

Primates

Eye preferences in capuchin monkeys (*Sapajus apella*)

--Manuscript Draft--

Manuscript Number:					
Full Title:	Eye preferences in capuchin monkeys (<i>Sapajus apella</i>)				
Article Type:	Original Article				
Keywords:	Eye preferences; Behavioural laterality; Hemispheric specialisations; Emotion; Capuchin monkeys				
Corresponding Author:	Duncan Andrew Wilson, MSc Primate Research Institute, Kyoto University Inuyama City, Aichi Prefecture JAPAN				
Corresponding Author Secondary Information:					
Corresponding Author's Institution:	Primate Research Institute, Kyoto University				
Corresponding Author's Secondary Institution:					
First Author:	Duncan Andrew Wilson, MSc				
First Author Secondary Information:					
Order of Authors:	Duncan Andrew Wilson, MSc Masaki Tomonaga, PhD Sarah-Jane Vick, PhD				
Order of Authors Secondary Information:					
Funding Information:	<table border="1"> <tr> <td>Japan Society for the Promotion of Science (15H05709)</td> <td>Dr. Masaki Tomonaga</td> </tr> <tr> <td>Japan Society for the Promotion of Science (U04)</td> <td>Not applicable</td> </tr> </table>	Japan Society for the Promotion of Science (15H05709)	Dr. Masaki Tomonaga	Japan Society for the Promotion of Science (U04)	Not applicable
Japan Society for the Promotion of Science (15H05709)	Dr. Masaki Tomonaga				
Japan Society for the Promotion of Science (U04)	Not applicable				
Abstract:	<p>This study explored whether capuchin monkey eye preferences differ systematically in response to stimuli of positive and negative valence. Eleven captive capuchin monkeys were presented with four images of different emotional valence and social relevance, and eye preferences for viewing the stimuli through a monocular viewing hole were recorded. Eye preferences were found at the individual-level but not at the population-level. Furthermore, the direction of looking, number of looks and duration of looks did not differ significantly with the emotional valence of the stimuli. These results are inconsistent with the main hypotheses about the relationship between eye preferences and processing of emotional stimuli. However, the monkeys did show significantly more arousal behaviours (vocalisation, door-touching, self-scratching and hand-rubbing) when viewing the negatively valenced stimuli than the positively valenced stimuli, indicating that the stimuli were emotionally salient. These findings do not provide evidence for a relationship between eye preferences and functional hemispheric specialisations, as often proposed in humans. Additional comparative studies are required to better understand the phylogeny of lateral biases, particularly in relation to emotional valence.</p>				
Suggested Reviewers:	<p>Tatyana Humle, PhD Senior Lecturer, University of Kent T.Humle@kent.ac.uk Dr. Humle has studied primate laterality.</p> <p>Alban Lemasson, PhD Professor, University of Rennes 1 alban.lemasson@univ-rennes1.fr Professor. Lemasson has studied primate laterality.</p> <p>Ralph Adolphs, PhD Professor, Caltech radolphs@hss.caltech.edu</p>				

Alistair P Mapp, PhD
Professor, York University
amapp@yorku.ca
Professor. Mapp has studied primate laterality.

1 **ORIGINAL ARTICLE**

2

3

4 **Eye preferences in capuchin monkeys (*Sapajus apella*)**

5

6

7 **Duncan A. Wilson · Masaki Tomonaga · Sarah-Jane Vick**

8

9

10

11 D. A. Wilson (✉)

12 Primate Research Institute, Kyoto University, Inuyama, Aichi, 484-8506, Japan

13 E-mail: duncan.wilson.76x@st.kyoto-u.ac.jp

14 Phone: (+81) 0568-63-0567

15 Fax: (+81) 0568-63-0085

16

17 M. Tomonaga

18 Primate Research Institute, Kyoto University, Inuyama, Aichi, 484-8506, Japan

19

20 S.-J. Vick

21 Division of Psychology, School of Natural Sciences, University of Stirling, Stirling,

22 FK9 4LA, UK

23

24 **Abstract**

25 This study explored whether capuchin monkey eye preferences differ systematically in
26 response to stimuli of positive and negative valence. Eleven captive capuchin monkeys
27 were presented with four images of different emotional valence and social relevance,
28 and eye preferences for viewing the stimuli through a monocular viewing hole were
29 recorded. Eye preferences were found at the individual-level but not at the population-
30 level. Furthermore, the direction of looking, number of looks and duration of looks did
31 not differ significantly with the emotional valence of the stimuli. These results are
32 inconsistent with the main hypotheses about the relationship between eye preferences
33 and processing of emotional stimuli. However, the monkeys did show significantly
34 more arousal behaviours (vocalisation, door-touching, self-scratching and hand-
35 rubbing) when viewing the negatively valenced stimuli than the positively valenced
36 stimuli, indicating that the stimuli were emotionally salient. These findings do not
37 provide evidence for a relationship between eye preferences and functional hemispheric
38 specialisations, as often proposed in humans. Additional comparative studies are
39 required to better understand the phylogeny of lateral biases, particularly in relation to
40 emotional valence.

41 **Keywords** Eye preferences · Behavioural laterality · Hemispheric specialisations ·
42 Emotion · Capuchin monkeys

43 **Introduction**

44 Behavioural laterality in primates has been widely and intensively studied for decades
45 (Fitch and Braccini 2013; Ward and Hopkins 1993), such as hand preferences (e.g.
46 Humle and Matsuzawa 2009), eye preferences (e.g. Westergaard and Suomi 1996b) and
47 auditory preferences (e.g. Lemasson et al. 2010). Studies on these lateral biases are
48 important because these are believed to be closely connected to cerebral hemispheric
49 specialisations (Rogers et al. 2013). In primates, for example, the left hemisphere is
50 responsible for focused attention to invariable stimuli, following learned rules and
51 categorising stimuli, and can inhibit the right hemisphere. The right hemisphere is
52 responsible for face perception (Tomonaga 1999; Dahl et al. 2013), spatial cognition,
53 non-focused attention to novel stimuli, emergency responses involving intense emotions
54 such as fear and rage, and negative cognitive bias (Rogers et al. 2013). These
55 hemispheric specialisations are thought to be reflected in the contra-lateral of the body
56 in preferences for movement (e.g. hand preferences) and perception (e.g. eye
57 preferences) (Bisazza et al. 1998).

58 How emotional processing is specialised in each hemisphere is still controversial.
59 There are two main hypotheses: the ‘right hemisphere hypothesis’ proposes that the left
60 hemisphere is dominant for cognitive processing and the right hemisphere is dominant
61 for emotional processing (Borod et al. 1998), whilst the ‘valence hypothesis’ proposes
62 that the right hemisphere is dominant for negative emotional processing and the left
63 hemisphere is dominant for positive emotional processing (Davidson 1995). In addition,
64 the ‘motivational approach-withdrawal hypothesis’ compliments the valence hypothesis
65 and proposes the left hemisphere drives approach behaviour towards stimuli, and the
66 right hemisphere drives withdrawal behaviour away from stimuli (Demaree et al. 2005).

67 In human and non-human primates, empirical evidence suggests the right
68 hemisphere is dominant for emotional processing (Lindell 2013). For example, in
69 humans, Adolphs et al. (1996) found damage to the right hemisphere impairs the ability
70 to identify and discriminate facial emotions, whereas damage to the left hemisphere
71 does not. In non-human primates, Vermeire and Hamilton (1998) found split brain
72 rhesus macaques were significantly better at discriminating emotional facial expressions
73 when presented through a single eyehole to the isolated right hemisphere than to the
74 isolated left hemisphere.

75 However, few studies have investigated the relationship between emotional
76 processing and visual laterality in non-human primates. Visual laterality is typically
77 investigated in non-human primates using eye preference (e.g. Kounin, 1938), visual
78 field (e.g. Vauclair et al. 1993) and head orientation (e.g. Casperd and Dunbar, 1996)
79 measures. The results of such studies do not provide consistent support for either the
80 right hemisphere or valence hypotheses (Chapelain and Blois-Heulin 2009).

81 In eye preference studies using stimuli of both positive and negative valence,
82 Hook-Costigan and Rogers (1998) found support for the valence hypothesis in common
83 marmosets; a right eye preference (left hemisphere dominance) for viewing food
84 (banana) and a shift to left eye preference (right hemisphere dominance) for viewing a
85 model snake (although see Rogers et al. 1994, for opposite findings in small-eared bush
86 babies). More recently, Braccini et al. (2012) found support for the valence hypothesis
87 when they examined eye preferences in captive adult chimpanzees for various stimuli;
88 the strongest right eye preference for food (banana) and the strongest left eye preference
89 for a plastic snake was found. In addition, the chimpanzees looked more frequently and

90 for longer at the positive stimuli, and less frequently and for shorter at the negative
91 stimuli, consistent with the motivational approach-withdrawal hypothesis.

92 The aim of the present study was two-fold. Firstly, to examine eye preferences
93 in capuchin monkeys, a species popular for behavioural and cognitive research. There
94 are some reports on eye preferences in capuchin monkeys for viewing food rewards
95 (Kounin, 1938) but the small sample size of three monkeys makes it difficult to
96 determine population-level, or species-level, eye preferences in this species. In a larger
97 scale study, Westergaard and Suomi (1996b) tested 40 capuchin monkeys and found
98 individual-level but not group-level eye biases. However, only a single stimulus (a
99 grape) was presented at the end of a tube. Therefore, secondly, we aimed to examine
100 whether eye preferences were modulated by the emotional valence of the stimuli
101 presented, including social stimuli not previously tested in this paradigm. In particular,
102 we tried to test whether capuchin monkeys also show a pattern of eye preference
103 consistent with the valence and motivational approach-withdrawal hypotheses. On this
104 basis, we predicted they would prefer to view positively valenced stimuli with their
105 right eye (more frequently and for a longer duration) and negatively valenced stimuli
106 with their left eye (less frequently and for a shorter duration).

107 **Methods**

108 *Participants and housing*

109 Eleven tufted capuchin monkeys (*Sapajus apella*) were studied at the Living Links to
110 Human Evolution Research Centre located at the Royal Zoological Society of
111 Scotland's Edinburgh Zoo (UK). Nine males and two females took part in the
112 experiment (age range two to thirteen years old) and all but one monkey was captive

113 born. The capuchin monkey's indoor enclosure measured 32.5 m². The monkeys were
114 habituated to the research cubicle environment and could voluntarily enter a test cubicle
115 for short periods of isolation. The study was approved by the Research Ethics Review
116 Committee at the University of Edinburgh, UK, and complied with regulations of the
117 Association for the Study of Animal Behaviour (ASAB 2012).

118 *Apparatus*

119 The experiment was conducted in research rooms, in which a set of eight research
120 cubicles (0.5m³ each) were arranged. The monkeys voluntarily accessed the research
121 cubicles through an entrance from their outdoor enclosure. Transparent or opaque slide
122 doors allowed individual cubicles to be opened to or closed off from each other. Each
123 cubicle had windows to allow the monkeys to be easily observed.

124 The viewing apparatus was a cardboard panel (37.0 cm x 33.8 cm) which slotted
125 into the front of the research cubicle door with an eight mm in diameter viewing hole
126 (11 cm from the top of the panel). A 17" LCD monitor (Dell, E177FPc, Round Rock,
127 Texas) was used to present stimuli using Microsoft PowerPoint. The monitor was
128 placed on a 120 cm high stand at a distance of 50 cm from the research cubicle door.

129 To record eye preferences a video camera was placed directly on top of the
130 research cubicle and angled downward to capture the position of the top of the
131 monkey's head in relation to the viewing hole. A second video camera was set at the far
132 end of the research cubicles to record general behaviour and hand preferences when
133 reaching for food rewards (Fig .1).

134 *Stimuli*

135 Four stimuli (trimmed photographs against a black background) were presented per test
136 session consisting of two positively and two negatively valenced stimuli, which were
137 either social (featured capuchin monkey facial expressions) or non-social (did not
138 feature capuchin monkeys). The non-social positively-valenced stimulus was a boiled
139 egg, a favourite food in their daily diet. The non-social negatively-valenced stimulus
140 was an open-mouth harpy eagle face, a natural predator (Fragaszy et al. 2004). The
141 monkeys had been habituated to model snakes in previous studies, and so the harpy
142 eagle was chosen as an alternative potentially emotive stimulus. The social positively-
143 valenced stimulus was a capuchin monkey raised eyebrow face, which is commonly
144 displayed by all sex and age classes during social affiliative interactions and play
145 (Fragaszy et al. 2004). The social negatively-valenced stimulus was a capuchin monkey
146 open-mouth threat face. The stimuli were presented successively and presentation order
147 was counterbalanced across monkeys.

148 *Procedure*

149 At the start of each session monkeys entered the research cubicles from outside. After
150 the cubicle slide door was closed, and the monkeys became briefly accustomed to the
151 inside of the cubicle, the stimuli were presented on a screen, positioned in front of the
152 door covered by the viewing hole panel. The monkeys were given three different cues to
153 signal the initial presentation and subsequent change of stimuli; a computer generated
154 camera shutter sound, calling the monkey's name by the experimenter, and tapping
155 gently five times at the viewing hole. The experimenter handling the monkeys was blind
156 to stimuli presentation order to avoid inadvertent cueing.

157 Each monkey was given up to 60 seconds to take an initial look at each stimulus.
158 The experimenter would repeat the monkey's name and tap at the hole at 15 second

159 intervals until they took an initial look, or one minute elapsed. After an initial look, the
160 image was retained for an additional 30 seconds (without providing any cues). At the
161 end of the trial, or if an initial look was not taken within 60 seconds, the next stimulus
162 was presented. Therefore, the shortest length of time a monkey could be in the research
163 cubicles on any one occasion was two minutes, and the longest time six minutes. If at
164 any point the monkeys showed specific behaviours, such as pacing rapidly, vocalising
165 excessively, or pushing the entrance slide door, the testing session was ended. After
166 testing, the monkeys were given food rewards and released. Participants were never
167 rewarded for looking into the viewing hole, as this may have reinforced the use of a
168 particular eye (Chapelain and Blois-Heulin 2009).

169 A look was defined as the monkey's head moving within at least two
170 centimetres of the viewing hole and ended when the head moved two centimetres or
171 more away. Eye use judgements were made by observing the position of the top of the
172 monkey's head in relation to cross hairs transecting the viewing hole. Ambiguous
173 looking behaviour, such as rapid eye switches, were excluded from the subsequent data
174 analyses.

175 From initial video observations four potential arousal behaviours were identified
176 and recorded; a 'hiccup' vocalisation (e.g. Wheeler 2010), door-touching (often
177 preceding pushing of the cubicle slide door), self-scratching (e.g. Dufour et al. 2011;
178 Yamanashi and Matsuzawa 2010), and hand-rubbing (often preceded by sudden
179 withdrawal from the viewing hole and accompanied by vocalisation). Arousal
180 behaviours were recorded within the stimulus presentation period of each session.

181 In addition, hand preferences were preliminarily measured by recording which
182 hand the monkeys used when reaching for food rewards given before the start of the
183 experiment. Three or more hand reaches were used to determine hand preference.

184 *Inter-rater reliability*

185 Inter-rater reliability scores were obtained by asking a second rater to code the video
186 recordings of three monkeys. Frequency and order of observed looks, and order of
187 arousal behaviours were recorded. Kappa coefficients were calculated for the frequency
188 of these measures (Bakeman and Gottman 1997). Inter-rater reliability for eye use
189 scores was .77 ($p < .001$) indicating ‘substantial agreement’ between raters (Landis and
190 Koch 1977). For arousal behaviours there was ‘fair agreement’ on the frequency of
191 behaviours in a particular category (Kappa = .40, $p < .001$) and ‘perfect agreement’ on
192 the category to which the behaviour belonged to (Kappa = 1.0, $p < .001$).

193 *Statistical analysis*

194 The data were analysed using SPSS (Version 19) and R (Version 3.2.2). For each
195 monkey, eye preferences were calculated using an eye use index measure. This was
196 done by subtracting the total number of right eye uses (R) from the total number of left
197 eye uses (L) and dividing by the total number = $(R - L) / (R + L)$. Eye use index values
198 ranged from 1.0 (complete preference for right eye use), through zero for no preference,
199 to -1.0 (complete preference for left eye use) (Westergaard and Suomi 1996a). We also
200 used binomial tests to evaluate the strength of eye preferences for each individual. Hand
201 preference was calculated using the same method to generate a hand use index measure.

202 The mean scores for the duration of initial, and subsequent looks, and collated
203 arousal behaviours (vocalisation, door touching, self-scratching and hand-rubbing) were

204 not normally distributed. Square root transformations were performed resulting in
205 normally distributed scores (Shapiro-Wilk tests) for initial looks ($S-W_{(28)} = .97, p = .65$),
206 subsequent looks ($S-W_{(28)} = .98, p = .94$) and arousal behaviours ($S-W_{(44)} = .97, p = .23$).
207 The square roots of the mean scores for all looking and behaviour dependent variables
208 were then analysed using a 2 x 2 repeated-measures analysis of variance (ANOVA),
209 with emotional valence and social relevance as independent variables.

210 **Results**

211 *Eye use*

212 The total number of looks at an individual stimulus ranged from 1 to 16 looks. Figure 2
213 shows the median of the total number of looks (combined across right and left eyes) for
214 each positively and negatively valenced category. Monkeys did not show any difference
215 in total looks between valence categories (Wilcoxon signed-rank test, $V = 8, N = 11, p =$
216 $.20$) and between social and nonsocial stimuli ($V = 14.5, N = 11, p = 1$).

217 Figure 3 shows the eye use index scores for each monkey. All monkeys
218 significantly preferred using either their left or right eye (binomial tests, all $ps < .05$).
219 However, there was no significant population-level eye preference; seven monkeys had
220 an overall left eye preference and four monkeys had an overall right eye preference,
221 irrespective of stimulus valence (binomial test, $p = .27$). The mean eye use index scores
222 for valence categories based on total number of looks did not differ significantly from
223 zero; for positively valenced stimuli the score was -0.18 ($t_{(10)} = .65, p = .53$) and for
224 negatively valenced stimuli -0.30 ($t_{(10)} = 1.08, p = .31$). There was also no significant
225 difference between valence categories ($t_{(10)} = 1.27, p = .23$). This tendency was
226 consistent when analysed on the basis of initial looks and subsequent looks.

227 Four monkeys did not take subsequent looks at all four stimuli, and so were
228 excluded from the initial and subsequent look duration analyses. For initial looks the
229 duration ranged from 0.1 to 5.4 seconds. Mean duration was 1.38 s (egg), 1.33 s (eagle
230 face), 1.37 s (monkey raised eyebrow face) and 1.86 s (monkey threat face). A 2 x 2
231 repeated measures ANOVA on the duration of initial look means found no significant
232 main effects of valence and social stimuli type (valence; $F_{(1, 6)} = .85$, $MSE = .05$, $p = .39$,
233 social type; $F_{(1, 6)} = 2.28$, $MSE = .04$, $p = .18$) and no interaction ($F_{(1, 6)} = 1.09$, $MSE =$
234 $.09$, $p = .34$). For subsequent looks the duration ranged from 0.2 to 3.6 seconds. Mean
235 duration was 0.58 s (egg), 0.55 s (eagle face), 0.44 s (monkey raised eyebrow face) and
236 0.75 s (monkey threat face). Subsequent looks were significantly shorter than first looks
237 ($t_{(6)} = 5.84$, $p = .001$). A 2 x 2 repeated measures ANOVA on the duration of subsequent
238 looks means found no significant main effects of valence and social stimuli type
239 (valence; $F_{(1, 6)} = 1.10$, $MSE = .07$, $p = .33$, social type; $F_{(1, 6)} = 0.05$, $MSE = 0.10$, $p =$
240 $.94$) and no interaction ($F_{(1, 6)} = 3.42$, $MSE = .03$, $p = .11$).

241 *Arousal behaviours*

242 Figure 4 shows the mean number of observed arousal behaviours per session as a
243 function of stimulus condition. Given the low frequency of arousal behaviours in some
244 sessions, all arousal behaviours were combined across sessions, and an overall mean
245 score calculated for each individual. The analysis found a significant main effect of
246 valence, $F_{(1, 10)} = 5.74$, $MSE = .04$, $p = .04$, which reflects more total arousal behaviours
247 in response to viewing the negatively valenced stimuli ($M = .66$ observations per
248 session) than positively valenced stimuli ($M = .40$ observations per session).

249 *Relationship between eye and hand preference*

250 Figure 3 also shows hand use index scores for each monkey. Three monkeys did not
251 make three or more hand reaches for food and so were excluded from the analyses. Left
252 hand preferences were shown by three monkeys and right hand preferences were shown
253 by five monkeys. However, as clearly shown in this figure, there was no significant
254 correlation between eye and hand use index scores ($r_{(6)} = -.17, p = .69$).

255 **Discussion**

256 This study found that eye preferences in capuchin monkeys were strongly lateralised at
257 the individual-level; all of the monkeys looked at all the stimuli consistently with either
258 their left or right eye. There are only two previous studies which have investigated
259 capuchin monkey eye preferences (Kounin 1938; Westergaard and Suomi 1996b). Our
260 results are consistent with Westergaard and Suomi (1996b), who also showed
261 individual-level, but not group-level eye preferences using a similar monocular viewing
262 task; 14 monkeys (41%) showed a left eye bias, 13 monkeys (38%) showed a right eye
263 bias, and seven monkeys (21%) showed no eye bias. In comparison, our study found
264 seven monkeys (64%) had a left eye bias and four monkeys (36%) had a right eye bias.

265 In both studies there was also no relationship between hand and eye preference.
266 This is consistent with studies in both non-human primates (Braccini et al. 2012; Fitch
267 and Braccini 2013) and humans (e.g. Mapp et al. 2003; Papousek and Schulter 1999;
268 Pointer 2001).

269 There was no difference in the direction of eye preference according to the
270 emotional valence or social relevance of the stimuli. Eye preferences did not change
271 between the first look and subsequent looks (when the monkeys had knowledge of the
272 stimuli). Therefore, our results do not provide support for either the valence hypothesis
273 or the right-hemisphere hypothesis of emotional processing.

274 More frequent looking and for a longer duration at the positively valenced
275 stimuli (approach behaviour) and less frequent looking and for a shorter duration at the
276 negatively valenced stimuli (withdrawal behaviour) was predicted (Braccini et al. 2012).
277 Although subsequent looks were significantly shorter than first looks, possibly due to
278 habituation, there was no difference in looking frequency or duration in regards to the
279 stimuli valence. Overall, these results do not provide any support for the motivational
280 approach-withdrawal hypothesis.

281 Previous eye preference studies providing support for the valence hypothesis in
282 non-human primates have used real objects as stimuli (e.g. Braccini et al. 2012; Hook-
283 Costigan and Rogers 1998). In the present study we presented stimuli as two-
284 dimensional images on a monitor screen, to allow for greater control of social stimuli
285 presentation, and to maintain consistency across all stimuli. One possibility is that two-
286 dimensional representation has a weaker emotional salience than three-dimensional
287 (real) representation (cf. Fagot et al. 2000). However, our monkeys showed more
288 arousal behaviours in response to viewing the negatively valenced stimuli than the
289 positively valenced stimuli, suggesting the images did have a degree of emotional
290 salience. Despite this, emotional valence did not impact upon eye preference and instead
291 the monkeys demonstrated consistent individual eye preferences across stimuli.

292 Another explanation is that there is no systematic causal relationship between
293 eye preference and hemispheric specialisations in primates. Primates have a crossing
294 optic chiasm, which means visual information from each eye is sent to both cerebral
295 hemispheres (Jeffrey 2001). The different thickness of the optic fibres means those
296 crossing to the contralateral hemisphere are more dominant and transfer information
297 faster than uncrossed fibres connected to the ipsilateral hemisphere (Bisazza et al. 1998).

298 Therefore, if mammals with greater crossing of optic fibres than primates (50%
299 decussation) such as horses (80-90% decussation) are tested (Brooks et al. 1999),
300 hemispheric specialisation for emotional processing may affect eye preference more
301 directly.

302 However, after reviewing the previous literature in humans, Mapp et al. (2003)
303 concluded that eye preference is determined by the constraint of the monocular viewing
304 task itself, and “the habit or ease of using the chosen eye”, independently of
305 hemispheric specialisations. The strong individual left or right eye lateralisation found
306 in this study may simply be a reflection of this constraint, and so eye preferences may
307 not be a good measure for testing the emotional valence hypothesis. A better approach
308 to examine hemispheric specialisations for emotional stimuli, may be to present stimuli
309 to either the left or right visual field for a brief duration, such as less than 200
310 milliseconds, during which the participant cannot make goal-directed saccades (e.g.
311 Fagot and Deruelle 1997; Vauclair et al. 1993).

312 In conclusion, the findings of this study do not provide convincing support for
313 eye preferences as a measure of emotional responses in captive capuchin monkeys. The
314 current data on emotional processing and eye preferences in non-human primates
315 remains inconsistent. Thus research with a greater number of species and larger sample
316 sizes is needed to better understand the potential of eye preferences as a measure of
317 emotional processing in non-human primates.

318 **Acknowledgements** We sincerely thank the Royal Zoological Society of Scotland’s
319 Edinburgh Zoo, and the staff at the Living Links to Human Evolution Research Centre.
320 We would especially like to thank Professor. Andrew Whiten and Dr. Nicolas Claidière
321 for permission to work at the centre, and Dr. Eoin O’Sullivan for his assistance with

322 monkey identification and handling. This paper is partially based on a dissertation for
323 the Degree of Master of Science in Applied Animal Behaviour and Animal Welfare at
324 the University of Edinburgh, UK. Preparation of the manuscript was financially
325 supported by the Ministry of Education, Culture, Sports, Science and Technology
326 Japan/Japan Society for the Promotion of Science Grants-in-Aid for Scientific Research
327 (#15H05709) and the Japan Society for the Promotion of Science Leading Graduate
328 Program in Primatology and Wildlife Science at Kyoto University, Japan (U04).

329 **Compliance with Ethical Standards** Conflict of Interest: The authors declare that
330 they have no conflict of interest. Ethical Approval: The study was approved by the
331 Research Ethics Review Committee at the University of Edinburgh, UK, and complied
332 with regulations of the Association for the Study of Animal Behaviour (ASAB 2012).

333 **References**

- 334 Adolphs R, Damasio H, Tranel D, Damasio AR (1996) Cortical systems for the
335 recognition of emotion in facial expressions. *J Neurosci* 16 23: 7678-7687
- 336 Association for the Study of Animal Behaviour (2012) Guidelines for the treatment of
337 animals in behavioural research and teaching. *Anim Behav* 83:301-309
- 338 Bakeman R, Gottman JM (1997) Observing interaction: An introduction to sequential
339 analysis. New York: Cambridge University Press. 2nd Edition
- 340 Bisazza A, Rogers LJ, Vallortigara G (1998) The origins of cerebral asymmetry: a
341 review of evidence of behavioural and brain lateralization in fishes, reptiles and
342 amphibians. *Neurosci Biobehav R* 22:411-426
- 343 Borod JC, Obler KL, Erhan HM, Grunwald IS, Cicero BA, Welkowitz J, Santschi C,
344 Agosti RM, Whalen JR (1998) Right hemisphere emotional perception:
345 evidence across multiple channels. *Neuropsychology* 12:446-458
- 346 Braccini SN, Lambeth SP, Schapiro SJ, Fitch WT (2012) Eye preferences in captive
347 chimpanzees. *Anim Cogn* 15:971-978
- 348 Brooks DE, Komaromy AM, Kallberg ME (1999) Comparative retinal ganglion cell and
349 optic nerve morphology. *Vet Ophthalmol* 2 1:3-11
- 350 Casperd JM, Dunbar RIM (1996) Asymmetries in the visual processing of emotional
351 cues during agonistic interactions by gelada baboons. *Behav Process*, 37 1:57-65
- 352 Chapelain AS, Blois-Heulin C (2009) Lateralization for visual processes: eye preference
353 in Campbell's monkeys (*Cercopithecus c. campbelli*). *Anim Cogn* 12:11-19
- 354 Dahl, CD, Rasch, MJ, Tomonaga M, Adachi I (2013) Laterality effect for faces in
355 chimpanzees (*Pan troglodytes*). *J Neurosci* 33:13344-13349

356 Davidson RJ (1995) Cerebral asymmetry, emotion, and affective style. In: Davidson RJ,
357 Hughdahl K (Eds.), Brain Asymmetry, Massachusetts: MIT Press 361-387

358 Demaree HA, Everhart DE, Youngstrom EA, Harrison DW (2005) Brain lateralization
359 of emotional processing: historical roots and a future incorporating
360 "dominance". Behav Cogn Neurosci Rev 4:3-20

361 Dufour V, Sueur C, Whiten A, Buchanan-Smith HM (2011) The Impact of Moving to a
362 Novel Environment on Social Networks, Activity and Wellbeing in Two New
363 World Primates. Am J Primatol 73:802-811

364 Fagot J, Deruelle C (1997) Processing of global and local visual information and
365 hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio
366 papio*). J Exp Psychol Hum Percept Perform 23 2:429

367 Fagot J, Martin-Malivel J, Dépy D (2000) "What is the evidence for an equivalence
368 between objects and pictures in birds and nonhuman primates". Picture
369 perception in animals 295-320

370 Fitch WT, Braccini SN (2013) Primate laterality and the biology and evolution of
371 human handedness: a review and synthesis. Ann N Y Acad Sci 1288:70-85

372 Fragaszy D, Visalberghi E, Fedigan L (2004) The Complete Capuchin: The Biology of
373 the Genus *Cebus*. Cambridge University Press

374 Hook-Costigan MA, Rogers LJ (1998) Eye preference in common marmosets
375 (*Callithrix jacchus*): influence of age, stimulus, and hand preference. Laterality
376 3:109-130

377 Humle T, Matsuzawa T (2009) Laterality in hand use across four tool - use behaviors
378 among the wild chimpanzees of Bossou, Guinea, West Africa. Am J Primatol 71
379 1:40-48

380 Jeffery G (2001) Architecture of the optic chiasm and the mechanisms that sculpt its
381 development. *Physiol Rev* 81 4:1393-1414

382 Kounin JS (1938) Laterality in monkeys (Book Review). *Pedagog Semin J Genet*
383 *Psychol* 52:375-393

384 Landis JR, Koch GG (1977) The measurement of observer agreement for categorical
385 data. *Biometrics* 33:159-174

386 Lemasson A, Koda H, Kato A, Oyakawa C, Blois-Heulin C, Masataka N (2010)
387 Influence of sound specificity and familiarity on Japanese macaques' (*Macaca*
388 *fuscata*) auditory laterality. *Behav Brain Res* 208: 286-289

389 Lindell AK (2013) Continuities in emotion lateralization in human and non-human
390 primates. *Front hum neurosci* 7

391 Mapp AP, Ono H, Barbeito R (2003) What does the dominant eye dominate? A brief
392 and somewhat contentious review. *Percept Psychophys* 65 2:310-317

393 Papousek I, Schuler G (1999) Quantitative assessment of five behavioural laterality
394 measures: Distributions of scores and intercorrelations among right-handers.
395 *Laterality* 4 4:345-362

396 Pointer JS (2001) Sighting dominance, handedness, and visual acuity preference: three
397 mutually exclusive modalities?. *Ophthal Physl Opt* 21 2: 117-126

398 Rogers LJ, Vallortigara G, Andrew RJ (2013) *Divided Brains: The Biology and*
399 *Behaviour of Brain Asymmetries*. Cambridge University Press

400 Rogers LJ, Ward JP, Stanford D (1994). Eye dominance in the small-eared bushbaby,
401 *Otolemur garnettii*. *Neuropsychologia* 32 2:257-264

402 Tomonaga M (1999) Inversion effect in perception of human faces in a chimpanzee
403 (*Pan troglodytes*). *Primates* 40:417-438

404 Vauclair J, Fagot J, Hopkins, WD (1993) Rotation of mental images in baboons when
405 the visual input is directed to the left cerebral hemisphere. *Psychol Sci* 4 2:99-
406 103

407 Vermeire BA, Hamilton CR (1998) Effects of facial identity, facial expression, and
408 subject's sex on laterality in monkeys. *Laterality* 3 1:1-20

409 Ward JP, Hopkins WD (1993) Primate laterality: Current behavioral evidence of
410 primate asymmetries. Springer Science & Business Media

411 Westergaard GC, Suomi SJ (1996a) Hand preference for bimanual task in tufted
412 capuchins (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). *J Comp*
413 *Psychol* 110:406-411

414 Westergaard GC, Suomi SJ (1996b) Lateral bias for rotational behavior in tufted
415 capuchin monkeys (*Cebus apella*). *J Comp Psychol* 110:199-202

416 Wheeler BC (2010) Production and perception of situationally variable alarm calls in
417 wild tufted capuchin monkeys (*Cebus apella nigrinus*). *Behav. Ecol. Sociobiol*
418 64 6:989-1000

419 Yamanashi Y, Matsuzawa T (2010) Emotional consequences when chimpanzees (*Pan*
420 *trogodytes*) face challenges: individual differences in self-directed behaviours
421 during cognitive tasks. *Animal Welfare* 19 1:25-30

422

423

424

425

426

427

428 **Figure captions**

429 **Fig. 1** A capuchin monkey 'Kato', adopting a bipedal standing position to look into the
430 viewing hole from inside the test cubicle

431 **Fig. 2** Boxplot of the total number of looks (combined across right and left eyes) for
432 each category of stimuli presented

433 **Fig. 3** Eye and hand use index scores for each monkey. Bars indicate eye use index and
434 circles indicate hand use index. Minus values indicate left eye or hand preference, and
435 plus values indicate right eye or hand preference

436 **Fig. 4** Mean number of arousal behaviours per session. Error bars represent the standard
437 error of the mean

Figure 1



Figure 2

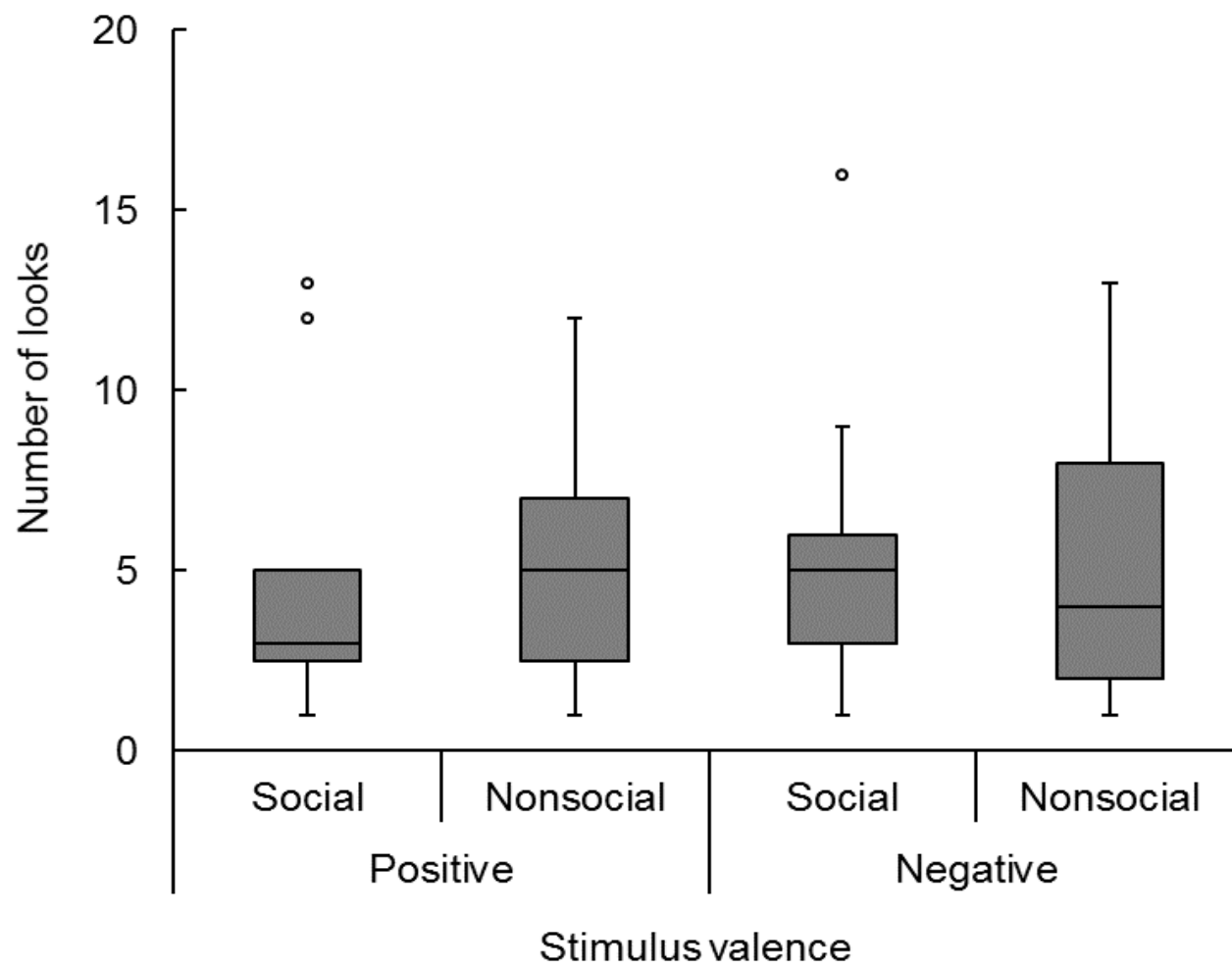


Figure 3

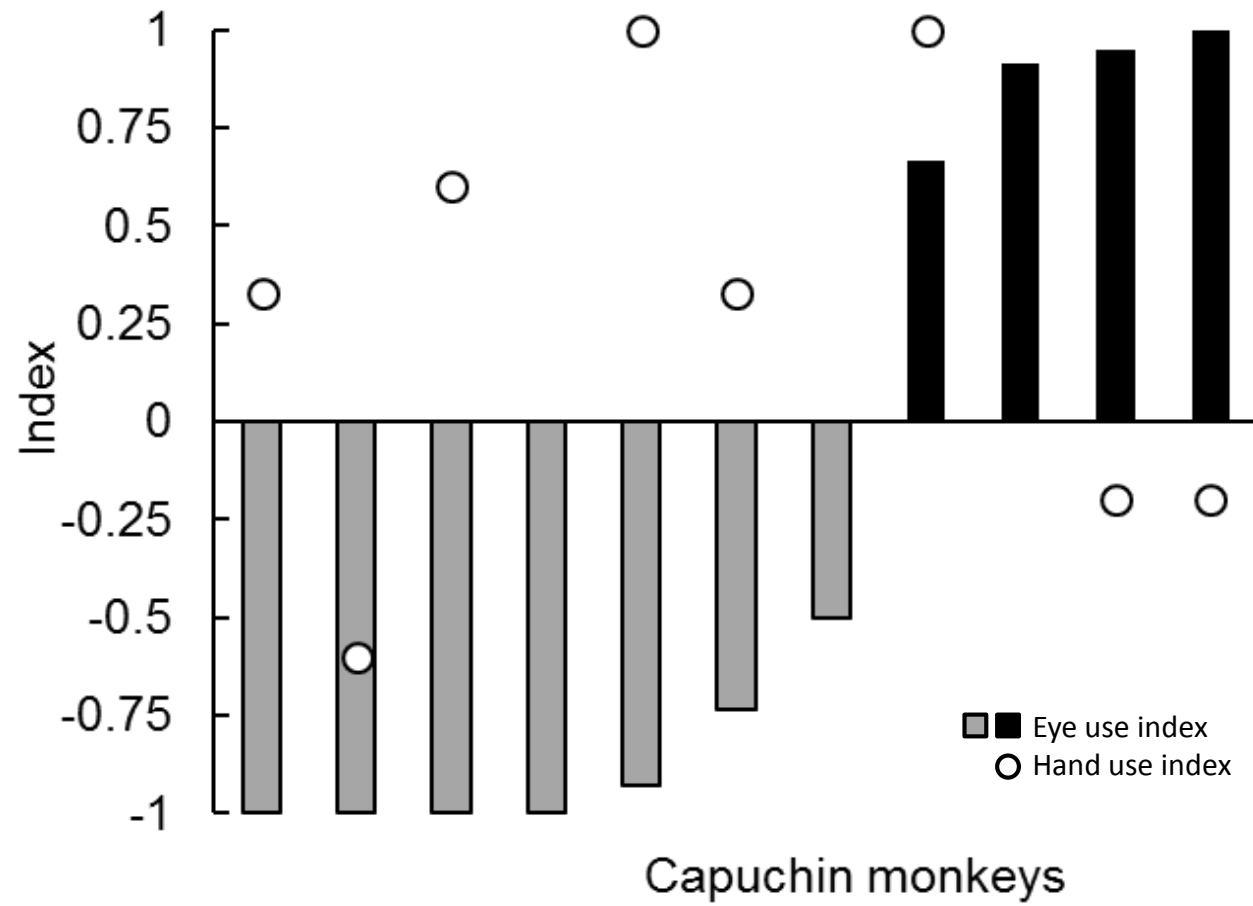


Figure 4

