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Plasticity in the Structure of Visual Space

Perceptual space

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Author contributions: CS conducted the experiment. CS, AH designed the experiment and analyzed the data. CS, AH, GT conceived the study and wrote the paper.

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None

52 **ABSTRACT**

53 Visual space embodies all visual experiences, yet what determines the topographical structure of visual space

54 remains unclear. Here we test a novel theoretical framework that proposes intrinsic lateral connections in visual

55 cortex as the mechanism underlying the structure of visual space. The framework suggests that the strength of lateral

56 connections between neurons in visual cortex shapes the experience of spatial relatedness between locations in

57 visual field. As such, an increase in lateral connection strength shall lead to an increase in perceived relatedness and

58 a contraction in perceived distance. To test this framework through human psychophysics experiments, we

59 employed a Hebbian training protocol where two point stimuli were flashed in synchrony at separate locations in

60 visual field, to strengthen the lateral connections between two separate groups of neurons in visual cortex. After

61 training, participants experienced a contraction in perceived distance. Intriguingly, the perceptual contraction

62 occurred not only between the two training locations that were linked directly by the changed connections, but also

63 between the outward untrained locations that were linked indirectly through the changed connections. Moreover, the

64 effect of training greatly decreased, if the two training locations were too close together, or too far apart and went

65 beyond the extent of lateral connections. These findings suggest that a local change in the strength of lateral

66 connections is sufficient to alter the topographical structure of visual space.

67 **SIGNIFICANCE STATEMENT**

68 Given that visual space underlies visual perception, it is easy to take its topographical structure for granted. Indeed,

69 most studies focus on object or feature perception that happens within visual space, without first considering the

70 structure of visual space itself. Here we studied plasticity in the structure of visual space. We found that a local

71 strengthening of lateral connections between retinotopically-tuned visual cortical neurons, induced by synchronized,

72 repetitive presentation of two point stimuli, could lead to a contraction in perceived distance and a change in visual

73 space structure. We propose lateral connections in visual cortex as the mechanism that relates locations perceptually

74 and shapes the structure of visual space.

75 **INTRODUCTION**

76   More than a third of the human cerebral cortex is occupied by retinotopic maps of the visual field, in which

77   individual neurons respond to specific locations in visual field and nearby neurons to nearby locations (Brewer &

78   Barton, 2012; Katzner & Weigelt, 2013; Sereno et al., 1995; Wang et al., 2014). This mapping between visual field

79   and cortex can explain *behavioral* aspects of spatial localization (Rose, 1999). However, it is unclear what underlies

80   the *experience* of spatial relations between locations: why do locations *feel* ordered in the specific way they do, apart

81   from our abilities to *behaviorally* localize targets?

82   Whereas individual neurons in visual cortex respond only to limited locations in visual field, the lateral connections

83   between these retinotopically-tuned neurons instead allow distinct locations to be related. We hypothesize that the

84   strength of lateral connections between neurons in visual cortex determines the degree of perceived relatedness

85   between locations in the visual field (Tononi, 2014; Tononi et al., 2016). This hypothesis explains how the

86   organization of lateral connections, where the connection strength between neurons decays with their cortical

87   separation (Clarke, 1994; Das & Gilbert., 1999), naturally gives rise to the topographical structure of visual space,

88   where the perceived relatedness between locations decays with their visual field separation. Importantly, this

89   hypothesis predicts that a *change* in the strength of lateral connections should *alter* the structure of visual space and

90   affect the perceived relatedness between locations. Specifically, an increase in lateral connection strength should

91   lead to an increase in perceived relatedness and a contraction in perceived distance. Moreover, the hypothesis

92   predicts that the perceptual changes should occur not only between locations linked directly by the changed

93   connections, but also between locations linked indirectly through the changed connections.

94   To test this hypothesis, we employed a Hebbian training protocol where two point stimuli were flashed in synchrony

95   at separate locations in visual field, to induce a short-term increase in the strength of lateral connections between

96   two separate groups of neurons in visual cortex (Caporale & Dan, 2008; Fu et al., 2002; Fu et al., 2004; Yao & Dan,

97   2001). A successful induction of synaptic plasticity requires the presence of direct connections between the two

98   neuronal groups (Ganguly et al., 2000; Li et al., 2004). It follows that, depending on the distribution of lateral

99   connection length, there should be an optimal separation between the two training locations at which the net increase

100   in lateral connection strength is maximal and the contraction in perceived distance is accordingly maximal. At

101   longer separation, the two neuronal groups would not be effectively connected; at shorter separation, the two

102   neuronal groups could be partially overlapping; either way, the number of lateral connections involved and the net

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103 change in lateral connection strength would be less (Fig. 1). We therefore varied the separation between the two

104 training locations from run to run, and measured the effect of training on the perceived distance between the training

105 locations, and on the perceived distance between the outward untrained locations.

106 **MATERIALS AND METHODS**

107 **Participants**

108 Thirty healthy young adults (eighteen female) gave written informed consent to participate in the experiment that

109 was approved by the Institutional Review Board of Author University. The experiments were conducted in a dark

110 room with the display (ASUS PG278Q, 27 inch, 2560 x 1440 pixels, 120 Hz) providing the only significant source

111 of light. Throughout the experiments, participants maintained central fixation and viewed the visual stimuli from a

112 chin rest at a distance of 25 cm.

113 **Procedures**

114 Each experiment run began with two testing sessions and was followed by three alternating cycles of training and

115 testing sessions. In the training session, we employed a Hebbian training protocol adapted from animal experiments

116 and shown to strengthen the lateral connections in cat primary visual cortex (Caporale & Dan, 2008; Fu et al., 2002;

117 Fu et al., 2004; Yao & Dan, 2001). To specifically target lateral connections in human primary visual cortex (V1),

118 we utilized the mirror-symmetry of human retinotopic organization, where V1 is the only early visual cortical region

119 whose ventral part (representation of upper visual field) and dorsal part (representation of lower visual field) are

120 contiguous and are directly connected by lateral connections (Brewer & Barton, 2012; Sereno et al., 1995; Wang et

121 al., 2014). By contrast, the ventral and dorsal parts of other early visual cortical regions (e.g., V2, V3) are segregated

122 by V1, and may have a different organization of lateral connections. We therefore placed the two training locations

123 in upper and lower visual fields, to activate two separate groups of neurons in the ventral and dorsal parts of visual

124 cortex, respectively. Specifically, we flashed two synchronized, vertically-separated point stimuli (5-pixel diameter)

125 in the right hemifield at a rate of ON for 8.33 msec, OFF for 425 msec, and 275 repetitions per training session (120

126 sec). Participants were instructed to passively view the stimuli and minimize eye blinks.

4

127   In the testing session, we used a psychophysical match-to-standard protocol to measure the perceived distance

128   between locations in visual field. In each trial, two pairs of vertically-separated dots (2-pixel diameter) were

129   presented simultaneously for 200 msec in the two hemifields. Participants were instructed to report which dot pair

130   appeared more separated or if the two dot pairs appeared equally separated. The separation between the dot pair in

131   the right hemifield was fixed at a standard value, and that in the left hemifield was adjusted by a one-up one-down

132   double-interleaved staircase with a step size of 0.1 degrees. A total of 108 trials were obtained, in two sessions of 54

133   trials each for the pre-training testing, and three sessions of 36 trials each for the post-training testing. The data were

134   fit with a logistic psychometric function to measure the point of subjective equality (PSE) where the two dot pairs

135   appeared equally separated. The difference between the pre- and post-training PSEs was taken to quantify the

136   training-induced change in perceived distance.

137   Each participant took part in seven experiment runs. A single experiment run lasted ten minutes and was followed

138   by a ten-minute compulsory rest to facilitate the recovery of pre-training baseline and minimize the accumulation of

139   training effect across runs. In different experiment runs, we used training locations separated by 3.2, 3.6, 4.0, 4.4,

140   4.8, 5.2, or 5.6 degrees (one run each in random order), at a horizontal eccentricity of 6 degrees. The separations

141   between testing locations were 0, 0.4, or 0.8 degree larger than the separations between training locations. These

142   visual field separations correspond to a cortical separation of 10 to 14 mm in human V1 (Schira et al., 2007) and

143   overlap with the reported extent of lateral connections in primate visual cortex (Ahmed et al., 2012; Burkhalter et al.,

144   1993; Kaas, 2000; Levitt & Lund, 2003; Lyon et al., 2014; Ringo, 1991; Voges, et al., 2010). Moreover, at an

145   eccentricity of 6 degrees, the number of neurons activated by a point stimulus (cortical point image) should be

146   minimal (Harvey and Dumoulin, 2011; Van Essen et al., 1984), thereby favoring the activation of distinct groups of

147   neurons. The choices of training parameters were determined from pilot experiments, where we tested the effect of

148   stimulus eccentricity (4, 6, 8 degrees), size (5, 15, 30-pixel diameter), pattern (single point, patches of dots,

149   checkboard wedges), and flashing profile (in synchrony, or with inter-stimulus-interval of 8.33, 16.67, 25.00, 33.33,

150   41.67, 50.00, 58.33, 66.67, 216.67 msec), through 276 experiment runs in three participants. Out of the pilot

151   parameters, those that favored focal activation of two separate groups of neurons (i.e. small-sized dots as opposed to

152   patches of dots or checkboard wedges) were used for formal experiments.

153   **Analysis**

154   We quantified the training-induced changes in the perceived distance between the training locations, and between

155   the outward untrained locations, as well as the dependence of training effects on the separation between training

156   locations. We first performed a repeated measures ANOVA on the raw data, with pre-/post-training and training

157   separation as the within-subjects factors. We then estimated how the training effect and its dependence on training

158   separation differed across participants, presumably as a consequence of inter-individual differences in cortical

159   architecture. For each participant, we fitted the training effect with a Gaussian function of the training separation,

160   and took the separation closest to the Gaussian peak as the optimal training separation. This procedure allowed us to

161   calculate the group average after aligning each participant's data to their optimal training separation.

162   **RESULTS**

163   After training, we observed a significant contraction in the perceived distance between the training locations, with

164   the degree of contraction dependent on the training separation (repeated measures ANOVA; effect of training on

165   perceived distance: $F(1,29) = 41.473$, $p < 10^{-6}$; quadratic trend in interaction between training effect and training

166   separation: $F(1,29) = 7.632$, $p = 0.010$). The contraction was maximal at a training separation of 4.4 degrees, which

167   corresponds to a cortical separation of 12 mm in human V1 (Schira et al., 2007) and falls within the extent of V1

168   lateral connections (Ahmed et al., 2012; Burkhalter et al., 1993; Kaas, 2000; Levitt & Lund, 2003; Lyon et al., 2014;

169   Ringo, 1991; Voges, et al., 2010). Due to the mirror-symmetry of human retinotopic organization, V1 is the only

170   early visual cortical region whose ventral part (representation of upper visual field) and dorsal part (representation of

171   lower visual field) are contiguous, while the ventral and dorsal parts of other early visual cortical regions (e.g., V2,

172   V3) are segregated by V1 (Brewer & Barton, 2012; Sereno et al., 1995; Wang et al., 2014). In these regions (e.g.,

173   V2, V3), a visual field separation of 4.4 degrees across horizontal midline would correspond to a cortical separation

174   much larger than 12 mm and would fall outside the extent of lateral connections. The observation of a maximal

175   training effect at a 4.4-degrees visual field separation thus suggests the existence of an optimal cortical separation at

176   which the net increase in V1 lateral connection strength is maximal.

177   Because the surface area of V1 and the length of V1 lateral connections both exhibit considerable inter-individual

178   variability (Andrews et al., 1997; Dougherty et al., 2003; Schwarzkopf et al., 2011; Schwarzkopf et al., 2013; Song

179   et al., 2011; Song et al., 2013; Song et al., 2013; Song et al., 2015), we expected the optimal training separation to

180 vary from participant to participant. To account for the influence of this inter-individual variability on the

181 calculation of group average, we aligned each participant's data to their optimal separation. The aligned group

182 average (Fig. 2) revealed a 7.2% contraction of perceived distance when training at the optimal separation, which

183 decreases to 2.6% when training at ±0.4 degrees from the optimal separation and to 0.8% when training at ±0.8

184 degrees from the optimal separation. Similar results were obtained from the pre-aligned raw data, which revealed a

185 group average of 3.5% contraction at the training separation of 4.4 degrees and a significant decrease to 1.1% when

186 training at ±1.2 degrees away (as reflected by the significant quadratic trend in the ANOVA).

187 The hypothesis that lateral connections underlie the structure of visual space further suggests that the perceived

188 distance should be changed not only between training locations, but also between outward untrained locations that

189 are linked indirectly by the changed connections (Fig. 3). In line with this prediction, after training at the optimal

190 separation, the perceived distance between the testing locations at 0.4 degrees and 0.8 degrees outward from the

191 training locations was contracted by a significant amount of 4.2% ($T(29) = 7.3$, $p < 10^{-7}$) and 3.6% ($T(29) = 5.3$, $p <$

192 10^{-5}), respectively. Moreover, the contraction (4.2%, 3.6%) produced by training at the optimal separation was even

193 larger than the contraction (2.6%, 0.8%) produced by training at these testing locations, illustrating again that the

194 effect of training is very weak at non-optimal training separation.

195 **DISCUSSION**

196 Taken together, these findings suggest that a local strengthening of lateral connections induced by synchronized,

197 repetitive presentation of two point stimuli can lead to a contraction in perceived distance. More broadly, they

198 suggest that lateral connections may underlie the topographical structure of visual space. The training protocol

199 employed in our study was adapted from animal studies shown to strengthen lateral connection between neurons in

200 cat V1 (Caporale & Dan, 2008; Fu et al., 2002; Fu et al., 2004; Yao & Dan, 2001). Due to the fine spatial scale over

201 which the changes are expected to happen (~ 10 mm) and the coarse spatial resolution of neuroimaging measures, it

202 is difficult to ascertain the exact neural-level changes induced by the protocol in human participants. The protocol

203 may have affected feedforward thalamocortical connections, and changed receptive fields or response gains at the

204 training locations (DeAngelis et al., 1995; Eyding et al., 2002; Ganguly et al., 2000; Hisakata et al., 2016; Kohler &

7

205 Wallach, 1994). Similarly, we cannot rule out the training-induced changes in attention and in feedback connections

206 from fronto-parietal cortices to visual cortex (Anton-Erxleben et al., 2007; Klein et al., 2016).

207 Such feedforward or feedback mechanisms have been proposed to account for the perceptual changes induced by

208 repetitive exposure to a visual stimulus, and the transfer of perceptual effects across locations, features, or tasks (Dill

209 & Fahle, 1997; Fahle et al., 1995; Goldstone, 1998; Sasaki et al., 2010; Zhang & Li, 2010). Usually, the transfer of

210 perceptual effects to an untrained location is taken to indicate a feedback mechanism, while the dependence of

211 perceptual effects on a retinotopic frame is taken to support a feedforward mechanism. However, neither

212 feedforward nor feedback mechanisms can account for a U-shape relation between the degree of perceptual changes

213 and the separation of training locations, as was found here (Fig. 2). Moreover, a feedforward mechanism cannot

214 explain the contraction in perceived distance between the untrained locations, as we also found (Fig. 3). Instead, our

215 findings are exactly as predicted by the hypothesis that lateral connections linking neighboring neurons in visual

216 cortex shape the structure of experienced space (Fig. 1).

217 Given that visual space underlies visual perception, it is easy to take its topographical structure for granted. Indeed,

218 most studies of visual perception focus on object or feature perception that happens *within* visual space, without

219 considering the *structure* of space itself. One exception is a recent report of a paradoxical co-occurrence between

220 decreased perceived density of dot textures and contracted perceived distance between dot pairs, after adaptation to a

221 large-field random dot stimulus (Hisakata et al., 2016). This finding cannot be explained by changes in neuronal

222 response properties, and the authors instead proposed the scaling of an "internal metric" in visual cortical system

223 that relates distinct locations and shapes perceived distance (Hisakata et al., 2016). Our study suggests that this

224 internal metric is provided by the organization and strength of lateral connections in retinotopic visual cortex.

225 While the lateral connections are present throughout visual cortex (Kaas, 2000; Levitt & Lund, 2003), different

226 visual cortical regions may play different roles in the structure of visual space. Due to cortical convergence, regions

227 higher up in the visual hierarchy usually occupy less cortical area and have fewer neurons (Dougherty et al., 2003;

228 Haug, 1987). Moreover, individual neurons in these regions inherit the aggregate receptive fields of their multiple

229 feedforward inputs (Brewer & Barton, 2012; Katzner & Weigelt, 2013; Sereno et al., 1995; Wang et al., 2014). By

230 contrast, V1 at the bottom of the visual hierarchy has the largest cortical surface area, the largest number of neurons,

231 and the smallest receptive fields. The lateral connections in higher-up visual cortical regions will therefore span

232 larger separations in visual field and specify a coarser visual space, whereas the lateral connections in V1 will

233 specify a finer visual space. These different spatial scales may jointly ensure a robust structure of visual space.

234 Following on this proposal, an important next step would be to apply protocols that can target different visual

235 cortical regions and selectively strengthen or weaken connections, such as theta burst TMS (Huang et al., 2005;

236 Rahnev et al., 2013; Salminen-Vaparanta et al., 2012; Silson et al., 2013), to examine the roles of individual visual

237 cortical regions in the structure of visual space.

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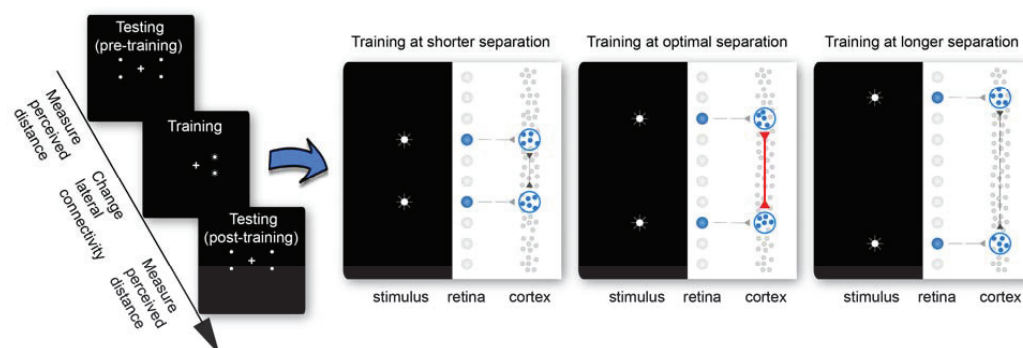
Figure 1. Experiment design. Each experiment run contained pre-training testing, training, and post-training testing

sessions. In the training session, we used synchronized, repetitive presentation of two point stimuli to strengthen the

lateral connections between two retinotopically-tuned neuronal groups. Since the successful induction of synaptic

plasticity requires the presence of direct connections between the two neuronal groups, there should be an optimal

separation between the two point stimuli for changing the lateral connection strength. At longer separation, the two

neuronal groups would not be effectively connected; at shorter separation, the two neuronal groups could be

partially overlapping; either way, the number of lateral connections involved and the net change in connection

strength would be less. In the testing session, we used a match-to-standard protocol to measure the perceived

distance. Participants adjusted the physical separation of a dot pair in the untrained hemifield to match the perceived

distance of a dot pair in the trained hemifield. The difference between the pre- and post-training matches was taken

to quantify the change in perceived distance and the effect of training.

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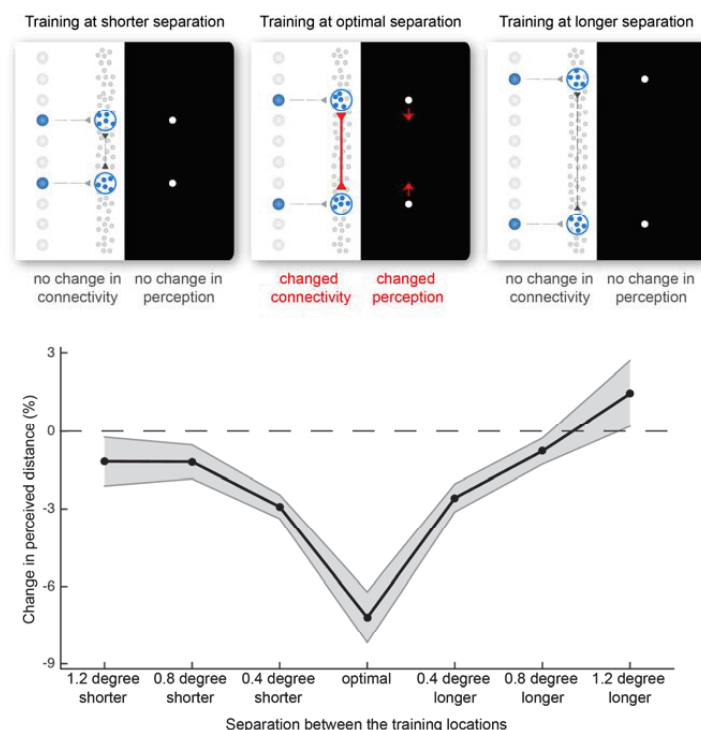
Figure 2. Change in perceived distance depends on training separation. The induction of synaptic plasticity and
the change in lateral connection strength should be dependent on the separation between training locations. We
measured the effect of training for a range of training separations. We observed a maximal contraction in perceived
distance, when training at a separation of 4.4 degree. The contraction declined when training at shorter or longer
separations. Black line represents group average and shaded area represents S.E.M. (N = 30).

357

14
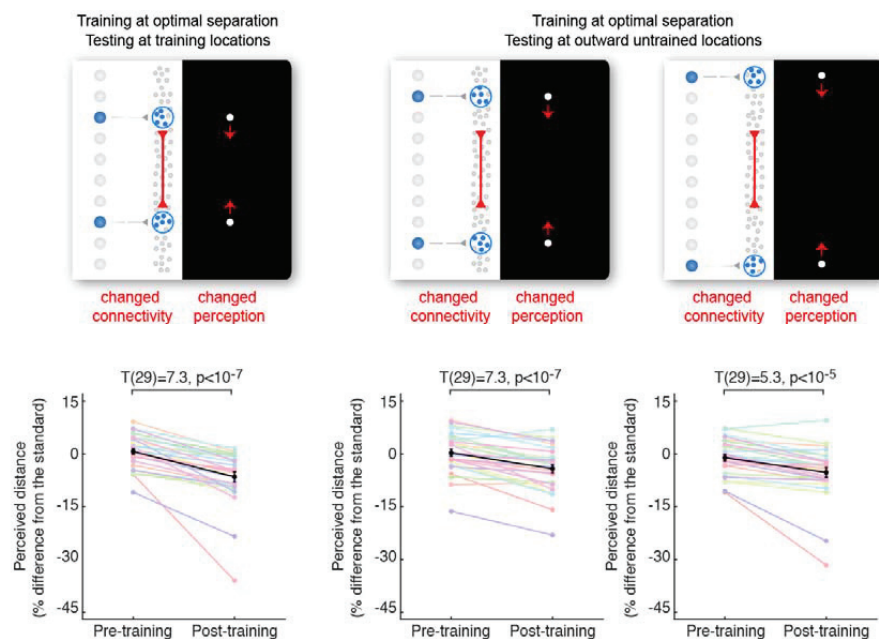
358

359 **Figure 3. Change in perceived distance between untrained locations.** A change in the strength of lateral

360 connections should affect the perceived distance, not only between the training locations, but also between the

361 untrained locations that span the training locations. We measured the effect of training for a range of testing

362 locations. After training at the optimal separation, the perceived distance between the testing locations at 0.4 and 0.8

363 degrees outward from the training locations was significantly contracted. Black line represents group average with

364 S.E.M. (N = 30). Colored lines represent individual participants. Paired-sample T-tests are shown.

15

Testing
(pre-training)

Measure
perceived
distance

Training

Change
lateral
connectivity

Testing
(post-training)

Measure
perceived
distance

Training at shorter separation

Training at optimal separation

Training at longer separation

stimulus   retina   cortex

stimulus   retina   cortex

stimulus   retina   cortex

Training at shorter separation   Training at optimal separation   Training at longer separation

no change in   no change in   changed   changed   no change in   no change in
connectivity   perception   connectivity   perception   connectivity   perception

Training at optimal separation
Testing at training locations

Training at optimal separation
Testing at outward untrained locations

changed
connectivity

changed
perception

changed
connectivity

changed
perception

changed
connectivity

changed
perception

T(29)=7.3, p<10^{-7}

T(29)=7.3, p<10^{-7}

T(29)=5.3, p<10^{-5}