1 **Global/local processing of hierarchical visual stimuli in a conflict-choice task by capuchin**
2 **monkeys (*Sapajus* spp.)**

3

4 Valentina Truppa^{a, *}, Paola Carducci^{a, b}, Diego Antonio De Simone^{a, c}, Angelo Bisazza^d, Carlo
5 De Lillo^e

6

7 ^aInstitute of Cognitive Sciences and Technologies, National Research Council (CNR), Via
8 Ulisse Aldrovandi 16/B, 00197 Rome, Italy

9 ^bEnvironmental and Evolutionary Biology PhD Program, Department of Environmental
10 Biology, Sapienza University of Rome, Piazzale Aldo Moro 5, 00185, Rome, Italy

11 ^cDepartment of Philosophy, Sapienza University of Rome, Via Carlo Fea 2, 00161 Rome, Italy

12 ^dDepartment of General Psychology, University of Padua, Via Venezia 8, 35131 Padua, Italy

13 ^eDepartment of Neuroscience, Psychology and Behaviour, University of Leicester, University
14 Road, Leicester, LE1 7RH, UK

15

16 *Corresponding author: Valentina Truppa Institute of Cognitive Sciences and Technologies,
17 National Research Council (CNR), Via Ulisse Aldrovandi 16/B, 00197 Rome, Italy.

18 Tel: +39 06 49936425; fax: +39 06 3217090.

19 E-mail address: valentina.truppa@istc.cnr.it

20

21 **Acknowledgements**

22 We thank two anonymous reviewers for their thoughtful suggestions and constructive comments on
23 the manuscript. We are also grateful to Tyrone Lucon Xiccato for his helpful statistical suggestions.

24 We wish to thank Cinzia Trapanese, Francesca Cosentino and Adrian Soldati for help with data
25 collection. We acknowledge Arianna Manciocco, Massimiliano Bianchi and Simone Catarinacci for

26 help with animal management and for technical help with the apparatus. We also thank the Comune
27 di Roma-Museo Civico Zoologia and the Fondazione Bioparco for hosting the Unit of Cognitive
28 Primatology and the Primate Center.

Abstract

In the last two decades, comparative research has addressed the issue of how the global and local levels of structure of visual stimuli are processed by different species, using Navon-type hierarchical figures, i.e., smaller local elements that form larger global configurations. Determining whether or not the variety of procedures adopted to test different species with hierarchical figures are equivalent is of crucial importance to ensure comparability of results. Among non-human species, global/local processing has been extensively studied in tufted capuchin monkeys using matching-to-sample tasks with hierarchical patterns. A local dominance emerged consistently in these New World primates. In the present study, we assessed capuchins' processing of hierarchical stimuli with a method frequently adopted in studies of global/local processing in non-primate species: the conflict-choice task. Differently from the matching-to-sample procedure, this task involved processing local and global information retained in long-term memory. Capuchins were trained to discriminate between consistent hierarchical stimuli (similar global and local shape) and then tested with inconsistent hierarchical stimuli (different global and local shape). We found that capuchins preferred the hierarchical stimuli featuring the correct local elements rather than those with the correct global configuration. This finding confirms that capuchins' local dominance, typically observed using matching-to-sample procedures, is also expressed as a local preference in the conflict-choice task. Our study adds to the growing body of comparative studies on visual grouping functions by demonstrating that the methods most frequently used in the literature on global/local processing produce analogous results irrespectively of the relative involvement of memory processes.

Keywords: visual perception, global/local processing, hierarchical stimuli, long-term memory, New World monkeys

Introduction

An important issue in visual cognition is the extent to which visual processing identifies local elements first and only subsequently integrates them into whole objects, or vice versa, detects the global properties of objects before an analysis of its component parts. The extent to which different species use one or the other of these perceptual strategies is a longstanding question in comparative cognition. A relative bias towards the processing of the local features of objects or their global configuration, in terms of accuracy or speed of processing, has often been regarded as indicative of the perceptual strategy used by a given species.

Comparative studies in this area are inspired by a seminal article by Navon (1977). Navon (1977, 1981) demonstrated that human adults tested with hierarchical visual patterns, i.e., local elements spatially arranged to form global configurations, process the global configuration more accurately and faster than the local elements. Evidence confirming this global advantage in humans has been provided in several other studies (e.g., Kimchi 1998; Kimchi and Palmer 1982; Kinchla and Wolfe 1979; Lamb et al. 1990; for reviews, see Kimchi 1992; Navon 2003).

In the last two decades, comparative research has largely made use of Navon-type hierarchical stimuli to assess global/local processing in an increasing number of species belonging to different taxa. Several studies have been conducted on pigeons (Cavoto and Cook 2001; Fremouw et al. 1998, 2002) and non-human primates (De Lillo et al. 2011; Deruelle and Fagot 1998; Fagot and Deruelle 1997; Fagot and Tomonaga 1999; Hopkins and Washburn 2002; Neiworth et al. 2006; Spinozzi et al. 2003, 2006; Tanaka and Fujita 2000; Tanaka et al. 2001; Truppa et al. 2016). Moreover, hierarchical stimuli have been recently used to study global/local preference also in honeybees (Avarguès-Weber et al. 2015), fish (Truppa et al. 2010b), domestic chicks (Chiandetti et al. 2014) and domestic dogs (Pitteri et al. 2014). Among studies that have used hierarchical patterns, a local dominance has been found mainly in monkeys (De Lillo et al. 2011, 2012; Deruelle and Fagot 1998; Fagot and Deruelle 1997;

79 Hopkins and Washburn 2002; Spinozzi et al. 2003, 2006; Tanaka and Fujita 2000; Tanaka et al.
80 2001; Truppa et al. 2016; for different results see Neiworth et al. 2006). More mixed results
81 have been reported for bird species. One study that used large local elements and a very small
82 separation between them reported a global dominance in pigeons (Goto et al. 2004). By
83 contrast, other studies have reported a local dominance in both pigeons (Cavoto and Cook
84 2001) and domestic chicks (Chiandetti et al. 2014). No clear dominance has been found in
85 domestic dogs (Pitteri et al. 2014), whereas a global dominance emerged in fish (Truppa et al.
86 2010b) and honeybees (Avarguès-Weber et al. 2015). However, there is some variability in the
87 procedures used to test animals in different studies, which may confound interspecies
88 differences in global-local processing inferred from the comparison of results reported in
89 different research articles.

90 A recent study specifically aimed at comparing different testing procedures for the
91 assessment of global/local processing in children diagnosed with Autistic Spectrum Disorder, a
92 population known for their local processing tendency, showed that different patterns of results
93 can be obtained with different testing procedures. Children with ASD showed a reduced
94 preference to report global properties of a stimulus when given a choice, whereas their ability
95 to process global properties, when instructed to do so, was unimpaired (Koldewyn et al. 2013).

96 Therefore, it is of crucial importance to determine whether or not the procedures adopted
97 to test different species' global and local processing are comparable. In fact, variations across
98 species may be ascribable to genuine differences in the way in which animals process global
99 and local aspects of hierarchical patterns only when potential differences in the results that may
100 stem from the use of a variety of testing methods are ruled out. For example, paradigms may
101 inadvertently differ in their memory requirements with possible consequences for the type of
102 visual system and resources that need to be recruited for the analysis of the stimuli.

103 Many comparative studies carried out on primate species used matching-to-sample (MTS)
104 procedures (e.g., De Lillo et al. 2011, 2012; Fagot and Deruelle 1997; Hopkins and Washburn
105 2002; Spinozzi et al. 2003, 2006; Truppa et al. 2016). In the MTS individuals are required to
106 choose which of two comparison stimuli (S+ and S-) resembles most closely a stimulus
107 presented as sample (SS). For example, to study global/local processing with an identity-MTS
108 procedure monkeys are faced with two different matching conditions, the Global condition and
109 the Local condition. In the Global condition, S+ is identical to the sample and S- differs from
110 the sample only at its global level. In the Local condition, S+ is identical to the sample and S-
111 differs from the sample only for the shape of its local elements. In this type of MTS based
112 studies, differences in accuracy and/or response time between the Global and the Local
113 condition are informative with respect to the visual processing style of the species under
114 investigation. Comparative studies so far have either used simultaneous MTS procedures which
115 do not require memory for the stimulus structure (e.g., De Lillo et al. 2011, 2012; Fagot and
116 Deruelle 1997; Hopkins and Washburn 2002; Spinozzi et al. 2003, 2006) or delayed MTS with
117 brief delays which require the short-term retention of stimulus structure (Truppa et al. 2016).

118 MTS tasks are relatively difficult to use with non-human animals. Even animals of species
119 that succeed in matching stimuli on the basis of an identity rule usually need a long training
120 before they can transfer this ability to novel stimuli (e.g., Truppa et al. 2010a). Therefore, many
121 comparative studies have adopted forced choice procedures rather than MTS for the study of
122 global/local processing in a variety of species (cotton-top tamarins: Neiwirth et al. 2006;
123 domestic dogs: Pitteri et al. 2014; pigeons: Cavoto and Cook 2001; Fremouw et al. 1998, 2002;
124 domestic chicks: Chiandetti et al. 2014; redbellied splitfins: Truppa et al. 2010b; honeybees:
125 Avarguès-Weber et al. 2015). Typically, in studies based on forced-choice tasks individuals are
126 initially trained to discriminate between consistent hierarchical stimuli (i.e., patterns where the
127 same shape is presented as the local and global level of stimulus structure) and then tested with

128 inconsistent hierarchical stimuli (i.e., patterns where a different shape is presented at the local
129 and global level). Thus, individuals are tested with hierarchical patterns in which the global
130 configuration and the shape of the local elements are in conflict. Moreover, this kind of task,
131 differently from the MTS procedures often adopted with non-human primates, requires the
132 long-term coding and retention of the hierarchical stimuli. In fact, when tested with inconsistent
133 stimuli individuals are evaluated for their ability to retrieve and select global or local features
134 of visual patterns reinforced during the preliminary training phase. The processing of visual
135 information in long-term memory involves brain structures, such as the hippocampus, that are
136 active in the encoding of the spatial organization of visual patterns in humans and animals
137 (Kumaran et al. 2007; Sanderson et al. 2006). Therefore, it is possible that during the long-term
138 encoding of compound stimuli the integration of the parts in global configurations is enhanced
139 compared to conditions that only require the short-term retention of the stimuli.

140 Among non-human species, global/local processing has been extensively studied in tufted
141 capuchin monkeys (De Lillo et al. 2011, 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016).
142 Studies that adopted MTS procedures have consistently revealed a local advantage in these
143 New World primates. This local advantage in capuchin monkeys has proved to be a very robust
144 finding. It emerges irrespectively of the size of the local elements, and their relative density and
145 distance (Spinozzi et al. 2006). The presence of a strong local dominance in monkeys under a
146 variety of manipulations of the separation of the local elements is consistent with seminal
147 findings in baboons showing a local advantage in that species even when the local elements are
148 connected by line segments (Fagot and Deruelle 1998). A local advantage in capuchin monkeys
149 also emerged in a delayed-MTS task with brief time intervals between the presentation of the
150 sample and the comparison stimuli (Truppa et al. 2016). However, capuchins have not been
151 tested in tasks requiring long-term memory, such as the conflict-choice discrimination task,
152 which has been used with several non-primate species (e.g., Chiandetti et al. 2014; Truppa et al.

2010b). Thus, we considered it important to assess if the encoding of visual information in long-term memory could potentially strengthen capuchins' ability to recognise the global configuration of hierarchical visual patterns.

The aim of this study was twofold. Firstly, we aimed to determine whether or not the local dominance previously observed in tufted capuchin monkeys also emerged when using a conflict-choice task. In this task, capuchins were first trained with pairs of consistent hierarchical stimuli (same shape featured at the local and global level of stimulus structure), and then tested with pairs of inconsistent stimuli (different shapes at local and global level of stimulus structure). We hypothesised that if the conflict-choice task was equivalent to the MTS for the assessment of global/local processing, then capuchins should have shown a preference for local properties of the stimuli in such task too. In addition, this study allowed us to evaluate whether or not capuchins' local dominance in short-term memory for hierarchical patterns, previously found by Truppa et al. (2016), also pertained to tasks involving the long-term retention of the stimuli.

Methods

Subjects

The subjects were six capuchin monkeys (see Table 1) considered to be unknown combinations of species of the genus *Sapajus* that, in accord with the current taxonomy, includes the “tufted/robust” species previously referred to the genus *Cebus* (Lynch Alfaro et al. 2012a, b, 2014). All subjects were adults born in captivity and housed at the Primate Center of the Institute of Cognitive Sciences and Technologies, CNR, Rome, Italy. They were kept in social groups, each housed in an indoor-outdoor enclosure (indoor: 5 m² x 2.5 m high; outdoor: 40-130 m² x 3 m high). To enrich the monkeys' living space, indoor enclosures were provided

177 with perches and ropes and outdoor enclosures were provided with logs, branches and ropes.
178 Moreover, outdoor enclosures were supplied with natural substrates, including woodchips on
179 the ground, to promote the monkeys' exploratory behaviour.

180 Capuchins were individually tested in an experimental cubicle (180 cm x 75 cm x 75 cm;
181 the cubicle floor is 80 cm higher than the floor of the rest of the room) to which they had access
182 through a sliding door from an adjacent indoor cage. Each subject was separated from the
183 group just before the daily experimental session solely for the purpose of testing
184 (approximately 20 min). Testing took place between 9:30 a.m. and 3:15 p.m. Water was freely
185 available at all times. Fresh fruit, vegetables and monkey chow were provided in the afternoon
186 after testing. All subjects were familiar with the experimental cage/cubicle, the experimental
187 routine and the experimenters. More details concerning the previous experience of our subjects
188 with relevant testing procedures and experimental protocols are provided in Table 1. None of
189 the subjects had been tested with the hierarchical figures used in this study before.

190 **Apparatus**

191 The apparatus consisted of a laptop (Acer Aspire 1400 Series) connected to a 17'' touch
192 screen (Tyco Electronics, ET1729L-7UEA-1-D-GY-G) and an automatic food dispenser (ENV-
193 203-45, MED Associates, Inc. Georgia, VT) (Figure 1). E-Prime software (Psychology
194 Software Tools, Inc.) was used to present the stimuli and to record the subjects' responses. The
195 food dispenser was programmed to deliver one 45-mg banana-flavoured pellet (TestDiet,
196 Richmond, IN, USA) when the monkey provided a correct response. The pellet was delivered
197 into a PVC feeding cup (with a diameter of 4 cm) located 14.5 cm below the touch screen, in
198 the centre. A wooden frame (58 cm wide x 54 cm high) with a central aperture (36 cm wide x
199 30 cm high) surrounded the touch screen. The food dispenser was placed behind the wooden
200 frame, out of sight of the subject. The laptop was placed at the back of the touch screen. The
201 touch screen, the food dispenser and the laptop were mounted on a trolley (90 cm long x 58 cm

202 wide x 85 cm high). The apparatus was placed 15 cm from the horizontal metal bars (0.5 cm in
203 diameter, separated by 4.5 cm) of the experimental cubicle, within the subject's arm reach.

204 **Stimuli**

205 The stimulus set included 16 pairs of non-hierarchical figures and 16 pairs of hierarchical
206 figures. Non-hierarchical pairs included 32 digital icons (2.30 cm x 2.30 cm, i.e. 8.7° of visual
207 angle, Figure 2a). Hierarchical pairs included 32 compound images composed of identical local
208 elements (0.35 cm × 0.35 cm). The elements subtended 1.3° of visual angle at a distance of 15
209 cm. This was the distance of the touch screen from the horizontal bars of the cubicle that
210 monkeys approached closely when responding and it was taken as the viewing distance. The
211 local elements (range 6-13) were spatially arranged to form global configurations (2.30 cm x
212 2.30 cm, i.e. 8.7° of visual angle). The distance between adjacent elements was kept
213 approximately at 0.35 cm (i.e., 1.3° of visual angle). Global configurations of comparable
214 density were obtained by varying the number of local elements. Each hierarchical figure was
215 paired with another one, which had approximately the same number of local elements in it. If
216 there was a difference, it was of two items maximum. Given that capuchins are unable to detect
217 a difference in numerosity of two items for quantities as those featuring the stimuli in our study
218 (see Addessi et al. 2008; vanMarle et al. 2006), it is unlikely that the monkeys could use the
219 numerosity of the local elements in the hierarchical figures to guide their choices. In fact, our
220 stimuli always contained at least six elements and any two stimuli could not differ for more
221 than two elements. Depending on the experimental phase (see below), hierarchical stimuli
222 could be either *consistent* (same shape at both local and global levels of the stimuli, Figure 2b)
223 or *inconsistent* (different shape at local and global levels of the stimuli, Figure 2c). Inconsistent
224 hierarchical stimulus pairs were created by switching the local elements of the two consistent
225 stimuli of each pair. All stimuli consisted of white images presented on a black background (8

226 cm high $\times$ 8 cm wide, i.e. 28.0° of visual angle); they were created using Microsoft PowerPoint
227 and then transformed into Bitmap images for stimulus presentation on the computer screen.

228 **Design and procedure**

229 The study included a training phase, a testing phase and a retesting phase (see Table 2). In
230 order to avoid experimental sessions with a large number of different stimuli for the monkeys
231 to memorise (training) and to recall (testing/retesting), the stimulus pairs were presented in two
232 separate blocks of trials. Each block included 16 pairs of stimuli. The first 16 pairs (8 pairs of
233 hierarchical stimuli and 8 pairs of non-hierarchical stimuli) were presented in a first training
234 phase, followed by the corresponding testing and retesting phases. The other 16 pairs were
235 presented in a second training phase followed by the corresponding testing and retesting
236 phases.

237 *Training phase.* Subjects were trained to select the rewarded positive stimulus (S+) within
238 a pair in a two-alternative forced-choice task. At the beginning of each trial, a white square (0.6
239 cm $\times$ 0.6 cm) appeared in the centre of the screen on a black background. When the monkey
240 touched the square, two stimuli were simultaneously displayed to the right and left, at a
241 distance of 5 cm apart. The initial touch of the central square was adopted to ensure that the
242 monkey was looking at the screen when the stimuli appeared. The subject had to indicate its
243 choice by touching one of the two stimuli on the screen; the touch-sensitive area included the
244 entire stimulus surface, i.e., both the white figure and the black squared background. The
245 computer automatically recorded the choice and the Response Time (RT). RT was measured as
246 the time between the appearance of the choice stimuli and the subject's choice (i.e., the touch
247 of the selected stimulus). After the response, the display was immediately extinguished and, if
248 the subject selected S+, a food pellet was delivered. A correct response was followed by a 5-s
249 inter-trial interval (ITI), whereas an incorrect response was followed by the 5-s ITI and an
250 additional 10-s time out (TO). During the experimental trials and the ITI, the screen was light

251 grey; during the TO, the screen was green. Monkeys received two 16-trial sessions per day. In
252 each session, half of the trials included pairs of consistent hierarchical stimuli and the other half
253 included pairs of non-hierarchical stimuli. Each S+ was presented an equal number of times in
254 both the right and the left position. To reduce the possibility of biased results due to the
255 particular shape of a given stimulus, half of the monkeys received one of the two stimuli in
256 each pair as S+, whereas the other half received the other stimulus as S+. The trials were
257 presented in random order. Sessions were administered 5 days per week. The learning criterion
258 was achieved when subjects responded correctly in at least 7 out of 8 trials (87.5%, binomial
259 test $P < 0.032$) during three consecutive sessions. The criterion was calculated separately for
260 consistent hierarchical stimuli and for non-hierarchical stimuli. After achieving the learning
261 criterion with both hierarchical and non-hierarchical stimuli, monkeys were tested with
262 inconsistent hierarchical stimuli.

263 *Testing phase.* Each testing phase consisted of 4 10-trial daily sessions. Each session
264 included two test trials with inconsistent hierarchical stimuli intermixed with eight training
265 trials with non-hierarchical stimuli. Non-hierarchical training stimuli were included in order to
266 check that the level of discrimination performance achieved during the training phase was
267 maintained throughout the testing phase. The two inconsistent hierarchical stimuli presented in
268 each test trial were both rewarded since each of them preserved one level (local or global) of
269 the hierarchical stimulus reinforced during the training phase. Therefore, to avoid biases due to
270 the reinforcement program, only one test trial for each pair of hierarchical stimuli was
271 presented. The trials were presented in random order. Sessions were administered 5 days per
272 week.

273 *Retesting phase.* To determine whether or not any pattern of preference shown by
274 capuchins during the testing was maintained after a long interval, a second trial for each block
275 of pairs of inconsistent hierarchical stimuli was presented as a retest after five months from the

276 end of the first testing phase. The stimuli, the number of sessions/trials and the procedure in the
277 retesting phase were the same adopted in the testing phase. The long interval between the first
278 (test) and the second (retest) presentation of the hierarchical inconsistent stimuli also helped to
279 prevent biases due to the fact that those stimuli were always rewarded at the first presentation.

280 During both test and retest, control trials with non-hierarchical stimuli maintained the same
281 reinforcing program scheduled for the training phase.

282 **Data analysis**

283 The Kolmogorov-Smirnov test showed that all distributions of data did not significantly
284 deviate from normality, therefore we employed parametric statistics. Statistical significance
285 was set at $P \leq 0.05$. In cases where no significant difference emerged with parametric statistical
286 analyses, we conducted Bayesian statistics (Dienes 2014; Wagenmakers 2007) using JASP
287 statistical software 0.7.5.6 (Love et al. 2015). According to Raftery (1995), a Bayes factor
288 (BF_{01}) greater than 3 represents substantial evidence in favour of H_0 (i.e., that the effect
289 investigated by the analysis does not occur), whereas a Bayes factor that falls within 1 and 3
290 means only weak evidence. Moreover, BF_{01} smaller than 1 indicates that the data are more
291 likely under H_1 (i.e., the effect investigated by the analysis does occur) than under H_0 .

292 *Training phase.* All individual data obtained from the first and the second block of pairs
293 were pooled and analysed together. We used two-tailed paired-samples t -tests to determine if
294 performance in hierarchical and non-hierarchical conditions differed in: (1) the number of trials
295 to achieve the learning criterion (i.e., learning speed); (2) the percentage of correct responses at
296 the attainment of the learning criterion (i.e., accuracy level); (3) the RT at the attainment of the
297 learning criterion.

298 *Testing phase.* A preliminary analysis demonstrated that the percentage of local choices of
299 the first block of stimulus pairs (mean = 70.0%, $SE = 10.90$) was not significantly different

300 from that of the second block of pairs (mean = 80.0%, $SE = 3.06$) [paired-samples t -test, $t(4) =$
301 -1.09 , $P = 0.338$]. Therefore, data from the first and the second block of pairs were pooled and
302 analysed together. We evaluated if: (1) the percentage of local choices was significantly higher
303 than the 50% expected by chance (two-tailed one-sample t -test); (2) the percentage of local
304 choices differed between the two groups of subjects reinforced with different hierarchical
305 figures (two-tailed independent samples t -test); (3) the RT differed between local and global
306 choices (two-tailed paired-samples t -test); (4) the percentage of correct choices for non-
307 hierarchical stimuli was significantly above chance level (two-tailed one-sample t -test).

308 *Retesting phase.* For the second presentation of the hierarchical inconsistent stimuli, we
309 evaluated if: (1) the percentage of local choices was still significantly above chance level (one-
310 tailed one-sample t -test); (2) the percentage of local choices differed between the testing and
311 the retesting phases (two-tailed paired-samples t -test); (3) the percentage of correct choices for
312 non-hierarchical stimuli was significantly above chance level (two-tailed one-sample t -test); (4)
313 the percentage of correct choices for non-hierarchical stimuli differed between the testing and
314 the retesting phases (two-tailed paired-samples t -test).

315

316 **Results**

317 All capuchins completed the scheduled experimental phases apart from the oldest female,
318 Roberta. Roberta took a very long time to complete the training with the first 16 pairs of stimuli.
319 After 2880 training trials with the second half of the stimuli we interrupted the training because she
320 had not approached the learning criterion for the discrimination of the hierarchical Navon-like
321 figures. Therefore, the following analyses included data for the first 16 pairs of stimuli for Roberta.

322 *Training Phase.* More trials were required to achieve the learning criterion with hierarchical
323 stimuli (mean = 1201.3, $SE = 404.6$) than with non-hierarchical stimuli (mean = 298.7, $SE = 85.6$)

324 [paired-samples t -test, $t(5) = 2.65$, $P = 0.045$, Figure 3a]. However, once the capuchins had
 325 achieved the learning criterion there were no significant differences between hierarchical and non-
 326 hierarchical stimuli in either the percentage of correct responses [hierarchical, mean = 90.6%, $SE =$
 327 1.17; non-hierarchical, mean = 91.3%, $SE = 1.13$; paired-samples t -test, $t(5) = -0.38$, $P = 0.721$,
 328 Bayesian paired samples t -test, $BF_{01} = 2.53$; Figure 3b] or RT [hierarchical, mean = 1034.41 ms, SE
 329 = 66.39; non-hierarchical, mean = 1134.52 ms, $SE = 86.57$; paired-samples t -test, $t(5) = -1.64$, $P =$
 330 0.162, Bayesian paired samples t -test, $BF_{01} = 1.10$, Figure 3c].

331 *Testing Phase.* At the first presentation of pairs of inconsistent hierarchical stimuli, the mean
 332 percentage of local choices was significantly higher than chance level [mean = 72.92%, $SE = 5.74$,
 333 one-sample t -test, $t(5) = 3.99$, $P = 0.005$, Figure 4]. However, capuchins had a similar mean RT in
 334 the local (mean = 1090.31 ms, $SE = 124.55$) and the global (mean = 1118.15 ms, $SE = 135.93$)
 335 choices [paired-samples t -test, $t(5) = -0.25$, $P = 0.810$, Bayesian paired samples t -test, $BF_{01} = 2.61$].
 336 No significant difference was found in the mean percentage of local choices between the two
 337 groups of subjects that were reinforced for choosing different stimuli [Group 1: mean = 68.75%, SE
 338 = 9.55; Group 2: mean = 77.08%, $SE = 7.51$; independent t -test, $t(4) = -0.69$, $P = 0.530$, Bayesian
 339 independent samples t -test, $BF_{01} = 1.56$]. Finally, capuchins maintained a percentage of correct
 340 responses with the non-hierarchical stimuli that was well above chance level [mean = 96.88%, $SE =$
 341 0.90; one-samples t -test, $t(5) = 51.95$, $P < 0.001$].

342 *Retesting Phase.* When capuchins were retested after five months, their mean percentage of
 343 local choices was still significantly higher than chance level [mean = 66.67%, $SE = 6.78$, one-
 344 sample t -test, $t(5) = 2.46$, $P = 0.028$, Figure 4]. Moreover, although the percentage of local choices
 345 made by the monkeys decreased, no significant difference was found between the percentage of
 346 local choices made immediately after training and after five months [paired-samples t -test, $t(5) =$
 347 1.58, $P = 0.175$, Bayesian paired samples t -test, $BF_{01} = 1.16$]. Finally, the percentage of correct
 348 responses recorded for the non-hierarchical stimuli was well above chance level [mean = 89.84%,

349 $SE = 2.45$; one-samples t -test, $t(5) = 16.29$, $P < 0.001$] and did not differ from the percentage of
350 correct responses observed in the testing phase administered immediately after the training [paired-
351 samples t -test, $t(5) = 2.16$, $P = 0.083$]. However, in this latter case the Bayesian analysis suggests a
352 weak evidence in favour of H_1 [Bayesian paired samples t -test, $BF_{01} = 0.55$]. This suggests that an
353 increase in sample size could have resulted in a significant difference.

354

355 **Discussion**

356 This study shows that tufted capuchin monkeys rely on local elements in a conflict-choice
357 task featuring Navon-type hierarchical stimuli. Monkeys were trained with consistent stimuli (same
358 global and local shape). They were subsequently tested with inconsistent stimuli (different global
359 and local shapes) obtained by exchanging the local elements between the consistent figures used in
360 the training. In the testing phase, capuchins preferred figures which included the correct local
361 elements even if they formed an incorrect global configuration, rather than figures with the correct
362 global shape but formed by incorrect local elements. A local preference was also found in a retest
363 presented after five months. These results are consistent with those of previous studies which
364 showed that capuchins are more accurate when required to match hierarchical stimuli on the basis
365 of the shape of their local elements in MTS tasks (De Lillo et al. 2011, 2012; Spinozzi et al. 2003,
366 2006; Truppa et al. 2016). The conflict-choice and the MTS tasks, therefore, provide converging
367 results concerning capuchins' processing style despite the different memory load or other
368 requirements of the two paradigms.

369 Capuchin monkeys already proved to be more proficient in processing the local level of
370 hierarchical stimuli in simultaneous MTS tasks without memory requirements (De Lillo et al. 2011,
371 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016) and in delayed-MTS tasks requiring the short-
372 term retention (0.5-3.0 s) of the sample stimulus (Truppa et al. 2016). This latter study showed that

373 whereas capuchins' recognition of local elements was above chance level with delays of up to 3.0 s,
374 their recognition of global configurations was above chance level in simultaneous, 0.0 and 0.5 s
375 delay conditions but not at delay intervals of 1.0 s or longer (Truppa et al. 2016). The present data
376 on a conflict-choice task provides the additional important information that capuchins' choice of
377 hierarchical stimuli is guided preferentially by the shape of their local elements, even when the
378 stimuli have been retained for an extended period of time. Thus, a clear local dominance in
379 capuchin monkeys is maintained even when the participation of integrative long-term memory
380 processes mediated by the hippocampus (Kumaran et al. 2007; Sanderson et al. 2006) may have
381 reduced it. The extent to which capuchins' propensity for the recognition of constituent parts of
382 familiar rewarded stimuli rather than their configuration is caused by a less efficient encoding
383 and/or recall of global information remains to be determined. Nevertheless, the fact that the local
384 dominance in capuchins has been reported in several studies using simultaneous or 0-delay MTS
385 (De Lillo et al. 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016) suggests that it emerges
386 relatively early during visual processing and without requiring the participation of recall processes.
387 At the same time, the finding that the local dominance of capuchin monkeys can be dramatically
388 reduced by inducing an attention bias towards the processing of the global level of stimulus
389 structure (De Lillo et al. 2011) suggests that it may not be an expression only of low-level, pre-
390 attentive visual processes.

391 In our study, we used a larger number of stimuli than it was previously done. An inspection
392 of 18 studies from the comparative literature on global-local processing indicates that a range of 2
393 to 6 stimuli has been used typically, with a variety of experimental paradigms and classes of
394 animals (insects: Avarguès-Weber et al. 2015; fish: Truppa et al. 2010b; birds: Cavoto and Cook
395 2001; Chiandetti et al. 2014; Fremouw et al. 1998, 2002; mammals: De Lillo et al. 2011; Deruelle
396 and Fagot 1998; Fagot and Deruelle 1997; Fagot and Tomonaga 1999; Hopkins and Washburn
397 2002; Neiworth et al. 2006; Pitteri et al. 2014; Spinozzi et al. 2003, 2006; Tanaka and Fujita 2000;

398 Tanaka et al. 2001; Truppa et al. 2016). In this study, we presented a total of 32 different
399 hierarchical figures combined in 16 pairs to our subjects. The testing phase featured only a single
400 presentation of each pair of inconsistent stimuli and a large number of stimuli was required to
401 generate a sufficient number of testing trials. Although, the use of a large number of stimuli was
402 motivated mainly by this procedural requirement, it also allowed us to demonstrate that a
403 spontaneous local preference in capuchins is present since their very first presentation with a given
404 compound stimulus. Moreover, the fact that the capuchins' local dominance was confirmed by
405 using several different stimuli gives more weight to the results of previous studies that observed a
406 similar pattern (e.g. De Lillo et al. 2011, 2012; Spinozzi et al. 2003, 2006; Truppa et al. 2016) and
407 suggests that the local dominance of capuchin monkeys is not contingent upon the specific stimuli
408 used there.

409 The present results together with previous findings suggest that capuchins' local dominance
410 emerges both when they are free to choose between the two types of information, as in the conflict-
411 choice task, and when they are required to attend the local or the global level of the hierarchical
412 stimuli, as in the MTS task (De Lillo et al. 2011; Spinozzi et al. 2003, 2006; Truppa et al. 2016). It
413 is important to note, however, that this local preference in capuchins is not due to an incapacity to
414 process the global configuration of hierarchical stimuli. In fact, MTS studies show that although
415 capuchins are more proficient in processing the local than the global level of the stimuli, they show
416 a high level of accuracy when required to match the stimuli on the basis of their global
417 configuration.

418 A further comment should be made on the implications of the procedure used in this study.
419 We used an intermixed presentation of hierarchical and non-hierarchical stimuli within the
420 experimental sessions. The use of non-hierarchical stimuli was motivated by the need to monitor
421 capuchins' memory performance during the entire course of the experiment. Such experimental
422 design also gave us the opportunity to observe differences in the processing of hierarchical and non-

423 hierarchical figures. In the training phase, capuchins learned to discriminate hierarchical consistent
424 stimuli very accurately (90.6% of correct responses). However, it required them significantly more
425 trials to achieve the learning criterion with hierarchical than non-hierarchical stimuli. Learning
426 speed was the only aspect of the performance that was affected by the type of stimuli presented. At
427 the attainment of the learning criterion, the accuracy and RT of capuchins were similar for
428 hierarchical and non-hierarchical figures. The fact that hierarchical figures needed a higher number
429 of presentations to be accurately discriminated indicates that they are more difficult to encode
430 and/or recall than non-hierarchical visual patterns. This suggests that, consistently with the results
431 of other studies, capuchins' processing of hierarchical stimuli is not confined to the analysis of the
432 shape of one level of stimulus structure only. In fact, if that were the case, the complexity of
433 hierarchical stimuli could have been reduced to that of each of its individual elements. This,
434 contrary to what has been observed here, should have resulted in a similar level of difficulty for the
435 acquisition of the criterion for hierarchical and non-hierarchical stimuli.

436 The investigation of how part-whole relations within visual patterns are processed by
437 different species yields important information concerning visual cognition. The observation of
438 differences in visual processing style in species that share a similar visual system, for example, may
439 suggest that they are mediated by higher cognitive functions. This suggestion is consistent with the
440 evidence that top-down attentional processes modulate global/local processing in monkeys and
441 humans (De Lillo et al. 2011). Particularly useful information can be obtained from the direct
442 comparison of taxonomically related species, with a similar neuroanatomy and analogous
443 ergonomic requirements. However, it is not always possible to carry out such comparisons in the
444 same study. When comparing patterns of results obtained in different studies with a variety of
445 organisms it is thus crucial to ensure that any alleged interspecies differences cannot be accounted
446 merely by methodological variations among the paradigms used. The present study, in conjunction
447 with previous investigations of level of processing in capuchin monkeys, shows that the local

448 advantage in capuchin monkeys is an extremely robust finding that can be replicated with different
449 task variations reported in the comparative literature and provides a useful template for comparison
450 across studies on animal visual cognition.

451

452 **Ethical approval:** The research protocol for this study was approved by the Italian Health Ministry
453 (Central Direction for the Veterinary Service, approvals n. 11/2011-C and n. DM132/2014-C to V.
454 Truppa). All applicable international, national and institutional guidelines for the care and use of
455 animals were followed. All procedures were in accordance with the ethical standards of the
456 National Research Council of Italy, where the study was conducted.

457 **Conflict of Interest:** The authors declare that they have no conflict of interest.

458 **Data availability:** The datasets generated and analysed during the current study is available from
459 the corresponding author on reasonable request.

460

461

462 **References**

- 463 Addessi E, Crescimbene L, Visalberghi E. (2008). Food and token quantity discrimination in
464 capuchin monkeys (*Cebus apella*). Anim Cogn 11:275-282. doi:10.1007/s10071-007-0111-6
- 465 Avarguès-Weber A, Dyer AG, Ferrah N, Giurfa M (2015) The forest or the trees: preference for
466 global over local image processing is reversed by prior experience in honeybees. Proc R Soc B
467 282: 20142384. <http://dx.doi.org/10.1098/rspb.2014.2384>
- 468 Cavoto KK, Cook RG (2001) Cognitive precedence for local information in hierarchical stimulus
469 processing by pigeons. J Exp Psychol Anim Behav Process 27:3-16.
470 <http://dx.doi.org/10.1037/0097-7403.27.1.3>
- 471 Chiandetti C, Pecchia T, Patt F, Vallortigara G (2014) Visual hierarchical processing and
472 lateralization of cognitive functions through domestic chicks' eyes. PLoS ONE 9(1): e84435.
473 doi:10.1371/journal.pone.0084435
- 474 De Lillo C, Palumbo M, Spinozzi G, Giustino G (2012) Effects of pattern redundancy and
475 hierarchical grouping on global-local visual processing in monkeys (*Cebus apella*) and humans
476 (*Homo sapiens*). Behav Brain Res 226:445-455. doi:10.1016/j.bbr.2011.09.040
- 477 De Lillo C, Spinozzi G, Palumbo M, Giustino G (2011) Attention allocation modulates the
478 processing of hierarchical visual patterns: a comparative analysis of capuchin monkeys (*Cebus*
479 *apella*) and humans. J Exp Psychol Anim Behav Process 37:341-352. doi:10.1037/a0022989
- 480 Deruelle C, Fagot J (1998) Visual search for global/local stimulus features in humans and baboons.
481 Psychon Bull Rev 5:476-481. doi:10.3758/BF03208825
- 482 Dienes Z (2014) Using Bayes to get the most out of non-significant results. Front Psychol 5:781.
483 doi:10.3389/fpsyg.2014.00781

484 Fagot, J, Deruelle C (1997) Processing of global and local visual information and hemispheric
 485 specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). J Exp Psychol Hum
 486 Percept Perform 23:429-442. <http://dx.doi.org/10.1037/0096-1523.23.2.429>

487 Fagot J, Tomonaga M (1999) Comparative assessment of global-local processing in humans (*Homo*
 488 *sapiens*) and chimpanzees (*Pan troglodytes*): Use of a visual search task with compound
 489 stimuli. J Comp Psychol 113:3-12. <http://dx.doi.org/10.1037/0735-7036.113.1.3>

490 Fremouw T, Herbranson WT, Shimp CP (1998) Priming of attention to global and local levels of
 491 visual analysis. J Exp Psychol Anim Behav Process 24:278-290.
 492 <http://dx.doi.org/10.1037/0097-7403.24.3.278>

493 Fremouw T, Herbranson WT, Shimp CP (2002) Dynamic shifts of pigeon local/global attention.
 494 Anim Cogn 5:233-243. doi:10.1007/s10071-002-0152-9

495 Goto K, Wills AJ, Lea SEG (2004) Global-feature classification can be acquired more rapidly than
 496 local-feature classification in both humans and pigeons. Anim Cogn 7:109-113. doi:
 497 10.1007/s10071-003-0193-8

498 Hopkins WD, Washburn D (2002) Matching visual stimuli on the basis of global and local features
 499 by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). Anim Cogn 5:27-31.
 500 doi:10.1007/s10071-001-0121-8

501 Kimchi R (1992) Primacy of wholistic processing and global/local paradigm: A critical review.
 502 Psychol Bull 112:24-38. doi:10.1037/0033-2909.112.1.24

503 Kimchi R (1998) Uniform connectedness and grouping in the perceptual organization of
 504 hierarchical patterns. J Exp Psychol Hum Percept Perform 24:1105-1118.
 505 <http://dx.doi.org/10.1037/0096-1523.24.4.1105>

506 Kimchi R, Palmer SE (1982) Form and texture in hierarchically constructed patterns. J Exp Psychol
507 Hum Percept Perform 8:521-35. <http://dx.doi.org/10.1037/0096-1523.8.4.521>

508 Kinchla RA, Wolfe JM (1979) The order of visual processing: “top down”, “bottom-up” or “middle
509 out”. Percept Psychophys 25:225-331. doi:10.3758/BF03202991

510 Koldewyn K, Jiang YV, Weigelt S, Kanwisher N (2013) Global/local processing in autism: Not a
511 disability, but a disinclination. J Autism Dev Disord 43:2329-2340. doi:10.1007/s10803-013-
512 1777-z

513 Kumaran D, Hassabis D, Spiers HJ, Vann SD, Vargha-Khadem F, Maguire EA (2007) Impaired
514 spatial and non-spatial configural learning in patients with hippocampal pathology.
515 Neuropsychologia 45:2699-2711. doi:10.1016/j.neuropsychologia.2007.04.007

516 Lamb MR, Robertson LC, Knight RT (1990) Component mechanisms underlying the processing of
517 hierarchically organized patterns: Interferences from patients with unilateral cortical lesions. J
518 Exp Psychol Learn Mem Cogn 16:471-483. <http://dx.doi.org/10.1037/0278-7393.16.3.471>

519 Love J, Selker R, Marsman M, Jamil T, Dropmann D, Verhagen AJ, Wagenmakers EJ (2015) JASP
520 (Version 0.7) [Computer software]. Retrieved from <http://jasp-stats.org>.

521 Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, Gutiérrez-Espeleta GA, Chiou KL,
522 Schulte M, Neitzel S, Ross V, Schwochow D, Nguyen MTT, Farias I, Janson C, Alfaro ME
523 (2012a) Explosive Pleistocene range expansion leads to widespread Amazonian sympatry
524 between robust and gracile capuchin monkeys. J. Biogeogr 39:272-88. doi:10.1111/j.1365-
525 2699.2011.02609.x

526 Lynch Alfaro JW, De Souza Silva J, Rylands AB (2012b) How different are robust and gracile
527 capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. Am J Primatol 74:273-86.
528 doi:10.1002/ajp.22007

529 Lynch Alfaro JW, Izar P, Ferreira R (2014) Capuchin monkey research priorities and urgent issues.
 530 Am J Primatol 76:705-720. doi:10.1002/ajp.22269

531 Navon D (1977) Forest before the trees: The precedence of global features in visual perception.
 532 Cogn Psychol 9:353-383. doi:10.1016/0010-0285(77)90012-3

533 Navon D (1981) The forest revisited: More on global precedence. Psychol Res 43:1-32.
 534 doi:10.1007/BF00309635

535 Navon D (2003) What does a compound letter tell the psychologist's mind? Acta Psychol 114:273-
 536 309. doi:10.1016/j.actpsy.2003.06.002

537 Neiwirth JJ, Gleichman AJ, Olinick AS, Lamp KE (2006) Global and local processing in adult
 538 humans (*Homo sapiens*), 5-year-old children (*Homo sapiens*), and adult cotton-top tamarins
 539 (*Saguinus oedipus*). J Comp Psychol 120:323-330. [http://dx.doi.org/10.1037/0735-](http://dx.doi.org/10.1037/0735-7036.120.4.323)
 540 7036.120.4.323

541 Pitteri E, Mongillo P, Carnier P, Marinelli L (2014) Hierarchical stimulus processing by dogs
 542 (*Canis familiaris*). Anim Cogn 17:869-877. doi:10.1007/s10071-013-0720-1

543 Raftery AE (1995) Bayesian model selection in social research. In: Marsden PV (ed) Sociological
 544 methodology, vol 25. Cambridge, MA: Blackwell, pp 111-196.

545 Sanderson DJ, Pearce JM, Kyd RJ, Aggleton JP (2006) The importance of the rat hippocampus for
 546 learning the structure of visual arrays. Eur J Neurosci 24:1781-1788. doi:10.1111/j.1460-
 547 9568.2006.05035.x

548 Spinozzi G, De Lillo C, Salvi V (2006) Local advantage in the visual processing of hierarchical
 549 stimuli following manipulations of stimulus size and element numerosity in monkeys (*Cebus*
 550 *apella*). Behav Brain Res 166:45-54. doi:10.1016/j.bbr.2005.06.043

551 Spinozzi G, De Lillo C, Truppa V (2003) Global and local processing of hierarchical visual stimuli
 552 in tufted capuchin monkeys (*Cebus apella*). J Comp Psychol 117:15-23. doi:10.1037/0735-
 553 7036.117.1.15

554 Tanaka HK, Fujita I (2000) Global and local processing of visual patterns in macaque monkeys.
 555 Neuroreport 11:2881-2884.

556 Tanaka HK, Onoe H, Tsukada H, Fujita I (2001) Attentional modulation of neural activity in the
 557 macaque inferior temporal cortex during global and local processing. Neurosci Res 39:469-472.
 558 doi:10.1016/S0168-0102(01)00202-4

559 Truppa V, Carducci P, Trapanese C, Hanus D (2015) Does presentation format influence visual size
 560 discrimination in tufted capuchin monkeys (*Sapajus* spp.)? PLoS ONE 10:e0126001.
 561 doi:10.1371/journal.pone.0126001

562 Truppa V, De Simone D, Piano Mortari E, De Lillo C (2014) Effects of brief time delays on
 563 matching-to-sample abilities in capuchin monkeys (*Sapajus* spp.). Behav Brain Res 271:240-
 564 248. doi:10.1016/j.bbr.2014.05.023

565 Truppa V, De Simone DA, De Lillo C (2016) Short-term memory effects on visual global/local
 566 processing in tufted capuchin monkeys (*Sapajus* spp.). J Comp Psychol 130:162-173.
 567 <http://dx.doi.org/10.1037/com0000018>

568 Truppa V, Garofoli D, Castorina G, Piano Mortari E, Natale F, Visalberghi E (2010a) Identity
 569 concept learning in matching-to-sample tasks by tufted capuchin monkeys (*Cebus apella*).
 570 Anim Cogn 13:835-848. doi:10.1007/s10071-010-0332-y

571 Truppa V, Piano Mortari E, Garofoli D, Privitera S, Visalberghi E (2011) Same/different concept
 572 learning by capuchin monkeys in matching-to-sample tasks. PLoS ONE 6:e23809.
 573 doi:10.1371/journal.pone.0023809

574 Truppa V, Sovrano V, Spinozzi G, Bisazza A (2010b) Processing of visual hierarchical stimuli by
575 fish (*Xenotoca eiseni*). Behav Brain Res 207:51-60. doi:10.1016/j.bbr.2009.09.039

576 vanMarle K, Aw J, McCrink K, Santos LR (2006) How capuchin monkeys (*Cebus apella*) quantify
577 objects and substances. J Comp Psychol 120:416-426. [http://dx.doi.org/10.1037/0735-](http://dx.doi.org/10.1037/0735-7036.120.4.416)
578 7036.120.4.416

579 Wagenmakers EJ (2007) A practical solution to the pervasive problems of p values. Psychol Bull
580 Rev 14:779–804.

581

582 **Table 1** Monkeys participating in this study: age, sex, previous experience with hierarchical stimuli
 583 and performance.

Name	Age (years)	Sex	Previous Experience	Training Trials to criterion NHS	Training Trials to criterion HS	Test % local choices	Retest % local choices
Roberta	29	F	a, b, c	480	2880	62.5	62.5
Robiola	17	F	a, b	300	1472	62.5	62.5
Rucola	15	F	a, b, c	100	440	87.5	75.0
Robot	20	M	a, b, c	124	448	87.5	93.7
Sandokan	15	M	a, b, c	172	360	56.2	43.7
Vispo	15	M	a	616	1608	81.2	62.5

584 Note: NHS = Non-hierarchical stimuli; HS = Hierarchical stimuli; a = computerised MTS tasks
 585 (e.g., Truppa et al. 2010a, 2011, 2014, 2016); b = two-alternative forced-choice procedure (Truppa
 586 et al. 2015); c = global/local processing of hierarchical stimuli using an MTS task (Truppa et al.
 587 2016).

588

589

590 **Table 2. Experimental design**

I Training phase	I Testing phase	I Retesting phase
I block of stimulus pairs 16-trial sessions, each including 8 pairs of NHS + 8 pairs of CHS until achievement of the learning criterion	I block of stimulus pairs four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS	I block of stimulus pairs four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS
II Training phase	II Testing phase	II Retesting phase
II block of stimulus pairs 16-trial sessions, each including 8 pairs of NHS + 8 pairs of CHS until achievement of the learning criterion	II block of stimulus pairs four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS	II block of stimulus pairs four 10-trial sessions, each including 8 pairs of NHS + 2 pairs of IHS

591 NHS = Non-hierarchical stimuli; CHS = Consistent hierarchical stimuli; IHS = Inconsistent
592 hierarchical stimuli

593

594

595

596 **Figure captions**

597 **Fig. 1** Experimental apparatus

598 **Fig. 2** Examples of (a) non-hierarchical stimuli used in both training and testing phase, (b)
599 hierarchical consistent stimuli used in the training phase and (c) hierarchical inconsistent stimuli
600 used in the testing phase

601 **Fig. 3** Capuchins' performance ($M+SE$) in the hierarchical consistent stimuli and non-hierarchical
602 stimuli used in the training phase in relation to (a) number of trials to achieve the learning criterion,
603 (b) percentage of correct responses at acquisition and (c) RT in correct responses at acquisition.
604 Dependent t -test: * $P < 0.05$

605 **Fig. 4** Percentage of local choices ($M+SE$) in the testing phase right after the training phase and in
606 the retesting phase after five months to the finish of the testing phase. One-sample t -test: * $P < 0.05$,
607 ** $P < 0.01$

608

609

610 **Fig. 1**

611

612

613

614 **Fig. 2**

615

616

617

618 **Fig. 3**

619

620

621

622 **Fig. 4**

623