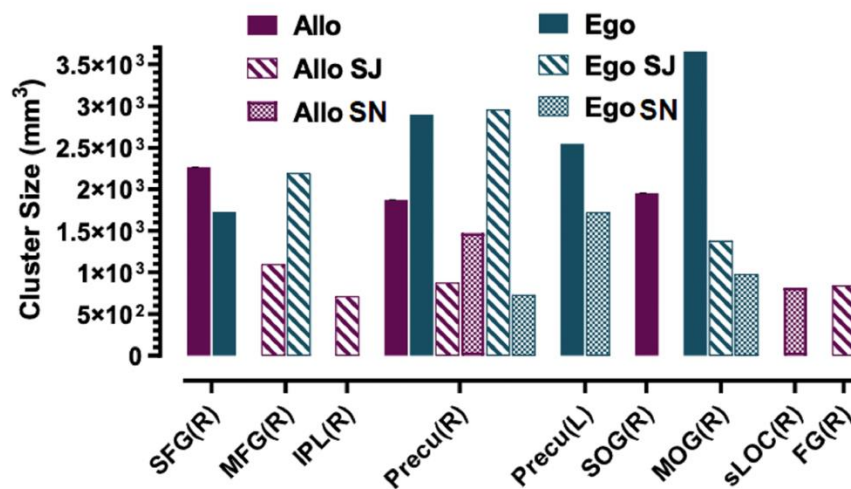
Figure 6. Summary of the results of the ALE in terms of cluster sizes (in mm3) showing

clusters of convergence in allocentric and egocentric spatial coding studies before and after

grouped according to the spatial judgment (SJ) or spatial navigation (SN) task-specific

features. SFG = superior frontal gyrus. MFG = middle frontal gyrus. IPL = inferior parietal

lobule. Precu = precuneus. SOG = superior occipital gyrus. MOG = middle occipital gyrus.

FG = fusiform gyrus. sLOC = superior lateral occipital cortex. Note: the cluster size in mm3

were taken from Table 2 and 3.

General Discussion

The allocentric and egocentric spatial coding types share comparable clusters of convergence in the precuneus and the SFG. The main convergence differences were in the occipital region — that is, in the SOG and MOG for the allocentric and egocentric representations, respectively. Additional controls set on task types revealed more differences in the convergences. For the SJ tasks, the MFG clusters of convergence were unique and common to both types. In contrast, the FG and IPL clusters were unique to the allocentric type, and the middle occipital gyrus cluster was unique to the egocentric type. For the SN tasks, the precuneus cluster of convergence was common to both spatial coding types, while the sLOC cluster was unique to the allocentric type and the middle occipital gyrus was unique to the egocentric type. It is noteworthy that the right precuneus cluster of convergence was found to associate with all the spatial coding and task types among all clusters. The left precuneus cluster of convergence was associated only with egocentric spatial coding, particularly with SN tasks. When compared to SJ tasks, functional lateralization of the precuneus suggests that SN tasks are likely to associate with the memory retrieval process. This evidence is in line with findings reported in previous studies that the left precuneus is involved in spatially guided behavior requiring spatial resolution and contextual association in space (for review see Cavanna & Trimble, 2006).

The precuneus cluster's convergent results supported the hypothesis that egocentric and allocentric spatial coding are mediated by common neural substrates — that is, by the precuneus, which falls within the SPL/FEF junction. However, the hypothesis that the egocentric spatial coding would involve the SOG, lateral/ventral IPS, and RSC, and that the allocentric spatial coding would involve the IPL and MTL (including hippocampus) cannot be supported. The task-specific hypothesis that the SJ tasks would be biased with the

convergence in the parieto-occipital clusters, and that the SN tasks would be biased with the convergence in the parieto-temporal clusters, including the MTL, is partially upheld.

Neural processes underlying spatial coding – similarities and differences

The finding of the convergence of the bilateral precuneus cluster as common to both spatial coding types is consistent with what has been reported in previous studies employing egocentric (Creem et al., 2001; Gomez et al., 2013; Parslow et al., 2004; Schindler & Bartels, 2013; Zaehle et al., 2007) or allocentric (Creem et al., 2001; Frings et al., 2006; Parslow et al., 2004; Shibata & Inui, 2011; Wegman et al., 2014; Zaehle et al., 2007; Zhang & Ekstrom, 2013) tasks. Similarly, the right SFG as the second cluster of convergence common to both spatial coding types is consistent with previous studies on egocentric (Committeri et al., 2004; Creem-Regehr et al., 2007; Creem et al., 2001; Fink et al., 2003; Galati et al., 2000; Gramann et al., 2006; Vallar et al., 1999) or allocentric (Frings et al., 2006; Shibata & Inui, 2011; Wegman et al., 2014; Zaehle et al., 2007) task-taking. These two clusters of convergence further indicated that the dorsal attention network mediates both spatial coding types. Neural processes, such as attention selection and response mapping (Corbetta & Shulman, 2002) and covert spatial attention maintenance (Corbetta & Shulman, 2002; Moore & Fallah, 2004; Thompson, Biscoe, & Sato, 2005), are essential for completing the tasks. Besides the dorsal attention network, the convergence revealed in the SFG cluster, and that in the precuneus cluster (as a larger part of the posterior cingulate cortex) suggests the involvement of the fronto-parietal attention network in both types of spatial coding. Additional neural processes for the tasks would be visuospatial attention (Galati et al., 2001; Galati et al., 2000; Liu et al., 2017; Neggers et al., 2006; Werner, 2005; Zhang & Ekstrom, 2013), encoding of objects in space (Foley, Whitwell, & Goodale, 2015; Goodale & Milner, 1992; Milner & Goodale, 2008), and maintenance of spatial representations in working memory (Corbetta et al., 2008; Ptak, 2012).

Coding of spatial navigations, especially when the processes involve visual working memory, is associated with the MTL's involvement (Burgess, 2008; Byrne et al., 2007; Committeri et al., 2004). As the MTL connects with the hippocampus (Parslow et al., 2004; Wegman et al., 2014; Zhang & Ekstrom, 2013) and parahippocampal (Parslow et al., 2004; Wegman et al., 2014), the MTL is expected to relate more to allocentric than egocentric processing (see Table 1). However, this study's findings failed to support this speculation as both aSC and eSC did not show any significant clusters of convergence in the hippocampus and parahippocampal areas regardless of the task types. One plausible reason for these negative results is that the hippocampus and its associated regions might have played a task-generic role in spatial navigation. An alternative explanation is that the relatively small number of experiments reported the hippocampus and parahippocampal involvement. The effect sizes were too small for producing a significant cluster required in this meta-analysis (see Table 1).

The main differences in the convergence of clusters between the two types of spatial coding were revealed in the occipital cortex. That is, in the SOG versus the MOG for the allocentric and egocentric types. Our results on the SOG are consistent with a few previous studies that showed activations in the SOG were higher in an allocentric than in an egocentric condition (Committeri et al., 2004; Galati et al., 2000; Neggers et al., 2006; Zaehle et al., 2007). The SOG (BA 19) is located in the anterior parieto-occipital region (Galletti et al., 2001), which mediates object-centered image processing (Crowe et al., 2008). Its close connection with the precuneus (van Asselen, Kessels, Kappelle, & Postma, 2008) suggests that the SOG may play a role in visualizing and maintaining the spatial relationships of the objects in space during the allocentric coding process (Boccia, Nemmi, & Guariglia, 2014; Derbie et al., 2021). The MOG, in contrast, is located rostrally to the parieto-occipital sulcus, which mediates encoding of object locations (Goodale & Milner, 1992). The role of the MOG

in egocentric coding is likely to encode the body-centered coordinates during the coding process (van der Stoep, Postma, & Nijboer, 2017). It is noteworthy that the convergent results of the SOG and MOG clusters revealed are not consistent with those reported in a few papers included in this meta-analysis. Three papers reported activations in the lateral occipital complex (comprising both the MOG and the SOG) in both spatial coding types (Liu et al., 2017; Saj et al., 2014; Werner, 2005), and two other papers reported activations in the SOG in the egocentric condition (Werner, 2005; Zaehle et al., 2007). A close look at the tasks used in these experiments indicated that the task processes involved some sort of SJ (see below). The similarity in the coding rules set for these supposedly allocentric and egocentric processes could have confounded the results. For instance, discriminating left/right with reference to the body in the egocentric condition (Saj et al., 2014) is largely comparable to differentiating the movement of an on-screen bar with reference to the midpoint of a line close to the bar in the allocentric condition (Neggers et al., 2006).

Task-specific confounding factor - spatial judgment versus spatial navigation

The complementary task-specific meta-analyses resulted in two main observations. First, the precuneus was confirmed once again to play a generic role, its convergence was found in both SJ and SN tasks. Second, the task-specific processes' influence on the convergence of clusters was more substantial for the allocentric than for the egocentric type. The generic role of the precuneus in both types of spatial coding has been covered in the last section and will not be repeated here. No task-specific influence was revealed for the egocentric spatial coding, which yielded the MOG cluster of convergence across SJ and SN conditions. In contrast, SJ task influences were found in the FG and IPL clusters for the allocentric spatial coding, whereas SN task influences were found in the sLOC cluster.

The results indicated that, during the SJ tasks, allocentric spatial coding might have been biased with increasing demands of object recognition (FG; Weiner & Zilles, 2016), spatial perception (IPL, see Husain & Nachev, 2007), sustained attention (IPL, see Husain & Nachev, 2007) and attention shifting and maintenance (IPL, see Ptak, 2012). The SJ tasks might also have changed the demands of the displacement-related process of the target image in allocentric spatial coding (FG, see Ferber, Humphrey, & Vilis, 2003). To support our proposition, subjects in a few SJ allocentric tasks were required to judge a left or right position against a self-perceived midpoint on the same line (Galati et al., 2000; Saj et al., 2014; Vallar et al., 1999). The orienting attention would have dominated the task-taking processes for continuous saccadic eye movements and online SJ, instead of by visualizing and maintaining spatial relationships through such means as memory-guided retrieval, as unique to allocentric spatial coding (see Saj et al., 2014). For the confounding factor in the SN tasks, the sLOC cluster also included the posterior parietal cortex. The posterior parietal cortex has been reported to be involved in maintaining visuospatial control of primed action (Goodale & Milner, 1992), and the sLOC in an animal study was found to modulate long-term representation of objects in the visual-field (James, Humphrey, Gati, Menon, & Goodale, 2002). SN tasks could inevitably bias allocentric spatial coding with excessive action controls and maintenance of object representations, such as environmental scenes, in the visual field (see Committeri et al., 2004). Another possible confound that might explain the results in sLOC is the difference in visual information load between SJ and SN. Spatial navigation tasks appear to have more visual information on the screen as compared to a visually simpler spatial judgment tasks in those selected studies.

Limitations

There are a few limitations associated with the meta-analytic method adopted in this study. First, we did not attempt to elucidate the theoretical basis for attentional spatial coding,

as ALE cannot examine temporal courses of the underlying neural processes. The results are meant to merely differentiate the main neural processes associated with the allocentric and egocentric types. Second, the conjunction analyses conducted yielded convergent neural clusters, and the results cannot reflect the within-group heterogeneity among the allocentric/egocentric and SJ/SN tasks. Third, the task-specific classifications adopted in this study (meta-analysis 3a,b & 4a,b) excluded several experiments and articles from the analyses. This somewhat would have compromised the generalization of the task-specific ALE results. In addition, some of the tasks included in SN (e.g. Committeri et al., 2004) may require SJ processing. Readers should be cautious when interpreting the findings of this part of the study.

Conclusion

Allocentric and egocentric spatial coding involves both similar and distinctive cognitive processes. The strong common clusters of convergence in the right precuneus and the right superior frontal gyrus suggest the recruitment of the parieto-frontal circuit in spatial coding. The distinctiveness of the two types of spatial coding was found in the parieto-occipital circuit. The SOG cluster dominated the allocentric coding of space, and the MOG cluster dominated the egocentric coding of space. These findings indicate that spatial coding, regardless of type, requires attention selection and maintenance, and response mapping. However, allocentric and egocentric types are unique in recruiting the SOG and MOG clusters for mediating the distinct processes required in the tasks. The allocentric coding process tasks are the visualization and maintenance of spatial relationships of objects in space. In the egocentric coding process, they are the encoding of body-centered coordinates.

The testing of task-specific influences indicated that egocentric spatial coding tasks used in previous studies are rather bias-free. Allocentric spatial coding tasks appear to have been significantly influenced, whether an SJ or an SN design was adopted as the task-taking

process. SJ designs were revealed to have been easily biased by decreases in demands of manipulating spatial relationships among the visual objects. SN designs were dominated by demands of action controls and maintaining visual scenes. Our findings offer insights to enhance spatial tasks' design for assessing spatial coding, particularly of those tasks targeting the allocentric type.

Author's contribution statement

Abiot Y. Derbie: conceptualization, analysis, investigation, method, writing - original draft, writing - review & editing. **Bolton K.H. Chau:** supervision, writing - review & editing. **Clive H. Y. Wong:** data analysis, writing - review & editing. **Li-dian Chen:** writing - review & editing. **Kin-hung Ting:** Resources, writing - review & editing. **Bess Y. H. Lam:** Resources, writing - review & editing. **Tatia M.C. Lee:** conceptualization, funding acquisition, resources, writing - review & editing. **Chetwyn C.H. Chan:** funding acquisition, conceptualization, supervision, validation, writing - original draft, writing - review & editing.

Data sharing statement

The data will be available on a reasonable request to the corresponding author.

References

Barra, J., Laou, L., Poline, J.-B., Lebihan, D., & Berthoz, A. (2012). Does an oblique/slanted perspective during virtual navigation engage both egocentric and allocentric brain strategies? *PloS one, 7*(11), e49537.

Bartsch, T., Schönfeld, R., Müller, F., Alfke, K., Leplow, B., Aldenhoff, J., . . . Koch, J. (2010). Focal lesions of human hippocampal CA1 neurons in transient global amnesia impair place memory. *Science, 328*(5984), 1412-1415.

Boccia, M., Nemmi, F., & Guariglia, C. (2014). Neuropsychology of Environmental Navigation in Humans: Review and Meta-Analysis of fMRI Studies in Healthy Participants. *Neuropsychology Review, 24*(2), 236-251. doi:10.1007/s11065-014-9247-8

Burgess, N. (2008). Spatial cognition and the brain. *Ann N Y Acad Sci, 1124*(1), 77-97. doi:10.1196/annals.1440.002

Burles, F., Slone, E., & Iaria, G. (2017). Dorso-medial and ventro-lateral functional specialization of the human retrosplenial complex in spatial updating and orienting. *Brain Struct Funct, 222*(3), 1481-1493. doi:10.1007/s00429-016-1288-8

Byrne, P., Becker, S., & Burgess, N. (2007). Remembering the past and imagining the future: a neural model of spatial memory and imagery. *Psychol Rev, 114*(2), 340-375. doi:10.1037/0033-295X.114.2.340

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain, 129*(Pt 3), 564-583. doi:10.1093/brain/awl004

Chafee, M. V., Averbeck, B. B., & Crowe, D. A. (2007). Representing spatial relationships in posterior parietal cortex: single neurons code object-referenced position. *Cereb Cortex, 17*(12), 2914-2932. doi:10.1093/cercor/bhm017

Chen, Q., Weidner, R., Weiss, P. H., Marshall, J. C., & Fink, G. R. (2012). Neural interaction between spatial domain and spatial reference frame in parietal-occipital junction. *J Cogn Neurosci,* **24**(11), 2223-2236. doi:10.1162/jocn_a_00260

Chen, Y., Monaco, S., Byrne, P., Yan, X., Henriques, D. Y., & Crawford, J. D. (2014). Allocentric versus egocentric representation of remembered reach targets in human cortex. *J. Neurosci.,* **34**(37), 12515-12526. doi:10.1523/JNEUROSCI.1445-14.2014

Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annu Rev Psychol,* **62**, 73-101. doi:10.1146/annurev.psych.093008.100427

Committeri, G., Galati, G., Paradis, A. L., Pizzamiglio, L., Berthoz, A., & LeBihan, D. (2004). Reference frames for spatial cognition: different brain areas are involved in viewer-, object-, and landmark-centered judgments about object location. *J Cogn Neurosci,* **16**(9), 1517-1535. doi:10.1162/0898929042568550

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron,* **58**(3), 306-324. doi:10.1016/j.neuron.2008.04.017

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci,* **3**(3), 201-215. doi:10.1038/nrn755

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annu Rev Neurosci,* **34**, 569-599. doi:10.1146/annurev-neuro-061010-113731

Creem-Regehr, S. H., Neil, J. A., & Yeh, H. J. (2007). Neural correlates of two imagined egocentric transformations. *Neuroimage,* **35**(2), 916-927. doi:10.1016/j.neuroimage.2006.11.057

Creem, S. H., Downs, T. H., Snyder, A., Downs III, J. H., & Proffitt, D. R. (2001). *Egocentric Versus Object-Relative Spatial Judgment Tasks Elicit Differences in Brain*

Activity. Paper presented at the Annual meeting of the Cognitive Neuroscience Society.

Crowe, D. A., Averbeck, B. B., & Chafee, M. V. (2008). Neural ensemble decoding reveals a correlate of viewer-to object-centered spatial transformation in monkey parietal cortex. *J. Neurosci., **28***(20), 5218-5228.

Derbie, A. Y., Chau, B., Lam, B., Fang, Y. H., Ting, K. H., Wong, C. Y. H., . . . Chan, C. C. H. (2021). Cortical Hemodynamic Response Associated with Spatial Coding: A Near-Infrared Spectroscopy Study. *Brain Topogr, **34***(2), 207-220. doi:10.1007/s10548-021-00821-9

Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *Neuroimage, **59***(3), 2349-2361. doi:10.1016/j.neuroimage.2011.09.017

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. *Hum Brain Mapp, **30***(9), 2907-2926. doi:10.1002/hbm.20718

Eickhoff, S. B., Nichols, T. E., Laird, A. R., Hoffstaedter, F., Amunts, K., Fox, P. T., . . . Eickhoff, C. R. (2016). Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *Neuroimage, **137***, 70-85. doi:10.1016/j.neuroimage.2016.04.072

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage, **25***(4), 1325-1335. doi:10.1016/j.neuroimage.2004.12.034

Ekstrom, A. D., Arnold, A. E., & Iaria, G. (2014). A critical review of the allocentric spatial representation and its neural underpinnings: toward a network-based perspective. *Front Hum Neurosci,* **8**, 803. doi:10.3389/fnhum.2014.00803

Ferber, S., Humphrey, G. K., & Vilis, T. (2003). The lateral occipital complex subserves the perceptual persistence of motion-defined groupings. *Cerebral Cortex,* **13**(7), 716-721.

Filimon, F. (2015). Are All Spatial Reference Frames Egocentric? Reinterpreting Evidence for Allocentric, Object-Centered, or World-Centered Reference Frames. *Front Hum Neurosci,* **9**, 648. doi:10.3389/fnhum.2015.00648

Fink, G. R., Marshall, J. C., Weiss, P. H., Stephan, T., Grefkes, C., Shah, N. J., . . . Dieterich, M. (2003). Performing allocentric visuospatial judgments with induced distortion of the egocentric reference frame: an fMRI study with clinical implications. *Neuroimage,* **20**(3), 1505-1517. doi:10.1016/j.neuroimage.2003.07.006

Foley, R. T., Whitwell, R. L., & Goodale, M. A. (2015). The two-visual-systems hypothesis and the perspectival features of visual experience. *Conscious. Cogn.,* **35**, 225-233. doi:10.1016/j.concog.2015.03.005

Frings, L., Wagner, K., Quiske, A., Schwarzwald, R., Spreer, J., Halsband, U., & Schulze-Bonhage, A. (2006). Precuneus is involved in allocentric spatial location encoding and recognition. *Exp. Brain Res.,* **173**(4), 661-672. doi:10.1007/s00221-006-0408-8

Galati, G., Committeri, G., Sanes, J. N., & Pizzamiglio, L. (2001). Spatial coding of visual and somatic sensory information in body-centred coordinates. *Eur J Neurosci,* **14**(4), 737-746. doi:10.1046/j.0953-816x.2001.01674.x

Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (2000). The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Exp. Brain Res.,* **133**(2), 156-164. doi:10.1007/s002210000375

Galletti, C., Gamberini, M., Kutz, D. F., Fattori, P., Luppino, G., & Matelli, M. (2001). The cortical connections of area V6: an occipito-parietal network processing visual information. *Eur. J. Neurosci.,* **13**(8), 1572-1588. doi:10.1046/j.0953-816x.2001.01538.x

Gamberini, M., Passarelli, L., Fattori, P., Zucchelli, M., Bakola, S., Luppino, G., & Galletti, C. (2009). Cortical connections of the visuomotor parietooccipital area V6Ad of the macaque monkey. *Journal of Comparative Neurology,* **513**(6), 622-642.

Ganesh, S., van Schie, H. T., Cross, E. S., de Lange, F. P., & Wigboldus, D. H. (2015). Disentangling neural processes of egocentric and allocentric mental spatial transformations using whole-body photos of self and other. *Neuroimage,* **116**, 30-39. doi:10.1016/j.neuroimage.2015.05.003

Geng, J. J., & Vossel, S. (2013). Re-evaluating the role of TPJ in attentional control: contextual updating? *Neurosci Biobehav Rev,* **37**(10 Pt 2), 2608-2620. doi:10.1016/j.neubiorev.2013.08.010

Gomez, A., Cerles, M., Rousset, S., Le Bas, J. F., & Baciu, M. (2013). Ongoing egocentric spatial processing during learning of non-spatial information results in temporal-parietal activity during retrieval. *Front Psychol,* **4**, 366. doi:10.3389/fpsyg.2013.00366

Gomez, A., Cerles, M., Rousset, S., Remy, C., & Baciu, M. (2014). Differential hippocampal and retrosplenial involvement in egocentric-updating, rotation, and allocentric processing during online spatial encoding: an fMRI study. *Front Hum Neurosci,* **8**, 150. doi:10.3389/fnhum.2014.00150

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci,* **15**(1), 20-25. doi:10.1016/0166-2236(92)90344-8

Gramann, K., Muller, H. J., Schonebeck, B., & Debus, G. (2006). The neural basis of ego- and allocentric reference frames in spatial navigation: evidence from spatio-temporal coupled current density reconstruction. *Brain Res,* **1118**(1), 116-129. doi:10.1016/j.brainres.2006.08.005

Hashimoto, R., Tanaka, Y., & Nakano, I. (2010). Heading disorientation: a new test and a possible underlying mechanism. *Eur Neurol,* **63**(2), 87-93. doi:10.1159/000276398

Husain, M., & Nachev, P. (2007). Space and the parietal cortex. *Trends in cognitive sciences,* **11**(1), 30-36.

James, T. W., Humphrey, G. K., Gati, J. S., Menon, R. S., & Goodale, M. A. (2002). Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. *Neuron,* **35**(4), 793-801.

Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nat Rev Neurosci,* **12**(4), 217-230. doi:10.1038/nrn3008

Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: an expanded neural framework for the processing of object quality. *Trends Cogn Sci,* **17**(1), 26-49. doi:10.1016/j.tics.2012.10.011

Liu, N., Li, H., Su, W., & Chen, Q. (2017). Common and specific neural correlates underlying the spatial congruency effect induced by the egocentric and allocentric reference frame. *Hum Brain Mapp,* **38**(4), 2112-2127. doi:10.1002/hbm.23508

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia,* **46**(3), 774-785. doi:10.1016/j.neuropsychologia.2007.10.005

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & Group, P. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS medicine,* **6**(7), e1000097. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2707599/pdf/pmed.1000097.pdf

Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *J Neurophysiol, 91*(1), 152-162. doi:10.1152/jn.00741.2002

Muller, V. I., Cieslik, E. C., Laird, A. R., Fox, P. T., Radua, J., Mataix-Cols, D., . . . Eickhoff, S. B. (2018). Ten simple rules for neuroimaging meta-analysis. *Neurosci Biobehav Rev, 84*, 151-161. doi:10.1016/j.neubiorev.2017.11.012

Neggers, S. F., Van der Lubbe, R. H., Ramsey, N. F., & Postma, A. (2006). Interactions between ego- and allocentric neuronal representations of space. *Neuroimage, 31*(1), 320-331. doi:10.1016/j.neuroimage.2005.12.028

Nori, R., Piccardi, L., Maialetti, A., Goro, M., Rossetti, A., Argento, O., & Guariglia, C. (2018). No gender differences in egocentric and allocentric environmental transformation after compensating for male advantage by manipulating familiarity. *Frontiers in neuroscience, 12*, 204.

Parslow, D. M., Rose, D., Brooks, B., Fleminger, S., Gray, J. A., Giampietro, V., . . . Morris, R. G. (2004). Allocentric spatial memory activation of the hippocampal formation measured with fMRI. *Neuropsychology, 18*(3), 450-461. doi:10.1037/0894-4105.18.3.450

Posner, M. I. (1980). Orienting of attention. *Q J Exp Psychol, 32*(1), 3-25. doi:10.1080/00335558008248231

Ptak, R. (2012). The frontoparietal attention network of the human brain: action, saliency, and a priority map of the environment. *Neuroscientist, 18*(5), 502-515. doi:10.1177/1073858411409051

Ptak, R., & Schnider, A. (2010). The dorsal attention network mediates orienting toward behaviorally relevant stimuli in spatial neglect. *J Neurosci, 30*(38), 12557-12565.

Ruggiero, G., D'Errico, O., & Iachini, T. (2016). Development of egocentric and allocentric spatial representations from childhood to elderly age. *Psychological research,* **80**(2), 259-272.

Rushworth, M., Behrens, T., & Johansen-Berg, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral cortex,* **16**(10), 1418-1430.

Saj, A., Cojan, Y., Musel, B., Honore, J., Borel, L., & Vuilleumier, P. (2014). Functional neuro-anatomy of egocentric versus allocentric space representation. *Neurophysiol Clin,* **44**(1), 33-40. doi:10.1016/j.neucli.2013.10.135

Schindler, A., & Bartels, A. (2013). Parietal cortex codes for egocentric space beyond the field of view. *Curr. Biol.,* **23**(2), 177-182. doi:10.1016/j.cub.2012.11.060

Shibata, H., & Inui, T. (2011). Brain activity associated with recognition of appropriate action selection based on allocentric perspectives. *Neurosci Lett,* **491**(3), 187-191. doi:10.1016/j.neulet.2011.01.033

Szczepanski, S. M., Pinsk, M. A., Douglas, M. M., Kastner, S., & Saalmann, Y. B. (2013). Functional and structural architecture of the human dorsal frontoparietal attention network. *Proc. Natl. Acad. Sci. U. S. A.,* **110**(39), 15806-15811. doi:10.1073/pnas.1313903110

Thaler, L., & Goodale, M. A. (2011). Neural substrates of visual spatial coding and visual feedback control for hand movements in allocentric and target-directed tasks. *Front Hum Neurosci,* **5**, 92. doi:10.3389/fnhum.2011.00092

Thompson, K. G., Biscoe, K. L., & Sato, T. R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *J. Neurosci.,* **25**(41), 9479-9487. doi:10.1523/JNEUROSCI.0741-05.2005

Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., & Fox, P. (2012). Minimizing within-experiment and within-group effects in Activation Likelihood Estimation meta-analyses. *Hum Brain Mapp, 33*(1), 1-13. doi:10.1002/hbm.21186

Vallar, G., Lobel, E., Galati, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (1999). A fronto-parietal system for computing the egocentric spatial frame of reference in humans. *Exp. Brain Res., 124*(3), 281-286. doi:10.1007/s002210050624

van Asselen, M., Kessels, R. P., Kappelle, L. J., & Postma, A. (2008). Categorical and coordinate spatial representations within object-location memory. *Cortex, 44*(3), 249-256.

van der Stoep, N., Postma, A., & Nijboer, T. C. W. (2017). Multisensory Perception and the Coding of Space. In A. Postma & I. J. M. van der Ham (Eds.), *Neuropsychology of Space* (pp. 123-158). San Diego: Academic Press.

Vann, S. D., Aggleton, J. P., & Maguire, E. A. (2009). What does the retrosplenial cortex do? *Nature Reviews Neuroscience, 10*, 792. doi:10.1038/nrn2733

Vossel, S., Geng, J. J., & Fink, G. R. (2014). Dorsal and ventral attention systems: distinct neural circuits but collaborative roles. *Neuroscientist, 20*(2), 150-159. doi:10.1177/1073858413494269

Walter, E., & Dassonville, P. (2008). Visuospatial contextual processing in the parietal cortex: an fMRI investigation of the induced Roelofs effect. *Neuroimage, 42*(4), 1686-1697. doi:10.1016/j.neuroimage.2008.06.016

Wegman, J., Tyborowska, A., & Janzen, G. (2014). Encoding and retrieval of landmark-related spatial cues during navigation: an fMRI study. *Hippocampus, 24*(7), 853-868. doi:10.1002/hipo.22275

Weiner, K. S., & Zilles, K. (2016). The anatomical and functional specialization of the fusiform gyrus. *Neuropsychologia, ***83**, 48-62. doi:10.1016/j.neuropsychologia.2015.06.033

Weniger, G., Siemerkus, J., Schmidt-Samoa, C., Mehlitz, M., Baudewig, J., Dechent, P., & Irle, E. (2010). The human parahippocampal cortex subserves egocentric spatial learning during navigation in a virtual maze. *Neurobiol Learn Mem, ***93**(1), 46-55. doi:10.1016/j.nlm.2009.08.003

Werner, S. (2005). *Allocentric spatial judgements by re-mapping egocentric coordinates: a fMRI study.* (MSc Thesis). Eberhard-Karls-Universität Tübingen, Tübingen, Germany.

Zaehle, T., Jordan, K., Wustenberg, T., Baudewig, J., Dechent, P., & Mast, F. W. (2007). The neural basis of the egocentric and allocentric spatial frame of reference. *Brain Res., ***1137**(1), 92-103. doi:10.1016/j.brainres.2006.12.044

Zanto, T. P., & Gazzaley, A. (2013). Fronto-parietal network: flexible hub of cognitive control. *Trends Cogn Sci, ***17**(12), 602-603. doi:10.1016/j.tics.2013.10.001

Zhang, H., & Ekstrom, A. (2013). Human neural systems underlying rigid and flexible forms of allocentric spatial representation. *Hum Brain Mapp, ***34**(5), 1070-1087. doi:10.1002/hbm.21494