1

2

3

4

5

6   Research article

7   The visual strategy specific to humans among hominids: A study using the gap-overlap

8   paradigm

9

10

11

12   Fumihiro Kano (1, 2)

13   Satoshi Hirata (3)

14   Josep Call (4)

15   Masaki Tomonaga (1)

1.   Primate Research Institute, Kyoto University, Inuyama, Japan

2.   Japan Society for Promotion of Science

3.   Great Ape Research Institute, Hayashibara Biochemical Laboratories, Inc.

4.   Max Plank Institute for Evolutionary Anthropology, Leipzig, Germany

fkanou@pri.kyoto-u.ac.jp

+81-80-6902-5013

23

24

25

Abstract

27 Although an extensive body of literature exists on the cognitive underpinnings of gaze

28 movements in macaques and humans, few studies have investigated this topic from a broader

29 evolutionary perspective. This study used the gap–overlap paradigm to examine the timing of

30 the gaze movements by four hominid species: humans, chimpanzees, gorillas, and orangutans.

31 The saccade latency involved in shifting the gaze from central to peripheral stimuli was

32 measured and compared under two conditions, gap and overlap. The central stimulus

33 disappeared shortly before the onset of the peripheral stimulus under the gap condition, but it

34 remained under the overlap condition. Although all species demonstrated similar saccade

35 latencies under the gap condition, the species clearly differed from one another under the

36 overlap condition, which may suggest their similar perceptual and motor mechanism of making

37 a saccade on the one hand and their differential strategies for coping with the competition

38 between two activities involving fixation and initiation of a saccade (i.e. central vs. peripheral

39 visual stimuli) on the other hand. In particular, humans showed longer saccade latency under the

40 overlap condition compared to the other great apes, which may reflect this species' unique

41 means of visual processing.

42 Key Words: Eye-tracking, Gap-Overlap, Great ape, Saccade latency

43

44

Eye-gaze movement constitutes one of the most comprehensively studied visually guided behaviors displayed by humans and macaque monkeys. The visual strategy common to human and nonhuman primates involves the alternation of fixation and saccade; fixation involves maintaining certain parts of the visual field fixed on the fovea, which optimizes retinal acuity and color sensitivity, whereas saccades involve bringing new parts of the visual field onto the fovea using rapid eye movements. Given that primates retrieve visual information primarily from the fovea, how they move their gaze inform us about the ways in which visual information from the external world is retrieved and processed, an operation that is critically important to survival.

When primates shift their gaze from one location to another via saccadic eye movements, competition occurs between two mutually exclusive activities: fixation and saccade initiation. Resolving this competition consumes time because it involves various perceptual and cognitive processes (Findlay & Walker, 1999). This time-consuming competitive process can be examined using a simplified experimental arrangement known as the gap–overlap paradigm. An extensive body of literature exists with regard to the use of this paradigm in humans (Braun & Breitmeyer, 1988; Kalesnykas & Hallett, 1987; Saslow, 1967) and macaque monkeys (Baizer & Bender, 1989; Fischer & Boch, 1983; Fischer & Weber, 1993). Following this paradigm, a central (fixated) and a peripheral target stimulus appear sequentially on a computer screen under two conditions. The central fixation stimulus disappears after a short period of time (200–400 ms) before the target is presented under the gap condition, whereas the central fixation stimulus remains under the overlap condition. The time between target presentation and initiation of a saccade directed at the target is then measured (i.e., the saccade latency). In humans and

67 monkeys, the saccade latency in response to peripheral stimuli has tended to be longer under the

68 overlap than under the gap condition (known as the "gap effect").

69   One well-established model of saccade generation (Findlay & Walker, 1999) assumes

70 that resolution of the competition between fixation and saccadic activities requires the

71 integration of various competing information signals to decide whether and where a saccade

72 should occur. This model suggests that resolving this competition involves a relatively slow

73 buildup in one activity and a decline in the other. Thus, when the saccadic activity overcomes

74 the fixation activity, a saccade is generated. The reduction of fixation activity is termed

75 disengagement. Physiologically, this competitive interaction can be observed in a subcortical

76 area, the *superior colliculus,* where a decline in fixation neurons and a buildup in

77 saccade-related neurons occur (Dorris & Munoz, 1995; Dorris, Pare, & Munoz, 1997; Munoz &

78 Wurtz, 1993a, 1993b). Saccade generation is also controlled by various cortical areas including

79 the parietal and frontal cortex (Müri et al., 1998; Munoz & Everling, 2004), especially the

80 frontal eye field (Dias & Bruce, 1994; Hanes & Schall, 1996). According to Findlay and

81 Walker's (1999) model, the gap effect occurs because the fixation activity is automatically

82 reduced by the offset of the fixation stimulus under the gap but not the overlap condition. The

83 offset of the fixation stimulus under the gap condition also works as a warning signal that

84 provides temporal information about the appearance of the target (L. E. Ross & Ross, 1980; S.

85 M. Ross & Ross, 1981).

86   It is well known that human infants from 1 to 4 months of age have difficulty in

87 shifting their gaze to peripherally presented stimuli, the so called "obligatory fixation" (Stechler

88 & Latz, 1966). The gap–overlap paradigm has revealed that infants in their first year of life

89 show an earlier maturation of saccade latency under the gap than under the overlap condition

90 (i.e., a larger gap effect in younger infants) (Farroni, Simion, Umilt, & Barba, 1999; Hood &

91   Atkinson, 1993; M. Matsuzawa & Shimojo, 1997). Thus, it is suggested that human infants have

92   difficulty in disengaging attention or reducing fixation activity under the overlap condition, in

93   which such disengagement does not occur in an automatic manner. Physiologically, this

94   phenomenon can be explained by the earlier maturation of subcortical compared with cortical

95   regulatory systems (e.g., the frontal eye field; (Johnson, 1990). Similar difficulties with

96   disengagement under the gap–overlap paradigm have also been reported among individuals

97   with autism (Landry & Bryson, 2004)

98   Numerous studies have been conducted in macaque monkeys to examine the neural

99   and behavioral mechanisms underlying saccade generation. Lesion studies, behavioral testing,

100   functional neuroimaging studies, single-unit recordings, and anatomical studies in macaques

101   and humans have shown that the neural circuitry controlling saccadic eye movements is

102   homologous, or qualitatively similar, in the two species (Munoz & Everling, 2004). Studies

103   comparing human and nonhuman primates have reported that trained macaques demonstrated a

104   shorter saccadic latency than did trained humans (Baizer & Bender, 1989). During free viewing

105   of a naturalistic dynamic scene, macaques scanned the scene more rapidly than did humans by

106   shifting their gaze to the next location at an earlier time (Berg, Boehnke, Marino, Munoz, & Itti,

107   2009; Shepherd, Steckenfinger, Hasson, & Ghazanfar, 2010).

108   A similar species difference was observed in comparisons of humans with one of their

109   closest living primate relatives, chimpanzees (*Pan troglodytes*), when freely viewing static

110   scenes (Kano & Tomonaga, 2009). A subsequent study (Kano & Tomonaga, in press) confirmed

111   that this species difference in the timing of gaze movements did not depend on the nature of the

112   stimuli (a scene containing humans/chimpanzees, fruit trees, only background, or texture) and

113   thus seemingly reflected general patterns of gaze movements rather than specific responses to

114   particular components of scenes. That subsequent study also examined the pattern of gaze

115   movements in chimpanzees and humans using the gap–overlap paradigm under free-viewing

116   conditions (no instruction/training) and found that chimpanzees and humans showed very

117   similar saccadic latencies under the gap condition, but that chimpanzees shifted their gaze to the

118   peripheral target at an earlier time than did humans under the overlap condition (i.e., a smaller

119   gap effect in chimpanzees). The species similarity under the gap condition suggested that

120   perceptual and motor abilities for making a saccade were comparable in both species, and the

121   species differences under the overlap condition suggested the operation of differential visual

122   strategies for resolving the competition between fixation and initiation of a saccade. In this

123   context, it might be argued that humans follow a different pattern than do other primates in the

124   timing of their gaze movements and that this species difference may derive from humans'

125   specific visual strategy for dealing with the aforementioned competition.

126   Despite their value, the current data have several shortcomings. First, there is the issue

127   of the representativeness of the existing samples. Kano and Tomonaga (in press) compared six

128   chimpanzees with 18 humans. However, the inclusion of additional individuals would be

129   necessary to confirm that these results reflect species rather than individual differences. This is

130   particularly important considering that these particular chimpanzees were previously

131   extensively trained in computerized tasks, some of which required rapid responses to stimuli

132   presented on a screen. Although these subjects were never trained to make saccades,

133   confirmation of the validity of the free-viewing paradigm as a way to reveal spontaneous

134   viewing patterns would require replication of the aforementioned results with chimpanzees with

135   different training experiences.

136   Second, there is the issue of the type of stimuli presented in the tasks. Using the

137   gap–overlap paradigm, Kano and Tomonaga (in press) presented naturalistic figures, faces, and

138   objects rather than simple geometric figures to attract the apes' and humans' spontaneous

139   attention to the stimuli. They found a minimal effect of different types of stimuli on species

140   differences in saccade latencies, even though both species discriminated faces from objects in

141   their gaze responses (in an experimental situation facilitating competition between the two

142   stimulus types). Thus, it was suggested that species differences reflected general (or habitual)

143   patterns of saccade generation rather than the immediate outcomes of the processing of

144   meaningful stimuli. However, one might argue that faces and objects are both meaningful and

145   that another type of stimulus, such as a meaningless figure, would be necessary to confirm these

146   findings.

147   Finally, the investigation of species of great apes other than chimpanzees can

148   contribute to clarifying the evolution of gaze-scanning patterns. As indicated above, the ways in

149   which primates move their gaze can inform us about how they retrieve and process visual

150   information that may be critically important for their survival. Thus, it is expected that each

151   species' gaze-scanning pattern sensitively reflects the phylogenetical and socioecological

152   constraints specific to each species. Phylogenetically, chimpanzees are the closest to humans,

153   followed by gorillas and orangutans. Thus, the comparison with the other apes may clarify whether

154   the differences between chimpanzees and humans represent derived or ancestral traits. Additionally,

155   each species has a differential socioecological background (Clutton-Brock & Harvey, 1977).

156   Thus, our comparative study may also help us to assess the potential impact of socio-ecological

157   variables on the gaze-scanning patterns.

158   The aim of the current study was to examine the timing of gaze movements from

159   comparative perspective using the gap–overlap paradigm. We tested humans and three

160   non-human great ape species, chimpanzees, gorillas and orangutans, living in three different

161   facilities. Additionally, we investigated the effect of the type of stimulus. Following previous

162   studies, we presented faces and objects, but also included a meaningless figure (texture).

163

Method

Participants

Four female gorillas (one adult, one infant, and two juveniles) and seven orangutans (one adult male, one infant male, four adult females, one juvenile female) housed at the Wolfgang Köhler Primate Research Center (WKPRC) at the Leipzig Zoo in Germany, eight chimpanzees (two adult males, three adult females, three juvenile females) housed at the Great Ape Research Institute (GARI) at Hayashibara Biomedical Laboratories, Inc. in Japan, and eight chimpanzees (two adult males, six adult females) housed at the Primate Research Institute at Kyoto University (KUPRI) participated in this study. Additionally, 16, six, and 18 humans (all adults) were recruited from WKPRC (all Europeans; six males, 10 females), GARI (all Japanese; two males, four females), and KUPRI (all Japanese; six males, 12 females), respectively, to participate in this study. Thus, 27 apes and 40 humans participated in this study. The data from six of the eight chimpanzees and the 18 humans at KUPRI were previously published (Kano and Tomonaga, in press). Two additional chimpanzees (an adult male and an adult female) were tested at KUPRI to increase the number of participants. All apes lived in social groups in a large outdoor compound attached to an indoor residence with regular feedings, enrichment, and water *ad libitum.* All apes were neither food- nor water-deprived. All apes and humans voluntarily participated in the study. Animal husbandry and research at WKPRC complied with the "European Association of Zoos and Aquaria (EAZA) Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria" and the "World Association of Zoos and Aquariums (WAZA) Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums," respectively. Animal husbandry at GARI and KUPRI complied with the "Care and Use of Laboratory Animals of Hayashibara Biochemical Laboratories, Inc." and the

187 2002 version of the "Guidelines for the Care and Use of Laboratory Primates of the Primate

188 Research Institute, Kyoto University," respectively. Research conducted at GARI and KUPRI

189 was approved by the Animal Welfare and Care Committee of KUPRI and the Animal Research

190 Committee of Kyoto University. Informed consent was obtained from all human participants.

191 Chimpanzees housed at KUPRI had extensive experience with participation in

192 computerized tasks using a touch-panel display, typically 15–21 inches in size, that required

193 them to respond by touching geometrical or naturalistic figures appearing on the screen (T.

194 Matsuzawa, Tomonaga, & Tanaka, 2006). Chimpanzees at GARI also had experience

195 participating in such touch-panel experiments, but to a lesser extent than those at KUPRI (Idani

196 & Hirata, 2006). Gorillas housed at WKPRC had begun participation in touch-panel

197 experiments only recently, and orangutans at this facility had neither experienced such

198 experiments nor been exposed to images on a computer screen. None of the apes or humans had

199 been explicitly trained to shift their gaze rapidly.

200 **Apparatus**

201 The same eye-tracking techniques were used for apes and humans to ensure the same

202 eye-tracking accuracy among species (Fig, 1 a–c). However, we slightly modified the

203 experimental arrangement in each facility to compensate for the specific constraints and

204 capitalize on the particular resources already present at each institution. Eye-tracking

205 experiments had been previously established with the chimpanzees at GARI and KUPRI

206 (Hattori, Kano, & Tomonaga, 2010; Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Kano &

207 Tomonaga, 2009, 2010, 2011, in press) and had recently been introduced to apes at WKPRC

208 (Kano, Call, & Tomonaga, in prep.). All apes were tested in an experimental booth. The

209 eye-tracking apparatus and experimenter were located outside the booth and were separated

210 from the apes via transparent acrylic panels at WKPRC and KUPRI. At GARI, the apparatus

211 and experimenter, who was highly familiar to the apes, stayed inside the booth. An eye tracker

212 with an infrared corneal reflection system measured participants' gaze movements. We used a

213 table-mounted apparatus at WKPRC and KUPRI (60 Hz; Tobii X120, Tobii Technology AB,

214 Stockholm, Sweden) and a monitor-integrated type at GARI (60 Hz; Tobii T60), both of which

215 were based on the same technology and thus possessed the same eye-tracking performance.

216 These eye trackers were equipped with wide-angle lenses (± 40 degrees in the semicircle above

217 the eye camera) and recorded both eyes, thereby allowing relatively large head movements by

218 participants. The eye tracker and 17-inch LCD monitor (1280 $\times$ 1024 pixels at WKPRC and

219 KUPRI and 1024 $\times$ 768 pixels at GARI) were mounted on a movable platform, and the

220 distance between the platform and the participants was adjusted to the point at which gaze was

221 most accurately recorded (approximately 60 cm). This flexible adjustment of the distance

222 between the platform and the participants enabled us to record the gaze movements of apes

223 without any head-restraining device. Four of the 11 apes (all juveniles) at WKPRC had

224 difficulty approaching the panel upon the request of experimenter. For this reason, we used a

225 nozzle and a tube attached to the panel, which continuously produced drops of grape juice

226 during the experiment, thereby keeping the participants' heads in front of the panel. Although

227 they were sipping grape juice during the presentation of stimuli, they did not attend to the

228 nozzle but freely moved their eyes. The experimenter at GARI sat beside the apes and held their

229 heads lightly during the recordings. The other apes at WKPRC and KUPRI sat still in front of

230 acrylic panels, and the experimenter encouraged them to face the eye tracker. The apes received

231 small pieces of fruit *ad libitum* before and after the calibration procedure and presentation of

232 pictures. No reward was given to reinforce any particular gaze behavior. At KUPRI, humans

233 were tested in the same experimental booth as apes, whereas humans were tested in another

234 room at GARI and WKPRC. Although the eye tracker recorded the eyes of humans and apes at

235 KUPRI and those of the apes at WKPRC through the transparent acrylic panel, we confirmed

236 that the acrylic panels (1.5–2 cm thick, absent of dirt or scratches) had no influence on the

237 eye-tracking data in the preliminary test for accuracy. Each participant's gaze was recorded as a

238 relative coordinate with respect to the monitor size (i.e., not as the gaze angle). One degree of

239 gaze angle corresponded to approximately 1 cm on the screen at a typical 60-cm viewing

240 distance.

241 An automated sequential calibration procedure was conducted for both apes and

242 humans. Five-point calibration was used for humans, but the calibration points were reduced to

243 two for apes to avoid interruption of the automated calibration process by participants averting

244 their gaze elsewhere. We asked humans to fixate on the small dot appearing on each calibration

245 point. For apes, we presented a small object or image at the calibration point for apes (a piece of

246 fruit or a small video clip; approx. 1-2 degree in width/height), thereby drawing their

247 spontaneous attention to the point. The calibration was repeated for the apes until maximum

248 accuracy was obtained. The calibration accuracy was checked *post-hoc* by presenting a small

249 object or image at several points on the screen and manually monitoring the participants' gaze

250 toward those points. To reduce the time required for a daily session, the same calibration data

251 were used for apes on separate days when the same level accuracy was achieved at the

252 beginning of a daily session. To avoid any calibration error due to changes in posture or eye

253 surface, the calibration accuracy was checked several times during the daily session, and the

254 calibration was repeated when the same accuracy was not obtained. To quantitatively estimate

255 the positional error, we conducted a preliminary session for each ape and human, in which we

256 recorded the position of the participant's gaze on the small object or image. We then calculated

257 the distance between the center of object/image and the recorded gaze position. The error was

258 found to be within 0.5–0.7-degree, on average, for all groups; this was sufficiently accurate for

259   the requirements of this study. Daily sessions lasted for 10–15 minutes for each ape and human.

260   **Procedure**

261   Each trial began after participants focused on a small red mark appearing at a central

262   position on the screen. We then presented a central fixation stimulus followed by a target

263   stimulus (approx. $4.8 \times 4.8°$ at a typical 60-cm viewing distance, approx. $9°$ apart). The

264   target appeared randomly to the left or right 560 ms after the onset of the trial (Fig. 1d). We

265   measured the time between target presentation and the initiation of a saccade directed at the

266   target (i.e., the saccade latency). Under the gap condition, the central fixation stimulus

267   disappeared 260 ms before target presentation, whereas the central fixation stimulus remained

268   under the overlap condition. The peripheral target stimulus remained for 940 ms, and thus each

269   trial lasted 1.5 s in total. Two types of stimulus, faces and objects, were initially used to test the

270   GARI and KUPRI groups. Another stimulus type, texture, was also used to test the WKPRC

271   group. Face stimuli included both ape and human faces. We prepared more than 50 exemplars of

272   each stimulus type. Different exemplars of the same stimulus type were presented at both

273   central and peripheral locations within each trial. Each exemplar was randomly selected from

274   the entire pool of exemplars. A previous study conducted at KUPRI (Kano and Tomonaga, in

275   press) involved six trials under each condition for each stimulus type ($6 \times 2 \times 2 = 24$ trials in

276   total). Because that study confirmed the minimal variance across trials, we reduced the number

277   of trials to three under each condition for each stimulus type at WKPRC ($3 \times 2 \times 3 = 18$ trials in

278   total) and GARI ($3 \times 2 \times 2 = 12$ trials in total).

279   We randomized the presentation order of conditions and stimulus type for each

280   participant. The entire session was conducted on a single day for humans at GARI (12 trials)

281   and KUPRI (24 trials) and on two separate days for humans at WKPRC (nine trials each day).

282   Six trials were conducted each day for apes at all facilities (3, 2, and 4 days in total at WKPRC,

283   GARI, and KUPRI, respectively). Preliminary analysis, however, revealed no significant effect

284   of day among those apes and humans tested on separate days.

285   After the completion of the whole session, we repeated trials in which participants

286   prematurely shifted their gaze before the onset of the peripheral target. If the same occurred in

287   those repeated trials, we excluded those trials from the analysis. This procedure resulted in the

288   total data loss of 0.0%, 1.3% and 19.8% of all trials for humans, gorillas, and orangutans,

289   respectively, at WKPRC; 6.9% and 11.4% for humans and chimpanzees, respectively, at GARI;

290   and 0.2% and 2.0% for humans and chimpanzees, respectively, at KUPRI. We found no bias for

291   a particular stimulus type or condition in those excluded trials. Additionally, for the quantitative

292   analysis, we excluded the trials in which the saccade latency of participants was longer than the

293   average for all trials (281 ms) plus 2.5 standard deviations (274 ms; i.e., longer than 555 ms) or

294   in which the participants did not shift their gaze by the end of a trial. This resulted in the total

295   data loss of 7.6%, 1.4%, and 0.0% of all trials for humans, gorillas and orangutans, respectively,

296   at WKPRC; 4.4 and 4.7% for humans and chimpanzees, respectively, at GARI; and 4.8% and

297   1.5% for humans and chimpanzees, respectively, at KUPRI. These trials appeared primarily

298   under the overlap condition, which probably reflects a characteristic of that condition, as

299   discussed below. We found no bias for a particular stimulus type in these excluded trials.

300   **Results**

301   Figure 2 presents the saccade latency of participants as a function of stimulus type

302   (face, object, and texture) and condition (gap and overlap). We conducted three separate

303   analyses of variance (ANOVAs) for the WKPRC, GARI, and KUPRI groups. We found a

304   significant interaction between condition and species in the WKPRC group (gorillas, orangutans,

305   and humans) ($F(2, 24) = 11.10$, $P < 0.001$, $\eta^2 = 0.48$), which was explained by the difference

306   in saccade latency among the species being more evident under the overlap ($F(2, 24) = 23.15$, P

307   < 0.001, $\eta^2 = 0.65$) than under the gap ($F(2, 24) = 3.92$, $P = 0.033$, $\eta^2 = 0.24$) condition.

308   Comparisons between orangutans and humans, between gorillas and humans, and between

309   gorillas and orangutans showed interactions between condition and species that were significant

310   ($F(1, 21) = 19.50$, $P < 0.001$, $\eta^2 = 0.48$), not significant ($F(1, 18) = 2.12$, $P = 0.16$, $\eta^2 = 0.10$),

311   and marginally significant ($F(1, 9) = 4.80$, $P = 0.056$, $\eta^2 = 0.34$), respectively. The analysis by

312   species showed that the effect of condition was significant for humans ($F(1, 15) = 159.97$, $P <$

313   0.001, $\eta^2 = 0.91$) and gorillas ($F(1, 3) = 615.80$, $P < 0.001$, $\eta^2 = 0.99$) and marginally

314   significant for orangutans ($F(1, 6) = 4.54$, $P = 0.07$, $\eta^2 = 0.43$). The effect of stimulus type was

315   not significant, either main effect or interaction with condition ($P > 0.05$).

316   We found a significant interaction between condition and species at GARI

317   (chimpanzees and humans) ($F(1, 12) = 14.51$, $P = 0.002$, $\eta^2 = 0.54$), which can be explained

318   by the species difference in saccade latency being more evident under the overlap ($F(1, 12) =$

319   7.72, $P = 0.017$, $\eta^2 = 0.39$) than the gap ($F(1, 12) = 3.77$, $P = 0.076$, $\eta^2 = 0.23$) condition.

320   The analyses by species showed that the effect of condition was significant for humans ($F(1, 5)$

321    $= 24.17$, $P = 0.004$, $\eta^2 = 0.82$) but not for chimpanzees ($F(1, 7) = 0.71$, $P = 0.42$, $\eta^2 = 0.093$).

322   The effect of stimulus type was not significant, either main effect or interaction with condition

323   ($P > 0.05$).

324   We found a significant interaction between condition and species at KUPRI

325   (chimpanzees and humans) ($F(1, 24) = 15.72$, $P = 0.001$, $\eta^2 = 0.39$), which can be explained

326   by the species difference in saccade latency being more evident under the overlap ($F(1, 24) =$

327   8.38, $P = 0.008$, $\eta^2 = 0.25$) than under the gap ($F(1, 24) = 0.002$, $P = 0.96$, $\eta^2 < 0.001$)

328   condition. The analyses by species showed that the effect of condition was significant for both

329   humans ($F(1, 17) = 59.05$, $P = 0.004$, $\eta^2 = 0.77$) and chimpanzees ($F(1, 7) = 12.25$, $P = 0.010$,

330    $\eta^2 = 0.63$), although the difference was small for chimpanzees (13 ms). We found a significant

331 effect of stimulus type ($F(1, 24) = 5.69$, $P = 0.025$, $\eta^2 = 0.19$) in the KUPRI group, although

332 the difference was small (8 ms).

333   We did not have a sufficient number of individual samples to examine the effects of

334 age and sex, but the exclusion of juveniles and males did not alter the aforementioned statistical

335 results. The effect of laterality (either right or left) was not significant in terms of either main

336 effects or interactions ($P > 0.05$) at any of the facilities. We confirmed the same statistical

337 results even when we limited the analyses to the first six trials at all facilities.

338   Figure 3 presents the distribution of saccade latencies from 0 to 500 ms. Apes and

339 humans showed a skewed distribution in their saccade latencies, with the peaks around 200 ms.

340 The distributions were similar across species under the gap condition. In contrast, the

341 distribution was skewed more leftward in apes than in humans, and the distribution of the

342 saccade latencies in humans was characterized by a long right tail exceeding 300 ms under the

343 overlap condition. This species difference was most pronounced between humans and

344 chimpanzees/orangutans, and the results for gorillas were between these two extremes.

345

346   **Discussion**

347   Humans, chimpanzees, gorillas, and orangutans from three research facilities were

348 compared in terms of their saccade latencies using the gap–overlap paradigm. Although all

349 species showed similar saccade latencies under the gap condition, the species clearly differed

350 from one another under the overlap condition. In general, humans showed longer saccade

351 latencies did than the other apes under that condition, which is explained by saccade latencies

352 longer than 300 ms being more frequent in humans than in other apes. We found little evidence

353 that stimulus type affected latencies.

354   The similarities among the various species under the gap condition suggest common

355 perceptual and motor abilities for responding to peripherally presented stimuli (e.g., the

356   sensitivity to salience of peripheral vision, the execution of saccadic eye movements).

357   Relatively consistent saccade latencies under the gap condition have also been observed among

358   human infants at various developmental stages (Hood & Atkinson, 1993; M. Matsuzawa &

359   Shimojo, 1997) and in autistic and typically developing children (Landry & Bryson, 2004).

360   These phylogenetic, developmental, and clinical consistencies suggest a relatively primitive or

361   fundamental operation underlying saccade generation under the gap condition.

362   In contrast, humans and apes differed under the overlap condition. Unlike

363   chimpanzees and orangutans, humans showed a clear overlap (or gap) effect. Interestingly,

364   gorillas showed a pattern that was somewhat similar to that displayed by humans in this regard.

365   Given that the species were similar in their saccade latencies under the gap condition, the

366   species differences under the overlap condition suggest the use of differential strategies for

367   dealing with the competition between fixation and initiation of a saccade. An alternative account

368   is that the participants anticipated the appearance of the target *via* the offset of the fixation

369   stimulus (or the gap) (Reuter-Lorenz, Hughes, & Fendrich, 1991; L. E. Ross & Ross, 1980).

370   However, this account is unlikely in the context of this study because any of our participants

371   were not trained in the task, as will be discussed in greater detail below.

372   Our study investigated participants' spontaneous (or "natural") pattern of gaze shifting

373   rather than their ability to control their gaze. Thus, they viewed the stimuli freely without any

374   instruction or training and without any head-restraining device. This arrangement differed

375   critically from those used in previous studies with instructed/trained humans and macaques as

376   subjects (e.g., (Fischer & Boch, 1983; Fischer & Ramsperger, 1984) and resembles those used

377   in previous studies with untrained human infants as subjects (Hood & Atkinson, 1993; M.

378   Matsuzawa & Shimojo, 1997). Several lines of evidence indicate that the participants in this

379   study showed their spontaneous patterns of gaze shifting. First, differing amounts of experience

380   in participating in computerized tasks or exposure to computer screens did not affect the data

381   obtained from apes. Second, the different reward schedule for apes (receiving a reward for

382   participating in the experiments, but not for their gaze behaviors) did not affect the results of

383   this study. Third, we observed few express or anticipatory saccades (fewer than 100 ms),

384   phenomena that have been frequently observed in trained subjects when the location at which

385   the target appeared was predictable (Fischer & Weber, 1993). Finally, analysis of the first six

386   trials of the session, in which an effect for (uninstructed) training or learning was unlikely,

387   yielded results identical to those for the entire session. Interestingly, the untrained humans in

388   this study showed a skewed distribution of saccade latency, with a long right tail extending

389   beyond 300 ms under the overlap condition, which has been commonly observed in humans

390   who were freely viewing naturalistic scenes. In contrast, trained humans in the previous studies

391   have often shown a symmetrical or inverted bell-shaped distribution of saccade latency under

392   the overlap condition (Braun & Breitmeyer, 1988; Fischer & Weber, 1993; Reuter-Lorenz, et al.,

393   1991).

394   Despite its theoretical importance, the free viewing design of this experiment may also

395   have shortcomings given that the possible differences in the motivational states of each species

396   may have had certain influence on the results (although we did not find any behavioral evidence

397   to show such motivational differences). We also recognize that genuine natural patterns of gaze

398   movements can be observed only during the course of daily activities. Thus, further studies

399   simulating naturalistic contexts (e.g., use of head-mounted eye-tracking devices) (Land, Mennie,

400   & Rusted, 1999) are necessary.

401   We found no effect of stimulus type on saccade latency. Thus, the saccade latency

402   elicited by the gap–overlap paradigm in this study may have reflected a habitual or

403   well-automated process for saccade generation rather than an immediate outcome of processing

404   meaningful stimuli. Kano & Tomonaga (in press) found a similar result in chimpanzees and

405   humans. That is, when an object and (a seemingly more salient) face were presented at central

406   and peripheral locations, respectively, under one condition and in the opposite locations,

407   respectively, under the other condition, the saccade latencies of both species were shorter when

408   the object was presented centrally and the face was presented peripherally than *vice versa*,

409   whereas the effect of overlap remained the same under both conditions. Therefore, although the

410   saccade latency of participants seems to be influenced by the stimulus type, the effect of overlap

411   seems to be influenced by the competition between the two stimuli, rather than by the stimulus

412   type *per se*.

413   Somewhat surprisingly, among the nonhuman great apes, gorillas showed the clearest

414   overlap effect. However, the small sample size ($n = 4$) precludes our reaching a definitive

415   conclusion, and further studies are necessary to confirm this result. One interpretation for this

416   possible species difference is the possible behavioral or cognitive uniqueness of gorillas among

417   the great apes, which has been suggested by previous studies (Peignot & Anderson, 1999;

418   Suarez & Gallup, 1981). Alternatively, gorillas may have been somewhat neophobic to the

419   presented stimuli. That is, their attention (or effective visual field) may have been temporarily

420   narrowed to the central stimuli, rendering them less sensitive to the appearance of peripheral

421   stimuli.

422   At least two ultimate (or evolutionary) interpretations are possible with regard to the

423   benefits (and costs) of the adoption of such specific visual strategies by humans and apes. First,

424   the specific visual strategy used by each species may have survival value in specific

425   socioecological environments. For example, it may be more beneficial to scan visual fields more

426   quickly by shifting gazes earlier in the context of arboreal living, where objects and animals

427   tend to appear in an unexpected manner, as may be the case for chimpanzees and orangutans. To

428   clarify the effect of socioecological factors, additional comparative studies in various primate

429   species are necessary.

430   Second, the pronounced effect of overlap (or competition) in humans may reflect their

431   unique means of information processing among hominids. That is, rather than constantly

432   retrieving new information, humans may keep their gaze stationary and thereby promote

433   time-consuming internal processing (e.g., for the sake of categorical and language processing).

434   In contrast, apes may switch their focus of attention (i.e., the fovea) more frequently than

435   humans and may thereby cover a wider visual field via gaze movements. Thus, a trade-off

436   between the depth and breadth of information processing/retrieval may occur in human and

437   nonhuman apes. However, two limitations must be considered with regard to this hypothesis.

438   First, no quantitative information is available about the information retrieval/processing in these

439   species in this study. Second, the hypothesis does not explain the effect of the overlap in gorillas

440   (although the effect was somewhat smaller in gorillas than in humans). One could assume that

441   this overlap effect in gorillas derived from a different cause than that in humans, as explained

442   above; however, further studies are necessary to clarify this issue.

443   In conclusion, this study found phylogenetic similarities and differences in saccade

444   latencies among hominid species. Although all species seem to have similar perceptual and

445   motor mechanisms for performing saccades, the species may differ in their strategies for coping

446   with the competition between two activities involving fixation and saccade initiation. In

447   particular, humans seem to spend a longer time resolving this competition than the other great

448   apes, which may reflect this species' unique means of information processing.

449

450

462

463

464

References

465

466 Baizer, J. S., & Bender, D. B. (1989). Comparison of saccadic eye movements in humans and

467   macaques to single-step and double-step target movements. *Vision Res., 29*(4), 485-495.

468 Berg, D. J., Boehnke, S. E., Marino, R. A., Munoz, D. P., & Itti, L. (2009). Free viewing of

469   dynamic stimuli by humans and monkeys. *J. Vision, 9*(5), 1-15.

470 Braun, D., & Breitmeyer, B. G. (1988). Relationship between directed visual attention and

471   saccadic reaction times. *Exp. Brain. Res., 73*(3), 546-552.

472 Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *J. Zool.,*

473   *183*(1), 1-39.

474 Dias, E. C., & Bruce, C. J. (1994). Physiological correlate of fixation disengagement in the

475   primate's frontal eye field. *J. Neurophysiol., 72*(5), 2532-2537.

476 Dorris, M. C., & Munoz, D. P. (1995). A neural correlate for the gap effect on saccadic reaction

477   times in monkey. *J. Neurophysiol., 73*(6), 2558-2562.

478 Dorris, M. C., Pare, M., & Munoz, D. P. (1997). Neuronal activity in monkey superior colliculus

479   related to the initiation of saccadic eye movements. *J. Neurosci., 17*(21), 8566-8579.

480 Farroni, T., Simion, F., Umilt, C., & Barba, B. D. (1999). The gap effect in newborns. *Dev. Sci.,*

481   *2*(2), 174-186.

482 Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing

483   and competitive inhibition. *Behav. Brain Sci., 22*(04), 661-674.

484 Fischer, B., & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in

485   the monkey. *Brain Res., 260*(1), 21-26.

486 Fischer, B., & Ramsperger, E. (1984). Human express saccades: extremely short reaction times

487   of goal directed eye movements. *Exp. Brain. Res., 57*(1), 191-195.

488   Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behav. Brain Sci.,*

489   *16*(03), 553-567.

490   Hanes, D. P., & Schall, J. D. (1996). Neural control of voluntary movement initiation. *Science,*

491   *274*(5286), 427-430.

492   Hattori, Y., Kano, F., & Tomonaga, M. (2010). Differential sensitivity to conspecific and

493   allospecific cues in chimpanzees and humans: A comparative eye-tracking study. *Biol.*

494   *Lett., 6*(5), 610-613.

495   Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., & Fujita, S. (2010). Facial perception of

496   conspecifics: chimpanzees (Pan troglodytes) preferentially attend to proper orientation

497   and open eyes. *Anim. Cogn., 13*(5), 679-688.

498   Hood, B. M., & Atkinson, J. (1993). Disengaging visual attention in the infant and adult. *Inf.*

499   *Behav. Dev., 16*(4), 405-422.

500   Idani, G., & Hirata, S. (2006). Studies at the Great Ape Research Institute, Hayashibara. . In D.

501   A. Washburn (Ed.), *Primate perspectives on behavior and cognition* (pp. 29-36).

502   Washington: American Psychological Association.

503   Johnson, M. H. (1990). Cortical maturation and the development of visual attention in early

504   infancy. *J. Cogn. Neurosci., 2*(2), 81-95.

505   Kalesnykas, R. P., & Hallett, P. E. (1987). The differentiation of visually guided and anticipatory

506   saccades in gap and overlap paradigms. *Exp. Brain. Res., 68*(1), 115-121.

507   Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures: a comparative

508   eye-tracking study. *Proc. Roy. Soc. B., 276*(1664), 1949-1955.

509   Kano, F., & Tomonaga, M. (2010). Face scanning in chimpanzees and humans: continuity and

510   discontinuity. *Anim. Behav., 79*(1), 227-235.

511   Kano, F., & Tomonaga, M. (2011). Perceptual mechanism underlying gaze guidance in

512   chimpanzees and humans. *Anim. Cogn., 14*(3), 377-386.

513   Kano, F., & Tomonaga, M. (in press). Species difference in the timing of gaze movement

514   between chimpanzees and humans. *Anim. Cogn.*

515   Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the

516   control of activities of daily living. *Perception, 28*(11), 1311-1328.

517   Landry, R., & Bryson, S. E. (2004). Impaired disengagement of attention in young children with

518   autism. *J. Child Psychol. Psychiat., 45*(6), 1115-1122.

519   Müri, R. M., Rivaud, S., Gaymard, B., Ploner, C. J., Vermersch, A. I., Hess, C. W., et al. (1998).

520   Role of the prefrontal cortex in the control of express saccades. A transcranial magnetic

521   stimulation study. *Neuropsychologia, 37*(2), 199-206.

522   Matsuzawa, M., & Shimojo, S. (1997). Infants' fast saccades in the gap paradigm and

523   development of visual attention. *Inf. Behav. Dev., 20*(4), 449-455.

524   Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). *Cognitive development in chimpanzees*.

525   Tokyo: Springer.

526   Munoz, D. P., & Everling, S. (2004). Look away: the anti-saccade task and the voluntary control

527   of eye movement. *Nature Rev. Neurosci., 5*(3), 218-228.

528   Munoz, D. P., & Wurtz, R. H. (1993a). Fixation cells in monkey superior colliculus. I.

529   Characteristics of cell discharge. *J. Neurophysiol., 70*(2), 559-575.

530   Munoz, D. P., & Wurtz, R. H. (1993b). Fixation cells in monkey superior colliculus. II.

531   Reversible activation and deactivation. *J. Neurophysiol., 70*(2), 576-589.

532   Peignot, P., & Anderson, J. R. (1999). Use of experimenter-given manual and facial cues by

533   gorillas (*Gorilla gorilla*) in an object-choice task. *J. Comp. Psychol., 113*(3), 253-260.

534   Reuter-Lorenz, P. A., Hughes, H. C., & Fendrich, R. (1991). The reduction of saccadic latency

535   by prior offset of the fixation point: an analysis of the gap effect. *Atten. Percept.*

536   *Psychophys., 49*(2), 167-175.

537   Ross, L. E., & Ross, S. M. (1980). Saccade latency and warning signals: Stimulus onset, offset,

538   and change as warning events. *Atten. Percept. Psychophys., 27*(3), 251-257.

539   Ross, S. M., & Ross, L. E. (1981). Saccade latency and warning signals: effects of auditory and

540   visual stimulus onset and offset. *Atten. Percept. Psychophys., 29*(5), 429-437.

541   Saslow, M. G. (1967). Effects of components of displacement-step stimuli upon latency for

542   saccadic eye movement. *J. Opt. Soc. Am., 57*(8), 1024-1029.

543   Shepherd, S. V., Steckenfinger, S. A., Hasson, U., & Ghazanfar, A. A. (2010). Human-monkey

544   gaze correlations reveal convergent and divergent patterns of movie viewing. *Curr. Biol.,*

545   *20*(7), 649-656.

546   Stechler, G., & Latz, E. (1966). Some observations on attention and arousal in the human infant.

547   *J. Am. Acad. Child Psychiatry, 5*, 517-525.

548   Suarez, S. D., & Gallup, G. G. (1981). Self-recognition in chimpanzees and orangutans, but not

549   gorillas. *J. Hum. Evol., 10*(2), 175-188.

550

551

552

553

Table 1

Distribution of Saccade Latency (ms) of Individuals. Each individual engaged in six, nine, and 12 trials respectively at WKPRC, GARI, and KUPRI.

	151–200	201–250	251–300	301–350	351–400	401-450	total
Gap condition							
WKPRC							
Human		7	9				16
Gorilla	1	2	1				4
Orangutan	2	5					7
GARI							
Human		4	2				6
Chimpanzee		2	4	2			8
KUPRI							
Human	3	12	3				18
Chimpanzee	1	5	1	1			8
Overlap condition							
WKPRC							
Human				5	8	3	16
Gorilla			2	1	1		4
Orangutan		4	2	1			7
GARI							
Human			2	2		2	6
Chimpanzee		1	5	2			8
KUPRI							
Human		4	4	6	2	2	18
Chimpanzee		6	1	1			8

554

555

556

557

558 Figure captions

559 *Figure 1*. (a)–(c) an ape on an eye tracker at WKPRC (Wolfgang Köhler Primate Research

560 Center, Germany), GARI (Great Ape Research Institute, Japan), and KUPRI (Primate Research

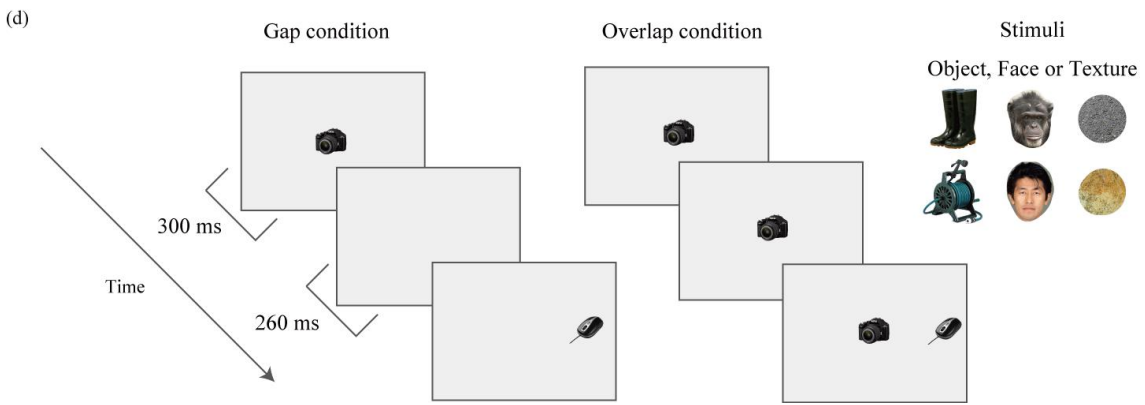561 Institute, Kyoto University, Japan), respectively. (d) Gap–overlap paradigm used in this study.

562

563 *Figure 2*. Saccade latency (ms) as a function of condition (gap and overlap) and stimulus type

564 (face, object, and texture) in humans, chimpanzees, gorillas, and orangutans from three research

565 facilities. Error bars represent ±95% confidence intervals.

566

567 *Figure 3*. Frequency distribution of saccade latencies from 0 to 500 ms in four species from

568 three research facilities. The data were pooled for all participants and stimulus types. The bin
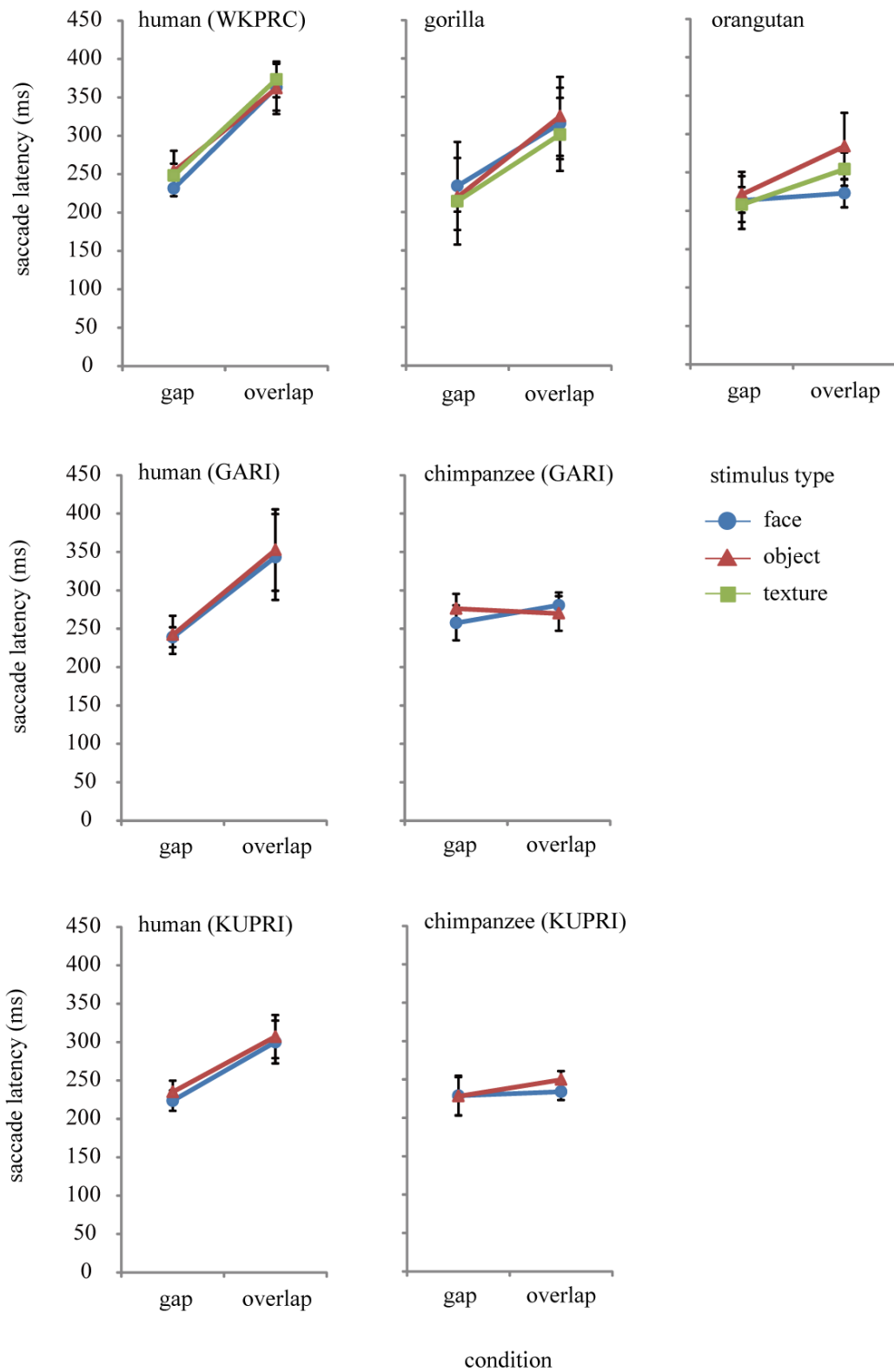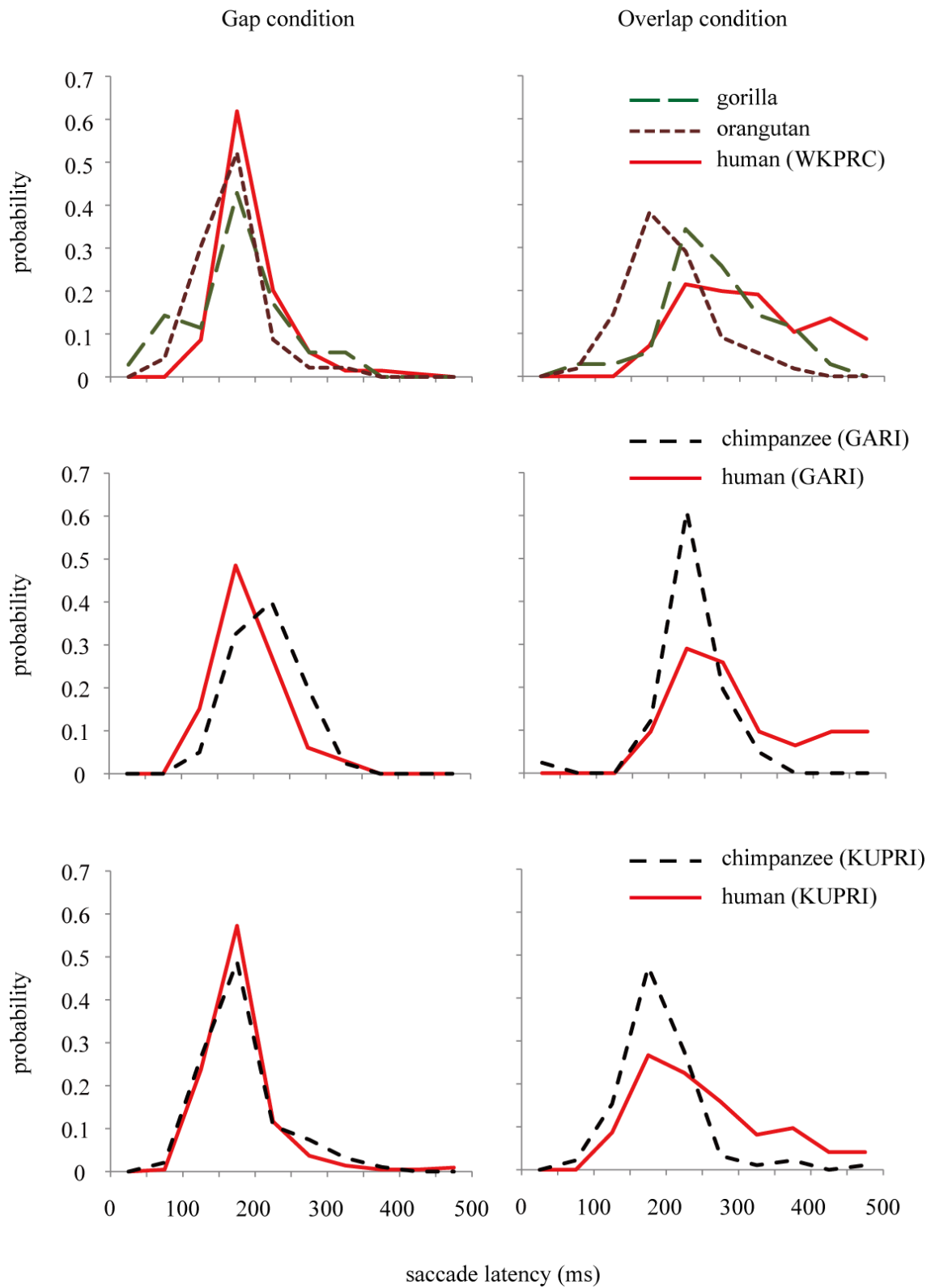
569 was 50 ms.

570

571

(a) (b) (c)

(d)

Gap condition   Overlap condition   Stimuli

Object, Face or Texture

Time

300 ms

260 ms

572

573   Figure 1

574

575   Figure 2

Gap condition Overlap condition

gorilla
orangutan
human (WKPRC)

chimpanzee (GARI)
human (GARI)

chimpanzee (KUPRI)
human (KUPRI)

saccade latency (ms)

576

577   Figure 3

578

579