



HAL
open science

Ego- and geo-centered references: a functional neuroimaging study

Arnaud Saj, Jacques Honore, Liliane Borel

► **To cite this version:**

Arnaud Saj, Jacques Honore, Liliane Borel. Ego- and geo-centered references: a functional neuroimaging study. *European Neurology*, 2024, *European Neurology*, 10.1159/000535725 . hal-04452893

HAL Id: hal-04452893

<https://hal.univ-lille.fr/hal-04452893v1>

Submitted on 22 Nov 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

Ego- and geo-centered references: a functional neuroimagery study

Arnaud Saj^{1,2,3}, Jacques Honoré⁴, Liliane Borel⁵

¹Neurology Department, Neuropsychology Unit, University Hospital of Geneva,
Switzerland

²Department of Psychology, University of Montréal, Montréal, QC, Canada

³CRIR/Institut Nazareth et Louis-Braille du CISSS de la Montérégie-Centre, Longueuil,
QC, Canada

⁴SCALab, UMR 9193, University of Lille, CNRS, F-59000 Lille, France

⁵ LNC, Aix-Marseille University, CNRS, 3 Place Victor Hugo, 13331 Marseille Cedex
03, France

Author corresponding : Pr Arnaud Saj, Department of Psychology, University of
Montréal, Montréal, QC, Canada. E-mail : arnaud.saj@umontreal.ca

Running title: Ego- and geo-centered in fMRI

21 **Ethics:** 2011-11-250 Cantonal Commission on Ethics in Human Research (CCER) -
22 authorisation for medical research on human beings. The written informed consent was
23 obtained for participation in this study.

24

25 **Funding:** AS is supported by Geneva Academic Society (Foremane Fund). LB was
26 supported by grants from CNRS, Ministère de l'Enseignement Supérieur et de la Recherche
27 (UMR 7260).

28 Conflict of Interest Statement: no conflict

29 **Author Contributions:** AS: study concept and design, analysis and interpretation of data,
30 and drafting the manuscript; LB: interpretation of data, revision of the manuscript for
31 intellectual content; JH: interpretation of data, revision of the manuscript for intellectual
32 content.

33 **Data Availability Statement:** All data generated or analysed during this study are included
34 in this article. Further enquiries can be directed to the corresponding author.

35

36

37 **Abstract**

38 Introduction - The integration of vestibular, visual, and somatosensory cues allows the
39 perception of space through the orientation of our body and surrounding objects with
40 respect to gravity. The main goal of this study was to identify the cortical networks
41 recruited during the representation of body midline and the representation of verticality.

42 Methods - Thirty right-handed healthy participants were evaluated using fMRI. Brain
43 networks activated during a subjective straight-ahead (SSA) task were compared to those

44 recruited during a subjective vertical (SV) task. Results - Different patterns of cortical
45 activation were observed, with differential increases in the angular gyrus and left
46 cerebellum posterior lobe during the SSA task, in right rolandic operculum and cerebellum
47 anterior lobe during the SV task. The activation of these areas involved in visuo-spatial

48 functions suggests that bodily processes of great complexity are engaged in body
49 representation and vertical perception. Discussion - Interestingly, the common brain

50 networks involved in SSA and SV tasks were areas of vestibular projection that receive
51 multisensory information (parieto-occipital areas) and the cerebellum, and reveal a

52 predominance of the right cerebral and cerebellar hemispheres. The outcomes of this first
53 fMRI study designed to unmask common and specific neural mechanisms at work in

54 gravity- or body-referenced tasks pave a new way for the exploration of spatial cognitive
55 impairment in patients with vestibular or cortical disorders.

56 **Key-word:** ego-centered reference frame; geo-centered reference frame; visual vertical;
57 visual straight ahead; fMRI

58

59 **Introduction**

60 The spatial positions and orientations of objects, bodies and of their parts may be
61 represented in distinct reference frames depending on the ongoing behaviour. In an ego-
62 centered frame (Vallar et al., 1999), they are referenced to our own body ('this can is on
63 my left'). When the reference is not bodily, the frame is said to be allo-centered (Galati et
64 al., 2010). In this case, it may be object-centered, the reference being an object ('the tag is
65 placed in the middle of the book cover', 'the line is not parallel to the edge of the sheet')
66 or geo-centered (Gentaz et al., 2008), the reference being the earth vertical ('the painting
67 is not hung vertically'). While there are a few papers comparing the neuronal network
68 subtending the ego-centered reference frame with the network subtending the object-
69 centered reference frame, the direct comparison with the geo-centered frame is still
70 missing.

71 In an ego-centered frame, positions are defined relative to the person's body or body
72 segment (head, trunk, or limb). One classical tool for assessing the ego-centered frame is
73 the subjective straight-ahead (SSA) task. The SSA is the participant's representation of the
74 direction "just ahead" of the body, which is contained in the midsagittal plane dividing the
75 body and surrounding spaces into two symmetrical right and left parts. Most often, to assess
76 this representation, the participant was asked to indicate in a horizontal plane where the
77 intersection with the midsagittal plane lay. Brain areas underlying the SSA have been
78 described in a few fMRI studies (Galati et al., 2000; Vallar et al., 1999; Saj et al., 2014).
79 Selective activity was found in the occipital, superior parietal, and inferior frontal cortices,
80 as well as in the precuneus and supplementary motor area in the right hemisphere. The
81 insula, thalamus, and cerebellum were also activated in the left hemisphere. In stroke

82 patients, in particular in those suffering from spatial neglect, damage of the same cortical
83 structures proved to be involved in ipsilesional SSA deviation (Barra et al., 2009;
84 Rousseaux et al., 2013). An ipsilesional SSA deviation has also been observed after
85 unilateral vestibular injury, in particular after left injury (Saj et al., 2013, 2021; Borel et
86 al., 2021). As they have been shown to be vestibular projection areas, the aforementioned
87 cortical areas could be involved, which remains an open issue.

88 The geo-centered reference frame makes it possible to reference the positions and
89 displacements of our body as well as surrounding objects with respect to gravity. The
90 classical evaluation task is the subjective vertical (SV). The SV is often assessed by asking
91 the subject to align a rod with the gravity. Neuroimaging studies using EEG (Lopez et al.,
92 2013) and fMRI (Saj et al., 2019) reported that gravity coding activates bilateral temporo-
93 occipital and parieto-occipital cortical networks associated with cerebellar and brainstem
94 areas. These activations, in healthy control, were characterized with a right dominance
95 tendency, involving notably the temporo-parietal junction and middle frontal gyrus. ~~by~~
96 ~~right hemisphere dominance~~. In stroke patients, damages to these regions were shown to
97 bias the SV toward the left (Barra et al., 2010), the bias counterclockwise more markedly
98 in cases of spatial neglect (Saj et al., 2012; Rousseaux et al., 2015). Furthermore, the SV
99 tilt, ipsilesional, is a frequent clinical sign of vestibular loss which occurs in unilateral
100 lesions from the brainstem to the parieto-insular vestibular cortex (Dieterich and Brandt,
101 2019).

102 To our knowledge, there is no available study directly comparing the networks underlying
103 ego-centered and geo-centered reference frames. Thus, in order to fill this gap, we recorded
104 the brain activity of the same healthy participants while they judged different spatial

105 properties of the same set of tilted (or not) and shifted (or not) lines. In separate blocks of
106 trials, they evaluated the verticality of these lines or their position relative to their
107 midsagittal plane.

108

109 **Methods**

110 **Subjects.** Thirty right-handed volunteers (mean age: 27.4 ± 2.8 years; 14 males and 16
111 females) were recruited from the general population. The participants were recruited
112 through advertisements on social media and on bulletin boards at the university and
113 hospital. The written informed consent was obtained for participation in this study (CCER-
114 2011-11-250). Exclusion criteria were past history of cerebral disease, epilepsy, head
115 trauma, vestibular or oculo-motor disorders or major psychiatric illness; visual acuity
116 below 20/40; left handedness; pregnancy; claustrophobia or contraindication to magnetic
117 field exposure (pacemaker, metallic prosthesis, dental apparatus, etc); addiction or intake
118 of any drug interfering with neuronal activity or cerebral blood flow.

119

120 **Behavioral design**

121 *Tasks*

122 In the subjective straight ahead task, the participants had to indicate whether or not the
123 center of visual lines (one per trial) were in their body midsagittal plane. In the subjective
124 vertical task, the participants judged whether or not the same visual lines (one per trial)
125 were aligned with the true vertical. In both tasks, the participant gave binary responses by
126 pressing keys with the index (yes) and middle fingers (no) of the right hand.

127 *Material*

128 The material and the stimuli were the same for SSA and SV tasks; only the instruction
129 differed. In each trial, a line (length = 10°; thickness = 1°) was projected on a vertical
130 screen reflected by a mirror mounted on the head coil in the MRI scanner. An irregular
131 frame was put around on the screen so as to avoid systematic strategies and minimize frame
132 effects. The lines were either straight (0°, 24 times) or tilted by -30°, -25°, -20°, -15°, -10°,
133 -5°, 5°, 10°, 15°, 20°, 25° or 30° (12 tilts, 3 times each). The center of the displayed line
134 was either in the midsagittal plane of the participant (0°) or deviated by 3° toward the left
135 or the right. In each of these 3 positions, the line was presented 8 times straight and once
136 with each of the 12 tilts. The order of the 60 visual stimuli was pseudo-random. Each was
137 presented in the first 1500 ms of the trial which lasted between 3000 and 4500 ms (pseudo-
138 randomly jittered). The participant could give his response during the whole duration of
139 the trial.

140 *Procedure*

141 The tasks were administered in a blocked design in order to maximize signal-to-noise ratio
142 and to minimize attentional demands. Two fMRI runs separated by a 30-sec pause, one per
143 task, were obtained in each participant. Instructions were given on the screen prior to each
144 run. A run included 10 blocks separated by 2-sec pauses, except the 5th which lasted 4 sec.
145 A block comprised 6 different stimuli, and lasted 24 sec. One half of the participants began
146 by the SSA task, the other by the SV task.

147

148 **Acquisition of fMRI data**

149 MRI data were acquired in the Brain and Behaviour Laboratory at the University Medical
150 Center in Geneva, Switzerland, using a 3-T whole-body TRIO system (Siemens) with the

151 standard head-coil configuration. Functional T2*-weighted images were obtained using
152 echoplanar imaging (EPI) with axial slices (TR/TE/Flip = 2200 ms/30 ms/85°, FOV = 235
153 mm, matrix = 128×128). Each functional volume was comprised of 32 contiguous 3.5 mm-
154 thick slices, parallel to the inferior surface of occipital and temporal lobes. For each patient,
155 a high-resolution anatomical image was also acquired after the functional scans, using a
156 3D-GRE T1-weighted sequence (FOV = 250 mm, TR/TE/Flip = 15 ms/5.0 ms/30°, matrix
157 = 256×256, slice-thickness = 1.25 mm). This anatomical image was co-registered with
158 functional images for subsequent normalization procedure.

159

160 **Analysis of fMRI data**

161 All fMRI data were processed and analysed using the general linear model for event-related
162 designs in SPM12 (Wellcome Department of Imaging Neuroscience, London, UK;
163 <http://www.fil.ion.ucl.ac.uk/spm>). Functional images were realigned, corrected for slice,
164 normalized to an EPI template (re-sampled at a voxel-size of 3x3x3 mm³), spatially
165 smoothed (8 mm FWHM), and high-pass filtered (cutoff: 180 sec). Statistical analyses
166 were performed on a voxelwise basis across the whole-brain, using a mixed blocked and
167 event-related design (Mechelli et al., 2003).

168 Individual visual events were modelled by a standard synthetic haemodynamic response
169 function (HRF). This HRF was estimated at each voxel by a General Linear Model (GLM)
170 using a least-square fit to the data, for each condition, and each individual participant.
171 Statistical maps (SPM[t]) generated from comparisons between conditions in individual
172 subjects were then included in a second-stage random-effect analysis, using one-sample t-
173 tests (Friston et al., 1998). The resulting maps SPM[t] were thresholded at conventional

174 statistical values (voxel threshold at $P < 0.001$ and cluster threshold at $P < 0.05$). In line
175 with previous imaging studies of our group (Saj et al., 2014), only the clusters comprising
176 more than 10 significant adjacent voxels were considered. Main comparisons were
177 performed between body representation and verticality perception tasks, whereas
178 conjunctions were tested for potential overlap between conditions. Thus, these analyses
179 enabled us to identify the neural networks selectively responsible for body representation
180 or verticality perception coding as well as those common to both spatial processes.

181

182 **Results**

183 **Behavioral data**

184 The behavioral data showed that the two tasks did not differ neither for the rate of correct
185 responses, nor for the response time. The average data showed similar rates of correct
186 responses (SSA: $94 \pm 4\%$; SV = $92 \pm 1\%$; SSA vs. SV: $p=0.245$) and response times (SSA:
187 644 ± 135 ms; SV: 629 ± 105 ms; SSA vs. SV: $p=0.862$) in both tasks.

188

189 **Neuroimager data**

190 *Common Activation for SSA and SV tasks*

191 During both the SSA and SV tasks, bilateral activations occurred in the postcentral gyrus
192 and the superior occipital lobe. Right middle temporal gyrus and inferior parietal lobule
193 were also activated. Activations also took place in the right posterior (lobule VI) and left
194 anterior (lobule V) cerebellar lobes. For both the brain and the cerebellum, the volume
195 activated was much greater on the right side (Table 1).

196

197 *Straight-ahead task*

198 The specific brain activations during SSA relative to the SV task were localized principally
199 in the right parieto-occipital cortices (Table 1). The contrast SSA > SV showed activations
200 within the right occipital, parietal (angular gyrus, precuneus), temporal (middle, fusiform
201 and parahippocampal gyri), and frontal (middle gyrus) lobes. In the left hemisphere,
202 activations were limited to the inferior frontal gyrus, precuneus and cerebellar posterior
203 lobe (Crus 1). The parameters of activity (beta values in arbitrary units) extracted from
204 these regions are shown for each task (Figure 1A).

205

206 *Verticality task*

207 The opposite contrast SV > SSA (Table 1) showed right side activations in the rolandic
208 operculum, the precentral gyrus and middle frontal gyrus, as well as the anterior and
209 posterior cerebellar lobe. The left anterior cerebellar lobe was also activated. The
210 parameters of activity (beta values in arbitrary units) extracted from these regions are
211 shown for each task (Figure 1B).

212

213 **Discussion**

214 The aim of this study was to reveal differences and similarities in the functional
215 neuroanatomical correlates of ego-centered and geo-centered representations. More
216 specifically, body midline (SSA) and vertical (SV) representations were directly compared
217 in fMRI for the first time. The major findings were a predominance of right hemisphere
218 activations and a strong involvement of cerebellum in both tasks. These data provide
219 insight into the anatomical basis of the ego-centered and geo-centered reference frames in

220 healthy participants and help to understand the consequences of brain lesions or vestibular
221 disorders.

222 Regarding the ego-centered representation, this study evidences the crucial role of parietal
223 lobe areas (angular gyrus and precuneus). These regions were found to be strongly
224 activated in body parts location tasks (Vuilleumier, 2013). They are involved in body
225 representation in healthy subjects (Saj et al., 2014). Moreover, damage to these regions
226 may be responsible for deficits in body representation. Comparing stroke patients, with or
227 without spatial neglect, Rousseaux et al. (2013) showed that, in patients with spatial
228 neglect, body representation alterations involved lesions of the inferior parietal cortex and
229 the middle part of the superior temporal gyrus. It is interesting to note here that these
230 cortical structures are also areas of vestibular projections, which could explain the
231 disturbance of the SSA in patients with vestibular impairment (Saj et al., 2013, 2021; Borel
232 et al., 2021). Another result of the present study was the involvement of the cerebellum in
233 body representation. Lesions of the cerebellum, more specifically damages to the left
234 cerebellum posterior lobe were also found in stroke patients with spatial neglect (Milano
235 and Heilman, 2014; Chaudhari et al., 2015). In addition, in healthy subjects, Marotta et al.,
236 (2021) recently showed that during movement, body position in space is coded by the
237 cerebellum. Other studies of ego-centered representation showed the involvement of
238 frontoparietal areas network including inferior parietal lobule, intraparietal sulcus and
239 precuneus, the temporoparietal and inferior frontal (premotor) cortices, as well as the
240 cerebellum (Vallar et al., 1999; Galati et al., 2000; Saj et al., 2014).

241 Concerning the subjective vertical task, the data showed an involvement of the rolandic
242 operculum (including the anterior insula), confirming previous results in EEG (Lopez et

243 al., 2011), and cerebellum in line with fMRI data of Saj et al. (2019). Indeed, the insular
244 cortex, known to be strongly influenced by vestibular stimulation (Bottini et al., 2001;
245 Dieterich and Brandt, 2008), constitutes a critical vestibular-somatosensory integration
246 center likely contributing to the perception of the vertical (Brandt and Dieterich, 1999;
247 Rousseaux et al., 2015). The specific lesion of the rolandic operculum may lead to impaired
248 perception of subjective visual vertical (Baier et al., 2021) as well as postural instability
249 (Dai et al., 2022). In stroke patients with or without spatial neglect, Rousseaux et al. (2014)
250 showed that lesions of insula were associated with altered judgments of verticality in both
251 visual and haptic modalities, confirming data of other studies (Barra et al., 2010, Baier et
252 al., 2012, Brandt et al., 1994). Barra et al. (2010) reveal the existence of a synthesis
253 involving the posterolateral thalamus between the vestibular and somaesthetic system for
254 developing and updating internal constructs of verticality. The posterolateral thalamus has
255 a direct link with the cerebellum (Bostan and Strick, 2018). A specific result of the present
256 study was the involvement of the cerebellum in the verticality representation, more
257 specifically the right cerebellar side. This region has already been observed in fMRI studies
258 in healthy participants (Saj et al., 2019) or during optokinetic stimulation (Bense et al.,
259 2006). The major role of the cerebellum, in particular the posterior part, in vertical
260 perception is confirmed by the consequences of cerebellar stroke (Barmack, 2003).

261 The last outcomes of this study concern the common regions involved in the SSA and SV
262 tasks, carried out in ego-centered and geo-centered reference frames, respectively. Both
263 tasks involved several cortical regions (postcentral gyrus, inferior parietal lobule and
264 superior occipital lobe) and the cerebellum (lobules V and VI). Noteworthy, these regions
265 are part of the multimodal vestibular projection network (Eickhoff et al., 2006; Lopez et

266 Blanke, 2011; zu Eulenburg et al., 2012; Frank and Greenlee, 2018). They are involved in
267 spatial representations generated from multiple sensory inputs and contributing to postural
268 control (Merfeld et al., 1999; Shadmehr and Krakauer, 2008), as well as in visuospatial
269 functions (Cojan et al., 2021). The postural and visuospatial disorders observed in stroke
270 or vestibular patients could be due, at least in part, to alterations of these reference frames.
271 Our data support the view that a sensory loss known to alter a given reference frame may
272 have consequences in the functioning of another frame. Thus, vestibular loss disrupted not
273 only ego-centered representation based on movements performed in the dark (Péruch et al.,
274 1999) but also allo-centered representation acquired on the basis of visual information
275 alone, in a virtual visual environment (Péruch et al., 2005). In the same vein, blind people
276 have difficulty in appreciating their body movements based on vestibular information alone
277 (von Breven et al., 1997).

278 **Conclusion**

279 In conclusion, this study evidenced some distinct neuro-anatomical correlates of geo-
280 centered and ego-centered representations. It also showed a strong predominance of right
281 hemisphere activations and an involvement of cerebellum in both representations. The
282 common structures underlying these representations proved to be multisensory integration
283 areas, and particularly areas of vestibular projection, which could explain deficits occurring
284 after both peripheral sensory damage and central damage. It could also provide a basis for
285 understanding the “multi-referenced” spatial deficits found in complex behaviours such as
286 spatial navigation and characterized by more extensive deficits than the initial sensory
287 damage would have suggested.

288

289 **References**

- 290 Baier B, Cuvenhaus HS, Müller N, Birklein F, Dieterich M. (2021) The importance of the
291 insular cortex for vestibular and spatial syndromes. *Eur J Neurol*, 28(5):1774-1778.
- 292 Barmack NH. (2003). Central vestibular system: vestibular nuclei and posterior
293 cerebellum. *Brain Res Bull*. 60(5-6):511-41.
- 294 Barra J, Marquer A, Joassin R, et al. (2010). Humans use internal models to construct and
295 update a sense of verticality. *Brain* 133: 3552–3563.
- 296 Barra J, Oujamaa L, Chauvineau V, et al. (2009). Asymmetric standing posture after stroke
297 is related to a biased egocentric coordinate system. *Neurology* 72: 1582–1587.
- 298 Bense S, Janusch B, Vucurevic G, Bauermann T, Schlindwein P, Brandt T, Stoeter P,
299 Dieterich M. (2006). Brainstem and cerebellar fMRI-activation during horizontal and
300 vertical optokinetic stimulation. *Exp Brain Res*, 174(2):312-23.
- 301 Bostan AC, Strick PL. The basal ganglia and the cerebellum: nodes in an integrated
302 network. *Nat Rev Neurosci*. 2018 Jun;19(6):338-350.
- 303 Bottini G, Karnath HO, Vallar G, Sterzi R, Frith CD, Frackowiak RS, Paulesu E. (2001).
304 Cerebral representations for egocentric space: Functional-anatomical evidence from
305 caloric vestibular stimulation and neck vibration. *Brain* 124,1182-96
- 306 Brandt T, Dieterich M. (1999) The vestibular cortex. Its locations, functions, and disorders.
307 *Ann N Y Acad Sci* 28;871:293-312.
- 308 Chaudhari A, Pigott K, Barrett AM. (2015). Midline Body Actions and Leftward Spatial
309 "Aiming" in Patients with Spatial Neglect. *Front Hum Neurosci*, 10;9:393
- 310 Cojan Y, Saj A, Vuilleumier P. (2021). Brain Substrates for Distinct Spatial Processing
311 Components Contributing to Hemineglect in Humans. *Brain Sci*, 11(12):1584.

312 Dai S, Lemaire C, Piscicelli C, Pérennou D. (2022). Lateropulsion Prevalence After Stroke:
313 A Systematic Review and Meta-analysis. *Neurology*. 98(15):e1574-e1584.

314 Dieterich M, Brandt T (2008) Functional brain imaging of peripheral and central vestibular
315 disorders. *Brain* 131,2538-2552

316 Eickhoff SB, Weiss PH, Amunts K, Fink GR, Zilles K (2006). Identifying human parieto-
317 insular vestibular cortex using fMRI and cytoarchitectonic mapping. *Human Brain*
318 *Mapping*, 27:611– 621.

319 Frank SM, Greenlee MW (2018). The parieto-insular vestibular cortex in humans: more
320 than a single area? *J Neurophysiol* 120: 1438 –1450, 2018.

321 Galati G, Lobel E, Vallar G, Berthoz A, Pizzamiglio L, Le Bihan D. (2000). The neural
322 basis of egocentric and allocentric coding of space in humans: a functional magnetic
323 resonance study. *Exp Brain Res* 133,156-64

324 Galati G, Pelle G, Berthoz A, Giorgia Committeri G (2010). Multiple reference frames
325 used by the human brain for spatial perception and memory. *Experimental Brain*
326 *Research*, 206:109–120.

327 Gentaz E, Gabriel Baud-Bovy G, Luyat M (2008). The haptic perception of spatial
328 orientations. *Experimental Brain Research*, volume 187, Article number: 331

329 Hugues A, Leplaideur S, Roy P, Fauvernier M, Allart E, Pérennou D, Boyer F, Paysant J,
330 Yelnik A, Rode G, Bonan I (submitted). Contribution of spatial reference frames and
331 unilateral spatial neglect on weight bearing asymmetry after right stroke. A cross-
332 sectional study.

333 Lopez C, Blanke O (2011). The thalamocortical vestibular system in animals and humans.
334 *Brain Res Rev*, 67(1-2):119-46.

335 Lopez C, Mercier MR, Halje P, Blanke O. (2011) Spatiotemporal dynamics of visual
336 vertical judgments: early and late brain mechanisms as revealed by high-density
337 electrical neuroimaging. *Neuroscience* 181:134–49.

338 Marotta A, Re A, Zampini M, Fiorio M. Bodily self-perception during voluntary actions:
339 The causal contribution of premotor cortex and cerebellum. *Cortex*. 2021 Sep;142:1-14

340 Merfeld DM, Zupan L, Peterka RJ. (1999) Humans use internal models to estimate gravity
341 and linear acceleration. *Nature*; 398: 615–618.

342 Milano NJ, Heilman KM. (2014) Cerebellar allocentric and action-intentional spatial
343 neglect. *Cogn Behav Neurol* 27(3):166-72.

344 Neal H Barmack 1. (2003) Central vestibular system: vestibular nuclei and posterior
345 cerebellum *Brain Res Bull* 60(5-6):511-41.

346 Rousseaux M, Honoré J, Vuilleumier P, Saj A. (2013). Neuroanatomy of space, body, and
347 posture perception in patients with right hemisphere stroke. *Neurology*. 81(15):1291-7.

348 Rousseaux M, Honoré J, Saj A (2014). Body representations and brain damage.
349 *Neurophysiol Clin*. 44(1):59-67.

350 Rousseaux M, Braem B, Honoré J, Saj A. (2015). An anatomical and psychophysical
351 comparison of subjective verticals in patients with right brain damage. *Cortex*. 69:60-7.

352 Saj A, Honoré J, Bernati T, Rousseaux M. (2012). Influence of spatial neglect, hemianopia
353 and hemispace on the subjective vertical. *Eur Neurol*. 68(4):240-6.

354 Saj A, Cojan Y, Musel B, Honoré J, Borel L, Vuilleumier P. (2014). Functional neuro-
355 anatomy of egocentric versus allocentric space representation. *Neurophysiol Clin*,
356 44(1):33-40.

357 Saj A, Borel L, Honoré J. (2019). Functional Neuroanatomy of Vertical Visual Perception
358 in Humans. *Front Neurol*, 10:142.

359 Saj A, Bachelard-Serra M, Lavieille JP, Honoré J, Borel L. (2021). Signs of spatial neglect
360 in unilateral peripheral vestibulopathy. *Eur J Neurol*. 28(5):1779-1783.

361 Saj A, Honoré J, Bernard-Demanze L, Devèze A, Magnan J, Borel L. (2013) Where is
362 straight ahead to a patient with unilateral vestibular loss? *Cortex*. 49(5):1219-28.

363 Shadmehr R, Krakauer JW. A (2008). computational neuroanatomy for motor control.
364 *Experimental Brain Research*; 185: 359–381.

365 Vallar G, Lobel E, Galati G, Berthoz A, Pizzamiglio L, Le Bihan D (1999) A fronto-parietal
366 system for computing the egocentric spatial frame of reference in humans. *Exp Brain*
367 *Res* 124,281-86.

368 Vuilleumier P (2013). Mapping the functional neuroanatomy of spatial neglect and human
369 parietal lobe functions: progress and challenges. *Ann N Y Acad Sci*. 296:50-74.

370 zu Eulenburg P, Caspers S, Roski C, Eickhoff SB (2012). Meta-analytical definition and
371 functional connectivity of the human vestibular cortex. *NeuroImage* 60:162–169.

372

373

374 **Legends**

375 **Table 1** - Anatomical location and statistical results for brain areas showing specific
376 activity during the SSA and SV tasks (Montreal Neurological Institute coordinates). L:
377 Left hemisphere; R: Right hemisphere; BA: Brodmann Area.

378 **Figure 1** - Activated brain regions are projected on a standard anatomical template.
379 Parameter estimates of activity (beta value, in arbitrary units, averaged across
380 responsive voxels in each cluster) are shown for main peaks in each task condition. A)
381 comparison between SSA vs SV (x,y,z: 30,-76,40); B) SV vs SSA (x,y,z: 20,-25,13). L:
382 Left hemisphere; R: Right hemisphere; BA: Brodmann Area; C) Full brain maps of
383 activations.

384

385

Area	hemi	MNI			BA	T	Z	p	vol (mm3)
		x	y	z					
SSA and SV : common regions									
Postcentral Gyrus	R	60	-16	34	BA2	4.56	4.24	<0.001	1647
Postcentral Gyrus	L	-42	-40	64		2.10	2.48	0.005	270
Inferior Parietal Lobule	R	39	-37	49		2.70	2.63	0.005	378
Middle Temporal Gyrus	R	51	-64	-2		4.18	3.92	<0.001	6048
Superior Occipital lobe	R	21	-91	22	BA19	4.47	4.17	<0.001	2781
Superior Occipital lobe	L	-6	-103	10	BA18	2.01	2.80	0.005	297
Superior Occipital lobe	L	-15	-94	19	BA19	1.99	2.60	0.005	108
Cerebellum Posterior Lobe (lobule VI)	R	18	-55	-20	C6	4.51	4.19	<0.001	5184
Cerebellum Anterior Lobe (lobule V)	L	-27	-58	-26	C6	1.97	2.54	0.005	135
SSA vs SV									
Inferior Frontal Gyrus	L	-57	23	4	BA45	3.13	3.00	0.001	270
Middle Frontal Gyrus	R	33	26	34		3.25	3.11	0.001	459
Angular gyrus	R	30	-49	37		3.17	3.04	0.001	297
Precuneus	L	-12	-67	52		3.44	3.02	0.001	378
Precuneus	R	27	-73	40		3.13	3.00	0.001	1512
Middle Temporal Gyrus	R	39	-82	19	BA19	2.95	2.84	0.002	810
Fusiform gyrus	R	39	-31	-20	BA20	2.34	2.52	0.004	567
Parahippocampal Gyrus	R	33	-43	-14	BA37	2.41	2.46	0.005	297
Occipital Lobe	R	30	-67	-2		3.68	3.48	<0.001	621
Occipital Lobe	R	33	-76	25		3.01	2.89	0.002	783
Cerebellum Posterior Lobe	L	-18	-76	-29		2.96	2.85	0.002	297
SV vs SSA									
Middle Frontal Gyrus	R	39	59	10	BA10	2.68	2.59	0.005	108
Precentral Gyrus	R	24	-25	52		2.70	2.61	0.004	108
Rolandic Operculum	R	45	-1	13		3.22	3.08	0.001	162
Cerebellum Anterior Lobe	R	21	-46	-32		2.81	2.71	0.003	540
Cerebellum Anterior Lobe	L	-21	-40	-38		2.80	2.71	0.003	297
Cerebellum Posterior Lobe	R	18	-61	-32	V8	3.32	3.17	0.001	351

Figure 1

