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Pseudoneglect in visual search: Behavioral evidence and connectional constraints in simulated neural circuitry

Pseudoneglect in visual search

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37 **Abstract**

38 Most people tend to bisect horizontal lines slightly to the left of their true center

39 (pseudoneglect), and start visual search from left-sided items. This physiological

40 leftward spatial bias may depend on hemispheric asymmetries in the organization

41 of attentional networks, but the precise mechanisms are unknown. Here we

42 modeled relevant aspects of the ventral and dorsal attentional networks (VAN and

43 DAN) of the human brain. First, we demonstrated pseudoneglect in visual search

44 in 101 right-handed psychology students. Participants consistently tended to start

45 the task from a left-sided item, thus showing pseudoneglect. Second, we trained

46 populations of simulated neurorobots to perform a similar task, by using a genetic

47 algorithm. The neurorobots' behavior was controlled by artificial neural networks,

48 which simulated the human VAN and DAN in the two brain hemispheres.

49 Neurorobots differed in the connectional constraints that were applied to the

50 anatomy and function of the attention networks. Results indicated that (1)

51 neurorobots provided with a biologically plausible hemispheric asymmetry of the

52 VAN-DAN connections, as well as with inter-hemispheric inhibition, displayed the

53 best match with human data; however, (2) anatomical asymmetry *per se* was not

54 sufficient to generate pseudoneglect; in addition, the VAN must have an excitatory

55 influence on the ipsilateral DAN; (3) neurorobots provided with bilateral

56 competence in the VAN but without inter-hemispheric inhibition failed to display

57 pseudoneglect. These findings provide a proof of concept of the causal link

58 between connectional asymmetries and pseudoneglect, and specify important

59 biological constraints that result in physiological asymmetries of human behavior.

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63 **Significance statement**

64 Most of us start our exploration of the environment from the left side. Here we

65 demonstrated this tendency in undergraduate students, and trained artificial agents

66 (neurorobots) to perform a similar visual search task. The neurorobots' behavior

67 was controlled by artificial neural networks, inspired by the human fronto-parietal

68 attentional system. In seven distinct populations of neurorobots, different

69 constraints were applied on the network connections within and between the brain

70 hemispheres. Only one of the artificial populations behaved in a similar way to the

71 human participants. The connectional constraints applied to this population

72 included known characteristics of the human fronto-parietal networks, but had also

73 additional properties not previously described. Thus, our findings specify biological

74 constraints that induce physiological asymmetries of human behavior.

75

76

77 **Keywords**: Spatial exploration, Visual search, Attention, Brain connections,

78 Spatial neglect

79 **1. Introduction**

80 A thorough exploration of the space around us is essential to everyday life.

81 However, spatial exploration is not perfectly symmetrical in humans. For example,

82 when we explore a scene in order to cancel out visual targets, we tend to start the

83 search from the left part of the scene (Azouvi et al., 2006; Bartolomeo, D'Erme, &

84 Gainotti, 1994). This physiological leftward spatial bias is analogous to the slight

85 physiological leftward shift typically observed in horizontal line bisection, termed

86 pseudoneglect (Bowers & Heilman, 1980) because it goes in the opposite direction

87 to the typical rightward bias showed by patients with left visual neglect after right

88 hemisphere damage (Schenkenberg, Bradford, & Ajax, 1980; Urbanski &

89 Bartolomeo, 2008).

90 Evidence shows that visuospatial attention is a major determinant of

91 pseudoneglect (McCourt, Garlinghouse, & Reuter-Lorenz, 2005; Toba, Cavanagh,

92 & Bartolomeo, 2011), which might thus result from asymmetries in the hemispheric

93 control of attention (McCourt & Jewell, 1999; Ossandón, Onat, & König, 2014).

94 However, the specific neural structures and the mechanisms at the basis of

95 pseudoneglect remain unknown.

96 In the human brain, visuospatial attention is controlled by fronto-parietal

97 networks, which demonstrate substantial asymmetries favoring the right

98 hemisphere (Corbetta & Shulman, 2002; Heilman & Van Den Abell, 1980;

99 Mesulam, 1999). Dysfunction of these networks after right hemisphere damage

100 can induce signs of neglect for left-sided events (Bartolomeo, Thiebaut de

101 Schotten, & Chica, 2012; Corbetta & Shulman, 2011). A bilateral dorsal attentional

102 network (DAN), composed by the intraparietal sulcus / superior parietal lobule and

103 the frontal eye field / dorsolateral prefrontal cortex, shows increased BOLD

104 responses during the orienting period (Corbetta & Shulman, 2002). A right-

105 lateralized ventral attentional network (VAN) includes the temporoparietal junction

106 and the ventrolateral prefrontal cortex. The VAN is important for detecting

107 unexpected but behaviorally relevant events, and induces the DANs to reorient

108 attention towards these events. Anatomically, three branches of a long-range white

109 matter pathway, the Superior Longitudinal Fasciculus (SLF), connect these

110 networks. The SLF has a ventro-dorsal gradient of hemispheric asymmetry

111 (Thiebaut de Schotten et al., 2011). The ventral branch (SLF III) connects the VAN

112 and is anatomically larger in the right hemisphere than in the left hemisphere,

113 whereas the dorsal branch (SLF I, connecting the DAN) is more symmetrical. The

114 lateralization of the intermediate branch (SLF II) displays interindividual

115 differences, and is strongly correlated to the individual amount of pseudoneglect in

116 line bisection and to differences in the speed of detection between left-sided and

117 right-sided targets. Specifically, larger SLF volumes in the right hemisphere

118 correlate with larger leftward bias (Thiebaut de Schotten et al., 2011).

119   A further potential source of performance asymmetry resides in the pattern

120 of inter-hemispheric connections. Behavioral and electrophysiological evidence

121 suggests that inter-hemispheric communication is not strictly symmetrical in

122 humans, but it is faster from the right to the left hemisphere (Marzi, 2010). Also,

123 the posterior callosal connections from the right parietal node of the DAN to its left

124 hemisphere homologue seem to be predominantly inhibitory (Koch et al., 2011).

125 Concerning the VAN, its right and left temporo-parietal caudal nodes are not

126 strongly connected by callosal fibers (Catani & Thiebaut de Schotten, 2012), and

127 thus work in relative isolation from one another.

128   It is tempting to relate these biological constraints to the widespread

129 leftward bias that occurs in human exploratory behavior. However, little is known

130 about the specific dynamic interplay between the attentional networks resulting in

131 pseudoneglect. On the one hand, methods used in humans have substantial

132 limitations of spatiotemporal resolution and of inferential power, which severely

133 limit their scope. On the other hand, it is difficult to draw firm conclusions from

134 monkey neurophysiology, because of important differences between humans and

135   primates in the organization of attention networks (Patel et al., 2015). In the

136   present study, we took a different approach to unravel these issues. First, we

137   tested a group of human participants to establish the presence and characteristics

138   of pseudoneglect in a visual search task (Experiment 1). In Experiment 2, we

139   trained neurally controlled robots (neurorobots) to perform a task as similar as

140   possible to the human one. We then articulated detailed implementations of

141   several instances of attention network architecture, which directed the neurorobots'

142   performance, in order to identify the structural and functional network constraints

143   crucial for simulating human performance.

144

145

146 **2. Experiment 1: Pseudoneglect in human visual search**

147 2.1 Introduction

148 Pseudoneglect has been mainly measured using tasks of perceptual estimation of

149 the length of horizontal lines (Bowers & Heilman, 1980; Jewell & McCourt, 2000;

150 Toba et al., 2011). Analogous leftward biases seem also to occur in visual search

151 tasks, as a tendency to find first targets on the left side of the display (Azouvi et al.,

152 2006; Bartolomeo et al., 1994), but evidence in this domain is much less

153 systematic. Thus, in the present context it was important to test our specific task in

154 order to ensure the validity of the human-robotic comparison of performance.

155

156 2.2. Methods

157 2.2.1. Ethics Statement

158 The procedure was approved by the local ethics committee.

159

160 2.2.2. Participants

161 A total of 101 right-handed psychology students (76 females; mean age ± SD,

162 22.24 ± 4.40) gave their informed consent to perform a visual search experiment

163 for course credit.

164

165 2.2.3. Procedure

166 Participants were instructed to cancel as fast as possible targets displayed on a

167 touch-sensitive tablet (Mediacom Winpad 801 8-inches, 120 dpi, 1280x800 pixels,

168 refresh frequency 60 Hz), by using a stylus pen. Participants were comfortably

169 seated with a viewing distance of ~40 cm. Each session consisted of 30 trials.

170 Each trial was initiated by the participant touching a green round button placed at

171 the center of the screen. Subsequently, a set of 5 dark-red (HEX #800000) filled

172 round targets, with a 40-pixel radius (0.76° visual angle), was presented. Targets

173   were randomly scattered on a display area of 512x512 pixels (9.7° x 9.7°), placed

174   at the center of the screen. Upon participant's touch, cancelled targets became

175   bright red (HEX #FF0000). To assess lateral bias, we first defined the center of the

176   display as 0, so that the values of the X coordinate went from -256 pixels (-4.85°)

177   on the extreme left to +256 pixels (+4.85°) on the extreme right. Second, we

178   measured the average position on the X axis of the first cancelled stimulus for

179   each trial.

180

181   2.3. Results

182   As expected with this easy task, accuracy was at ceiling, with all participants

183   correctly cancelling all the targets. Results showed a left-biased distribution of the

184   first found target. The average X value was -80.23 pixels (-1.52°), which

185   significantly differs from the central position at X = 0 (Wilcoxon-Mann-Whitney two-

186   tailed test, Z=-6.37, p<0.001).

187

188   2.4. Discussion

189   During a visual search task similar to that used for our simulations, normal

190   participants exhibited a leftward bias (pseudoneglect), consisting of a tendency to

191   start the visual search from a left-sided target. This result was observed in an

192   experimental setting as close as possible to that used for neurorobots, and

193   replicates and extends previous results obtained with different types of visual

194   search tasks, such as the line cancellation test (Bartolomeo et al., 1994) and the

195   bells test (Rousseaux et al., 2001).

196

197 **3. Experiment 2: Visual Search in Neurorobots**

198 3.1. Introduction

199 A neurorobot is a real or simulated robot whose behavior is controlled by an

200 artificial neural network. For the present experiment, we developed distinct

201 populations of simulated neurorobots controlled by artificial neural networks with

202 different connectivity constraints. The neurorobots' task was designed to be as

203 close as possible to that performed by human participants in Experiment 1.

204

205 3.2. Models

206 Code Accessibility: The code is available as extended data and in GitHub

207 repository (Gigliotta, 2017).

208   The simulated robot (Fig. 1) has a single artificial eye and an actuator

209 (simulated hand) able to perform the cancellation task. The robot's eye can move

210 and zoom, and can thus be described as a pan/tilt/zoom camera, because it can

211 move along the horizontal and vertical axes and can zoom in a range between 1x

212 to 12x. The use of a zoom was inspired by models of attention, which stipulate that

213 attention can either be distributed over the whole field, but with low resolving

214 power, or be continuously constricted to small portions of the visual field with a

215 concomitant increase in processing power (Eriksen & Yeh, 1985).

216   The artificial eye is equipped with a retina made up of a 7x7 grid of light

217 receptors (see Fig. 1). Each receptor outputs an activation value computed by

218 averaging the luminance of the perceived stimuli across the receptive field, with

219 radius set to 80 pixels. Receptors are evenly distributed within the artificial retina,

220 which has a square form with a side varying from 1120 pixels (no zoom) to 96

221 pixels (maximum zoom). Thus, each stimulus can occupy a retinal surface ranging

222 from 0.8% to 100% of the artificial retina. Horizontal and vertical movements of the

223 eye are controlled by four simulated muscles (Massera, Ferrauto, Gigliotta, & Nolfi,

224 2014) (see Fig. 1), in analogy to the medial, lateral, inferior and superior recti of the

225 human eye.

226 3.2.1. Neural network

227 We used a standard neural network model in which each node of the network has

228 a sigmoid activation function $\varphi(x)=1/(1+e^{-x})$ and an adjustable threshold ϑ. The

229 output, O, is computed for each node i by using the following equation:

$$O_i = \varphi(A_i)$$

230 Where:

$$A_i = \vartheta_i + \sum_{i,j} w_{ij}\, O_j$$

231 w_{ij} is the synaptic weight connecting unit j with unit i. The pattern of connections

232 between nodes has been chosen according to biological evidence on dorsal and

233 ventral attentional networks in human brains (see below, section 3.5).

234   Fig. 2A depicts the general template network. The 7x7 retina, consisting of

235 49 artificial neurons, constituted the input layer. The output layer controlled the

236 zoom with two artificial neurons, the extraocular muscles with four neurons, and a

237 decision unit for target detection, which triggered the touch response when

238 exceeding a criterion threshold of 0.7. The hidden layer contained the attention

239 networks and a hidden network devoted to control vertical eye movements (4

240 neurons, not depicted in Fig. 1). We modeled the DAN and the VAN by building a

241 neural model organized across two hemispheres, with visual information from each

242 visual field projecting to the contralateral hemisphere. Each DAN had 5 artificial

243 neurons; each VAN had 4 artificial neurons. These parameters were based on pilot

244 work, and reflect a tradeoff between network complexity and the time needed to

245 run simulations. With these parameters, each simulation required about a week to

246 be completed on our hardware. The VAN-DAN connections in the right hemisphere

247 outnumbered those in the left hemisphere, in order to simulate analogous results

248 for the human SLF II (Thiebaut de Schotten et al., 2011).

249   The inter-hemispheric connections were also modeled by following

250 anatomical and functional results obtained in the human brain, and outlined in the

251 Introduction. Thus, (1) they connected only the DANs, but not the VANs, which

252 thus worked in relative isolation from one another (see Fig. 9.4D in Catani &

253 Thiebaut de Schotten, 2012) and (2) they were inhibitory, such that each DAN

254 inhibited the contralateral one (Koch et al., 2011): each DAN induced

255 contralaterally-directed eye movements and inhibited ipsilaterally-directed eye

256 movements. The DANs controlled zooming and cancellation behaviors. All the

257 hidden units within the DANs also had reentrant connections, which integrate the

258 previous input with the current one, thus simulating a sort of simplified visual

259 memory, in analogy to similar mechanisms occurring in the primate brain (Salazar,

260 Dotson, Bressler, & Gray, 2012). Thus, reentrant connections resulted in some

261 persistence of the previous inputs across steps within a given trial.

262   Given the importance of eye position in visually-guided target reaching

263 (Lewis, Gaymard, & Tamargo, 1998), we provided eye position information to

264 neurorobots through an efference copy of the motor output. In particular, motor

265 outputs controlling the four ocular muscles were connected one to one with the

266 four input neurons, with a fixed weight of 1 (i.e., perfect copy from input to output).

267

268 3.2.2. Cancellation task

269 Similar to the human experiment (see section 2), neurorobots performed a 30-trial

270 cancellation task. The human and robotic tasks were designed with the explicit

271 constraint of being as similar as possible. Targets were presented on a virtual

272 display measuring 512 x 512 pixels. At the start of each trial, the gaze of the

273 artificial eye was initialized at the center of the display, with no zoom. Again,

274 similarly to the human experiment, each trial consisted of a set of 5 round targets,

275 with a luminance value of 0.5 (in conventional units ranging from 0 to 1.0) and a

276   radius of 40 pixels, randomly scattered in the virtual display. Upon cancellation,

277   targets increased their luminance to the maximum value of 1.0.

278

279   3.2.3. The Adaptive/Learning process

280   For the present work, neurorobots were trained by means of a Genetic Algorithm,

281   a form of evolutionary computation that implements a Darwinian process of

282   adaptation that can model cognitive development and trial-and-error learning,

283   especially when only distal rewards are available (Di Ferdinando, Parisi, &

284   Bartolomeo, 2007; Stefano Nolfi & Floreano, 2000). Genetic algorithms are a

285   useful alternative to supervised learning in settings such as the present one,

286   because we employed a fitness function based on the number of cancelled targets,

287   and not a set of input-output pairings which could be used to minimize the error by

288   a supervised learning mechanism such as back-propagation. A typical experiment

289   starts with the generation of a random set of individual neurorobots (each defined

290   by a specific set of parameters of a neurocontroller). Each individual is then

291   evaluated according to a fitness function representing the desired performance on

292   a requested task. Due to genetic operators such as mutation and crossover, the

293   best individuals will populate the next generation. The process iterates until a

294   specific performance or a fixed number of generations is reached. In the present

295   work, each genetic string encodes the value of synaptic connections w_{ij} and

296   neuron thresholds in the range (-5, 5). Initially, for each evolutionary experiment a

297   set of 100 random individuals (i.e., competing sets of parameters for the neural

298   network of the neurorobot) were generated and evaluated for their ability to find

299   targets. Targets had to be found as fast as possible on each of 30 cancellation

300   trials, lasting 700 time steps each. At the end of the evaluation phase, individuals

301   were ranked according to their performance, and the best 20 were used to

302   populate the next generation after having undergone a mutation process. Each

303   parameter was encoded by an 8-bit string, thus mutations were implemented by

304   bits switching with probability p=0.01. The number of generations was set to 3,000.

305   Three behavioral components contributed to the overall fitness, *F*: an

306   exploration component, a component proportional to the number of target correctly

307   cancelled, and a reward for responses promptness.

308   The exploration component, which was introduced to avoid the bootstrap

309   problem (Stefano Nolfi & Floreano, 2000), rewarded the ability of the neurorobot to

310   explore its visual field. In particular, the area that can be explored through eye

311   movements was split in 100 cells. Exploration fitness (*EF*) was then computed for

312   each trial by dividing the number of visited cells by 100. A second fitness

313   component (*TF*) was represented for each trial by the number of correctly

314   cancelled targets divided by 5 (i.e., the total number of presented targets). Finally,

315   a reward for promptness (*PF*) was given when all the five targets were cancelled.

316   *PF* was inversely proportional to the number of time steps *nt*, used to cancel all the

317   stimuli:

318   $$PF=nt/700$$

319   The overall fitness was calculated as

320   $$F=EF+TF+PF.$$

321   After training, neurorobots' performance in the cancellation task was

322   evaluated on 30 new trials, in order to measure their accuracy in finding the targets

323   and the position of the first cancelled target, as estimated by the average value of

324   the X coordinate of the first cancelled stimulus across trials.

325

326   3.2.4. Valence of VAN-DAN connections and of inter-DAN connections

327   A set of 5 populations of neurorobots, each composed of 40 individuals, featured

328   neurocontrollers with different connectional constraints. Neurocontrollers A, B and

329   C (Fig. 2) had left-right asymmetric connections between VAN and DAN (i.e., the

330   simulated SLF II), with a greater number of connections in the right hemisphere

331   (120) than in the left hemisphere (108). The ratio of this asymmetry difference

332   (0.05) corresponds to the average asymmetry ratio of SLF II in 20 human subjects,

333   as described by Thiebaut de Schotten et al. (2011) (see their supplementary Table

334   1). In neurocontroller A (Fig. 2A) there were no constraints in terms of type of

335   connections (inhibitory or excitatory) along the ventral and dorsal attentional

336   networks. In neurocontroller B a further constraint was added: VAN to DAN

337   pathways were set to be excitatory during the training process (see Fig. 2B).

338   Finally, in neurocontroller C also the connections projecting from the retina to the

339   VAN were set to be excitatory (see Fig. 2C). To better evaluate the effect on

340   performance of SLF II asymmetry, we trained two additional control populations

341   based on neurocontroller C: C0 with completely symmetrical VAN-DAN

342   connections (laterality ratio = 0); C1 with VAN-DAN connections only present in the

343   right hemisphere, and absent VAN-DAN connections in the left hemisphere

344   (complete right lateralization of SLF II).

345   Earlier models of spatial attention (Heilman & Van Den Abell, 1980;

346   Mesulam, 1981) postulated a bilateral competence of the right hemisphere for both

347   hemispaces, without explicit consideration of inter-hemispheric interactions. To

348   simulate these models, we trained two additional populations of neurorobots

349   (neurocontrollers D and E in Fig. 2; 40 individuals for each population). In these

350   neurocontrollers, the right hemisphere received visual information from both the

351   right and the left visual hemifields, while the left hemisphere received information

352   only from the right, contralateral visual hemifield. Moreover, there were no

353   inhibitory connections between the right DAN and its left homolog. The rest of the

354   architecture was the same as for all the other neurocontrollers. The only difference

355   between neurocontroller D and neurocontroller E was the valence of the

356   connections running from the visual fields to VAN and DAN. In neurocontroller D,

357   the valence of the visuo-attentional connections was not constrained, and could

358   thus assume either a positive or a negative valence. In neurocontroller E, visuo-

359   attentional connections were constrained to be excitatory, similar to neurocontroller

360   C.

361   Two additional control simulations were designed to assess the importance

362   of the inhibitory valence of inter-DAN connections. In these simulations, we used

363   neurorobots identical to model C, except that the inter-DAN connections were (1)

364   let free to evolve as excitatory or inhibitory (neurocontroller F), or (2) constrained to

365   be facilitatory (neurocontroller G).

366

367   **3.3. Results**

368   3.3.1. Behavioral Results

369   Figure 3 shows the ability of the five populations of neurobots to correctly solve the

370   task. The mean percentages of correct cancellations are reported for each

371   population. Figure 4 reports the performance of the three populations equipped

372   with neurocontrollers A-E on correct cancellations. Each boxplot contains data

373   collected for 40 neurorobots tested on 30 cancellation trials.

374   There were significant differences in the amount of correct cancellations

375   across the populations A-E [Kruskal-Wallis test, $\chi^2_{(4,\ n\ =\ 200)}$ = 38.96, p = 7.10e-08].

376   Neurocontrollers with inter-hemispheric inhibition (A-C) performed better than

377   neurocontrollers without inter-hemispheric inhibition (D-E; Post-hoc pairwise

378   comparisons using Dunn's-test, all ps < 0.05).

379   Importantly, the spatial position of the first canceled target (X coordinate

380   value for each trial, Fig. 4) did differ across the populations A-E, $\chi^2_{(4,\ n\ =\ 200)}$ =

381   34.198, p =4.65e-07. The position of the first canceled target was not different from

382   0 (central position) in neurorobots equipped with neurocontroller A   (Wilcoxon-

383   Mann-Whitney, p=0.1, two-tailed) and neurocontroller D (p=0.5). Neurorobots E,

384   with bilateral competence in the right hemisphere and excitatory visual-attentional

385   connections, showed a rightward bias, opposite to human pseudoneglect

386   (Md=58.81, z=-2.8802, p=0.004). Neurorobots B and C tended instead to start their

387 exploration from a left-sided target (neurocontroller B, Md = -33.27, z = -2.057, p =

388 0.02; neurocontroller C, Md = 63.29, z = -5.35, p < .001), thus showing a leftward

389 bias reminiscent of human pseudoneglect. The control populations with complete

390 SLF II symmetry (C0), or extreme rightward SLF II asymmetry (C1) showed the

391 predicted patterns of performance: no pseudoneglect for C0 (Md=20.435, z=-

392 0.823, p=0.411), and large pseudoneglect for C1 (Md=-96.526, z=-7.406,

393 p=1.299e-13) (Fig. 5).

394   The additional control populations F (unconstrained inter-DAN connections)

395 and G (excitatory inter-DAN connections) achieved an overall worse performance

396 as compared with neurorobots C [Kruskal-Wallis test, $\chi^2_{(2,\ n\ =\ 119)}$ = 49.67, p =

397 1.635e-11]. However, neurorobots F (median correct cancellations, 83.33%; 1st

398 quartile, 79.33%; 3rd quartile, 88.00%) performed better than neurorobots G

399 (median correct cancellations, 75.33%; 1st quartile, 70.33%; 3rd quartile, 79.67%;

400 Dunn's test, all ps < 0.05). There were also differences between populations C, F

401 and G in the initial spatial bias [Kruskal-Wallis test, $\chi^2_{(2,\ n\ =\ 119)}$ = 9.24, p = 0.0099].

402 Interestingly, in population F inter-DAN connections had a strong tendency to

403 evolve towards inhibition; at the end of the evolutionary process, only 2 of 40

404 individuals (5%) had evolved excitatory connections. Perhaps as a consequence,

405 neurorobots F tended to start their exploration from the left side (median X value

406 for the 1st canceled target, −77.94 pixels; 1st quartile, −119.76; 3rd quartile,

407 −39.20), similar to neurorobots C. In contrast, neurorobots G, with excitatory inter-

408 DAN connections, did not show any consistent lateral bias (median X value for the

409 1st target, −2.92 pixels; 1st quartile, −84.53; 3rd quartile, 61.95; Wilcoxon-Mann-

410 Whitney, p = 0.45, two-tailed). These results strongly suggest that in our setting

411 inhibitory inter-DAN connections (1) conferred an evolutionary advantage in terms

412 of cancellation accuracy and (2) were important to the development of

413 pseudoneglect behavior.

414

18

415

416   3.3.2. Neural results

417

418   To better understand the neural dynamics leading to the exploratory bias, we

419   examined the average activations of the DANs across all the individuals for each

420   population, equipped with neurocontrollers C (biologically-inspired asymmetry) and

421   C_0 (symmetrical attention networks). We then computed a laterality index of DAN

422   average activations between the two hemispheres: (Mean Right DAN activation -

423   Mean Left DAN activation)/(Mean Right DAN activation + Mean Left DAN

424   activation), with a possible range from -1 (prevalent left DAN activity) to +1

425   (prevalent right DAN activity). Figure 7 reports the course of the laterality index

426   across time steps. As expected, left and right DAN activations were balanced with

427   neurocontroller C_0. On the other hand, in neurocontroller C activations were

428   unbalanced toward the right hemisphere DAN. A crucial aspect for pseudoneglect

429   concerns the initial time steps in which the exploratory bias occurs. A higher

430   imbalance toward the right hemisphere DAN is present at the outset of the

431   cancellation task for neurorobots C, as a consequence of asymmetries in their

432   network architecture, while it is obviously absent for neurorobots C_0, with

433   symmetrical networks. The initial imbalance favoring the right hemisphere DAN is

434   the likely basis of the spatial bias towards the initial cancellation of a left-sided item

435   in neurorobots C.

436   Figure 8 shows the average activation of the hidden DAN neurons in the

437   left and in the right hemisphere during the first 30 time steps of the cancellation

438   task, for agents equipped with the biologically inspired neurocontroller C, and for

439   those equipped with the symmetrical neurocontroller C_0. The initial activation is

440   symmetrical for the C_0 agents, but it is higher in the right hemisphere than in the

441   left hemisphere for the C agents. Thus, an asymmetry of VAN connections results

442   in a corresponding activation asymmetry in the anatomically symmetrical DANs.

443   The DAN asymmetry in the initial phases of the task is the simulated neural

444   correlate of behavioral pseudoneglect. After the initial phase, the left-right

445   differences are absorbed by the increased activity of the hidden units; when left

446   and right activities reach saturation, the behavioral asymmetry decreases (see Fig.

447   7, where asymmetry of performance decreases around time step 150 for

448   neurocontroller C).

449

450   3.3.3. Comparison between human and robotic performance

451   Human participants and robotic populations as a whole did not show the same

452   distribution of the position of the first cancelled targets (Kruskal-Wallis test, χ^2(5, n

453   = 301) = 67.88, p < .001) (see Fig. 6). Post-hoc tests (Dunn's test with Bonferroni

454   correction) demonstrated a difference in distribution between humans and

455   neurocontrollers A (p <0.001), B (p=0.0394), C_0 (p < 0.001), C_1 (p = 0.0153).

456   However, the position distribution derived from human performance and

457   neurocontroller C's performance showed a similar degree of leftward asymmetry

458   (Fig. 9; Dunn's test, p = 1.0; Levene test of homogeneity, p = 0.39). Thus, all

459   robotics agents performed differently from humans, with the notable exception of

460   the neurorobot population C, whose performance provided a good approximation

461   to human performance.

462   We then compared the performance over time of human participants and

463   model C neurorobots not only for the first canceled target (Fig. 9), but also across

464   all the remaining targets. We performed a Bayesian repeated measures ANOVA

465   (JASP software, version 0.8.2), with agents (human, neurorobots C) as between-

466   group factor, and the spatial position (X coordinate) of the sequence of all the five

467   canceled targets as within-group factors. The Inclusion Bayes Factor, which

468   compares ANOVA models that contain a given effect to equivalent models stripped

469   of the effect, showed decisive evidence (BF$Inclusion$= 2.137e +42) for the

470   cancellation order main effect. Thus, the order of cancellation of all the five targets

471 depended on their spatial position (Fig. 10). Importantly, this effect was statistically

472 equivalent for the human and the neurorobot C populations. In particular, there

473 was substantial evidence against the existence of a group main effect (BF*Inclusion*

474 = 0.144), and strong evidence against the existence of a group X cancellation-

475 order interaction (BF*Inclusion* = 0.046). These results show that the neurorobots

476 from population C and human subjects behave similarly over time when canceling

477 all the five targets.

478

479 **4. Discussion**

480 In this study, we established specific connectivity constraints leading to a lateral

481 spatial bias (pseudoneglect) in artificial organisms trained to perform a visual

482 search task by using genetic algorithms. A form of pseudoneglect that was

483 qualitatively and quantitatively similar to that shown by normal participants did

484 emerge in artificial neurorobots, but only in those harboring hemispheric

485 asymmetries of connectivity that simulated those typically occurring in the human

486 brain. As a further condition, a general excitatory influence of VAN on the

487 ipsilateral DAN was necessary for pseudoneglect to occur in neurorobots. This

488 novel result suggests that hemispheric asymmetry alone is not sufficient to

489 generate a leftward bias, and thus further specifies the likely connectional

490 constraints of pseudoneglect.

491 We first consider our results in the light of neurophysiological studies of

492 pseudoneglect, and then in relation to existing modeling studies of the human

493 attentional system. A particular instance of pseudoneglect occurs with the

494 landmark task: When judging lines pre-bisected to the left of their true center,

495 normal participants consider the left segment as being longer than the right one

496 (Milner, Brechmann, & Pagliarini, 1992). Spatial attention has been shown to be a

497 major determinant of this phenomenon (Toba et al., 2011). Szczepanski et al.

498 (2013; 2010) tested normal participants' spatial bias on convert attention tasks and

499   on the landmark task by using a multimodal approach, combining psychophysics,

500   fMRI and TMS. They tested only frontal and parietal ROIs in the DAN, and did not

501   explore the VAN. Their subjects' sample showed a mixed spatial bias: some

502   subjects had a leftward bias (pseudoneglect), but most subjects showed a

503   rightward bias (Szczepanski & Kastner, 2013). On average, the bias was

504   rightward, unlike most of the literature results. The lateralization of the bias

505   correlated with the lateralization index of the fMRI activation in the ensemble of the

506   DAN ROIs during a covert spatial attention task. Specifically, subjects that had

507   more left hemisphere activation also had a contralateral, i.e. rightward, bias in the

508   landmark task; conversely, subjects with more right hemisphere activation tended

509   to have a leftward behavioral bias. TMS-induced interference on the left- or right-

510   hemisphere parietal nodes during the landmark task caused an ipsilateral shift of

511   the bias: right parietal TMS caused a rightward shift compared to the initial bias,

512   and left parietal stimulation caused a leftward shift. Stimulating both right and left

513   parietal ROIs did not cause a shift. Szczepanski and Kastner (2013) suggested

514   that there is an inter-hemispheric competition between the DAN nodes, and the

515   lateralization of the sum of the weights in the DAN activation shifts the attentional

516   focus contralaterally. The possibility of long-range suppression, which might

517   involve the DANs in both hemispheres, was shown in the monkey LIP: firing rate

518   was suppressed when a saccade target was as far as 50° from the neuron

519   receptive field (Falkner, Goldberg, & Krishna, 2013).

520   Thus, these results are broadly consistent with the functioning of the

521   present neurorobot population C. In agreement with Szczepanski and Kastner's

522   (2013) conclusions, the DAN in the current model is conceptualized as a whole,

523   and not as separated nodes. Additionally, Szczepanski and Kastner's data showed

524   that there is large variability between participants in the direction and degree of

525   lateralization of DAN activation, that on average did not significantly differ between

526   the hemispheres. Here we aimed to explore the typical functional architecture in

527 the human population. Therefore, we chose to model the DAN as laterally

528 symmetrical and the VAN as right-lateralized. However, there are several

529 differences between the current models and the Szczepanski et al's studies. First,

530 they used a landmark task while here we used a search task. Second, the overall

531 behavioral pattern here was of a leftward classical pseudoneglect bias and not the

532 rightward bias found by Szczepanski et al. This might result from substantial

533 differences in the studied samples or in the tasks used. Third, and more

534 importantly, the VAN, which has a major contribution in the current model, was not

535 tested in their studies.

536 The architecture of neurorobot C is partly inspired by the results of Koch et

537 al (2011), which might oversimplify the nature of interhemispheric interactions.

538 Several fMRI studies of human attention areas found evidence of bilateral

539 activation of attention areas, with a contralateral bias (see, e.g., Patel et al., 2015).

540 In neurorobots D and E, we introduced bilateral competence in the right

541 hemisphere networks (Heilman & Van Den Abell, 1980; Mesulam, 1981). However,

542 performance this model showed no consistent spatial bias. This suggests that right

543 hemisphere bilateral competence by itself might not be crucial to the emergence of

544 pseudoneglect. Moreover, in our setting the inhibitory valence of inter-DAN

545 connections was important for the development of an initial leftwards spatial bias,

546 as well as to reach optimal levels of performance, as stressed by additional control

547 simulations in which inter-DAN connections were either set free to evolve as

548 inhibitory or excitatory (neurorobots F), or constrained to assume only excitatory

549 valence (neurorobots G). On the other hand, evidence from neglect patients

550 (Bartolomeo & Chokron, 1999) challenges models of attention exclusively based

551 on inter-hemispheric rivalry (Kinsbourne, 1970, 1977, 1993). In addition, bilateral

552 competence in attentional areas might be important in long-term compensation of

553 neglect (Bartolomeo & Thiebaut de Schotten, 2016; Lunven et al., 2015). Our

554 results stressing the importance of both right-hemisphere bilateral competence and

555 inter-hemispheric competition for pseudoneglect may thus pave the way for an

556 integrated interpretation of different lines of research on normal or dysfunctional

557 human attention networks.

558   In their recent review, Borji and Itti (2013) provided a taxonomy of nearly 65

559 computational models of visual attention. Many of these models focused on

560 reproducing eye movements [e.g., the saliency-based models reported in Borji and

561 Itti (2013)], following a bottom up approach. Typically, these models extract a set

562 of features, represented as maps, from an incoming image. Then, feature maps

563 are combined in a saliency map where a winner-take-all mechanism will designate

564 the spatial region to be attended. Saliency-based attention models in general do

565 not account for exploration biases, with the exception of a recent model (Ali Borji &

566 Tanner, 2016), where an object center bias (the tendency to focus on the center of

567 objects) is reproduced by adding an ad-hoc bias map to the saliency map. While

568 important for building predictive models, this result seems little relevant to lateral

569 biases such as pseudoneglect. Other models (Deco & Rolls, 2004; Deco & Zihl,

570 2004) simulate attention as emerging from the competition of several brain areas

571 subjected to bottom-up and top-down biases. These models do not drive eye

572 movements; the scan path is simulated as a sequence of activations of the

573 simulated posterior parietal cortex. Lanyon and Denham (2004, 2010) added to

574 these models simulated eye movements and an adjustable attention window

575 scaled according to stimuli density. Despite being successful at reproducing scan

576 paths in healthy individuals and neglect patients, these models do not address the

577 issue of pseudoneglect. Other models of attention did not consider pseudoneglect

578 because of their training procedure or design constraints (Di Ferdinando et al.,

579 2007; Monaghan & Shillcock, 2004; Mozer, 2002; Pouget & Sejnowski, 2001). Di

580 Ferdinando et al. (2005) explored line bisection and target cancellation

581 performance in four biologically inspired neural networks. The networks' patterns

582 of connectivity varied along different degrees of asymmetry, inspired by specific

583   theories. Pseudoneglect occurred in line bisection but not in visual search. In these

584   models, motor outputs were only used for target selection; there was no active

585   exploration of the environment, whereas when our neurorobots explored their

586   environment the corresponding input information changed as a function of eye

587   movements. Nonetheless, the present study shares with Di Ferdinando et al.

588   (2005) and other work from the Zorzi group (Casarotti, Lisi, Umiltà, & Zorzi, 2012)

589   the stress on accounts of attentional phenomena relying on sensory-motor

590   transformations, as stated by the premotor theory of attention (Rizzolatti, Riggio,

591   Dascola, & Umilta, 1987). Specifically, our results support the hypothesis that the

592   way in which the movements of the actuators are controlled affects the

593   performance on a cancellation task (Gigliotta, Bartolomeo, & Miglino, 2015).

594   Thus, contrary to most available models of attention, our artificial robots are

595   trained to correctly cancel target stimuli, and are free to self-organize in order to

596   find a proper solution, within the sole limits of the imposed connectivity constraints.

597   These constraints were inspired by available data concerning the anatomical and

598   functional organization of the attentional networks in the human brain. To the best

599   of our knowledge, this is the first attempt to simulate pseudoneglect as a

600   consequence of activity in the dorsal and ventral attention networks in the two

601   hemispheres of the human brain. While this article was under review, two

602   theoretical papers were published that also took into account the dorsal/ventral

603   architecture of the attentional networks (Parr & Friston, 2017; Seidel Malkinson &

604   Bartolomeo, 2017), but neither endeavored to simulate pseudoneglect. Another

605   original feature of the present models is the embodiment factor, consisting of the

606   explicit modeling of eye movements (see also Bartolomeo, Pagliarini, & Parisi,

607   2002; Di Ferdinando et al., 2007; Gigliotta et al., 2015; Lanyon & Denham, 2004;

608   Miglino, Ponticorvo, & Bartolomeo, 2009). In particular, the present models

609   extended the models devised by Di Ferdinando et al. (2007), by increasing the

610   complexity of the organisms' retina, the biological plausibility of the motor system

611 and that of the neural controllers. Conti et al. (2016) also adopted an embodied

612 perspective, based on a humanoid robot platform. In their study, an iCub robot was

613 trained to remove objects from a table, a task reminiscent of a cancellation task.

614 Intra-hemispheric disconnections were able to produce neglect-like behavior.

615 However, the embodiment of the model was limited by the facts that selection of a

616 visual target was carried out independently of the motor behavior, and that robot's

617 eyes were kept fixed during the cancellation task. Moreover, although hemisphere

618 asymmetry was modeled by increasing the number of right hemisphere processing

619 units, no bias in normal performance is reported.

620   Moreover, contrary to most published work, our model attempted to

621 simulate the relationships between the visual pathways and the attentional

622 networks by respecting important biological constraints. Visual pathways project

623 mainly to the hemisphere contralateral to each visual field. However, theoretical

624 models of visual attention posit that the left hemisphere mainly deals with the

625 contralateral hemispace, whereas the right hemisphere has a more bilateral

626 competence (Heilman & Van Den Abell, 1980; Mesulam, 1981). In previous

627 computational models this asymmetry has not always been simulated in a

628 biologically plausible way. In some cases, both simulated hemispheres received

629 visual information from the whole visual field, with attention asymmetries being

630 represented in inner layers (Di Ferdinando et al., 2007; Monaghan & Shillcock,

631 2004). In the Conti et al.'s model (Conti et al., 2016), the right hemisphere received

632 information from both visual hemifields, whereas the left hemisphere processes

633 only the contralateral visual hemifield. Our models D and E had similar

634 architecture, but were unable to mimic human performance. Moreover, there is no

635 anatomical evidence of such asymmetries in the visual pathways, and information

636 exchange in the occipital visual areas is mainly limited to the vertical meridian

637 (Berlucchi, 2014). In our model, these important biological constraints of visual

638 information processing were respected, because each artificial hemisphere

639 received visual information from the contralateral hemifield; inter-hemispheric

640 connections were only present at a later stage of processing, between the artificial

641 DANs.

642   It might be argued that in our model C a leftward bias was simply

643 transferred or amplified from the input to the output layers. If so, however, we

644 would have expected to observe a constant leftward bias, akin to right-sided

645 neglect. What we found, instead, was just an initial leftward bias, at the onset of

646 the exploration task, analogous to human physiological pseudoneglect. In order to

647 observe this initial bias, the VAN-DAN connections had to have an excitatory

648 valence. This occurrence does not result from existing empirical data and is thus a

649 novel prediction of the model. Also, neurorobot populations D and E, which also

650 had more right hemisphere than left hemisphere resources, and should then entail

651 a similar input-to-output amplification, did not show pseudoneglect, presumably

652 because of the lack of inter-hemispheric inhibition.

653   The level of detail of the models is not a trivial matter, because it has to

654 provide meaningful novel information while remaining tractable. A potential

655 limitation of our study is the use of simplified versions of the fronto-parietal cortical

656 networks, without taking into consideration the substructures of the DAN and VAN,

657 which are both broad and partly heterogeneous networks (Colby & Goldberg,

658 1999), nor subcortical structures such as striatum, thalamus and superior colliculus

659 (Krauzlis, Bogadhi, Herman, & Bollimunta, 2017). For example, the connectional

660 anatomy of VAN components such as the temporoparietal junction (e.g., with the

661 ventral cortical visual stream) and of the ventrolateral prefrontal cortex (e.g., with

662 limbic structures) is likely to be crucial to the functioning of the VAN. Yet, our

663 simplified model, with a VAN receiving visual input and sending excitatory

664 connections to the ipsilateral DAN, was able to mimic human performance to an

665 impressive level of accuracy.

666   More generally, our modeling is consistent with evidence from healthy

667   subjects and neglect patients, stressing the importance of entire fronto-parietal

668   networks, or of their dysfunction, in behavioral patterns such as pseudoneglect

669   (Szczepanski & Kastner, 2013), or visual neglect (Bartolomeo et al., 2012;

670   Corbetta & Shulman, 2011), respectively. Also, integrated fronto-parietal activity,

671   with subtle, task-dependent differences in network dynamics, occurs during

672   attention orienting in monkeys (Buschman & Miller, 2007). Concerning visual

673   neglect, evidence suggests that a major determinant of this condition is indeed a

674   dysfunction of the right hemisphere VAN (Corbetta & Shulman, 2011; Urbanski et

675   al., 2011), or of its connections with the ipsilateral DAN (Thiebaut de Schotten et

676   al., 2005).

677   Finally, we note that the present population-based model can be potentially

678   used to explore in a natural manner the universal properties (the basic brain

679   architecture) and individual differences in network efficiency, two aspects recently

680   underlined by Michael Posner (2014) as appropriate features for future models of

681   attention.

682   In conclusion, we have demonstrated the emergence of pseudoneglect

683   behavior in artificially evolving neurorobots searching for visual objects, under

684   specific connectional constraints. These neurorobots provide a plausible model for

685   the dynamic interactions between fronto-parietal attention networks in the human

686   brain.

687

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866
867

868 **Figure Legends**

869

870 Figure 1. Schema of the neurorobot equipped with an artificial eye, provided with a

871 7x7 light receptor retina, and controlled by two pairs of simulated extraocular

872 muscles.

873

874 Figure 2. Panels A, B and C depict different implementations of the attentional

875 networks with inter-hemispheric inhibition (Koch et al., 2011) and DAN/VAN

876 architecture (Corbetta & Shulman, 2002). Panels D and E represent two

877 implementations of right-hemisphere networks with bilateral competence (Heilman

878 & Van Den Abell, 1980; Mesulam, 1981) and no inter-hemispheric inhibition.

879 Arrows indicate connections that can be either excitatory or inhibitory; red

880 connections with triangular arrowheads denote excitatory connections; blue round

881 arrowheads represent inhibitory connections. LH, left hemisphere; RH, right

882 hemisphere; Canc., cancellation units; LDAN and RDAN, dorsal attention networks

883 in the left and in the right hemisphere, respectively; LVAN and RVAN, ventral

884 attention networks in the left and in the right hemisphere; LVF and RVF, left and

885 right visual field. Right and left VANs have the same number of neurons, but

886 different patterns of connection strength.

887

888 Figure 3. Mean percentage of correct cancellations computed across 30 trials for

889 each population of 40 neurorobots provided with neurocontrollers A-E. The middle

890 bar of the boxplot indicates the median of the tested population. The top and the

891 bottom of the box indicate respectively the first (q1) and the third (q3) quartiles.

892 Whisker length extends until the last data point that is not considered as an outlier,

893 I.e. a point that is greater than $q3 + 1.5 \times (q3 - q1)$ or less than $q1 - 1.5 \times (q3 -$

894 $q1)$. There were no outliers in the current dataset.

895

896   Figure 4. Average x values of the first cancelled target, computed across 30 trials

897   for each population of 40 neurorobots provided with neurocontrollers A, B, C, D

898   and E.

899

900   Figure 5. Average x values of the first cancelled targets, for all the neurorobots

901   provided with neurocontrollers C, C0, and C1. Average x values of neurorobots C0

902   is not significantly different from 0, while average x values of neurocontrollers C

903   and C1 significantly differ from 0.

904   Figure 6. Average position on the X axis of the first cancelled targets for human

905   participants (H) and artificial neurorobots equipped with neural networks A, B, C,

906   C0, C1, D and E.

907

908   Figure 6. Average position on the X axis of the first cancelled targets for human

909   participants (H) and artificial neurorobots equipped with neural networks A, B, C,

910   C0, C1, D and E.

911

912   Figure 7. Laterality indexes of DAN activation computed for individuals equipped

913   with neurocontroller C and C0. A value of 0 means that activation in left and right

914   hemisphere DANs is balanced; positive values denote prevalence of right

915   hemisphere DAN, negative values indicate prevalence of left hemisphere DAN.

916

917　Figure 8. Average activation of hidden neurons in right hemisphere DAN (RDAN)

918　and in left hemisphere DAN (LDAN), for the first 30 steps of individuals equipped

919　with neurocontrollers C and C0. The activity scale goes from 0 (black) to 1 (white).

920　Note the early, large left-right asymmetry in neurobiologically inspired C agents

921　(arrows), which subsequently decreases. The symmetrical C0 agents do not show

922　any asymmetry of performance.

923

924　Figure 9. Relative frequencies of the distribution of the position of the first

925　cancelled target for 101 human participants (see Experiment 1) and for the

926　populations of neurorobots C (equipped with the biologically inspired

927　neurocontroller), C0 (presenting symmetrical DAN) and C1 (with VAN-DAN

928　connections only present in the right hemisphere).

929

930　Fig. 10. Coordinates of canceled targets as a function of the temporal sequence of

931　cancellation in human participants and in neurorobot population C. Error bars represent

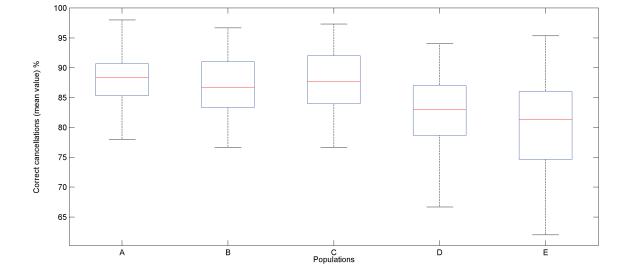932　credible interval of 95%

933

934   **Extended Data 1.** Neurobots and cancellation task have been implemented on the

935   basis of Evorobot*, an open source tool for running evolutionary experiments

936   (http://laral.istc.cnr.it/evorobotstar/) (S. Nolfi & Gigliotta, 2010). The present code,

937   written in C++, includes header (.h) and source (.cpp) files of the modified version

938   of Evorobot*. In particular, the motor control is defined in file epuck_sm.cpp

939   (function move_robot retinaMotorControlType 20); neurorobots and task are

940   initialized in file epuck.cpp (functions: initialize_robot_cancellationTask3();

941   initialize_world_cancellationTask; update_sensors; update_motors). The fitness

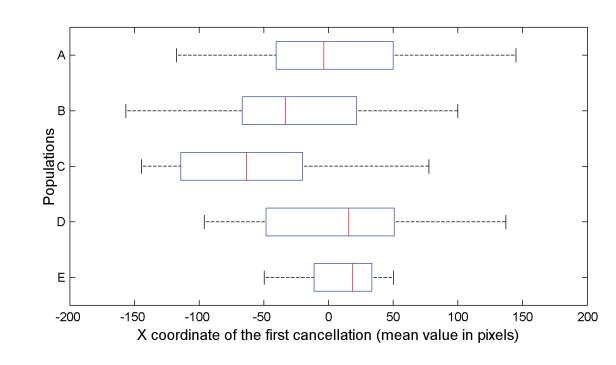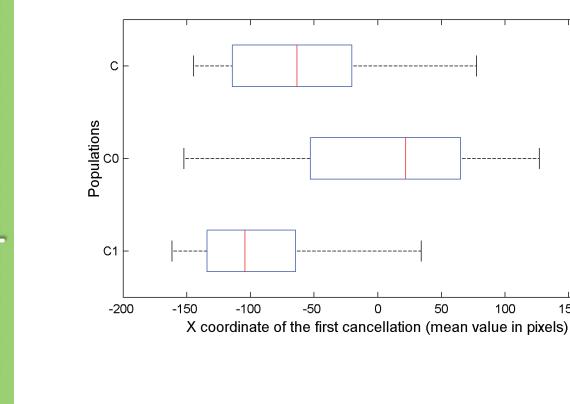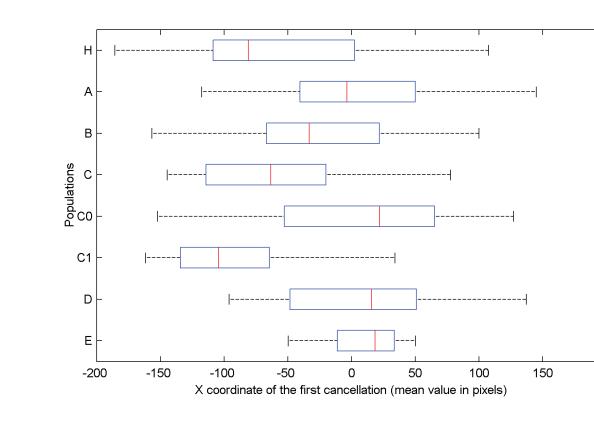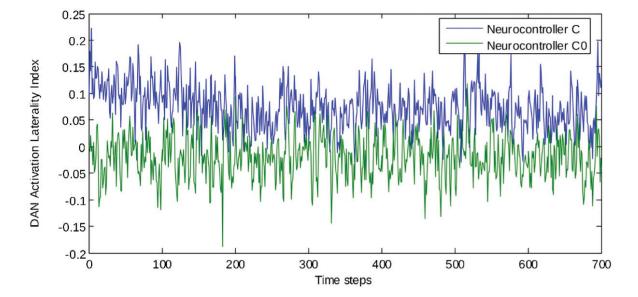942   function is defined in fuction ffitness_cancellationTask3.

943

Medial
Rectus

Lateral

Inferior
Rectus

Superior
Rectus

Human participants (H)

Population C

Population C0

Population C1

X coordinate of the first cancellation (mean value in pixels)