

1 CUED REPETITION OF SELF-DIRECTED BEHAVIORS IN MACAQUES

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19 **ABSTRACT**

20 Two macaques were trained to perform three self-directed behaviors on signal, and to  
21 repeat behaviors after a 'repeat' signal. The cognitive processes underlying the  
22 monkeys' repeat performance were evaluated using multiple repetitions of the repeat  
23 signal, extended delay periods between target behavior and repeat signal, and by  
24 transferring the repeat signal to novel behaviors. The monkeys appear to have used  
25 representations of their own past behaviors as a basis for repetition performance, but  
26 they mostly failed to correctly repeat target behaviors after extended delays and  
27 during transfer tasks. Implications for episodic memory abilities are discussed.

28

29 **Keywords:** pigtailed macaques; self-directed behavior; repeat signal; internal  
30 stimulus; episodic memory

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32 **Running head:** cued repetition in macaques

33

34 **Word count:** 5504 words without references

35 6166 words with references

36 The assessment of cognitive processes in humans and non-human animals typically  
37 relies on the use of objects, external events and other environmental stimuli. The  
38 advantage of externally presented stimuli is that they can be easily controlled and  
39 manipulated, and that the resulting overt behavior can provide valuable insight into  
40 the operation of hypothetical cognitive processes. However, external stimuli are not  
41 the only source of input that give rise to cognitive processes. Humans and other  
42 animals may also act on the perception of internal stimuli, which may be powerful  
43 motivators of behavior (e.g., hunger, thirst and pain experiences). Similarly, an  
44 organism's own behavior, perceived via proprioceptive feedback and/or coded in  
45 memory, may have a profound effect on future behavior. Here we investigate how  
46 self-generated movement may be stored and processed by pigtailed macaques.

47

48 In humans, the processing of internal stimuli is commonly assessed through verbal  
49 self-reports. For non-human animals, researchers have to rely on the assessment of  
50 other overt behaviors that are taken to indicate processing of internal stimuli. For  
51 example, Beninger et al. (1974) gave rats the opportunity to earn food rewards by  
52 pressing one of four levers, each associated with one distinct behavior (face washing,  
53 rearing, walking and immobility). If a rat performed one of those behaviors and  
54 subsequently pressed the corresponding lever, it received a food reward. All four rats  
55 learned to select the correct lever above chance levels for at least three behaviors.

56 These results indicate that rats can form an association between their own past  
57 behavior and an external object. Importantly, however, they do not clarify how their  
58 own behaviors were processed and stored by the animals (see also Morgan and  
59 Nicholas, 1979, and Shimp, 1982, for similar results in rats and pigeons respectively).

60

61 Recently, Mercado and colleagues have studied processing of internal stimuli in  
62 bottlenosed dolphins. Two dolphins were trained to perform distinct behaviors in  
63 response to hand gestures by a human trainer, and to repeat these behaviors following  
64 an abstract repeat gesture. Both dolphins transferred the repeat signal to new  
65 behaviors that had never been previously reinforced, with one dolphin reaching an  
66 accuracy of 79% correct repetitions. To clarify whether the dolphins remembered the  
67 trainer's hand gestures or their own behaviors, they were also tested on double-  
68 repetitions and self-selected behaviors that were not prompted by hand signals. One  
69 dolphin succeeded at both these tasks. Ruling out several other possible explanations,  
70 Mercado et al. (1998) concluded that the dolphins based their repetition performance  
71 on representations of their own past behaviors (see also Mercado et al., 1999).

72

73 Little is known about how primates might perform on such tasks, or how internal  
74 stimuli are processed in primates. The present study employs a paradigm based on  
75 that of Mercado et al. (1998) to assess whether pigtailed macaques' (*Macaca*  
76 *nemestrina*) are able to perform tasks that rely on internal representations of their own  
77 behaviors. Two monkeys were first trained to perform three distinct self-directed  
78 behaviors in response to auditory signals, and subsequently to repeat two of the  
79 behaviors after hearing an abstract 'repeat' signal (described in part A). We then ran  
80 several manipulations to answer the following questions: 1. Do monkeys remember  
81 their own past behavior (rather than associated signals) as assessed by two  
82 consecutive repeat signals (part B)? 2. How much delay can monkeys tolerate  
83 between past behavior and repeat signal (part C)? 3. Can monkeys successfully  
84 transfer the repeat signal to novel, untrained behaviors and thereby demonstrate an  
85 understanding of the repeat signal beyond learned reward contingencies (part D)? The

86 answers to these questions will help us to draw a clearer picture of the processing of  
87 internal stimuli in primates.

88

## 89 **PART A: GENERAL METHODS AND BASIC TRAINING**

### 90 **Subjects**

91 Subjects were two male pigtailed macaques (*Macaca nemestrina*), Alcatraz and  
92 Charlie, both captive born, aged 18 and 4 years respectively. Although both monkeys  
93 were housed individually, their home cages (cage measures: 100x160x100cm) were  
94 part of an interconnected system that allowed daily social interactions with other  
95 individuals. The monkeys were not food deprived for the experiment, but received  
96 part of their normal diet during testing and the rest thereafter. Water was available ad  
97 libitum.

98

### 99 **Procedure**

100 Both monkeys were individually trained and tested in their home cages. Two training  
101 sessions were administered on a daily basis, one in the morning and one in the  
102 afternoon. Each session lasted between 15 and 30 minutes depending on the number  
103 of trials administered. The experimenter sat in front of the cage with the apparatus for  
104 producing auditory stimuli and a clipboard for recording the monkeys' responses. A  
105 white cardboard screen (ca. 40x70cm) covered the apparatus to avoid visual cueing of  
106 the target behavior. Small pieces of various fruits and vegetables were used as food  
107 rewards. Whenever a monkey performed a desired response, a metallic clicking noise  
108 was sounded as a secondary reinforcer before a food reward was given.

109

110 The first step in training the monkeys to repeat self-directed behaviors on signal was  
111 to increase the spontaneous occurrences of these behaviors. The second training phase  
112 consisted of bringing these behaviors under signal control, i.e. training the monkeys to  
113 associate a distinct auditory signal with each behavior. In the third training phase, the  
114 monkeys were taught to repeat two of these behaviors after hearing a novel ‘repeat’  
115 signal.

116

### 117 **Training 1: Establishing three self-directed responses**

118 Three self-directed behaviors were selected for training. Scratching and grooming are  
119 both trainable through operant conditioning techniques (e.g. Louboungou and  
120 Anderson, 1987). Mouthing of one hand was chosen as the third behavior on the basis  
121 that mouthing forms part of the monkeys’ natural behavioral repertoire.

122

#### 123 **a. Scratching**

124 A scratch was defined as a quick succession of two or more movements of the  
125 fingertips drawn rapidly across the skin at the same body area. Training started with  
126 eight 30-min sessions of baseline measures of scratching. During the first four  
127 baseline sessions, no rewards were given and any occurrences of scratching were  
128 noted. During the next four baseline sessions, 30 rewards were given to the monkey at  
129 one minute intervals independently of the monkey’s behavior, and all occurrences of  
130 scratching were noted. During each training session thereafter, all occurrences of  
131 scratching were rewarded. After several training sessions, Charlie’s grooming and  
132 scratching responses became largely indistinguishable from each other. In order to  
133 obtain clear responses, scratching with the foot directed to the shoulder was  
134 considered the only acceptable scratching response for Charlie.

135

136 **b. Grooming**

137 Grooming was defined as a self-directed manual response accompanied by intense  
138 visual interest in the body part being groomed, e.g. manipulating hairs or skin and  
139 removing single hairs or particles from it. At least two such movements had to occur  
140 to be counted as a grooming response. Six baseline measurements of grooming were  
141 taken during training of signal control for scratching, i.e. when rewards were given  
142 after scratching behaviors in response to the scratch signal (see Training 2 below). All  
143 sessions after baseline sessions involved reinforcement of all grooming responses.

144

145 **c. Mouthing**

146 Mouthing was defined as licking a hand or wrist, or inserting a hand or wrist into the  
147 mouth. Baseline measures of mouthing were collected during six sessions of signal  
148 control for scratching and grooming, i.e. when rewards were available contingent on  
149 scratching and grooming responses after the respective scratch and groom signal had  
150 been sounded (see Training 2 below). Since mouthing responses never occurred  
151 spontaneously during baseline, a small number of additional training sessions were  
152 conducted in which the experimenter applied some fruit juice onto the monkeys'  
153 wrists and hands with a syringe. Every lick of the hand was then additionally  
154 reinforced with a food reward. Monkeys were rewarded for all occurrences of  
155 mouthing after baseline sessions.

156

157 **Results and Discussion**

158 Contingent reinforcement had a dramatic effect on the monkeys' behaviors, increasing  
159 scratching responses from an average of 8 responses per session during baseline to up

160 to 139 responses per session during reinforcement. Similar effects were obtained for  
161 grooming (average of 1 response per session during baseline and up to 62 responses  
162 per session during reinforcement) and mouthing (average of 1 response per session  
163 during baseline and up to 72 responses per session during reinforcement).

164

165 Increases in performance after introduction of contingent continuous reinforcement  
166 suggest that all three behaviors were under voluntary control of the monkeys, not  
167 “hard-wired” behavioral repertoires (Louboungou and Anderson, 1987), and therefore  
168 suitable for the repetition paradigm.

169

#### 170 **Training 2: Bringing the self-directed behaviors under signal control**

171 Having established an increased frequency, the behaviors were brought under signal  
172 control defined as each behavior occurring reliably after an auditory signal had been  
173 given. Auditory signals were one high-pitched sound and one low-pitched sound, both  
174 generated with an electronic keyboard, and a metallic clicking noise. These sounds are  
175 referred to as discriminative stimuli, or DC signals.

176

177 At the beginning of training, the DC signals were delivered in random order, and were  
178 sounded continuously (for up to 30 seconds) until the corresponding target behavior  
179 occurred. The DC signal then stopped and the monkey received a food reward. If the  
180 target behavior was not performed within 30 s, no food reward was given, and the  
181 signal was repeated after 20 s. Once responses were more reliable, DC signal length  
182 was reduced to 10 s. If the corresponding behavior occurred within this period, the  
183 DC signal stopped and a reward was given. If the wrong behavior or no observable  
184 behavior occurred, trials were ended immediately or after the 10 s DC signal



185 respectively. Inter-trial intervals were set at 20 s. Thirty trials for each behavior were  
186 administered during each session. Both monkeys were first trained on scratching and  
187 grooming responses. Training of the mouthing response was introduced after scores of  
188 at least 80% correct for scratching and grooming in two consecutive sessions was  
189 achieved.

190

### 191 **Results and Discussion**

192 After an average of 117 sessions, both monkeys responded to all three DC signals  
193 with appropriate self-directed behaviors (over 80% correct in two consecutive  
194 sessions). More trials were required to learn appropriate scratch (mean=77 sessions)  
195 and groom (mean=66 sessions) responses compared to mouthing (mean=23 sessions).

196

### 197 **Training 3: Repetition of two behaviors following an abstract repeat signal**

198 Two behaviors were selected for each monkey (Alcatraz: scratch and groom; Charlie:  
199 scratch and mouth) for training of repetition following a novel 'repeat' (RE) signal. A  
200 small metal whistle was used to give the RE signal.

201

202 Each trial consisted of a DC signal (max. 10 s), which stopped as soon as the monkey  
203 performed the appropriate behavior, followed by presentation of a food reward. After  
204 a 3 s delay, the RE signal was given for up to 10 s. If the monkey repeated the  
205 previous behavior, the signal stopped, the monkey received a food reward, and a 10 s  
206 inter-trial interval ensued. If no behavior or a wrong behavior was performed  
207 following the RE signal, the trial was ended, no reward was given, and a new trial  
208 started after a 15 s delay.

209

210 Each session consisted of 30 DC signals for each behavior, followed by the RE signal.  
211 In case of an incorrect or no response to a DC signal, the trial was ended and followed  
212 by a 15 s inter-trial interval. These ‘lost’ trials were re-run at the end of each session.  
213 To prevent forgetting of the third response, 20 signals for the third behavior were also  
214 given but never combined with the RE signal. DC signals were first presented in  
215 blocks of five trials, and once the monkey responded correctly, in random order.  
216 Monkeys were judged to have learnt the RE signal if they performed both repeat  
217 behaviors at over 80% correct in two consecutive sessions.

218

219 **Results and Discussion**

220 Alcatraz averaged around 65% correct responses to the repeat signal from the start of  
221 training, whereas Charlie’s responses were initially random, but improved slowly as  
222 training progressed. Alcatraz required 55 sessions and Charlie 113 sessions to  
223 accurately repeat two behaviors following the RE signal.

224 -----

225 Insert Figure 1 about here

226 -----

227 To our knowledge, the only animals to have previously been trained to respond to a  
228 repeat signal are bottlenosed dolphins (Mercado et al., 1998). However, a related  
229 gesture, “Do this”, or perhaps, “Do-what-I (the experimenter)-did”, has been used in  
230 primate research. Using this command, human demonstrators have made self- or  
231 object-directed gestures that are then replicated by chimpanzees and orangutans  
232 (Hayes and Hayes, 1952; Custance et al., 1995; Miles et al., 1996). A few attempts  
233 have been made to train monkeys a “Do-what-I-did” command, without success  
234 (Mitchell and Anderson, 1993; Visalberghi and Fragaszy, 2002). If the repeat signal in

235 the current study is regarded as a recursive “Do-what-I-did” command, it is  
236 noteworthy that our two macaques were able to correctly repeat their own self-  
237 directed behaviors following the RE signal.

238

## 239 **PART B: TEST WITH MULTIPLE REPEAT SIGNALS**

240 Part A described the training of a paradigm involving signal-controlled, self-directed  
241 responses. One interpretation could be that the monkeys had to remember what  
242 actions they performed in order to successfully repeat them. There is a clear  
243 alternative however; the monkeys might simply retrieve a memory of the initial DC  
244 signal so that the representation of this external stimulus may affect correct  
245 performance. In part B, we asked the monkeys to repeat target behaviors twice  
246 following repeat signals. If they based their repetitions on the previous DC signal, it  
247 would be difficult for them to repeat a target behavior with the previous signal being a  
248 repeat signal (because repeat signals were not associated with any one behavior). By  
249 contrast, if repetitions were based on memories of the previously performed behavior,  
250 they might easily repeat the target behavior multiple times. We restricted test  
251 performances to 30 trials per behavior in order to avoid performance improvements  
252 on the basis of prolonged reinforcement series.

253

### 254 **Test B**

255 For Alcatraz, 60 trials of scratch signal and 60 trials of groom signal followed by the  
256 RE signal were administered in random order over three sessions (for Charlie: scratch  
257 and mouth signals). For 30 trials for each behavior, the DC signal was sounded and  
258 the monkey was rewarded if the corresponding behavior was performed within 10 s.  
259 After a 3 s delay the RE signal was given, and if the target behavior was repeated

260 correctly, the monkey received a second food reward. Following a 3 s delay the  
261 experimenter presented the RE signal a second time, and rewarded the monkey if the  
262 target behavior was performed within 10 s. To ensure that the monkeys were not  
263 simply spontaneously performing the target behavior, the remaining 30 trials for each  
264 behavior were identical to those described, except that the second RE signal was not  
265 given. Instead, the experimenter noted if the target behavior was repeated in the 10 s  
266 control period. Trials were separated by 20 s inter-trial intervals.

267

268 **Results and Discussion**

269 -----

270 Insert Figure 2 about here

271 -----

272 As Figure 2 shows, Charlie repeated both scratching and grooming behaviors  
273 following the second RE signal. He did not repeat these behaviors in the absence of  
274 the second RE signal. For both behaviors, the difference in repetitions between trials  
275 with and without second RE was significant (binomial tests: both  $p < 0.001$ ). Alcatraz  
276 showed similar performances: he repeated grooming behaviors more often when the  
277 second RE signal was sounded ( $p = 0.029$ ), and there was a non-significant trend for  
278 repetitions of scratching behaviors ( $p = 0.11$ ). Both monkeys were equally successful  
279 during the first 10 trials of testing as during the last 10 trials of testing for both  
280 behaviors (all  $ps=NS$ ).

281

282 These results suggest that both monkeys used internal representations of their own  
283 past behaviors as the basis for repetition performances. Possible simple explanations  
284 for the repeat behaviors, such as a continuation of target behaviors until the repeat

285 signal was sounded, do not apply. Both monkeys always ceased target behaviors  
286 immediately following the sound of the secondary reinforcer and whilst consuming  
287 the offered food reward. Furthermore, we did not observe evidence of strategies that  
288 the monkeys might have used to remember target behaviors, such as performing target  
289 behaviors in a particular part of the home cage. Instead, both monkeys appear to have  
290 remembered their motor output following the first DC signal, and based the  
291 repetitions of the target behaviors upon this memory.

292

### 293 **PART C: INCREASING THE DELAY PERIOD BETWEEN TARGET** 294 **BEHAVIOR AND RE SIGNAL**

295 In part C, we increased the delay between target behavior and RE signal in order to  
296 evaluate how long the target behavior was retained in memory. Test C1 increased the  
297 delay between DC signal and RE signal from 3 s to 10 s. In Test C2, the delay was  
298 increased to 30 s. Trials were separated by 20-s inter-trial intervals.

299

#### 300 **Test C1**

301 Monkeys received a total of 120 trials in random order over three test sessions using  
302 scratch and groom behaviors for Alcatraz and scratch and mouth behaviors for  
303 Charlie. Thirty trials of each behavior consisted of the DC signal followed by a 10-s  
304 delay and 10 s of RE signal. A correct repetition of the target behavior during the RE  
305 signal was rewarded. To control for random repetitions of the target behaviors  
306 following the delay period, an additional 30 trials for each behavior were followed by  
307 a 10-s observation period in the absence of the RE signal. Trials were separated by  
308 20-s inter-trial intervals.

309

310 **Test C2**

311 Test C2 was identical to Test C1, except that the delay between DC signals and RE  
312 signals was increased to 30 s. RE signals and control periods without signal continued  
313 to be 10 s long.

314

315 **Results and Discussion**

316 -----

317 Insert Figure 3 about here

318 -----

319 **Test C1**

320 Alcatraz’s repetition of both target behaviors was significantly better with the RE  
321 signal than without the RE signal (binomial tests: scratching:  $p=0.009$ , grooming:  
322  $p=0.012$ ; Figure 3a). There was no learning curve evident in Alcatraz’ data: he was as  
323 successful during the first 10 trials as during the last 10 trials (both behaviors: 6 vs. 7  
324 trials correct,  $p=NS$ ). At the same delay period, Charlie’s repetitions of mouthing but  
325 not scratching were significantly better with the RE signal than without the RE signal  
326 (scratching:  $p=NS$ , mouthing:  $p=0.001$ ; Figure 3a). On scratching trials, Charlie  
327 showed a significant bias for mouthing after hearing the RE signal (21 trials out of  
328 30). Charlie’s mouthing repetitions therefore seem to stem from a generalized  
329 tendency for mouthing upon hearing the RE signal at this delay period, rather than  
330 from memory of the target behaviors.

331

332 **Test C2**

333 At 30 s delay, Alcatraz continued to repeat scratching and grooming significantly  
334 better in trials with the RE signal than in trials without the RE signal (binominal tests:

335 scratching:  $p=0.024$ ; grooming:  $p=0.024$ ; Figure 3b). However, the percentage of  
336 correct grooming responses to the RE signal was relatively low with only 33% of  
337 trials correct. As Charlie was considered to have failed the 10-s delay condition, he  
338 was not tested at 30-s delay.

339

340 Although it is not clear what the exact time span of working memory is in monkeys, it  
341 is usually estimated to be between 30 s and 1 min (Schwartz and Evans, 2001).  
342 Furthermore, monkeys do not appear to actively rehearse information held in working  
343 memory (Washburn and Astur, 1998), which makes it likely that information recalled  
344 after a 1-min delay is retrieved from long-term memory. Assessment of recall abilities  
345 showed that monkeys struggle to retrieve declarative memories after a delay of more  
346 than 60 s (Hampton, 2001), possibly suggesting a failure to form long-term  
347 declarative memories. In the present study, the difficulty to repeat target behaviors at  
348 30 s delay suggests that both monkeys' repetition performances were mediated by  
349 working memory of the self-generated movement.

350

#### 351 **PART D: TRANSFER TO NEW BEHAVIORS**

352 So far, two aspects have been tested: retrieval of the memory for specific behaviors  
353 and retrieval after extended delays. However, both tests relied on target episodes of  
354 behaviors that were learnt through positive reinforcement. To test if the monkeys  
355 could correctly respond to the RE signal in combination with novel, unexpected  
356 behaviors, we conducted two transfer tests: Test D1 applied the RE signal to the third  
357 trained behavior, which was never combined with the RE signal during training. Test  
358 D2 assessed transfer of the RE signal to new, untrained behaviors. Successful transfer  
359 to new behaviors would indicate that the monkeys had generalized the repetition rule.

360

361 **Test D1**

362 Over 3 sessions, the monkeys received 30 trials with both trained repetition behaviors  
363 followed by RE signals. The crucial test trials of 30 mouth trials for Alcatraz and 30  
364 groom trials for Charlie followed by RE signals were randomly interspersed among  
365 these trials. To ensure that repetition was prompted by the RE signal, both monkeys  
366 also received 30 trials each of scratch, groom and mouth DC signal followed by a 10 s  
367 observation period without RE signal. Trials were separated by 20 s inter-trial  
368 intervals.

369

370 **Test D2**

371 Two new untrained behaviors were selected based on observations of their frequent  
372 spontaneous occurrence, namely yawning for Alcatraz and vocalization (coo-calls) for  
373 Charlie. It has been shown that both of these behaviors can be operantly conditioned  
374 (Louboungou and Anderson, 1987; Pierce, 1985), suggesting that they may be  
375 brought under voluntary control. When a target behavior occurred, monkeys received  
376 a food reward, followed by a 3-s delay. On half the trials, the RE signal was then  
377 given, and if the monkeys repeated the target behavior they received a second food  
378 reward. On the remaining trials, the monkeys were simply observed for 10 s without  
379 RE signal, and any occurrences of the target behavior was noted. Sessions lasted for  
380 30 minutes with alternating RE and non-RE signal trials. Alcatraz was tested over 4  
381 sessions, and received 22 trials with and 23 trials without the RE signal. Charlie was  
382 tested over 2 sessions, and received 30 trials with and 30 trials without the RE signal.

383

384 **Results and Discussion**



385 **Test D1**

386 -----

387 Insert Figure 4 about here

388 -----

389 Figure 4 shows that both monkeys repeated the trained behaviors significantly above  
390 chance in response to the RE signal, but not in the absence of the RE signal (Alcatraz:  
391 scratching:  $p=0.013$ , grooming:  $p=0.036$ ; Charlie: scratching:  $p<0.001$ , mouthing:  
392  $p<0.001$ , all binomial tests). Alcatraz (Figure 4a) also repeated the transfer behavior -  
393 mouthing - more often during trials with the RE signal than without the RE signal, but  
394 this trend failed to reach statistical significance (binomial test:  $p=0.092$ ). The  
395 percentage of correct mouthing repetition in response to the RE signal was relatively  
396 low; he performed correctly in only 1/3 of trials. Looking at each behavior across  
397 trials, correct repeats occurred equally often during the first 10 trials as during the last  
398 10 trials ( $p=NS$ ). Charlie (Figure 4b) never repeated the transfer behavior - grooming  
399 - in either type of trial.

400

401 **Test D2**

402 Both monkeys failed to repeat yawning or vocalization, regardless of whether the RE  
403 signal was given or not. Instead, Alcatraz performed scratching 12 times and Charlie  
404 performed scratching 29 times in response to the RE signal.

405

406 Together the results from Test D1 and D2 provide little evidence for successful  
407 transfer to novel behaviors, and suggest that the monkeys did not form an abstract  
408 understanding of the repeat signal. Instead, it seems possible that the monkeys learnt  
409 the correct repetition of the trained behaviors through rote learning, e.g. to scratch if

410 the previous behavior was scratch, groom if the previous behavior was groom, etc.  
411 Although the monkeys' learning was limited, it is important to note that rote learning  
412 does not contradict the hypothesis of internal stimuli underlying repetition  
413 performance.

414

## 415 **GENERAL DISCUSSION**

416 While much is known about the processing of external stimuli, much less research has  
417 been devoted to the processing of internal stimuli in non-human animals. The  
418 presented series of experiments aimed to clarify if, and how, internal stimuli in the  
419 form of self-generated behaviors are processed and stored by macaques. To this end,  
420 we adopted a paradigm that relies on an abstract repeat signal. The following sections  
421 summarize the results from the previous sections, evaluating their interpretations as  
422 evidence for internal representations of past behaviors and detailing the paradigm's  
423 potential for future experiments.

424

### 425 **Training of three self-directed behaviors and the repeat signal**

426 Alcatraz and Charlie both learnt to perform three self-directed target behaviors upon  
427 hearing an associated auditory signal. To our knowledge, this is the first report of  
428 conditioned auditory stimuli controlling the performance of self-directed behaviors.  
429 Scratching and grooming have previously been increased in frequency through  
430 operant conditioning (e.g. Iversen et al., 1984; Louboungou and Anderson, 1987), but  
431 have not been produced "on command". To our knowledge, mouthing has not  
432 featured in previous operant conditioning experiments. All three responses were  
433 initially indistinguishable from non-cued responses, but through training became

434 highly stereotyped. Increasing rigidity of the response form was expected (Iversen et  
435 al., 1984), and was not considered to compromise the experimental paradigm.

436

437 In the final training phase, the monkeys learnt to repeat target behaviors after hearing  
438 a “repeat” signal. Since all behaviors were distinct movements that had ceased by the  
439 time of the repeat signal, there were no cues within the immediate environment that  
440 could have prompted the required behavior. We argue that the experimental design is  
441 therefore a recall paradigm that relies on the processing of internal stimuli. It is not  
442 clear whether the monkeys relied on a representation of the previously performed  
443 behavior, or whether they used internal cues about their previous self-directed action  
444 (e.g. proprioceptive or somatosensory aftereffects on the involved body) as a basis for  
445 their responses. However, it seems likely that any internal cues would be especially  
446 salient at the start of a session and that habituation would make somatosensory  
447 feedback an unreliable indicator of the target behavior after several target responses.  
448 Successful performances in parts B and C were not noticeably better at the start  
449 compared to the end of tests, which supports the view that representations of past  
450 behaviors affected repetition performance.

451

#### 452 **Multiple repeat signals**

453 Part B assessed whether the monkeys could repeat target behaviors twice without  
454 intervening DC signals. The logic of part B was simple: successful performance might  
455 indicate that the monkeys used the memories of their own past behaviors as the basis  
456 for repetition performance rather than the associated DC signals. Except for one  
457 behavior by Alcatraz, all behaviors were correctly repeated following a second RE  
458 signal. We suggest that the combined results of parts A and B indicate that the

459 monkeys relied on representations of their own past behaviors for successful  
460 repetition performances. To be clear, we do not claim that the monkeys' own past  
461 behavior is the only basis for repetition performance. Other factors, such as a  
462 representation of the initial DC signal, may also mediate the monkeys' responses.  
463 Nonetheless, we believe that the present results provide evidence that macaques are  
464 able to use internal stimuli in the form of representations of their own past behavior as  
465 the basis for current behavior.

466

#### 467 **Increasing delay between DC signal and RE signal**

468 In part C, we tested the monkeys' ability to repeat the target behavior after increased  
469 delays. Although one monkey failed to repeat target behaviors after a 10-s delay, the  
470 other was more likely to repeat target behaviors after a repeat signal than without a  
471 repeat signal at both 10-s and 30-s delays. We note, however, that overall response  
472 rates to the repeat signal were low. One problem is that only a small number of trials  
473 were conducted with each delay period. Our results might also have been affected by  
474 the novel test conditions which are known to diminish performance (Shettleworth and  
475 Sutton, 2003). A further complication is added by the recent finding by Fritz et al.  
476 (2005) that macaques may have difficulties in forming long-term memories of  
477 arbitrary auditory stimuli. The results of part C therefore suggest that the monkeys in  
478 the present study relied on their working memory for successful repeat performance.

479

#### 480 **Transfer of the repeat signal to new behaviors**

481 Part D assessed whether the monkeys could transfer the RE signal to previously  
482 untrained behaviors. Transfer is important for validating the experimental paradigm;  
483 success would indicate a general application of the repeat signal to past behaviors and

484 would further reinforce the view that successful repetition is not simply an artifact of  
485 intensive training. Both monkeys largely failed to transfer the RE signal to new  
486 trained and untrained behaviors. The only evidence for transfer was that Alcatraz  
487 showed significantly more correct mouthing responses following the RE signal than  
488 without the RE signal, but overall responsiveness to the transfer behavior was low.

489

490 One possible explanation for this failure may lie in constraints in understanding  
491 abstract concepts. Previous research has shown that monkeys can learn abstract  
492 concepts, but the size of the stimulus set is a critical factor. Katz et al. (2002) trained  
493 rhesus monkeys to make same/different judgments and found no transfer after 8-item  
494 set training, but good transfer after 128-item set training. Therefore, rather than  
495 relying on trial-and-error learning, monkeys with extensive experience of applying an  
496 abstract concept appear more likely to use an abstract rule in a novel situation.

497 Application of the repeat signal to over 30 different behaviors may also have  
498 facilitated an abstract understanding in Mercado et al.'s (1998) dolphins. We conclude  
499 that the monkeys in the present study were unlikely to have formed an abstract  
500 concept of the repeat signal based on its application to only two behaviors during  
501 training, which may be largely responsible for the failure to transfer to novel  
502 behaviors. It remains to be seen whether monkeys with more varied experience of the  
503 repeat signal would be able to fully transfer the repeat signal. A rote learning  
504 approach to repetition performance is nonetheless consistent with internal  
505 representations of the past behaviors.

506

507 **Can self-repetition reflect episodic memory abilities?**

508 One reason for our interest in internal representations is their possible link to episodic  
509 memory (EM). Tulving (1972) defined EM as a long-term, declarative memory  
510 system that is involved in the recollection of events from one's personal past set in a  
511 unique spatio-temporal context (i.e., what, where and when). Importantly, EM is  
512 characterized by a "re-living" of events (Tulving, 1985) and has a phenomenological,  
513 "autonoetic" (self-referential) quality (Wheeler et al., 1997). In humans, EM is  
514 commonly assessed via verbal self reports, e.g. using the 'Remember/Know'  
515 procedure (Tulving, 1985). In contrast, EM research in nonhumans has typically  
516 relied on the assessment of what, where and when aspects of an event. For example,  
517 Clayton and Dickinson (1998) showed that scrub jays remember what type of food  
518 (larvae or peanuts) was stored where (distinct caching sites), and when (whether the  
519 food is likely to have decayed by the time of recovery). Although such tests satisfy the  
520 what, where and when requirements, it is unclear whether they provide any insight  
521 into the subjective experience of an individual. For example, scrub jays may adjust  
522 their behavior according to whether a caching site was previously recovered or not  
523 (Clayton and Dickinson, 1999), but whether the birds remember their own behavior  
524 during recovery or merely the consequences of recovery, is not clear. In other words,  
525 these tests may not necessarily require self-referential memory of one's own behavior,  
526 a critical feature of EM.

527

528 Given the evidence that our monkeys' memories of their own recent behaviors  
529 appeared to be relatively frail, can they be judged to have the same "autonoetic"  
530 experience as humans? Our study does not provide compelling evidence for true EM.  
531 Perhaps most damning is the fact that EM is a form of long-term memory, and the  
532 monkeys in the present study did not conclusively repeat target behaviors after

533 extended yet relatively brief delays. Our finding is in line with the results of a recent  
534 study by Hampton et al. (2005), which tested rhesus monkeys in a what-where-when  
535 paradigm similar to Clayton and Dickinson's (1998), and failed to find any evidence  
536 of EM. In sum, it is doubtful that our monkeys exhibited true EM.

537

538 Nevertheless, the repeat paradigm offers new avenues for assessing EM in non-verbal  
539 subjects. What-where-when paradigms typically carry the potential confound of  
540 recognition memory, which is not necessarily associated with EM (see Yonelinas,  
541 2002, for a review). As a result, most relevant animal studies have not unequivocally  
542 revealed EM (Griffiths et al., 1999). One important strength of our repeat paradigm is  
543 that it relies specifically on recall rather than on recognition of a presented cue. In  
544 addition, if it can be shown that a repeat signal has been generalized to novel contexts,  
545 the paradigm can also be used to assess the memory of unique one-trial experiences,  
546 another indicator of episodic memory (Zentall et al., 2001).

547

548 In conclusion, we have demonstrated that macaques remember their own past  
549 behaviors through the use of representations, and furthermore that these internal  
550 stimuli influence the ability to repeat previous behaviors following short delays. We  
551 believe that an examination of the influence of internal stimulation on cognitive  
552 processing is important, and presents an alternative to the traditional reliance on the  
553 manipulation of external objects and events. Although it is clear that macaques can  
554 remember, it remains unclear whether they were able to genuinely utilize a self-  
555 referential representation of their past behavior. Finally, the paradigm used here may  
556 have the potential to reveal episodic memory in non-verbal populations, but in the  
557 case of macaques, provides no evidence for true episodic memory.

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627

## 628 **Acknowledgements**

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630 drafts of this paper.

631 **FIGURE CAPTIONS**

632 Figure 1. Demonstration of cued repetition. Percentage of correct repetitions for  
633 Alcatraz (1a) and for Charlie (1b). Broken line = scratching responses, dotted line =  
634 grooming responses, solid line = mouthing responses. Criterion line shown at 80%  
635 correct.

636

637 Figure 2. Test with multiple repeat commands. Percentage of correct repetitions for  
638 two target behaviors presented for Alcatraz and Charlie. Black bars = repetition with  
639 RE signal; white bars = repetitions without RE signal. \*\* indicates  $p < 0.05$ .

640

641 Figure 3. Increase in delay between DC and RE signal. Percentage of correct  
642 repetitions for two target behaviors for Alcatraz and Charlie at 10-s delay (3a) and 30-  
643 s delay (3b). Black bars = repetition with the RE signal, white bars = repetitions  
644 without the RE signal. \*\* indicates  $p < 0.05$ .

645

646 Figure 4. Transfer tests to new behaviors. Percentage of correct repetitions for three  
647 target behaviors for Alcatraz (4a) and Charlie (4b). Black bars = repetition with the  
648 RE signal, white bars = repetitions without the RE signal. \*\* indicates  $p < 0.05$ .

649

650

651

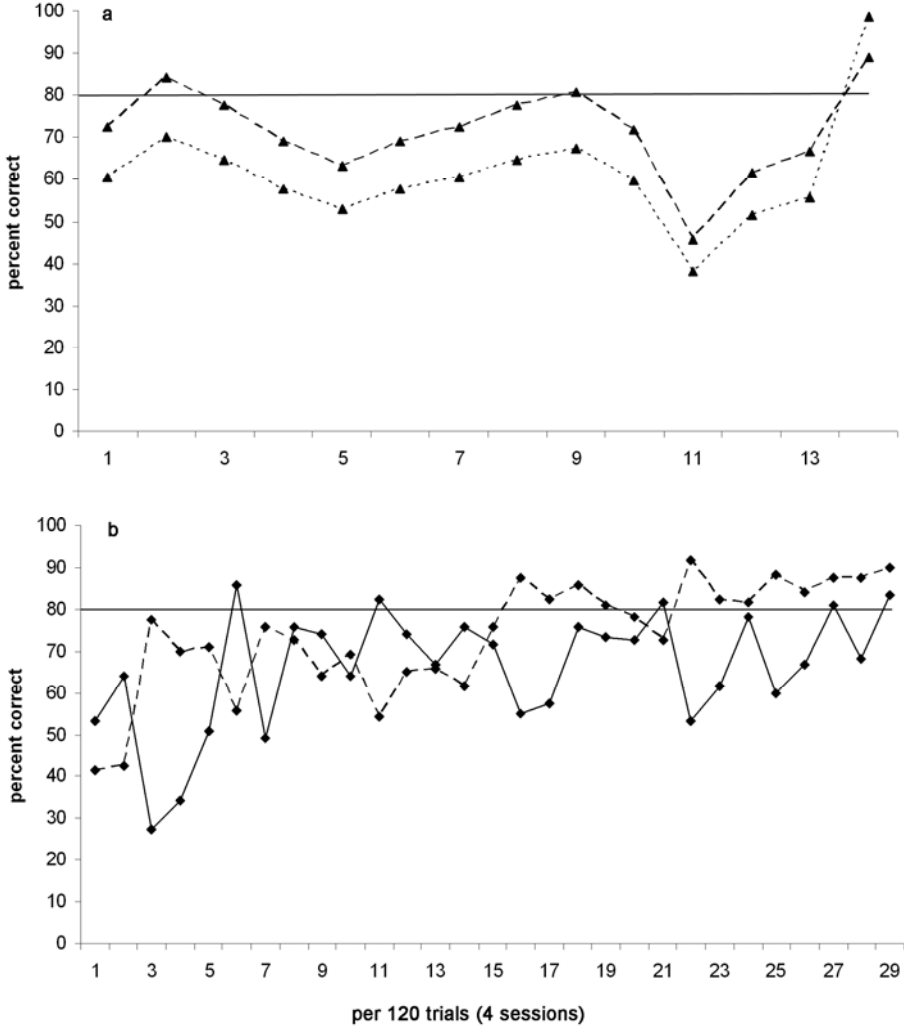
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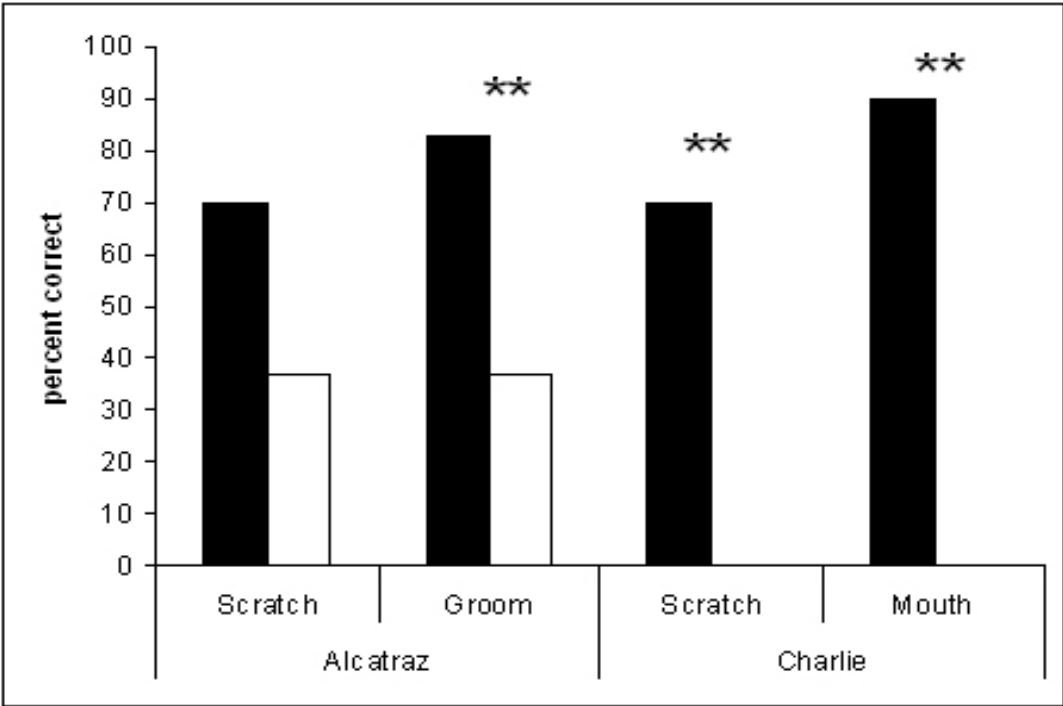
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656 Figure 1

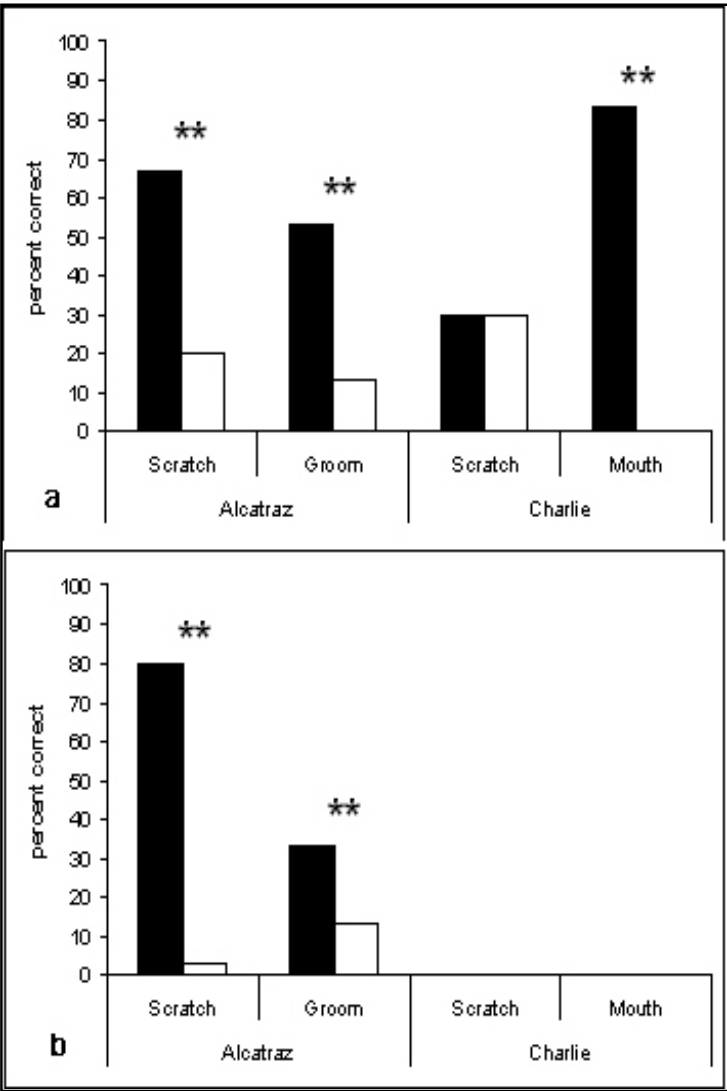


657 Figure 2



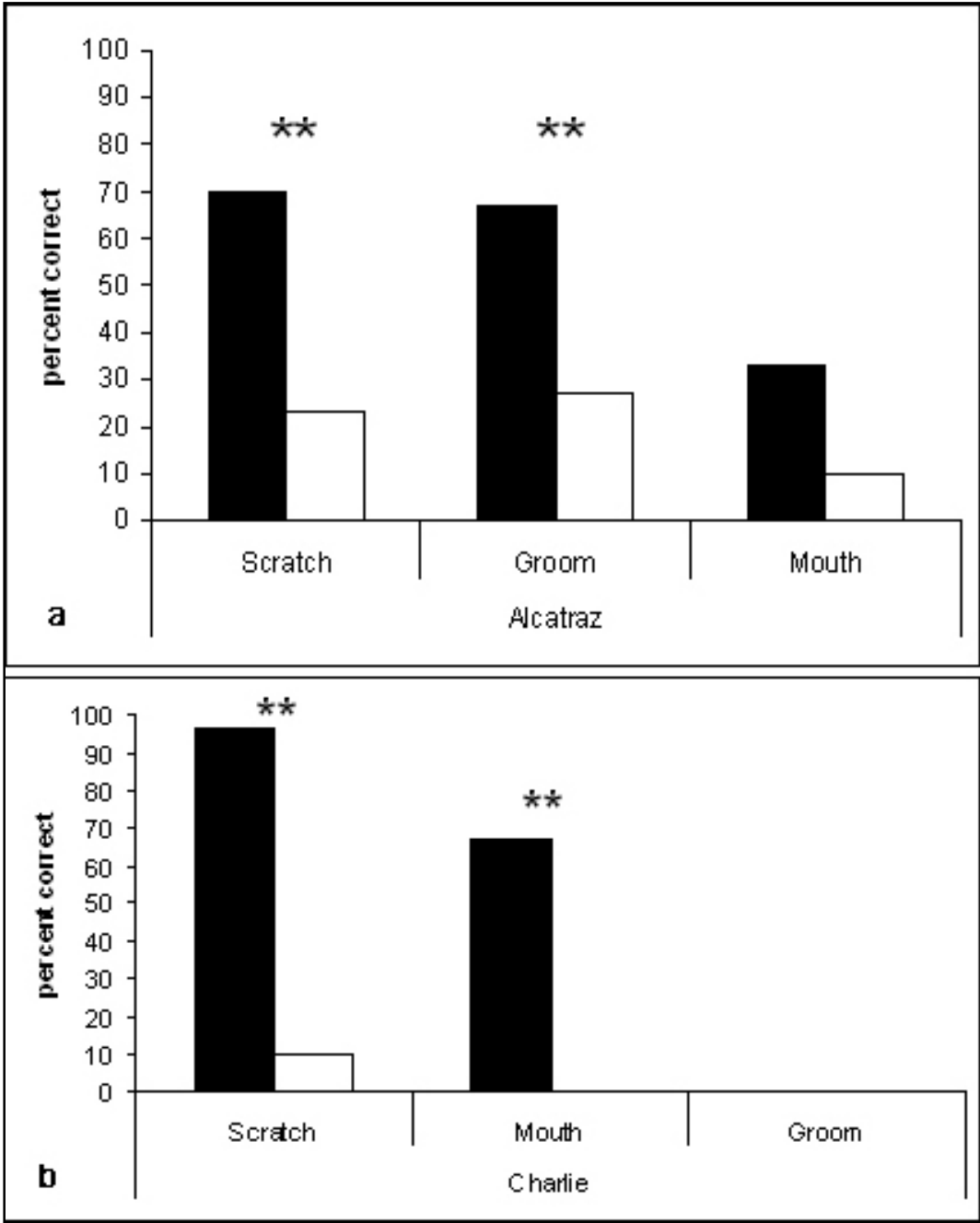
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659 Figure 3.



660

661 Figure 4.



662