What did you choose just now? Chimpanzees' short-term retention of memories of their own behavior

Many recent comparative studies have addressed "episodic" memory in nonhuman animals, suggesting that birds, rodents, great apes, and others can remember their own behavior after at least a half-day delay. By contrast, despite numerous studies regarding long-term memory, few comparable studies have been conducted on short-term retention for own behavior. In the current study, we addressed the following question: Do chimpanzees remember what they have just done? Four chimpanzees performed matching-to-sample and visual search tasks on a routine basis and were occasionally (every four sessions) given a "recognition" test immediately after their response during visual search trials. Even though these test trials were given very rarely, all four chimpanzees chose the stimulus they selected in the visual search trials immediately before the test trial significantly more frequently than they chose the stimulus they selected in another distractor trial. Subsequent experiments ruled out the possibility that preferences for the specific stimuli accounted for the recognition test results. Thus, chimpanzees remembered their own behavior even within a short-term interval. This type of memory may involve the transfer of episodic information from working memory to long-term episodic-like memory (i.e., an episodic buffer).

2   What did you choose just now?

3   Chimpanzees' short-term retention of memories of their own behavior

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8   Episodic memory is defined as long-term memory for personally experienced events (Tulving, 1985).
9   Some researchers have suggested that episodic memory should contain information about "what" occurred,
10   "when" it occurred, and "where" it occurred (e.g., Clayton & Dickinson 1998; Skov-Rackette et al., 2006). Due
11   to recent advances in comparative cognitive science, many species have been found to show some degree of
12   this "episodic" memory (e.g., food-caching jays (Clayton & Dickinson, 1998), rhesus macaques (Hampton et
13   al., 2005; Hoffman et al., 2009), rats (Crystal & Babb, 2008), and dolphins (Marcado III et al., 1998). For
14   example, great apes showed "episodic" memory (Menzel, 1998; Schwartz et al., 2005; Martin-Ordas, 2010).
15   Menzel (1998) reported that one symbol-trained chimpanzee remembered where an object was hidden in an
16   outdoor enclosure for 16 hours.

17   However, controversy about whether these examples of long-term memory satisfy the criteria of
18   human-like episodic memory persists (Suddendorf & Busby, 2003; Tulving, 2005). Thus, the term "episodic-
19   like" memory is often used to describe this type of memory in nonhuman animals (e.g., Clayton & Dickinson,
20   1998). One reason for this is that many of the studies mentioned above seemingly lack components of "what,"
21   "when," and "where." For example, Hampton et al. (2005) administered a memory task to rhesus monkeys that
22   was functionally equivalent to those used by Clayton and Dickinson (1998); however, unlike the latter's results
23   with jays, Hampton et al. found intact memory for the "what" and "where" of past events but not for the
24   "when."

25   Most previous studies of episodic-like memory in nonhuman animals have focused intensively on the
26   "long-term" retention of episodes, primarily because of the definition of episodic memory mentioned above.
27   However, the other aspects of memory of past episodes should also be examined. One neglected area is the
28   transition from working (or short-term) memory to long-term episodic-like memory. In terms of human
29   working memory, Baddeley (2000) proposed the "episodic buffer," a link between the working and long-term
30   memory systems. However, how the short-term retention of working memories is crystalized into long-term
31   episodic-like memories in nonhuman animals remains unclear (cf. Zhou et al., 2012). To address this issue,
32   research regarding the short-term properties of episodic-like memory is necessary.

33   Another aspect of episodic-like memory is the retroactive retrieval of incidentally encoded
34   information. Humans can recall past events that have not been actively encoded, and several researchers have
35   recently become interested in this aspect of memory in nonhuman animals, conducting relevant experimental
36   studies (dogs: Fujita et al., 2012; rats: Zhou et al., 2012; pigeons: Singer & Zentall, 2007; Zentall et al., 2001,
37   2008).

38   Zentall and his colleagues (Singer & Zentall, 2007; Zentall et al., 2001, 2008) tested pigeons for
39   episodic-like memory under the matching-to-sample paradigm. For example, pigeons were trained to match the
40   left position to red and the right position to green (position–color matching) and to match yellow to vertical
41   lines and blue to horizontal lines (color–line matching). After learning to perform these two types of matching
42   tasks, they completed probe trials in which red and green choices were occasionally presented after participants
43   chose the vertical or horizontal stimulus in the color–line trials. When pigeons selected the left key for vertical
44   lines, they chose the red key and vice versa. Pigeons exhibited significantly better performance than would be

45 expected by chance (71.6%) during such probe trials (Singer & Zentall, 2007). This result indicates that
46 pigeons remember their own behavior even when they are unexpectedly prompted to do so. The same
47 experimental paradigm was also used by Zhou et al. (2012), who also reported that rats can respond correctly to
48 unexpected probe trials during maze-learning tasks. Some researchers have emphasized this unexpectedness in
49 the episodic memory system (Zentall et al., 2008); however, pigeons underwent eight probe trials in each of 24
50 104-trial sessions in Singer and Zentall's study (2007). Given such a relatively large number of probe trials,
51 pigeons might have learned the specific procedure for the probe trials or the probe trials might have become
52 less unexpected.

53 Consistent with the approach adopted by Zentall et al. (Singer & Zentall, 2007; Zentall et al., 2001,
54 2008) and Zhou et al. (2012), we also focused on chimpanzees' retroactive retrieval of incidentally encoded
55 information. To this end, we tested the short-term retention ability of chimpanzees for their own behavior.
56 Chimpanzee participants performed matching-to-sample and visual search trials. In the matching trials, the
57 chimpanzees were initially shown a single sample stimulus on a touch-screen monitor and were required to
58 touch it. After a delay interval, two choice stimuli, one of which was the same as the sample, were presented. In
59 contrast, the search display, which contained one target and five distractor stimuli, was presented during the
60 visual search trials, and the chimpanzees were required to touch an odd item among the uniform distractors. As
61 a probe test, chimpanzees were occasionally presented with two stimuli after they selected the target in the
62 visual search trial. One of the stimuli was the one that the subject had chosen from the search display, and the
63 other differed from the stimuli in the previous search display. These probe trials were presented once per test
64 session, and the test session appeared every four baseline sessions to maintain the rarity and unexpectedness of
65 the probe trials. If the chimpanzees remembered their own choice just before the probe test, they could choose
66 the "correct" stimulus during the probe trial.

METHODS

Participants

69 Four chimpanzees (*Pan troglodytes*) from the Primate Research Institute, Kyoto University (KUPRI),
70 participated: Pendesa (female, 28 years old at the onset of the present experiment), Ayumu (male, 7 years old),
71 Cleo (female, 7 years old), and Pal (female, 7 years old). As these chimpanzees have a long history of
72 comparative cognitive experiments involving matching-to-sample and visual search tasks (Fagot & Tomonaga,
73 1999; Goto et al., 2012; Tomonaga 2001; Tomonaga & Imura, 2010; and Matsuzawa et al., 2006), it was not
74 necessary to train them for these tasks before the present experiments. They live in a social group of 14
75 individuals in an environmentally enriched outdoor compound (770 m^2) connected to the experimental room by
76 a tunnel.

Ethical Considerations

78 The care and use of the chimpanzees adhered to the 2nd edition of the Guide for the Care and Use of
79 Laboratory Primates issued by KUPRI in 2002. The design of the current research was approved by the Animal

80 Welfare and Animal Care Committee of KUPRI and by the Animal Research Committee of Kyoto University

81 (Approval No. 07-1554). All procedures adhered to the Japanese Act on the Welfare and Management of

82 Animals.

83 **Apparatus and Stimuli**

84 Experimental sessions were conducted in a booth (1.8 × 2.15 × 1.75 m) in an experimental room. A

85 17-inch LCD monitor (IO-Data, Tokyo, Japan, Model LCD-AD171F-T, 1280 × 1024 pixels, pixel size: 0.264 ×

86 0.264 mm) with a touch screen was placed on a wall of the booth (Fig. 1) at a viewing distance of

87 approximately 40 cm. A food reward was delivered via a food tray connected to a universal feeder located

88 under the monitor (Bio-Medica Ltd., Osaka, Japan, Model BUF-310). Experimental events and data collection

89 were controlled by a PC using a customized program written in Microsoft Visual Basic 6.0©.

90 We prepared 2,500 color photographs (6.0 × 6.0 cm in size) depicting various kinds of objects and

91 scenes as stimuli. We did not control any of the parameters of these pictures, such as the distribution of colors,

92 average brightness, and so on. These stimuli were presented only once to each chimpanzee.

93 **Procedure**

94 **Matching-to-sample trials**

95 Figure 2A shows the flow of a matching-to-sample trial. In each trial, a blue square (3.0 × 3.0 cm)

96 was presented at the bottom center of the monitor as a warning signal. When the chimpanzee touched the

97 square, it disappeared, and a sample stimulus was presented at a random position on the monitor. Touching the

98 sample stimulus terminated it, and a green circle (3.0 cm in diameter) was presented at a random location on

99 the monitor. A single touch to this circle was followed by the presentation of the two choice stimuli. This

100 interval was defined as a self-paced delay interval. Touching the choice stimulus that was the same as the

101 sample delivered a food reward (a piece of apple or a raisin) followed by a chime. If the chimpanzee chose a

102 stimulus that differed from the sample, this response was recorded as an error, and a buzzer sounded. The

103 intertrial interval was 3 s.

104 **Visual search trials**

105 As in the matching trials, each trial began with the presentation of a warning signal. After touching

106 this, the search display was presented. We prepared two types of visual search trials. In the homogeneous-

107 distractor trials, one target and five identical distractors were presented as a search display (Fig. 2B), whereas

108 six different stimuli appeared in the heterogeneous-distractor trials (Fig. 2C). The chimpanzees were required to

109 touch the target stimulus during the homogeneous-distractor trials, but any choice of stimulus was non-

110 differentially reinforced during the heterogeneous-distractor trials. When the chimpanzees touched the target

111 during the homogeneous-distractor trials and touched any stimulus during the heterogeneous-distractor trials,

112 the search display disappeared, and a green circle was presented at a random location, as in the matching trials.

113 Touching the green circle delivered a food reward accompanied by a chime. If the chimpanzees touched one of

114 the distractors during the homogeneous trials (error response), the search display disappeared, and a buzzer

115 sounded. The presentation of the green circle was intended to equalize the flow of the trials across the

116 matching, visual search, and test trials (described later).

117 **"What-did-you-choose" test**

118  The third type of trial was called a "what-did-you-choose" test trial (Figs. 2D and 2E). In this trial,

119 two choice stimuli occasionally appeared after the self-paced delay interval following the visual search task.

120 One of the two stimuli was the one that the subject chose from the search display, and the other was the one that

121 was different from any stimulus in the previous search display. Any touch to a stimulus caused the termination

122 of the stimuli, but was not followed by feedback or a food reward. It should be noted that if the chimpanzees

123 made an error during the homogeneous-distractor visual search component of the test trials, the subsequent

124 two-choice component was cancelled.

125  Each baseline session consisted of 28 trials, in which the first four trials were matching trials. Among

126 the remaining 24 visual search trials, 16 were homogeneous- and eight were heterogeneous-distractor trials.

127 These trials were randomly presented. Test sessions were presented after every four sessions of the baseline

128 trials, and either a homogeneous or heterogeneous test trial appeared as 29th trial. Each chimpanzee received 64

129 test sessions, i.e., one session per day, four or five times per week, yielding 64 test trials (32 for each type of

130 test trial). All stimulus positions were randomly assigned across trials. The correct stimulus position was also

131 randomized among trials.

132 **Control tests**

133  The present experiment used various kinds of stimuli, which were not controlled for color, brightness,

134 or content. Thus, some stimuli may have been more salient than others based on these low-level features. As is

135 the case for humans, chimpanzees' visual search patterns are controlled by salient "pop-out" features

136 (Tomonaga, 1993, 2001). To evaluate the effect of this phenomenon, we prepared two types of control tests. If

137 degree of salience controlled choices, one would hypothesize that (1) chimpanzees would choose the same

138 stimulus they had chosen previously when only the two choice stimuli presented during the "what-did-you-

139 choose" test trials were presented again and that (2) chimpanzees would choose the same stimulus they had

140 chosen previously when the visual search display that had appeared during the test trials was presented again. If

141 the chimpanzees' behavior were not governed simply by these non-memory stimulus factors, they would

142 choose randomly in the control test trials.

143  In the first type of control test trial, called the no-sample two-choice test, only two stimuli were

144 presented (Fig. 2F). These two stimuli were identical to those that appeared in the choice phase of the "what-

145 did-you-choose?" test trials (with both homogeneous- and heterogeneous-distractor visual search displays)

146 given to each chimpanzee. If the choice response in the test trial were controlled by the chimpanzees' stimulus

147 preference, they would choose the same stimulus selected during the test trials. In the other control test, we

148 presented the same search display that had been presented in the previous "what-did-you-choose" test trials

149 with homogeneous and heterogeneous distractors, but in the form of a visual search trial, to determine whether

150 the chimpanzees chose the stimulus based on their own stimulus preferences under the heterogeneous-distractor

151 condition. If this were the case, the chimpanzees would choose the same stimulus when the same search display

152 was presented. We administered 32 additional test sessions to each chimpanzee. Each session consisted of two

153 matching trials, 20 visual search trials (12 with homogeneous distractors and eight with heterogeneous

154 distractors), two no-sample two-choice test trials, and two visual search test trials. Test trials were presented

155 randomly during a session, and no food reward or feedback was given after the choices in the test trials.

RESULTS

157   All data from each chimpanzee are presented in the supplementary file. All chimpanzees completed

158 the experimental sessions (258 sessions on average, range: 255–260) within 578 days on average (range: 481–

159 664); test trials were given every 9 days. Participants performed very accurately on matching (97.1%, standard

160 error of the mean, $SEM = 0.7$) and homogeneous visual search (94.0%, $SEM = 1.3$) trials. The self-paced delay

161 interval lasted 1.05 sec, on average, across all types of trials. Figure 3 (black bars) shows the results of the test

162 trials. All chimpanzees chose the stimulus that was chosen immediately before significantly more often than

163 they chose the other stimulus under both distractor conditions (the significance level at 0.05 was 65.6%,

164 binomial test): 77.4% ($SEM = 1.5$) for the homogeneous- and 85.2% ($SEM = 7.0$) for the heterogeneous-

165 distractor test trials, respectively.

166   Because the current experiments were conducted over a long period of time, it is possible that

167 performance on the test trials improved during the course of the experimental sessions. To evaluate these

168 learning effects, we divided the 32 test trials under each distractor condition into four eight-trial blocks and

169 compared the performance across blocks. As shown in Table 1, no systematic improvement was observed

170 across blocks. We found a significant difference in Cleo's performance under the homogeneous-distractor

171 condition ($p = 0.038$, Fisher's exact probability test); however, when the data were analyzed based on the first

172 16 versus the second 16 trials (68.8% vs. 81.25%), this difference was not significant ($p = 0.685$).

173   During the control test sessions, chimpanzees performed very accurately on both the matching

174 (98.4%, $SEM = 1.1$) and visual search trials (94.0%, $SEM = 1.7$). For the first type of test trials (i.e., the no-

175 sample two-choice tests), the stimulus choice made by the chimpanzees was random in comparison with their

176 previous choices [41.4% ($SEM = 6.8$) in the homogeneous-display control and 42.2% ($SEM = 2.7$) in the

177 heterogeneous-display control test trials; see Fig. 3, gray bars]. Actually, the performance of two chimpanzees

178 (Ayumu and Pal) significantly differed from chance in the homogeneous-display control two-choice test trials,

179 but they avoided the stimulus that they had previously chosen. In the other control test of the repeated visual

180 search test trials (Table 2), the chimpanzees chose the same stimulus they had chosen in the previous

181 homogeneous-distractor test trial in 92.2% ($SEM = 2.7$) of the trials. However, they chose the same stimulus as

182 in the previous heterogeneous-distractor test trial in only 21.1% ($SEM = 5.3$) of the trials. Although one

183 chimpanzee exhibited significantly better performance (Ayumu, 31.3%, $p < 0.05$, binomial test) than would be

184 expected by chance (16.7%), the other three chimpanzees chose stimuli randomly.

185 **DISCUSSION**

186   Irrespective of the type of distractors, all chimpanzees exhibited significantly better recognition of the
187 stimulus chosen immediately before testing than would be expected by chance. These results indicate short-
188 term retention of memories of their own behavior. Furthermore, they performed at the level of chance on
189 control test trials. These data suggest that the results of "what-did-you-choose" test trials cannot be explained
190 by only the salience of the stimuli.

191   Our results clearly show that chimpanzees can remember choices they made immediately before an
192 incidental memory task. Unlike the pigeons studied in previous research (Singer & Zentall, 2007; Zentall et al.,
193 2001, 2008), the chimpanzees in our study experienced a very long interval (one trial/9 days) between test
194 trials. In contrast with the situation involving pigeons, this long inter-test interval may have made it less likely
195 that the chimpanzees expected to be asked, "what did you choose?" immediately after an individual trial. Thus,
196 the present results do not support rule learning or semantic memory (Singer & Zentall, 2007). Their choice
197 behavior during the test trials cannot be explained by simple association learning on the basis of differential
198 reinforcement because the choice of the stimulus on the search display and the subsequent choice between the
199 two stimuli were not actually differentially reinforced by a food or sound reward. Additionally, it would be
200 difficult to explain our results in terms of non-memory strategies such as stimulus preference. The choices of
201 the chimpanzees during the heterogeneous-distractor trials and the choice phase during the test trials were not
202 consistent enough to explain our results. In the test trials, one of the two choice stimuli was selected from the
203 stimuli in the previous search display. This may have led to different degrees of familiarity with the two choice
204 stimuli, and the chimpanzees may have utilized these differences in the choice of a stimulus. This possibility
205 should be examined further in the near future. Of course, it is still rather difficult to distinguish between
206 semantic memory and episodic recollection using the current experimental procedure. It remains plausible that
207 the chimpanzees chose the stimuli based on semantic memory ("that is the stimulus I chose") rather than based
208 on episodic recollection ("I remember choosing that stimulus"). In the future, we should devise a new
209 procedure to differentiate these possibilities more clearly.

210   Previous studies have reported that chimpanzees have the ability to form long-term episodic-like
211 memories (e.g., Menzel, 1998). In our experiments, the delay interval between the choice behavior and the
212 incidental question was only 1 second. Can our findings be connected with the previous results showing long-
213 term retention of memories of their own behavior? Some researchers may argue for a critical gap between the
214 short- and long-term properties of episodic memory, whereas others may not make this argument (Singer &
215 Zentall, 2007). We think that our results can be closely related to the "episodic buffer" in the components of
216 working memory proposed by Baddeley (2000). This component is considered to act as a bridge between
217 working memory and long-term episodic memory. Chimpanzees may temporally store memories of their own
218 behavioral episodes in this episodic buffer. As Baddeley proposed, the episodic buffer plays a critical role in
219 feeding information into and retrieving information from long-term episodic memory. Thus, we should focus
220 on the temporal dynamics of episodic-like memory and its underlying mechanisms. However, these

221 mechanisms remain unclear from the perspective of comparative cognition. More detailed comparative studies
222 should be conducted in the future.

223 In our experiment, only the "what" component of short-term episodic-like memory was examined, as
224 our experimental design did not allow us to determine the "when" and "where" components. For example, the
225 "when" component, was always fixed: the choice "just before" the current testing phase. Furthermore, the
226 "where" component could not be manipulated in our setting as we always tested the chimpanzees in the same
227 apparatus in the same room. Although controversy concerning the necessary conditions for testing episodic-like
228 memory in nonhuman animals persists (Zentall et al., 2008), we plan to modify the experimental procedure
229 enough to test the "when" and "where" components in a well-controlled setting. These further attempts will tell
230 us more about episodic-like memory in chimpanzees as well as about the evolution of episodic memory.

231 **CONCLUSION**

232 In the present study, we examined the ability of chimpanzees to recognize what they had just done
233 using matching-to-sample and visual search paradigms. In the memory-test trials, chimpanzees chose the
234 stimulus that they had chosen previously. These results seem to support the operation of short-term episodic-
235 like memory in chimpanzees. The comparative cognition domain has emphasized the long-term aspects of
236 episodic-like memory more than short-term storage of episodes, which may be attributable to the original
237 definition of episodic memory. However, the present results suggest the need for additional comparative
238 cognitive investigations of the temporal dynamics involved in role of episodic-like memory in the transition
239 from short-term to long-term storage.

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297   Table S1. Raw data for each chimpanzee in the present experiment. Microsoft Excel 2003 file format (.xls)

298   Figure Captions

299   Figure 1. Chimpanzee Cleo performing the "what-did-you-choose?" test. Photo Courtesy: Masaki Tomonaga

300   (Kyoto University)

301   Figure 2. Flow of each type of trial in the present experiment. Photo Courtesy: Masaki Tomonaga (Kyoto

302   University)

303   Figure 3. Mean percentage of correct choices during the "what-did-you-choose?" tests and the no-sample

304   control tests. Error bars indicate the standard errors. Data from each chimpanzee are also shown.

Learning effects in the "what-did-you-choose" test trials.

Each number represents the number of correct trials in each eight-trial block.

Table 1. Learning effects in the "what-did-you-choose" test trials. Each number represents the number of correct trials in each eight-trial block.

Eight-trial block	Pendesa		Ayumu		Cleo		Pal	
	homo DSTs	hetero DSTs	homo DSTs	hetero DSTs	homo DSTs	hetero DSTs	homo DSTs	hetero DSTs
1	5	5	8	7	3	8	8	8
2	6	6	6	7	8	8	5	8
3	7	6	4	5	7	7	5	7
4	6	5	7	6	6	8	8	8
Fisher's Exact p	0.942	1.000	0.145	0.791	0.038	1.000	0.053	1.000

homoDSTs: trials with homogeneous distractors; heteroDSTs: trials with heterogeneous distractors

Results of the second control test sessions.

The percentages of correct trials under baseline conditions and the percentage of trials in which chimpanzees chose the same stimuli they had chosen previously in the repeated visual search test trials.

Table 2. Results of the second control test sessions. The percentages of correct trials under baseline conditions and the percentage of trials in which chimpanzees chose the same stimuli they had chosen previously in the repeated visual search test trials.

| Chimpanzee | Baseline | | Test | |
| | MTS | Visual Search (homoDSTs) | Visual Search | |
			homoDSTs	heteroDSTs
Pendesa	98.4	94.5	96.9	6.3
Ayumu	100	98.4	96.9	31.3
Cleo	95.3	90.4	87.5	21.9
Pal	100	92.7	87.5	25
Average	98.4	94	92.2	21.1
SE	1.1	1.7	2.7	5.3

homoDSTs: trials with homogeneous distractors; heteroDSTs: trials with heterogeneous distractors

Figure 1

Chimpanzee Cleo performing the "what-did-you-choose?" test.

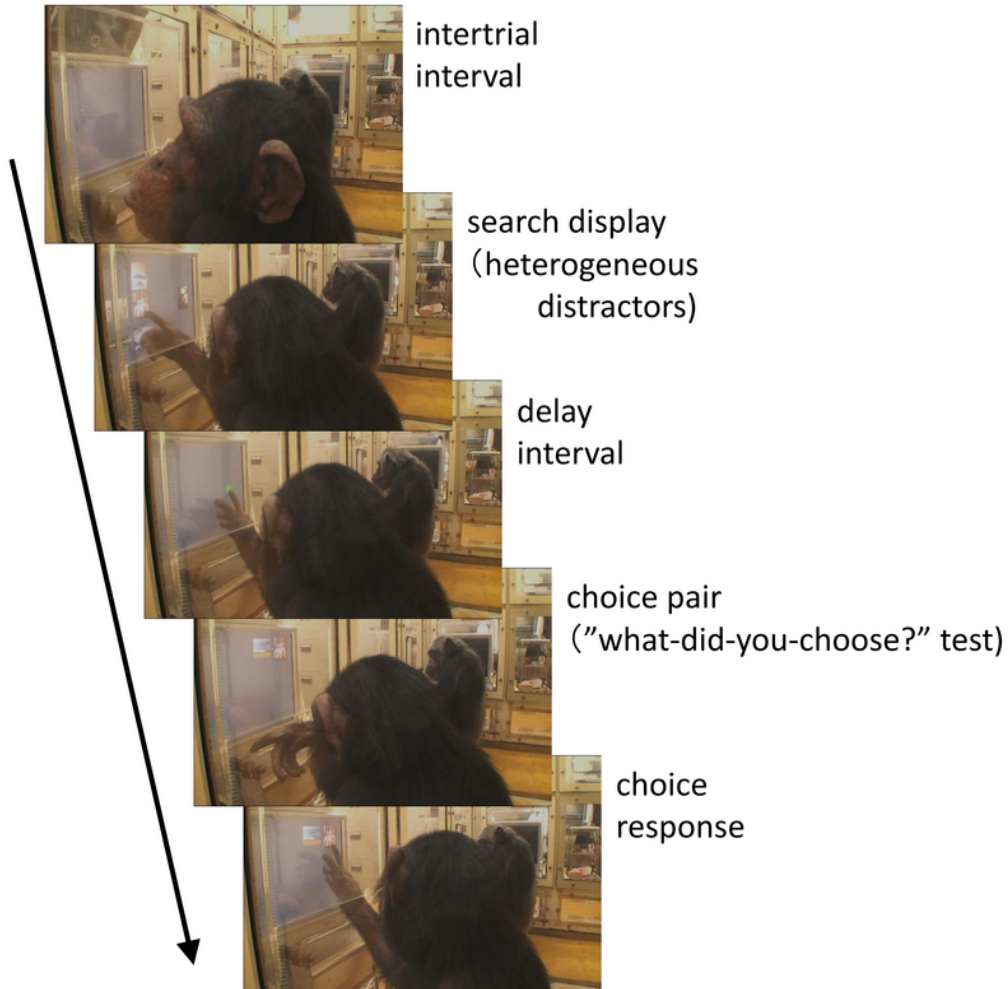
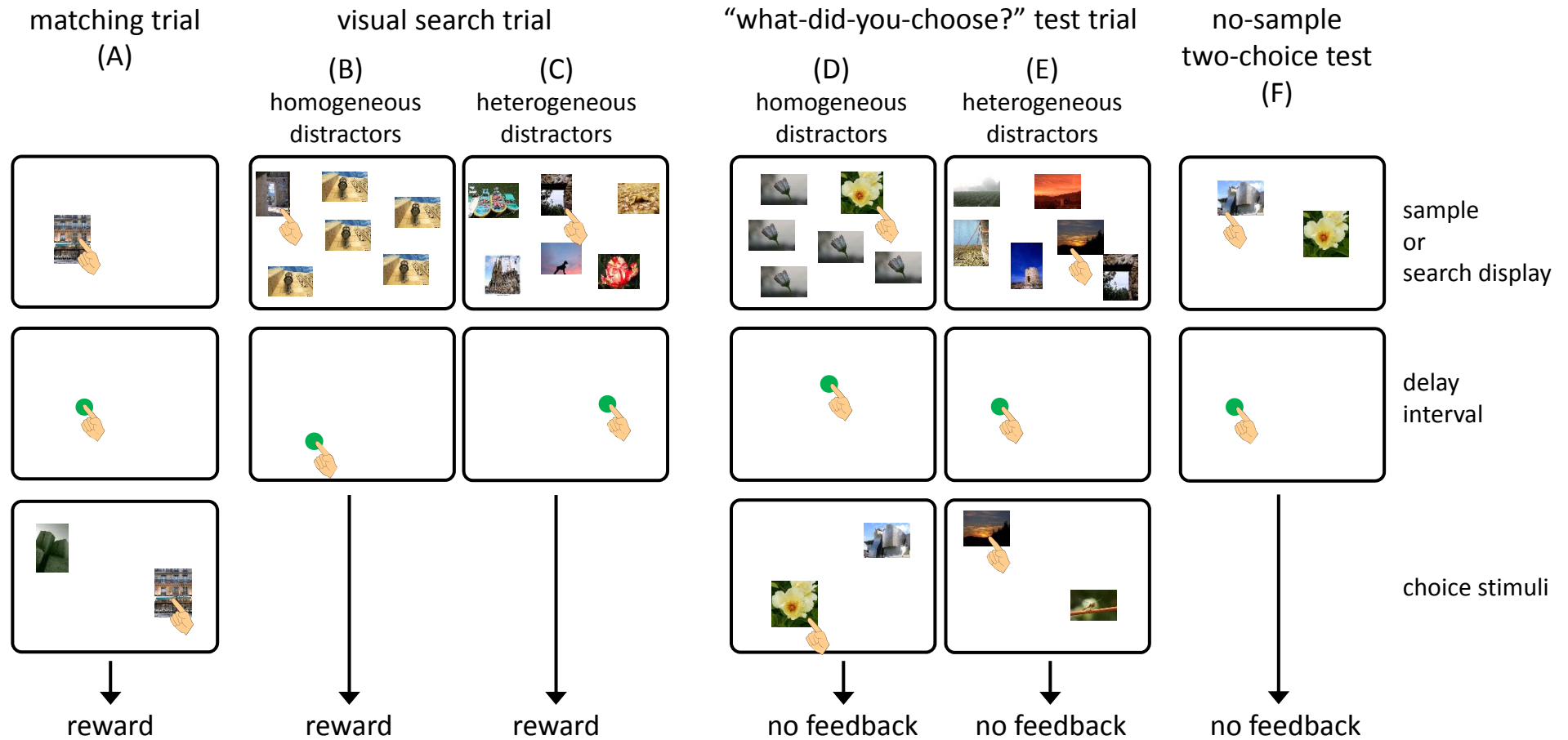



Photo Courtesy: Masaki Tomonaga (Kyoto University)

Flow of each type of trial in the present experiment.

Photo Courtesy: Masaki Tomonaga (Kyoto University)

Mean percentage of correct choices during the "what-did-you-choose?" tests and the no-sample control tests.

Error bars indicate the standard errors. Data from each chimpanzee are also shown.