1 **Spatial frequency and global-local visual processing in capuchin monkeys (*Sapajus* spp.)**

2 **and humans (*Homo sapiens*)**

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Abstract

Two experiments employing an identity Matching-To-Sample (MTS) procedure were carried

out to clarify the factors affecting global-local visual processing of capuchin monkeys

(*Sapajus* spp.) in comparison with humans. In a first experiment we assessed the relative

ability of the two species to discriminate High, Medium or Low spatial frequencies (HSFs,

MSFs, LSFs). Then, in a second experiment we determined if the use of a procedure designed

to induce a bias towards attending given spatial frequencies could produce a top-down or

selection-history modulation of global-local visual processing in capuchins and humans. In

the first experiment, monkeys discriminated better the HSFs. By contrast, humans

discriminated better the MSFs and LSFs. The second experiment showed an effect of SF

processing on global-local processing in both species. However, this effect was confined to

local trials only and occurred under different conditions in the two species. In monkeys it

occurred following a bias towards attending HSFs, whereas in humans it occurred following a

bias towards attending LSFs. These results provide new information about the relative

sensitivity of humans and capuchins to different spatial frequencies in vision. Moreover, they

suggest that global-local visual processing can be modulated in both humans and monkeys by

processes that are not confined to attending one or the other level of stimulus structure.

Keywords: visual perceptual grouping, global-local, spatial frequencies, primates, capuchin

monkeys

59   An important issue in the study of visual cognition of humans and other species is the

60   identification of the factors involved in the processing of the relationship between wholes and

61   their component parts. In an extremely influential study, Navon (1977) showed that healthy

62   human adults are faster and more accurate when processing the global rather than the local

63   level of hierarchical visual stimuli (i.e. compound stimuli where small local shapes or letters

64   are arranged in larger configurations depicting a global shape or letter).

65   A large body of literature on humans shows that such a global-advantage is affected

66   by several stimulus features such as visual angle (Kinchla & Wolfe, 1979), position in the

67   visual field (Pomerantz, 1983), spatial frequency (Badcock et al., 1990; Hughes et al., 1990;

68   Lamb & Yund, 1993; 1996), relative size (Amirkhiabani, 1998), Gestalt principles (Han &

69   Humphreys, 1999; Han et al., 1999; LaGasse, 1993) and some disorders such as autism

70   (Happè, 1999) and age of the participants (Cassia et al., 2002; De Lillo et al., 2005).

71   From a comparative standpoint, it is of interest to determine whether or not a global

72   mode of processing is also typical of species closely related to us, and, by doing so, to attempt

73   to trace its evolutionary origin. A local advantage has been found in baboons (*Papio papio*,

74   Fagot & Deruelle, 1997), macaques (*Macaca mulatta*, Hopkins & Washburn, 2002) and

75   capuchin monkeys (*Sapajus* spp.*,* Spinozzi et al., 2003). Studies carried out on chimpanzees

76   (*Pan troglodytes*) showed sometimes a local but also sometimes a global advantage (Fagot &

77   Tomonaga, 1999; Hopkins & Washburn, 2002) indicating that there may not be a strong bias

78   towards global or local processing in species taxonomically closer to humans. All together

79   these findings suggest a possible evolutionary trend in the emergence of the global advantage

80   in primates. One of the very few findings showing a global advantage in monkey species is

81   reported in a study on *Saguinus oedipus* by Neiworth et al. (2006). The study reports that

82   these monkeys show a global advantage but only when the density of the stimuli was

83   manipulated and made very high. Nevertheless, the global advantage disappeared when the

84   local elements were presented in a less dense condition.

85   The widely replicated finding that monkeys show a local advantage has attracted a

86   significant interest in comparative cognition (De Lillo et al., 2005; Fagot & Deruelle, 1997;

87   Lea et al., 2006; Spinozzi et al., 2003). However, it has proved difficult to identify a key

88   factor which can explain local advantage in monkeys (Fagot & Deruelle, 1997). Robust

89   capuchins (*Sapajus* spp.) are the monkeys whose local advantage has been under scrutiny

90   most often. These *platyrrhine* monkeys show a local advantage even when the global level of

91   hierarchical stimuli subtends the same visual angle of the local level (Spinozzi et al., 2005)

92   and this advantage extends to short- (Truppa et al., 2016) and long-term memory traces of the

93   stimuli (Truppa et al., 2017). The local advantage in these monkeys cannot be explained by a

94   failure to use gestalt principles such as proximity, shape similarity and orientation to group

95   local elements into coherent wholes; even though each grouping cue may have a different

96   relative weight in capuchins and humans (Spinozzi et al., 2009). Neither can the local

97   advantage in capuchins be explained by a deficit in the processing of the spatial relationship

98   between stimulus parts. Similarly to humans, capuchins are highly sensitive to the spatial

99   relationships between stimulus parts. Disrupting such relationship in a matching-to-sample

100   task produces a dramatic decrement of performance in both humans and monkeys (De Lillo et

101   al., 2007). Moreover, capuchins and humans are similarly sensitive to global properties of

102   goodness of shape and redundancy of hierarchical visual patterns (De Lillo et al., 2012).

103   Thus, two decades of research show that capuchins' local advantage is a very robust

104   phenomenon and cannot be accounted for by a deficit in the processing of stimulus structure

105   or Gestalt properties. This suggests that some attentional processes, other than bottom-up

106   (stimulus driven) forms of control, might be involved in explaining the difference between

107   humans and monkeys in this domain.

108   In humans, processes that modulate global and local processing rely on attention

109   allocation and have traditionally been considered as top-down. Attentional biases towards one

110   or the other level of hierarchical stimuli produce a shift from global to local advantage in

111   humans (Kinchla et al., 1983). Interestingly, this effect does not pertain to humans only. In a

112   previous study on humans and capuchin monkeys, we manipulated attentional bias to each

113   level of hierarchical stimulus structure by administering trials in blocks containing a large

114   proportion of either global or local trials. Monkeys showed a local advantage in the local bias

115   condition (86% local trials, 14% global trials). By contrast, they displayed a global advantage

116   in the global bias condition (86% global trials, 14% local trials). Humans exhibited an overall

117   global dominance in the accuracy scores. However, attention bias towards one or the other

118   level of the stimuli produced a significant reduction of processing time for the attended level

119   (De Lillo et al., 2011). These results indicate that attention modulates the processing of

120   hierarchical stimuli in monkeys too.

121   Although attention bias, as induced in the experiments described above, cannot be a

122   bottom-up process, it is worth noting that recent experimental results (Awth et al., 2012;

123   Failing & Theeuwes, 2018) and theoretical consideration (Theeuwes, 2019; for a discussion in

124   a comparative context see also Smith & De Lillo, 2022; Washburn & Taglialatela, 2012)

125   challenge the simple dichotomy top-down/bottom-up of attentional processes. Selection

126   history (e.g., repeatedly attending particular spatial position as in probability and contextual

127   priming in foraging or visual search studies) can bias selection processes in a way that is

128   certainly not bottom-up but, at the same time, does not involve conscious goal-driven

129   processes. It may well be that similar effects induced by selection-history apply to processing

130   biases towards one level or other of the structure of hierarchical visual stimuli.

131   A visual property affecting human global-local processing is the spatial frequency of

132   the stimulus. Spatial frequency (SF) refers to the number of light intensity changes over space

133   in an image (e.g., produced by presenting a dark grating on a light background) and is

134   measured by cycles per degree (cpd) of visual angle. Global perception typically involves the

135   processing of LSFs, whereas local perception requires processing HSFs (Robertson, 1996;

136   Shulman et al., 1986; Shulman & Wilson, 1987). Lamb and Yund (1993) found that filtering

137   out the LSF content of hierarchical stimuli, increased RTs in the global trials but not in the

138   local ones, indicating that the LSFs mediate the global advantage in humans. Further studies

139   have shown that after removing the LSFs from hierarchical stimuli, the global advantage is

140   reduced (Badcock et al., 1990; Boeschoten et al., 2005; Hughes et al., 1990).

141   Following the 'zoom-lens' model proposed by Eriksen and Yeh (1985), Shulman and

142   Wilson (1987) suggest that, in humans, sensitivity to particular SFs is controlled by the areal

143   spread of attention to local or global information. According to this proposal, when attention

144   is spread more widely there is a loss of sensitivity to HSFs and an increased sensitivity to

145   LSFs. By contrast, when the spotlight of attention becomes narrower there is a loss of

146   sensitivity to LSFs and an increased sensitivity to HSFs. In support of this hypothesis Flevaris

147   et al. (2011) demonstrated that allocating attention to global or local levels of hierarchical

148   patterns biases the selection of LSFs or HSFs, respectively. The finding supports the idea that

149   a flexible attentional mechanism links SF processing and global-local processing in humans.

150   The aim of the present study is to assess if the allocation of attention to high or low

151   SFs affects global-local processing in capuchin monkeys and humans. Capuchins' sensitivity

152   to different SFs in relation to that of humans is not known. Thus, in order to select SFs that

153   each species was able to discriminate, we carried out a preliminary experiment (Experiment

154   1) to clarify which one, in a spectrum of low, medium or high SF sine-wave grating patterns,

155   is discriminated above chance by the two species. To do so, we presented an identity MTS

156   task with six different SF sine-wave grating patterns ranging from 0.25 cpd to 8.0 cpd of

157   visual angle. SFs within this range of cpd patterns can be discriminated by humans (De Valois

158   & De Valois, 1990). However, very little research has been carried out to highlight potential

159   differences between human and other primates on their ability to detect particular SFs. A few

160   studies addressing this issue have been carried out on catarrhine species such as macaques

161   (De Valois et al., 1974), chimpanzees (Matsuno & Tomonaga, 2006) and orangutans (Adams

162   et al., 2017), whereas platyrrhines have rarely been assessed (e.g., squirrel monkeys, Merigan,

163   1976) and there are no data on capuchin monkeys. Therefore, the purpose of Experiment 1

164   was to identify levels of SFs which can be accurately discriminated by capuchin monkeys and

165   humans at both the lower and higher end of the SF spectrum. Once identified, the appropriate

166   SF gratings could then be used in a main experiment (Experiment 2) to bias attention towards

167   high or low SF. We have previously demonstrated that it is possible to manipulate global-

168   local processing by biasing attention towards one or other level of stimulus structure in both

169   humans and capuchins (De Lillo et al., 2011). The purpose of this study (Experiment 2) was

170   to clarify whether or not biasing attention allocation towards either HSFs or LSFs can also

171   modulate global and local visual processing in capuchin monkeys and humans. This would

172   provide further information about the cause of the well-established differences in global-local

173   processing in humans and monkeys. Our reasoning was that if the preferential level of

174   processing of hierarchical structure of visual stimuli is mediated by a preferential processing

175   of particular bands of SF, then it should be affected by manipulations of the number of trials

176   within a session which require focusing on particular SFs. Therefore, in Experiment 2 we

177   administered sessions of trials containing many discriminations of either high or low SF

178   gratings intermixed with a few trials featuring global-local processing to determine if being

179   repeatedly exposed to particular SFs affected global-local processing in capuchin monkeys

180   and humans.

181

182   **Experiment 1**

183   In this preliminary experiment, we assessed the range of low, medium or high SF that

184   can be discriminated by capuchin monkeys and humans in order to select the appropriate

185   gratings to be used in Experiment 2 to produce an attention bias.

186   **Experiment 1a: Monkeys**

187   *Method*

188   *Standards of openness and transparency*

189   We report how we determined our sample size, all data exclusions (if any), all

190   manipulations, and all measures in the study.

191   *Participants*

192   The sample size of our monkeys was determined opportunistically, based on the

193   availability of the monkeys for the period when testing took place. Three adult capuchin

194   monkeys (*Sapajus* spp.) participated in this experiment: 1 female (Pippi) and 2 males (Gal

195   and Rubens) aged 29, 23 and 8 years, respectively. All individuals were captive born and

196   housed at the Primate Center of the Institute of Cognitive Sciences and Technologies

197   (I.S.T.C.), National Research Council (C.N.R.), in Rome, Italy. Each monkey lived in a social

198   group in an indoor-outdoor enclosure (outdoor: 40-130 m^2 x 3 m high; indoor: 5 m^2 x 2.5 m

199   high). The monkeys were tested individually in an experimental cubicle (0.76 m long x 1.70

200   m wide X 0.73 m high) which they could access through a sliding door from the adjacent

201   indoor enclosure. Each subject was separated from the group exclusively for the purpose of

202   testing, just before each daily testing session. The monkeys spontaneously entered into the

203   indoor enclosure in order to obtain highly preferred food as a rewad for taking part in the test.

204   They were never food or water deprived. Fresh fruit and vegetables were provided after

205   testing and water was available ad libitum. All three subjects were already familiar with the

206   MTS procedure and had been previously tested with hierarchical patterns (De Lillo et al.,

207   2005, 2011; Spinozzi et al., 2006). In particular, all three subjects had taken part in the study

208   by De Lillo et al. (2011), where they were tested with hierchcal stimuli and a similar

209   procedure to manipulate attention bias. However, they had never been tested with SF gratings

210   before.

211   The research protocol for this study was approved by the Italian Health Ministry

212   Central (Direction for the Veterinary Service, approval n. 11/2011-C). All procedures

213   complied with APA ethical standards and other applicable national and international

214   guidelines for the care and use of animals.

215   *Apparatus*

216   The apparatus used with capuchins (see supplementary material, Figure S1) consisted

217   of a vertical panel (35 cm high x 45 cm wide x 2 cm thick) with two lateral walls (35 cm high

218   x 35 cm wide x 2 cm thick). It was fixed perpendicularly onto a board (45 cm x 35 cm), which

219   could be moved forward and backward on a support, mounted on a trolley (55 cm high x 50

220   cm wide x 50 cm long). The vertical panel had two symmetrical rectangular openings (9 cm

221   high x 5 cm wide), each 10 cm from the centre. Three polyvinyl-chloride (PVC) lids (11 cm

222   high x 6 cm wide x 0.3 cm thick) were used for stimulus presentation. Two lids were placed

223   in front of the rectangular openings of the vertical panel. They could be slid laterally in both

224   directions along two parallel metal tracks (45 cm long x 1 cm high), which were mounted

225   horizontally on the panel, 1 cm above and below the openings. The two comparison stimuli

226   were placed on these two sliding panels. The third lid, on which the sample stimulus (SS) was

227   placed, was fixed in the centre of the vertical panel, between the two openings and equidistant

228   from the comparison stimuli.

229   The apparatus was placed in front of the experimental box behind a transparent

230   Plexiglas panel (45 cm wide x 40 cm high) mounted on the front wall of the experimental

231   cubicle. The Plexiglas panel had two symmetrical lateral armholes (15 cm wide x 5.5 cm

232   high) at the level of the rectangular openings of the apparatus, to allow the monkey to insert

233   an arm through one of the two holes and thereby move one of the sliding lids covering the

234   rectangular openings in order to retrieve a piece of peanut. The rectangular openings of the

235   apparatus were positioned at the subjects' eye level. The hands of the experimenter were

236   always occluded by the apparatus and out of view of the subjects when placing the reward. As

237   the monkeys were always free to move in the enclosure during every experimental session,

238   two lateral vertical panels were mounted on the trolley to prevent the monkey from being able

239   to see the back of the apparatus when moving around the experimental cage.

240   *Stimuli*

241   Figure 1a shows the set of stimuli adopted in Experiment 1 as SS and S+. The

242   complete stimulus set, including all the non-matching stimuli (S-) is provided in the

243   supplementary material (Figure S2).

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245   Figure 1 about here

246   ---------------------------

247   Each stimulus consisted of a sinusoidal grating plus a Gabor-Mask. The stimuli were

248   obtained by converting a sinusoidal function into an image using the software *Mat-*

249   *lab.r2010a*. The Gabor mask allowed a higher level of contrast in the centre of the grating that

250   dropped down toward the edge of the pattern. Each grating pattern measured about 4.0 cm x

251   4.0 cm. Capuchins initially viewed the stimuli from approximately 30 cm and then made their

252   choice from approximately 15 cm. At these distances the stimuli subtended about 7° and 15°

253   of visual angle, respectively.

254   The stimulus set consisted of 6 main SF gratings (0.25 cpd, 0.5 cpd, 1.0 cpd, 2.0 cpd,

255   4.0 cpd and 8.0 cpd) adopted as SS and correct comparison stimuli (S+) and 12 gratings

256   derived from the main gratings either adding or removing 30% of the cpd values. These last

257   stimuli were adopted only as negative comparison stimuli (S-). The entire set of stimuli

258 adopted is listed in table 1. This spectrum of cpd patterns has been proved to be detectable by

259 humans (De Valois & De Valois, 1990) and it falls within the range of SF patterns previously

260 used in similar experiments (Flevaris et al., 2011; Shulman et al., 1986; Shulman & Wilson,

261 1987).

262 The gratings were grouped in LSFs, MSFs and HSFs categories for the purpose of

263 experimental manipulation, as described in Table 1.

264 -------------------------

265 Table 1 about here

266 ---------------------------

267 *Procedure and Design*

268 An Identity MTS task was adopted. Each matching condition involved one SS, one S+

269 identical to SS and one S-, which was different from SS. S- was always a sinusoidal grating

270 obtained by adding or removing 30% of the value in cpd of SS. Figure 1b reports an example

271 of a trial.

272 In order to test the monkeys, the apparatus was placed in front of the experimental

273 cubicle, at a distance of 30 cm. At the beginning of each trial, the experimenter, while

274 standing behind the trolley in a central position, placed SS at the centre of the panel and the

275 two comparison stimuli, S+ and S-, on the sliding lids covering the rectangular openings of

276 the panel. Finally, she placed the reward behind the lid featuring S+. Once the animal showed

277 a preference by inserting the arm through one of the armholes, the experimenter moved the

278 panel within the subject's arm reach, at about 15 cm from the front wall of the experimental

279 cubicle. The monkey could obtain the reward only if it moved the lid featuring S+. After the

280 monkey had moved one of the two lids with either hand, the panel was moved away from the

281 cubicle. Trials were separated by an interval of about 30s, during which the experimenter

282 recorded the choice and selected stimuli for the next trial.

283   As a precaution measure, the experimenter moved both hands simultaneously behind

284   the sliding lids when placing the bait. This was done to avoid that particular movements of the

285   neck or shoulders could provide spurious cues to the animal concerning the location of the

286   bait. The experimenter was trained to keep her head in a fixed position while looking ahead

287   once the baiting had occurred and until the subject made a response.

288   Each monkey performed 8 sessions of 36 trials each; one session a day, for a total of

289   288 trials. Each daily session included as SS all the 6 main gratings shown in Figure 1a. S-

290   (SS+30% or SS-30%) appeared in the same proportion in each session. The order of

291   presentation of each SF main grating was randomized, however, they appeared in equal

292   number across each session.

293   ***Results***

294   *Accuracy*

295   The overall mean percentage of correct responses was 67.8% (Pippi: 71.9%, Gal:

296   63.0%, Rubens: 68.3%). Figure 2a reports the overall mean percentage of correct responses

297   obtained by the monkeys in each of the six types of SF condition: 0.25 cpd, 0.5 cpd, 1.0 cpd,

298   2.0 cpd, 4.0 cpd, 8.0 cpd.

299   One-sample *t*-tests were conducted to assess whether or not, at the group level, the

300   mean percentage of correct responses observed for each condition was significantly above the

301   chance level of 50% correct. The monkeys performed significantly above the chance level

302   only for the 8 cpd condition [$M = 74.0\%$, $t(2) = 15.34$, $p < .005$, $d = 8.85$, $_{95\%}$CI: 17.27-30.37].

303   A repeated measures ANOVA comparing the accuracy scores obtained on each SF condition

304   did not reveal a significant difference between the six cpd conditions. Individual data,

305   together with results of binomial tests, carried out on the frequency of correct responses of

306   each individual in each of the 6 SF conditions are reported in Table 2. From Table 2 it can be

307   noted that all subjects performed significantly above chance for the 8 cpd condition. By

308 contrast, none of the subjects performed above chance level in the 0.25 cpd condition. The

309 condition with the lowest SF where at least 2 subjects performed above chance was the 0.5

310 cpd.

311   ---------------------------

312   Figure 2 about here

313   ---------------------------

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315   Table 2 about here

316   ---------------------------

317   Finally, the relatively high level of accuracy recorded in the 8.0 cpd condition raised

318 the doubt that monkeys may have used alternative clues to solve the task. Given that the 10.4

319 cpd patterns consisted of extremely thin bars, they might have been perceived by the monkeys

320 as a grey pattern. Had this been the case, the trials featuring S- 10.4 cpd pattern could have

321 resulted in a matching task between a grating versus a grey pattern which would have been

322 easier to solve than a discrimination comparison between two SF gratings. If this was the

323 case, we should have observed a higher level of performance in the trials featuring the 10.4

324 cpd grating as S- in comparison with trials featuring the 5.6 cpd as S-. In order to test this

325 possibility, a paired-sample *t*-test was carried out to compare accuracy in the trials featuring

326 5.6 cpd and the trials featuring 10.4 cpd as S-. This analysis did not reveal any significant

327 difference between the two non-matching conditions (10.4 cpd = 71.7% *vs.* 5.6 cpd $M =$

328 76.4%) suggesting a genuine proficiency of capuchins in discriminating gratings with SF of

329 8.0 cpd.

330   **Experiment 1b: Humans**

331   *Method*

332   *Participants*

333   The sample of human participants was determined opportunistically. It was considered

334   inappropriate to have a sample much larger than the monkey sample to make comparisons

335   meaningful. At the same time, we did not want to miss the opportunity to test a larger number

336   of people than the three monkeys that were available for the study. Thus, 16 volunteers (8

337   males and 8 females) from the participant panel of the School of Psychology, University of

338   Leicester, UK, were given a small participation fee to participate in this experiment.

339   *Apparatus*

340   The experimental set up comprised a Pentium PC with a 17" SVGA monitor with a

341   resolution of 1024 x 768 pixels. A response box connected with the PC allowed the subjects

342   to make a choice between two response keys, respectively located on the left and the right of

343   the response box. The software used to generate stimuli on the computer screen and to collect

344   the responses of the subjects was developed at the University of Leicester, using E-prime

345   (Psychology Software Tools Inc.).

346   *Stimuli*

347   The stimuli were the same as those of Experiment 1a (see Figure 1). As for the

348   monkeys, the visual angle subtended by the stimuli was approximately 7 degrees. The

349   distance of 30 cm between the computer screen and the participant's eyes was kept constant

350   by using a chin rest.

351   *Procedure and Design*

352   The same identity MTS used for Experiment 1a was adopted for Experiment 1b.

353   S+ was always identical to SS, whereas S- was a sinusoidal grating obtained by the SS

354   adding or removing 30% of the value in cpd. Each session included all six main grating

355   patterns (SS) with their relative matching (S+) and non-matching stimuli (S-) and the

356   sequence was random. Each trial started with the three stimuli appearing at the same level on

357   the screen. As for Experiment 1a, the SS appeared always at the centre of the screen. The

358 subject's task was to indicate, by pressing the "L" or the "R" key, respectively located on the

359 left and right of an array of keys of a response box, which of the two patterns was identical to

360 the centrally presented pattern. All the three stimuli remained present on the screen until a

361 response was made, after which a blank screen would appear. Then, to move to the next trial

362 the subject had to press a different button on the response box.

363 Each participant performed 48 trials featuring each main SF pattern for a total of 288

364 SF trials in one session. S- stimuli (SS - 30% or SS + 30%) were in equal number and

365 appeared randomly.

366 The PC allowed the recording of accuracy scores and reaction time (RT) with a

367 precision of 1 msec.

368 ***Results***

369 *Accuracy*

370 The overall percentage of correct responses across the six SF conditions was 88.65%

371 (see Figure 2b).

372 One-sample t-tests revealed that the accuracy level of the humans was significantly

373 above the chance level of 50% for all the SF conditions [0.25 cpd: $t(15) = 26.08$, $p = .005$, $d = $

374 6.52; 0.5 cpd: $t(15) = 44.39$, $p = .005$, $d = 11.1$; 1.0 cpd: $t(15) = 30.03$, $p = .005$, $d = 7.51$; 2.0

375 cpd: $t(15) = 30.06$; $p = .005$, $d = 7.51$; 4.0 cpd: $t(15) = 25.69$, $p = .005$, $d = 6.42$; 8.0 cpd:

376 $t(15) = 20.86$, $p = .005$, $d = 5.21$].

377 A repeated measures ANOVA carried out to compare the mean percentages of correct

378 responses obtained for each SF condition proved significant [$F (2.98, 44.78) = 6.89$, $p = .005$,

379 $\eta_p^2 = .315$]. Please note that, here and below, whenever fractional degrees of freedom are

380 reported, this is because the Greenhouse-Geisser correction for violation of the sphericity

381 assumption was applied.

382   Paired-sample *t*-tests were performed as pairwise comparisons and, after applying the

383   Bonferroni correction for 15 comparisons (α = .0033), revealed that the accuracy level for the

384   0.25 cpd condition was significantly lower than for the 0.5 cpd (*p* = .0033), 1.0 cpd (*p* = .001)

385   and 2.0 cpd (*p* = .0033) conditions. Moreover, the accuracy level for the 8.0 cpd condition

386   was significantly lower than for the 1.0 cpd condition (*p* = .0033).

387   In experiment 1a, monkeys proved to process the 8.0 cpd significantly better than the

388   0.25 cpd. In order to assess the presence of interspecies differences in the processing of these

389   two SFs, independent sample *t*-tests were performed on accuracy scores recorded by monkeys

390   and humans for the 0.25 cpd condition and the 8.0 cpd condition, respectively. They revealed

391   that the accuracy score recorded for the monkeys in the 0.25 cpd condition was lower than

392   that recorded for humans [*t*(17): 3.720, *p* = .005, *d* = 2.98, $_{95\%}$CI: 0.124 – 0.447]. However, no

393   significant interspecies difference emerged for the 8.0 cpd condition.

394   *Response Times (RT)*

395   The apparatus adopted with humans allowed to record RT. Therefore RT was used as

396   an additional dependent variable for humans. Only the RTs for correct answers were included

397   in the data analysis. The median RT for each condition was computed for each subject to

398   compensate potential effects of extreme values. Figure 3 reports the means of medians and SE

399   of the RTs recorded for each SF condition. A repeated measures ANOVA carried out on these

400   values revealed an overall significant difference between conditions [$F(2.38,35.65) = 5.06$, *p*

401    $= .01$, $\eta_p^2 = .252$].

402   However, after applying the Bonferroni correction for 15 comparisons ($\alpha = 0.0033$),

403   none of the paired-sample *t*-tests revealed a significant difference between the different

404   conditions.

405   --------------------------

406   Figure 3 about here

407 --------------------------

408 ***Discussion***

409 The main purpose of this preliminary experiment was to determine which SFs were

410 appropriate to use in Experiment 2 for each species. Nonetheless, some of the differences

411 observed between the two species are of interest in themselves, considering the paucity of

412 information available in the literature. The results of this experiment show interspecies

413 differences between the processing of Low, Medium and High SFs by humans and capuchin

414 monkeys.

415 In humans the performance in all the six SF conditions was above the level expected

416 by chance, demonstrating that humans can accurately discriminate the range of frequencies

417 used in our MTS task. However, humans proved more accurate in trials featuring SFs

418 ranging between 0.5 cpd and 4.0 cpd than conditions with gratings featuring 0.25 cpd and 8.0

419 cpd.

420 Capuchins showed a different pattern. In fact, their accuracy was above chance level

421 only in the 8.0 cpd condition. In addition, their accuracy was higher in trials featuring SS with

422 gratings of 8.0 cpd, than in trials featuring SS with gratings of 0.25 cpd. This difference seems

423 to be genuinely due to their ability to discriminate HSF patterns particularly accurately.

424 The results of the interspecies analysis performed on the accuracy recorded on the 8.0

425 cpd and 0.25 cpd condition indicate that monkeys process these last frequencies significantly

426 less accurately than humans, whereas the two species do not differ in their processing of 8.0

427 cpd. These findings support the conclusion, supported also by within-species analyses, that

428 monkeys process the 8.0 cpd condition significantly better than the 0.25 cpd condition.

429 Overall, from the first experiment it emerges that the peak of SF sensitivity is located

430 around medium SFs in humans and around higher SFs in monkeys. In addition, both species

431 had more difficulty processing the 0.25 cpd condition.

432   Therefore, in Experiment 2 the 8.0 cpd value was selected as the HSF stimulus as it

433   was processed above chance in monkeys. The 0.5 cpd, value was selected as the LSF stimulus

434   as two monkeys' performance was significantly above chance there. The same stimuli were

435   suitable for use with humans as they matched both above chance level (as they did with all

436   SFs used in this experiment).

437

438   **Experiment 2**

439   In a previous study (De Lillo et al., 2011), we showed that it is possible to induce, in

440   both monkeys and humans, an attention set towards the global or the local level of structure of

441   hierarchical visual patterns by manipulating the proportion of trials requiring the processing

442   of one or the other level within a testing session. Such attention bias affects the quality of

443   processing of the levels of structure of the stimuli and can produce an inversion of the global-

444   local dominance shown by a given species (De Lillo et al., 2011; Fremouw et al., 1998). The

445   aim of Experiment 2 was to evaluate whether or not the allocation of attention to HSFs or

446   LSFs can affect local and global processing in monkeys and humans in a similar way. It was,

447   therefore important to identify with the previous experiment appropriate values of SF to be

448   used to in Experiment 2, i.e. the 8.0 cpd and the 0.5 cpd patterns as the HSF and LSF samples,

449   respectively.

450   In Experiment 2, we attempted to induce an attention bias towards HSF and LSF,

451   respectively, by administering 85.7% of trials requiring matching either HSFs or LSFs,

452   randomly intermixed with a 14.3% of trials requiring, either global or local processing. These

453   particular percentages were used following the procedure by De Lillo et al. (2011) with

454   monkeys and previously adopted by Kinchla et al. (1983) with humans and Fremouw et al.

455   (1998) with pigeons. In the previously mentioned studies, the use of these percentages of

456   trials has proved to be effective to bias attention towards global or local levels of stimulus

457   structure in hierarchical stimuli. Therefore, the same percentages were adopted here. The use

458   of trials featuring discrimination of SFs in order to bias attention towards global or local

459   processing, however, has not been attempted before with capuchin monkeys or, to our

460   knowledge with any other nonhuman animal species. Our reasoning was that if the

461   preferential processing of one level or the other of the hierarchical structure of visual stimuli

462   is mediated by a preferential processing of particular bands of SF, then it should be affected

463   by manipulations of the number of trials within a session which require focusing on particular

464   SFs. The combination of the two SF bias conditions, HSF and LSF, with the two global-local

465   conditions, resulted in a total of four conditions: HSFs bias - Global trials condition, HSFs

466   bias - Local trial condition, LSFs bias - Global trial condition, LSFs bias - Local trial

467   condition.

468   **Experiment 2a: Monkeys**

469   ***Method***

470   *Participants*

471   Participants were the same as in Experiment 1.

472   *Apparatus*

473   The apparatus was the same as in Experiment 1.

474   *Stimuli*

475   The stimulus set comprised a sub-set of SF patterns and a sub-set of hierarchical

476   stimuli patterns (see Figure 4a, b).

477   The first sub-set of SF stimuli comprised the 0.5 cpd pattern as LSF and the 8.0 cpd

478   pattern as HSF. As in Experiment 1, S+ was identical to SS, whereas S- could include grating

479   patterns obtained by adding or removing 30% of cpd to/from SS.

480   The second sub-set comprised hierarchical patterns where a global shape was formed

481   by the spatial arrangement of smaller geometrical shapes, along the lines described by Navon

482   (1977). The hierarchical stimuli appeared as white shapes on a black background and were

483   created using Microsoft PowerPoint. The stimulus sub-set comprised eight compound forms

484   similar to the ones used in previous experiments (De Lillo et al., 2011; Spinozzi et al., 2003;

485   2005). It included large circles (C), squares (S), rhombi (R), or letter *X*s (X) made up of

486   smaller circles (c), squares (s), rhombi (r), or letter *X*s (x). The shape of the global level could

487   be identical (consistent stimuli) or it could be different (inconsistent stimuli) from the shape

488   of the local level. The stimuli measured 4.0 x 4.0 cm at global level and had 12 local elements

489   measuring 0.5 x 0.5 cm. Capuchins initially viewed the stimuli from approximately 30 cm and

490   then made their choice from approximately 15 cm. At a distance of 30 cm, the stimuli

491   subtended about 7° of visual angle at global level and 0.9° at local level, whereas at a distance

492   of 15 cm they subtended about 15° of visual angle at global level and 2° at local level.

493   ---------------------------

494   Figure 4 about here

495   ---------------------------

496   *Procedure and Design*

497   An identity MTS task was adopted using both SF stimuli and hierarchical patterns.

498   The matching between the SF stimuli is the same reported in Experiment 1, with the

499   only difference that the SF patterns adopted here were only the 8.0 cpd as high SF pattern and

500   0.5 cpd as low SF pattern. The MTS with hierarchical stimuli involved two conditions: in the

501   global trials, S+ was identical to SS and S- was differed from SS only at the global level; in

502   the local trials, S+ identical to SS and S- was differed from SS only for local elements.

503   Examples of one global and of one local trial are presented in Figure 4c.

504   The procedure adopted resembled closely that adopted by De Lillo et al. (2011). Each

505   daily session consisted of a sequence of 4 control trials (either global or local), followed by 24

506   SF trials pseudo-randomly intermixed with either 4 global or 4 local trials. The randomisation

507 had as the only constraint that the global-local trials should not appear in the first 7 trials. This

508 was done to avoid global-local trials appearing in the first positions and before an attention

509 bias could be developed on the basis of the SF discriminations. To clarify further, as stated

510 above, each daily session was preceded by a control session of 4 trials comprising either

511 global or local trials, depending on the type of trials in the session with hierarchical stimuli

512 that followed. So, a global session was preceded by global control trials and a local session

513 was preceded by local control trials. Each monkey performed a total of 16 sessions, one

514 session per day, for a total of 512 trials, which comprised 64 control trials (32 global, 32

515 local), 384 SF trials (192 HSF, 192 LSF) and 64 global or local trials (32 global, 32 local).

516   There were three conditions: (1) HSF Bias (Global trials, 85.7% HSF trials and 14.3%

517 global trials; Local trials, 85.7% HSF trials and 14.3% local trials); (2) LSF Bias (Global

518 trials, 85.7% LSF trials and 14.3% global trials; Local trials, 85.7% LSF trials and 14.3%

519 local trials) and (3) CONTROL (Global trials, 100% Global trials; Local trials, 100% Local

520 trials). The conditions were administered in the following order to all the three subjects: HSF-

521 Local, HSF-Global, LSF-Local and LSF-Global. As only three subjects were tested, it was not

522 possible to fully counter balance the order of which monkeys started the experiment.

523 Similarly, within a total of 16 sessions, it would not have been possible to fully

524 counterbalance the sequence of presentation of the 4 conditions across sessions. As such,

525 rather than using an arbitrary subset of possible sequences, it was decided to repeat the same

526 order 4 times, and it was considered more appropriate to follow the same order with all

527 subjects. We had no specific reason for using any specific order. However, we ensured that

528 global and local sessions alternated on consecutive days.

529   ***Results***

530   *Accuracy for Spatial Frequency Matching Trials*

531   The overall mean percentage of correct responses for the group of monkeys for high

532   and low SF trials combined was 71.4%. Table 3 shows the individual percentages of correct

533   responses for trials involving HSFs and LSFs pattern discrimination registered during the

534   local and global tasks. The average percentage of the group obtained combining the

535   performance recorded on SF trials during the global and local condition was 68.1% for the

536   LSF trials and 74.7% for the HSF trials. One-sample t-tests performed on the percentage of

537   correct answers obtained combining the performance recorded on the SF trials during the

538   global and local tasks, revealed that the accuracy level shown by the monkeys was above the

539   50% level expected by chance in both HSF (global and local) [$t(2) = 6.64$, $p < .05$, $d = 3.84$,

540    $_{95\%}$CI: 8.68 – 40.63] and LSF (global and local) [$t(2) = 5.77$, $p < .05$, $d = 3.33$, $_{95\%}$CI: 4.59 –

541   31.53] trials. In addition, a paired-sample t-test performed on the accuracy scores recorded

542   between these 2 conditions, always combined for local and global tasks, did not reveal any

543   significant difference, demonstrating again that monkeys' performance in the LSF trials was

544   as good as in the HSF trials.

545   --------------------------

546   Table 3 about here

547   --------------------------

548   *Accuracy for Compound Stimuli Matching Trials*

549   The overall mean percentage of correct responses for global and local trials was

550   70.7%. Table 4 reports the individual percentages of correct responses shown by each

551   monkey in the local and global trials of the Control, HSFs bias (8.0 cpd), and LSFs bias (0.5

552   cpd) conditions.

553   --------------------------

554   Table 4 about here

555   --------------------------

556   A bar graph depicting the percentage of correct responses for the group of monkeys

557   across the different conditions is presented Figure 5a.

558   A 2 (Level of Processing: Global, Local) x 3 (Condition: Control, HFS, LSF) repeated

559   measures ANOVA, performed on the percentage of correct responses, did not reveal a

560   significant main effect for either Level of Processing (local: $M = 71.2$ %; global: $M = 70.1$%),

561   or condition (Control: $M = 73.4$ %; HSFs: $M = 66.7$ %; LSFs: $M = 71.9$ %). Importantly,

562   however, there was a significant interaction Level of Processing by SF Bias [$F_{(1,2)} = 7.611$,

563    $p < .05$, $\eta_p^2 = .792$]. None of the post-hocs carried out to interpret the interaction yielded

564   significant results. Nevertheless, an inspection of Figure 5a suggests that the interaction can

565   be explained by the reversal of the relative accuracy observed in local and global trials in the

566   control and LSF bias condition (with higher values for the Local trials, compared to the

567   Global trials), on the one hand, and the HSF bias condition (with higher values for the Global

568   trials compared to the Local trials), on the other.

569   ---------------------------

570   Figure 5 about here

571   ---------------------------

572   **Experiment 2b: Humans**

573   In Experiment 2b we used the same stimuli and design of experiment 2a to test

574   humans and procedures as similar as possible to those used with monkeys.

575   *Method*

576   *Participants*

577   Experiment 2b was carried out on 8 participants among those who took part in

578   Experiment 1b and were still available to take part in Experiment 2. In order to replicate the

579   procedure used with monkeys, with half of the human sample the sessions were administrated

580   exactly in the same order in which they were administrated to the monkeys. Therefore, these 4

581   subjects started with the session HSF-Local followed by HSF-Global, then LSF-Local

582   followed by LSF-Global. The other half of the sample received the opposite order, with the

583   session LSFs-Global followed by LSF-Local and then the sessions HSF-Global followed by

584   HSF-Local. In this way, a partial counter balancing of presentation order was achieved.

585   *Apparatus*

586   The experimental set-up was the same as for Experiment 1b.

587   *Stimuli*

588   The stimuli were the same as in Experiment 2a.

589   *Procedure*

590   The same MTS procedure used with monkeys was adopted with humans. However,

591   each human subject performed 4 alternated sessions per day, instead of one session per day.

592   Possible undesired adaptation effects were minimised by administering only 4 sessions

593   per day, each session consisting of one condition (e.g., HSF-Local bias, HSF-Global bias,

594   LSF-Local bias, LSF-Global bias). The same sequence was repeated for 4 consecutive days.

595   Each session was separated by a time of approximately one minute and every trial was

596   followed by a blank screen so that participants had to press a button to move to the next trial.

597   **Results**

598   *Accuracy for Spatial Frequency Trials*

599   The overall mean percentage of correct responses on SFs trials (high and low)

600   recorded by the whole group of humans was high (94.7%). The average percentage of the

601   group obtained combining the performance recorded on the SF trials during the global and

602   local condition was 98.6% for the LSF trials and 90.8% for the HSF trials. A one-sample *t*-

603   test performed on the percentage of correct answers obtained combining the performance

604   recorded on the SF trials in the global and local conditions, revealed that the accuracy level

605   was above the 50% level expected by chance in both LSF [$t(7) = 69.91$, $p < .001$, $d = 24.7$,

606    $_{95\%}$CI: 46.92 – 50.21] and HSF [$t(7) = 14.63$, $p < .001$, $d = 5.17$, $_{95\%}$CI: 34.22 – 47.42].

607   Finally, a paired-sample t-test performed on the percentage of correct answers recorded in the

608   two conditions demonstrated that humans processed the LSFs significantly better than the

609   HSFs [$t(7) = 2.830$, $p < .05$, $d = 12.19$, $_{95\%}$CI: 14.22 – 1.27].

610   *Response Times for Spatial Frequency Trials*

611   Only the RTs for correct answers were included in the data analysis. The median RT

612   for each condition was computed for each subject to attenuate potential effects of extreme

613   values. The average of the group obtained combining the performance recorded on the SF

614   trials during the Global and Local condition was 1500.8 ms for the HSF trials and 1262.0 ms

615   for the LSF trials. Paired sample t-test performed on the medians of RTs recorded in the two

616   conditions did not reveal any significant difference between the speed of processing of the

617   two different SF trials.

618   *Accuracy for Compound Stimuli Matching Trials*

619   The level of accuracy displayed by human participants was extremely high in both the

620   global ($M = 100.0\%$) and the local ($M = 99.7\%$) trials, making formal statistical comparisons

621   inappropriate. Hence, the analysis was confined to RTs, as described below.

622   *Response Times for Compound Stimuli Matching Trials*

623   RTs for correct responses only were included in the analysis.

624   A 2 (Level of Processing: Global, Local) x 3 (Condition: Control, HSF bias, LSF bias)

625   repeated measures ANOVA was performed on the medians of the RTs data recorded for each

626   of human participants.

627   The ANOVA did not reveal any significant effect for Level of Processing and

628   Condition but revealed a significant interaction between these two factors [$F (2, 14) = 3.89$, p

629    $< .05$, $\eta_p^2 = .357$]. However, after applying the Bonferroni correction, none of the pairwise

630   comparisons carried out using paired-sample *t*-tests, revealed a significant difference (Figure

631   5b).

Discussion

633   The results of Experiment 2 suggest that attending to different grating patterns can

634   affect global-local processing in both humans and capuchin monkeys. In fact, a significant

635   interaction between high-low SF processing and global-local processing emerged in both

636   species. In both species the effect is mostly confined to local trials. There are, however, some

637   important differences between the two species. In monkeys this effect emerges as a worsening

638   of performance in the local trials presented as part of the HSFs condition. In humans the

639   effect emerges as a reduction of RT's for local trials in the LSFs condition.

640   To help the interpretation of the above pattern of results, it was of interest to evaluate

641   the presence of any potential effects caused by perceptual adaptation. It is a well-known

642   phenomenon that neuron responses to grating patterns drop down along the time of exposure

643   to the same grating (Blakemore & Campbell, 1969; De Valois & De Valois, 1990). Given our

644   results, we thought that it was worth considering the possibility that subjects were

645   experiencing adaptation to specific SFs due to repetitive exposure to several trials featuring

646   the similar SFs. On the basis of the considerations that follow, we have reasons to believe that

647   perceptual adaptation did not occur in this study. Our procedure aimed at biasing attention

648   toward either HSFs or LSFs and not at inducing adaptation to particular SFs, as has been done

649   in other studies (e.g., Shulman et al., 1986). With a procedure like ours, it is extremely

650   unlikely that low level perceptual adaptation to SFs could have occurred. Adaptation typically

651   occurs when gratings of a certain frequency are presented continuously for an extended period

652   of time. Our testing sessions were relatively short and were presented only once per day to

653   monkeys and four per day to humans, always alternating HSFs and LSFs. Furthermore, in

654   humans each trial was separated by consecutive trials using a blank screen, and the

655   participants decided when to interrupt the presentation of the blank screen to progress onto the

656   following trial. Similarly, with the procedure adopted for testing monkeys at least a few

657   seconds elapsed between each trial to allow the experimenter to slide the images of the stimuli

658   into the apparatus.

659   Nevertheless, in order to confidently rule out that perceptual adaptation to either HSFs

660   or LSFs influenced our results, we looked at how discrimination performance in our subjects

661   changed with time within each testing session. Our reasoning was that, if perceptual

662   adaptation developed as participants were exposed to repeated SF trials in the course of a

663   testing session, then their performance in the SF trials should have decreased as the session

664   progressed. In order to test this possibility, we divided each session into six blocks (four trials

665   each) and we averaged, each block across testing sessions. We did so separately for each

666   condition and we used percentages of correct responses for monkeys and median RTs for

667   humans.

668   One-way ANOVAs comparing the six blocks did not show significant differences or

669   trends across blocks for any condition in monkeys: HSF-global, HSF-local, LSF-global and

670   LSF-local. This suggests that monkeys' performance on SF trials remained constant as

671   exposure to particular SF increased, ruling out that adaptation occurred.

672   Similarly, one-way ANOVAs carried out on humans' RTs recorded in SF trials, did

673   not reveal significant differences across blocks or significant trends for the HSF-global, HSF-

674   local and LSF-global conditions. Only the ANOVA carried out on humans' RTs in the HSF-

675   local condition revealed a significant difference between blocks [$F(5, 35) = 2.94$, $p < .05$]

676   with a significant quadratic component of the trend [$F(1, 7) = 9.36$, $p < .05$]. This significant

677   quadratic component of the trend suggests that RTs decreased and then increased across each

678   block. This pattern would be inconsistent with the occurrence of adaptation processes which

679   would instead predict a more linear trend.

680   Therefore, considering the procedure adopted together with the results of this last

681   analysis, it seems extremely unlikely the either of the two species developed an adaptation to

682   given SFs in the course of testing.

683

684   **General Discussion**

685   The present study aimed to elucidate the mechanisms responsible for the difference in

686   global and local visual processing observed between monkeys and humans, whereby humans

687   typically show a global advantage and several monkey species show a local advantage (*Papio*

688   *papio*, Fagot & Deruelle, 1997; *Macaca mulatta*, Hopkins & Washburn, 2002; *Sapajus* spp.,

689   Spinozzi et al., 2003; but see Neiworth et al., 2006 for different results on *Saguinus oedipus*),

690   despite the alleged similarity of their visual system.

691   In particular, this study builds on the key discovery that monkeys' local advantage can

692   be reversed with manipulations affecting their attention bias towards the global level of

693   hierarchical visual stimuli (De Lillo et al., 2011). Using a similar methodology to that of De

694   Lillo et al. (2011), we wanted to determine whether or not this effect on global-local

695   processing is likely to be mediated by selective attention towards SFs of a particular range,

696   since HSF pertain mostly to local details of visual stimuli and LSF to global configurations.

697   Before we could use particular SFs as the basis for the main manipulation of Experiment 2,

698   we had to carry out a preliminary experiment (Experiment 1) in order to determine SF ranges

699   which were discriminable by both species and thus appropriate to use.

700   Apart from their practical use for the selection of the appropriate stimuli for

701   Experiment 2, the results of Experiment 1, provide information regarding which ranges of SF

702   are processed more accurately by capuchin monkeys and people. It emerged that in an MTS

703   task monkeys discriminated HSF gratings (8.0 cpd) more accurately than LSF ones. By

704   contrast, humans performed better in conditions featuring gratings with SF ranging from 0.5

705   cpd and 4.0 cpd of visual angle rather than 8.0 cpd and 0.25 cpd. This pattern indicates that

706   the peak of SF sensitivity is shifted toward medium SFs in humans and toward higher SFs in

707   monkeys. In addition, both species found the 0.25 cpd condition difficult.

708   This pattern of interspecies similarities and differences in SF processing between

709   capuchin monkeys and humans can be relevant for the interpretation of their well-documented

710   differences in global *vs* local dominance. Because global perception typically requires LSF

711   processing, whereas local perception requires HSF processing (Robertson, 1996; Shulman et

712   al., 1986; Shulman & Wilson 1987) it is possible that their ability to discriminate between SF

713   may affect their global-local processing styles.

714   Nonetheless, the results of Experiment 2 provide further support for the notion that

715   context and higher level non-perceptual processes affect global-local processing in both

716   species. In Experiment 2, we investigated if non stimulus-driven modulation of global-local

717   processing can be achieved by manipulating the frequency of exposure to HSF or LSF trials,

718   respectively.

719   A significant interaction emerged between exposure to SF of a given range and global-

720   local processing of hierarchical stimuli, in both species. Nevertheless, this interaction was in

721   both cases in an unexpected direction. Monkeys performed at a lower level of accuracy in the

722   local trials when interspersed with HSF trials within the same testing session, while humans

723   performed faster in these trials when they were interspersed with LSF trials. In both species

724   the global trials were not affected by this manipulation. It is of interest to note that, similarly

725   to what was observed here, the local trials were those affected by manipulation of attention

726   bias in our previous study (De Lillo et al., 2011). In that study, the direction of the effect was

727   consistent with an interpretation based on an attention bias. By contrast, here we observe an

728   effect that goes in the opposite direction from what was predicted and as such it is difficult to

729   explain.

730   Several studies suggest that in humans global processing can be mediated by LSF

731   processing and local processing by HSF processing (Robertson, 1996; Shulman et al., 1986;

732   Shulman & Wilson, 1987). This is not due to the ability to discriminate the SFs in itself

733   though, because the global structure of images is still visible when LSFs are removed or

734   attenuated (Badcock et al., 1990; Carlson et al., 1984; Hughes et al., 1990; Fiorentini et al.,

735   1983; Norman & Ehrlich, 1987; Parker et al., 1996; Peli, 1992; Schyns & Oliva, 1994).

736   Moreover, Lamb and Yund (1993) showed that the removal of LSFs can slow global

737   processing but does not eliminate the global bias. Also, it does not affect the ability to switch

738   attention from global to local forms.

739   Importantly, SFs should not be considered global or local in themselves (see also

740   Sierra-Vázquez et al., 2006). Flevaris et al., (2011) adopted compound gratings where each

741   pattern included both relatively low and relatively high SFs, which overlapped

742   perpendicularly to each other. Then, they measured the effect of exposure to global-local trials

743   on the detection of these compound gratings. Their results demonstrated that the exposition to

744   global-local tasks can affect SF recognition. However, this effect did not depend on the

745   absolute value of each SF. Instead, the same SF could elicit different responses depending on

746   its relative role in the compound stimulus and not on its absolute value (e.g., relatively high or

747   relatively low SF in comparison with the other SF present in the compound stimulus).

748   Therefore, the fact that in our experiment 8.0 cpd patterns were considered as HSFs, while 0.5

749   cpd gratings were considered as LSFs, does not necessarily imply that these SFs should

750   trigger perceptual reactions toward local or global processing, respectively. Another study

751   which does not support the idea of a strict relationship between LSFs and global processing or

752   HSFs and local processing respectively, has been carried out by Dale and Arnell (2014). The

753   main purpose of their study was to evaluate if dispositional global-local biases can be altered

754   by various manipulations of high/low SFs in humans. In two experiments participants were

755   asked to discriminate 0.76 cpd as LSF trials and 7.2 cpd as HSF trials. Before and after the

756   discrimination tasks, subjects were asked to perform some global-local trials and scores were

757   compared. Interestingly, they adopted LSFs and HSFs with cpd values very similar to those

758   adopted in the current experiment. Overall, they did not find substantial differences following

759   SF manipulations with the single exception of an effect on global performance after exposure

760   to HSFs. However, since it was the only significant result out of five different experiments,

761   authors argued that this effect could possibly have been found by chance and that it was not

762   necessarily meaningful, thus, they concluded that exposing to HSFs or LSFs does not affect

763   global-local processing.

764   Shulman and Wilson (1987) suggested that the distribution of attention to the local or

765   the global structure of hierarchical stimuli can affect subsequent SF recognition. Our results

766   are consistent with this, in showing that symmetrically to Shulman and Wilson's (1987)

767   findings, SF can affect global-local processing, an effect that cannot be bottom-up.

768   As mentioned in the introduction, the traditional dichotomy top-down/bottom-up has

769   been challenged and a third type of attention deriving from selection history has been

770   proposed (Awth et al., 2012; Failing & Theeuwes, 2018; Theeuwes, 2019). Similarly to some

771   of these experimental findings, our effect is likely to be context driven. However, its direction

772   does not support an interpretation based on selective attention, even of this selection-history

773   type.

774   In conclusion, the present study provides, for the first time, some information about

775   capuchin monkeys' ability to process different SFs. Furthermore, it suggests that it is possible

776   to produce an effect on global-local trials even in the condition when the prevalent MTS trials

777   feature stimuli which are not hieratical visual shapes. As the effect does not seem to be related

778   to low level perceptual processes, such as adaptation, our findings suggest that it cannot be

779   bottom-up. At this stage we cannot explain, on theoretical grounds, the particular direction of

780   the effect we obtained. A replication of this effect with a larger pool of subjects would help

781   determine its consistency, whereas other basic manipulations of the procedure adopted here

782   could reveal the psychological determinants of contextual effects on global-local processing

783   with more precision.

784

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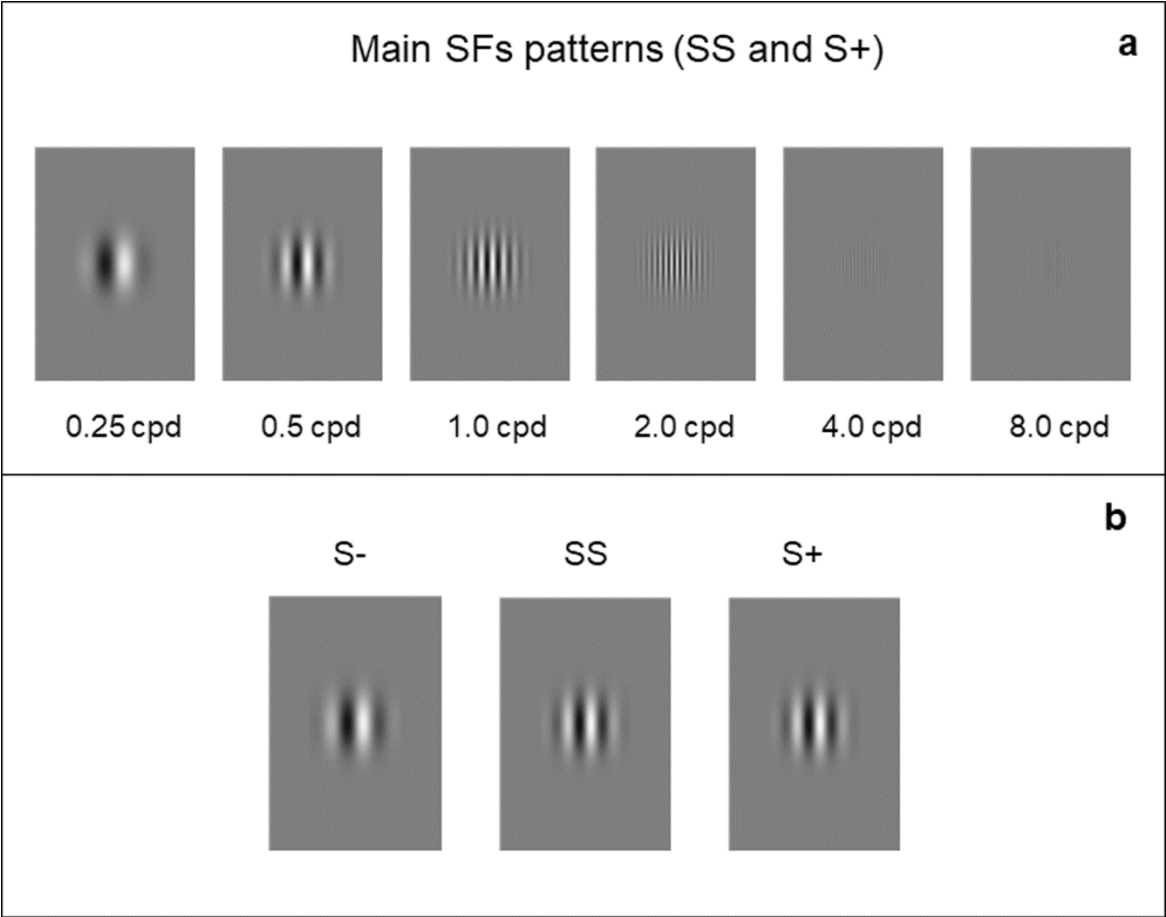
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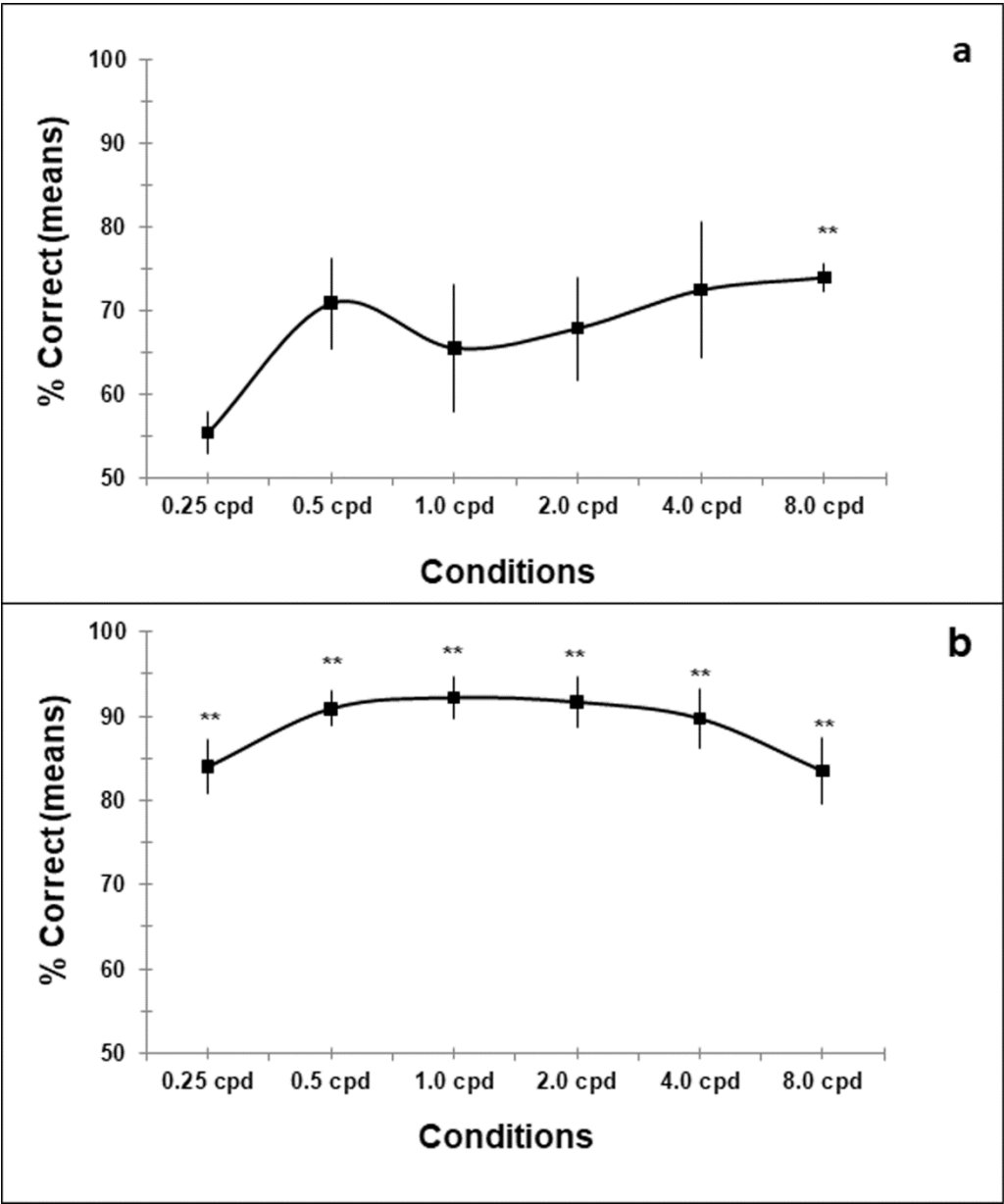1009   *comparative cognition* (pp. 100–116). Oxford, UK: Oxford University Press.

1010

1011   **Figure 1**

1012   *Stimulus Set Adopted in Experiment 1 as SS and S+ and Example of SF Matching Trial*

1013   *Performed in Experiments 1 and 2*

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1015
1016

1017   *Note.* Stimulus set adopted in Experiment 1 as sample (SS) and correct comparison stimuli

1018   (S+) (a). Example of SF matching trial performed in Experiments 1 and 2 (b). In this example

1019   as sample and matching stimuli (SS/S+) 0.5 cpd are adopted, and as non-matching stimulus
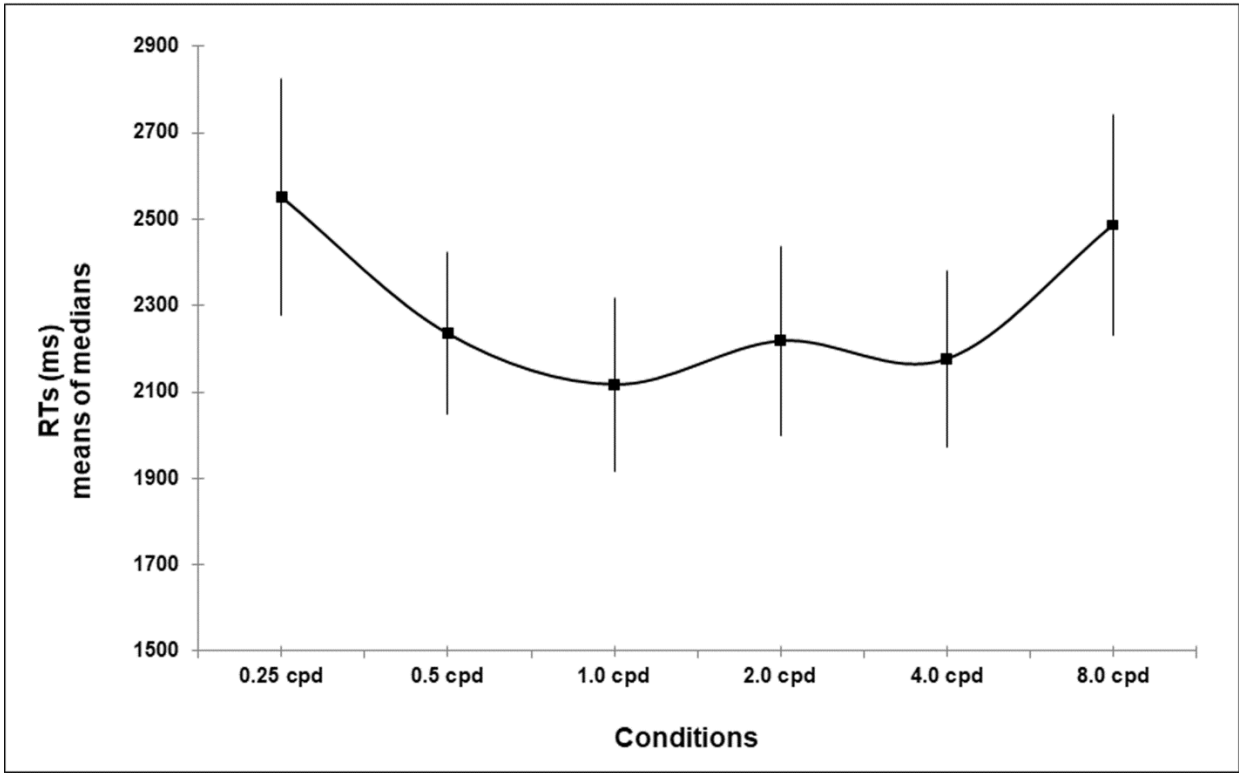
1020   (S-) 0.35 cpd (equal to 0.5 cpd -30%) is adopted.

1021 **Figure 2**

1022 *Percentages of Correct Responses Observed in Monkeys and Humans in Experiment 1*

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1024

1025 *Note*. Percentages of correct responses observed in the different cpd conditions (0.25 cpd,

1026 0.5 cpd, 1.0 cpd, 2.0 cpd, 4.0 cpd, 8.0 cpd) in capuchin monkeys (a) and humans (b); error

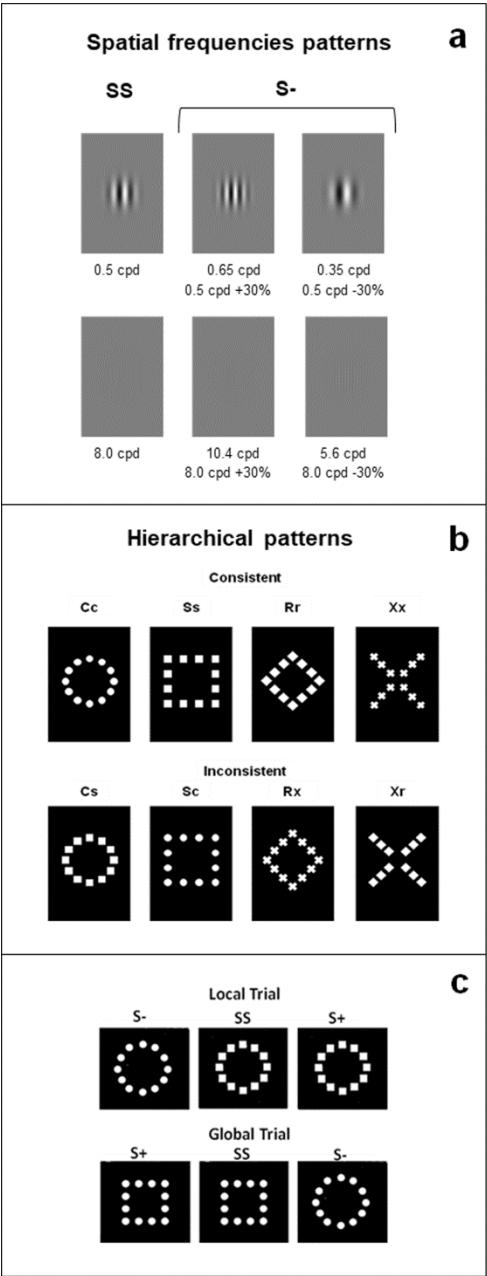1027 bars represent standard errors. **: $p < .01$; one-sample *t*-test.

1028

1029   **Figure 3**

1030   *Response Times Observed in Humans in Experiment 1*

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1034   *Note.* Median RTs observed in the different conditions in humans. Error bars represent

1035   standard errors.

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1040   **Figure 4**

1041   *Stimulus Set and Examples of Local and Global Trials Adopted in Experiment 2*

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1045   *Note.* SF stimuli (a) and hierarchical stimuli (b) adopted in Experiment 2. Both SF stimuli and

1046   hierarchical stimuli are reduced in the same scale. Example of local and global matching trials

1047   (c).

1048

1049 **Figure 5**

1050 *Percentage of Correct Responses (Monkeys) and Response Times (Humans) in Experiment 2*

1051

1052

1053

1054 *Note*. Percentages of correct responses observed in monkeys for local and global trials,

1055 according to the different conditions of the task (a). Means of the medians of the Response

1056 Times recorded in human subjects for local and global trials, according to the different

1057 conditions of the task (b). Error bars represent standard errors.

1058

1059 **Table 1**

1060 *Spatial Frequency Gratings Used in Experiment 1*

	Sample (SS) and matching stimuli (S+)	Non-matching stimuli (S-)	
	cpd	-30% cpd	+30% cpd
Low	0.25	0.175	0.325
	0.5	0.35	0.65
Medium	1.0	0.7	1.3
	2.0	1.4	2.6
High	4.0	2.8	5.2
	8.0	5.6	10.4

1061

1062

Table 2

Individual Percentages of Correct Responses for Gratings of Different SFs in

Experiment 1a (Monkeys)

Subject	0.25 cpd	0.50 cpd	1.0 cpd	2.0 cpd	4.0 cpd	8.0 cpd
Pippi	52.1	81.25***	68.8*	79.2***	72.9**	77.1***
Rubens	53.9	62.7	76.9***	58.0	86.3***	72.0**
Gal	60.4	68.8*	51.0	66.7*	58.3	72.9**

Note. *$p < .05$, **$p < .01$, *** $p < .001$ (Binomial test).

1069 **Table 3**

1070 *Individual Percentages of Correct Responses for HSF and LSF Gratings Observed*

1071 *During the Local and the Global Tasks in Experiment 2a (Monkeys)*

	HSF (8.0 cpd)		LSF (0.5 cpd)	
Subject	**Local**	**Global**	**Local**	**Global**
Pippi	72.9	72.9	69.8	75.0
Rubens	67.7	70.8	75.0	64.6
Gal	78.1	85.4	65.6	58.3

1072

1073

1074 **Table 4**

1075 *Individual Percentages of Correct Responses for Local and Global Trials in the Different*

1076 *Conditions of Experiment 2a (Monkeys)*

	Local Trials			Global Trials		
		HSF	**LSF**		**HSF**	**LSF**
Subject	**Control**	**(8.0 cpd)**	**(0.5 cpd)**	**Control**	**(8.0 cpd)**	**(0.5 cpd)**
Pippi	81.3	62.5	62.3	84.4	87.5	62.5
Rubens	71.8	68.8	75.0	68.8	75.0	75.0
Gal	75.0	56.3	87.5	59.4	50.0	68.8

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1079 **Supplementary Material of the article:**

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1081

1082 **Spatial frequency and global-local visual processing in capuchin monkeys (*Sapajus***

1083 spp.**) and humans (*Homo sapiens*)**

1084

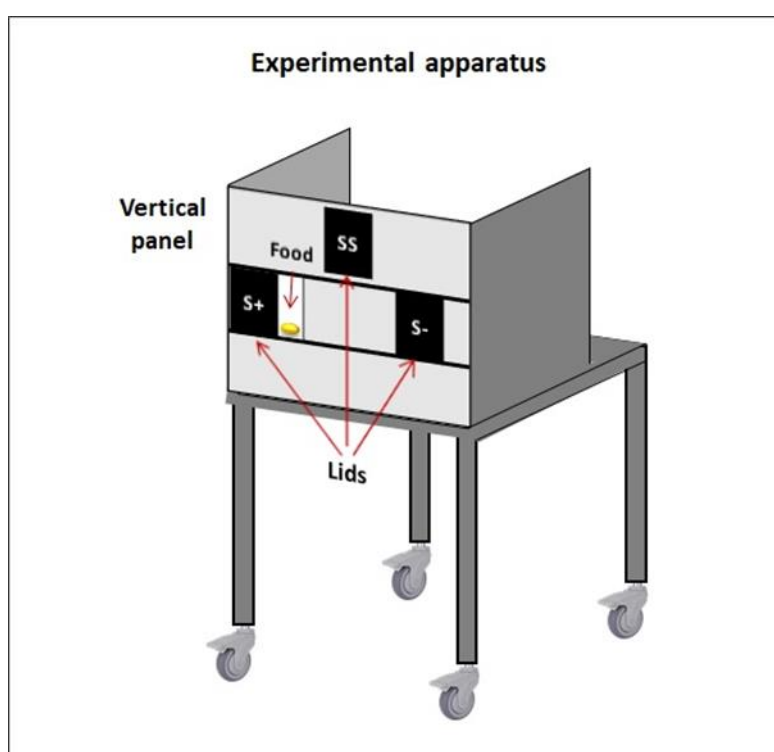1085 Milena Palumbo[1,2], Giovanna Spinozzi[2], Valentina Truppa[2] & Carlo De Lillo[1]

1086 [1]School of Psychology and Vision Sciences, University of Leicester, Leicester, UK

1087 [2]Institute of Cognitive Sciences and Technologies, National Research Council, Rome, Italy

1088

1089 **Experiment 1**

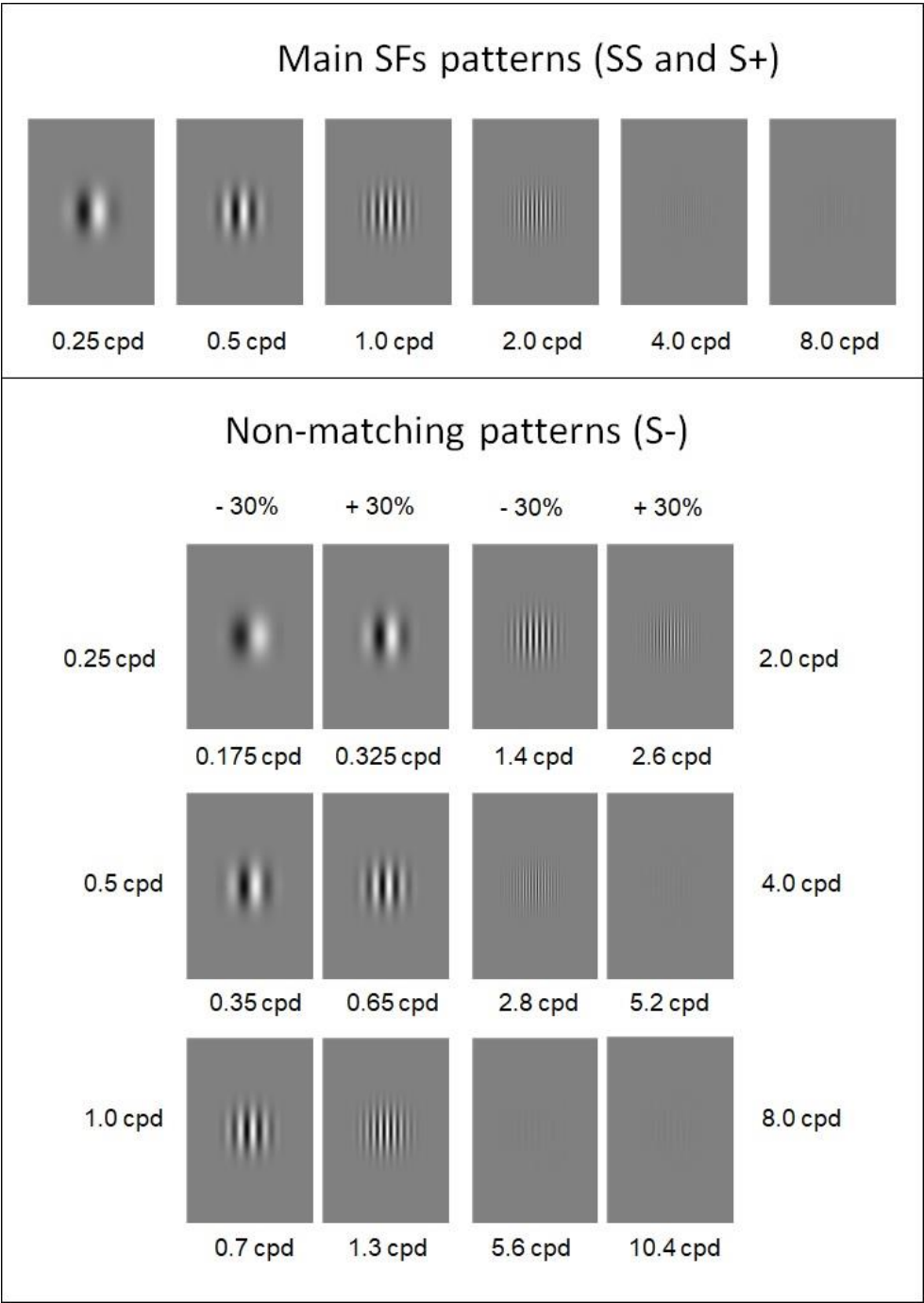1090 **Experiment 1a: Monkeys**

1091 *Method*

1092 *Apparatus*

1093

1094

1095 **Figure S1.** Apparatus adopted in the experiments with monkeys.

1096

1097

1098 *Stimuli*

1099

1100 **Figure S2.** Complete stimulus set adopted in Experiment 1. The set
1101 consisted of 6 main spatial frequency gratings (0.25 cpd, 0.5 cpd, 1.0 cpd,
1102 2.0 cpd, 4.0 cpd and 8.0 cpd) adopted as sample (SS) and correct comparison
1103 stimuli (S+) and 12 gratings, derived from the main gratings either adding or
1104 removing 30% of the cpd values, which were adopted as negative
1105 comparison stimuli S-.

1106

1107   *Results*

1108   A repeated measures 8 (session) x 6 (spatial frequency condition) ANOVA was carried out.

1109   The ANOVA did not reveal any significant main effect or interaction. Individual performance

1110   (percentage of correct responses) across sessions is reported in figure S3.
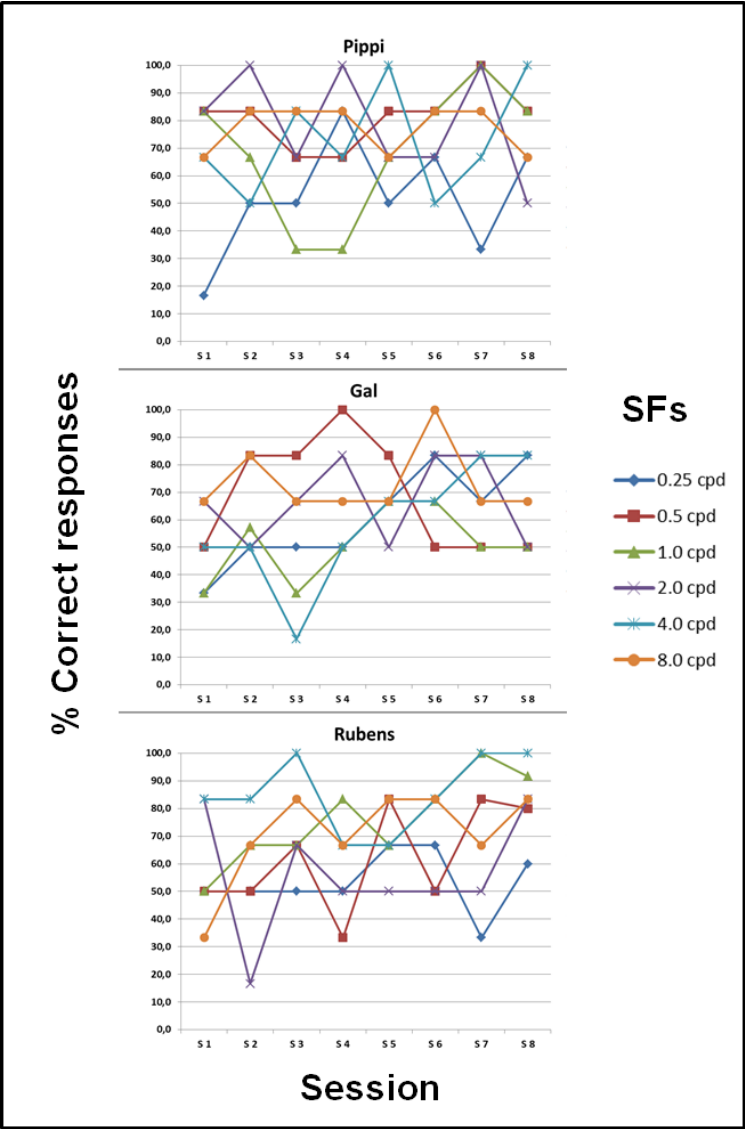
1111

1112   **Figure S3.** Individual percentage of correct responses in
1113   each SF condition for each session.

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