

1                   **Social learning, culture and the ‘socio-cultural brain’ of**  
2                   **human and non-human primates**

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16  
17     running head: Primate cultural cognition and socio-cultural brains

18  
19     Noting important recent discoveries, we review primate social learning, traditions and  
20     culture, together with associated findings about primate brains. We survey our current  
21     knowledge of primate cultures in the wild, and complementary experimental diffusion  
22     studies testing species’ capacity to sustain traditions. We relate this work to theories that  
23     seek to explain the enlarged brain size of primates as specializations for social  
24     intelligence, that have most recently extended to learning from others and the cultural  
25     transmission this permits. We discuss alternative theories and review a variety of recent  
26     findings that support cultural intelligence hypotheses for primate encephalization. At a  
27     more fine-grained neuroscientific level we focus on the underlying processes of social  
28     learning, especially emulation and imitation. Here, our own and others’ recent research  
29     has established capacities for bodily imitation in both monkeys and apes, results that are  
30     consistent with a role for the mirror neuron system in social learning. We review  
31     important convergences between behavioural findings and recent non-invasive  
32     neuroscientific studies.  
33

34	Keywords:
35	Social learning
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43	Cultural intelligence hypothesis
44	Mirror neurons
45	Autism
46	
47	
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## 68 1. Introduction

69

70 Recent decades have seen enormous strides in our knowledge and understanding of  
71 many aspects of primate social cognition (de Waal and Ferrari, 2012; Mitani et al.,  
72 2012; Seyfarth and Cheney, 2015a,b) and discoveries about primate social learning,  
73 traditions and culture have been prominent in the progress made (Whiten et al., 2011;  
74 Whiten, 2012; Hoppitt and Laland, 2013; Watson et al., in press). These latter topics  
75 provide the focus for the present review. In discussing ‘social learning’ we take a broad  
76 perspective, taking this to include all learning from others, whether from their actions or  
77 the results of those actions (Heyes, 1994). Some outcomes of such social learning may  
78 be relevant only for a short while, such as which trees are currently in fruit, but others  
79 are longer lasting and may give rise to traditions (Whiten and van Schaik, 2007). We  
80 follow Fragaszy and Perry (2003, p. xiii) in defining traditions as “a distinctive behavior  
81 pattern shared by two or more individuals in a social unit, which persists over time and  
82 that new practitioners acquire in part through socially aided learning”. Of course “two  
83 or more individuals” is a minimal criterion and traditions can be regarded as more  
84 robust the more widely they spread between individuals, between groups and through  
85 larger populations. In relation to “persists over time”, they are similarly more robust the  
86 longer they last, which may or may not involve multiple generations. ‘Culture’ is a  
87 more contentious term. Many authors treat ‘culture’ and ‘tradition’ as essentially  
88 synonyms, but others, often mindful of how much more complex human culture is than  
89 anything encountered in other species, suggest we gain more insight by requiring  
90 additional criteria for culture, such as being based on imitation and teaching (Galef,  
91 1992) or involving multiple and diverse traditions (Whiten and van Schaik, 2007),  
92 features thought to be particularly distinctive in human culture.

93 We relate discoveries about primate social learning and culture to neuroscience in  
94 two main ways. First, at a relatively ‘macro’ level we review evidence that the size of  
95 the brain or major parts of it are associated with an emphasis on the extent or nature of  
96 social learning in the species concerned. This perspective invokes what has accordingly  
97 been called the ‘cultural intelligence hypothesis’ (Whiten and van Schaik, 2011). This  
98 in turn can be considered a special case of the ‘social intellect’ (Whiten and Byrne,  
99 1988a) or ‘social brain’ (Dunbar, 1998) hypotheses to explain primate intelligence, so

100 we begin our review with a brief overview of these ideas and the evidence bearing on  
101 them, relevant for the overarching topic of ‘social cognition’ in this journal theme issue.  
102 At a second, more ‘micro’ level we note the relevance of discoveries about the scope of  
103 imitative matching and learning in primates to the operation of mirror neurons, that fire  
104 both when an animal executes a certain action or observes it performed by others. This  
105 discussion begins with non-human primates, in which mirror neurons were first  
106 discovered (Rizzolatti et al., 2001), but extends importantly to humans, in which  
107 associations with imitation were first identified (Iacoboni et al., 2001; see Molenberghs  
108 et al., 2009, Iacoboni, 2010, and Ferrari and Rizzolatti, for reviews) and where  
109 distortions in the mirror system have been hypothesized to be linked with autism  
110 (Williams et al. 2001).

111

## 112 **2. Social intelligence and the ‘social brain’ of primates**

113

114 Humphrey (1976) was the key originator of what came to be called the “the social  
115 intellect hypothesis”. The core of his proposition was that the acknowledged lively  
116 intelligence of non-human primates (henceforth ‘primates’) was not adapted so much  
117 for dealing with physical problems in domains such as foraging and avoiding predators,  
118 but instead reached its highest sophistication in grappling with the special complexity  
119 being discovered in primates’ social lives. Such ideas were prefigured by some earlier  
120 speculations about primate social complexity (e.g. Jolly, 1966) but Humphrey expressed  
121 the theory in an explicit and articulate fashion with major impacts on primatologists  
122 conducting empirical studies, who were beginning to record the social complexities he  
123 alluded to.

124

### 125 *2.1 Social and Machiavellian intelligence hypotheses*

126

127 Just over a decade later, sufficient empirical work on primate social cognition and  
128 complexity that included shifting alliances and coalitions (de Waal, 1982), social  
129 knowledge (Cheney et al., 1986) and tactical deception (Whiten and Byrne, 1988b) had  
130 accumulated, collated in the first integrative volume on the topic: *Machiavellian*  
131 *Intelligence* (Byrne & Whiten, 1988). The title echoed de Waal’s account of the

132 dynamic power manoeuvrings amongst chimpanzees (*Chimpanzee Politics*, 1982)  
133 which could quote the advice given by Nicolo Machiavelli (1531) about how politicians  
134 could socially manipulate their subjects, because it so well matched chimpanzees'  
135 tactics. Byrne and Whiten emphasized not only the devious social scheming for which  
136 Machiavelli has bequeathed his name to everyday language, but rather, the key mix of  
137 competitive *and cooperative* manoeuvres that Machiavelli identified. Management of  
138 such social tactics creates pressure for greater skill in others, in the potentially spiralling  
139 Machiavellian arms races that Humphrey first sketched. Humphrey (1976) compared  
140 primate social life to a game of chess, in which one's gambits were played out in a  
141 social arena where the other players are constantly reactive and responsive. This may  
142 create a selection pressure for increasingly nimble social tactics, that can be expected to  
143 evolve up to a ceiling of social cognition limited only by the economics of devoting  
144 sufficient neural and other resources to such functions (see Isler and van Schaik, 2014,  
145 on the 'expensive brain framework').

146 Whiten & Byrne (1988a) distinguished three levels of the social or 'Machiavellian'  
147 intellect hypothesis ('MIH'). The most basic is the hypothesis that in contrast to much  
148 early work that focused on intelligence in relation to physical problems typical of  
149 comparative psychologists' laboratories, primate intelligence in the wild is actively  
150 engaged with social life. This version of the hypothesis may appear elementary today,  
151 but has driven over two decades of ingenious research identifying the complexities of  
152 primate social cognition, in both wild and captive primates (Seyfarth & Cheney,  
153 2015a,b, and papers in this journal issue).

154 The second and more ambitious version of the hypothesis proposes that intelligence  
155 has been moulded more by social life than by physical demands such as foraging and  
156 predator evasion. Version three goes further, to propose that the very nature and scope  
157 of intelligence has been shaped by these social selection presses, so that primates'  
158 brains and cognitive potentials have become specifically adapted for dealing with  
159 complexities characteristic only of the social realm. What Humphrey (1976) called  
160 'natural psychology', later called 'Theory of Mind' or mindreading, offers a striking  
161 example, that stimulated productive empirical research with primates particularly in the  
162 present century (Call and Santos, 2012; Whiten, 2013; Krupenye et al. 2016; Meunier,  
163 this issue).

164 To many primatologists who in their research on primate social life have daily been  
165 impressed by its intricacies, these hypotheses may have an inherent plausibility, but  
166 testing them rigorously is challenging. One early approach to this was due to Dunbar  
167 (1995), who examined the relationship between measures of a primate species' relative  
168 brain size – encephalization – and the average size of social groups in the species,  
169 adopted as an initial, if very basic, measure of social complexity. Remarkably, despite  
170 the crudeness of both measures, Dunbar found the positive relationship between them  
171 that the second version of the MIH predicts (Fig. 1). Dunbar dubbed the neural version  
172 of the MIH supported by such discoveries the 'Social Brain Hypothesis' (Dunbar, 1998;  
173 and see Brothers (1990) for a pioneering exploration of the concept of a 'Social Brain').  
174 The variables involved in such tests, group size and neural volumes, may be crude but  
175 are more amenable to straightforward measurement than either social complexity or the  
176 sophistication of social cognition. The tractability of the approach has generated a  
177 substantial corpus of studies further exploring these relationships, that we briefly review  
178 next.

179

180 &lt; insert figure 1 about here &gt;

181

182 *2.2 Social complexity and encephalization: empirical tests*

183

184 Although social complexity and degrees of encephalization are in principle subject  
185 to empirical measurement, this does not mean the process is straightforward. For  
186 example, larger animals tend to have larger brains, so such allometric relationships must  
187 be allowed for; and concerning social complexity, a meaningful social unit needs to be  
188 focused on, which is inherently challenging in fluid or hierarchically structured primate  
189 communities.

190 Controlling for body size has been addressed by controlling directly for this  
191 variable by regressing brain size first on body size and then considering residuals – but  
192 this is not straightforward because the effects are nonlinear. A variety of alternative  
193 approaches have been developed. For example, Dunbar (1998) measured the 'neocortex  
194 ratio', the ratio of neocortex volume to the volume of the remainder of the brain, and  
195 found this index to be positively correlated with a species' average group size. This was

196 not the case for other, ‘ecological variables’ like home range size, which would be  
197 expected if primate intellect has evolved for dealing with physical complexities such as  
198 navigation and foraging on a complex distribution of foods. Accordingly Dunbar’s  
199 results supported the social brain hypothesis. More refined measures of social  
200 complexity have also been explored, such as the size of the social ‘cliques’ that concern  
201 an individual’s most intense social relationships (Kudo & Dunbar, 2001), and the  
202 frequency of ‘tactical deception’ episodes reported in the research literature (Whiten &  
203 Byrne, 1988b; Byrne & Corp, 2004), with the predicted relationships with neocortex  
204 ratio again confirmed.

205       When such analyses have been extended to birds, it was not the size of social  
206 communities or social systems that explained relative brain size, but rather the mating  
207 system, with the greatest encephalization in those species with long-term pair bonding  
208 (Emery et al. 2007). Shultz and Dunbar (2007) further explored the sociality-  
209 encephalization relationship in carnivores, bats and ungulates as well as primates and  
210 found that pair-bonding was most strongly related to relative brain size in all of these  
211 taxa except primates. What might explain this? Emery and colleagues as well as Shultz  
212 and Dunbar shared the interpretation that in both birds and mammals, pair-bonding and  
213 the bi-parental care associated with it involve the management of intimate co-ordination  
214 and synchrony, which selects for encephalization. In primates it is suggested that  
215 analogous, bonded, and intricately negotiated relationships extend the same principles  
216 across larger social networks (Emery et al. 2007; Shultz & Dunbar, 2007). Shultz and  
217 Dunbar (2010) further showed that encephalization is most marked in those taxa of  
218 mammals with higher degrees of sociality, of which primates typically offer prime  
219 examples, supporting the social brain hypothesis from another perspective.

220       These broader taxonomic analyses suggest interesting implications for the evolution  
221 of the human ‘social brain’ (for reviews of this work, see Dunbar & Shultz, 2007,  
222 2010). First, we humans are primates, so this body of research suggests that our  
223 sophisticated social brains did not emerge ‘out of the blue’, but instead have evolved on  
224 the back of socially-driven neural adaptations widespread amongst primates, implying  
225 an important shared pre-human ancestry. Second, we are unusual amongst the apes to  
226 have developed pair-bonding, found to be a modal characteristic of those hunter-  
227 gatherer societies that offer the best models for our evolutionary past ways of life

228 (Marlowe, 2005; Whiten and Erdal, 2012). In such societies, there is bi-parental  
229 investment because fathers invest in the development of their offspring in a variety of  
230 ways from food provisioning to education, for example in relation to hunting (Hewlett  
231 et al. 2011). These two features, the complex social life we share with other primates  
232 (and have made even more elaborate: Whiten and Erdal, 2012) and more unusual pair-  
233 bonded parental investment embedded within band life, may together help to explain the  
234 unique degree of encephalization that has tripled the brain size of our species in just  
235 over two million years. As we shall see below, these characteristics take on special  
236 significance in the realm of social learning and culture.

237       Of course, such effects of selection for social cognitive sophistication on primate  
238 brains have been enmeshed in a complex web of other factors. Such benefits are  
239 energetically costly, so can only evolve if they achieve payoffs that more than  
240 compensate for this, which in turn can be expected to be associated with adaptations to  
241 particular types of ecological niche and other factors such as life history variables. Such  
242 dynamics are beyond the scope of this review but have been explored in some depth for  
243 both non-human and human primates by Isler and van Schaik (2014).

244       Despite such complexities, further explorations of relationships between social  
245 complexity and brain variation in both human and non-human primates have extended  
246 to consider particular parts of the brain (Platt et al. 2016). In humans, for example, the  
247 size of peoples' social networks predicts the volume of regions such as the amygdala,  
248 implicated in emotional responses and vigilance (Bickart et al. 2011) as well as other  
249 parts involved in social functions such as the orbitofrontal cortex (Powell et al. 2012 )  
250 and ventromedial prefrontal cortex (Lewis et al. 2011). Kanai et al. (2011) showed that  
251 the number of people's Facebook friends is correlated with the density of grey matter in  
252 the superior temporal sulcus (STS) and temporal gyrus.

253

### 254 **3. Cultural intelligence and the 'cultural brain'**

255

256 In more recent years a 'cultural intelligence hypothesis' (CIH) has been developed in  
257 part to address findings that the MIH does not explain well, notably the large absolute  
258 and relative brain sizes of the great apes, not all of which live recognizably complex  
259 social groups (van Schaik, 2006; Whiten and van Schaik, 2007; van Schaik and Burkart,



260 2011). However the CIH should apply to all species where cultural transmission  
261 becomes extensive and/or complex in nature.

262 The CIH can be regarded as in some respects a descendant or subsection of the  
263 MIH, and in some respects a competitor to it. It can correctly be thought of as a  
264 subsection insofar as it focuses on *social learning*, which provides one component of  
265 social complexity. Thus, Whiten and Byrne (1988a), in dissecting a suite of facets of  
266 ‘Machiavellian intelligence’ such as social knowledge and theory of mind, already  
267 included social learning and cultural transmission. Allusions to these dimensions of  
268 complexity in the social worlds of primates had in fact been made earlier in the  
269 foundational articles of Jolly (1966) and Humphrey (1976). As Whiten and van Schaik  
270 (2007) noted, the largest part of a major compilation of work under the title of ‘social  
271 complexity’ was already headed ‘cultural transmission’ (de Waal and Tyack, 2005).  
272 However, to properly explicate the CIH, we need first to offer an overview of what we  
273 have learned of the scope of culture in non-human primates.

274

### 275 3.1 *The scope of ‘culture’ in primates*

276

277 The study of potential cultural behaviours in wild primates has long been led by  
278 chimpanzee researchers, from Goodall (1986) through McGrew (1992) to Boesch and  
279 Tomasello (1996) charting accumulating evidence that, like people, chimpanzees  
280 behaved in different ways across their distribution in Africa, with circumstantial  
281 evidence such as youngsters’ intense peering at adult tool use indicating a cultural basis.  
282 The first systematic syntheses became possible when the leaders of nine long-term  
283 projects collaborated to agree behavioural definitions and pool their data (Whiten et al.,  
284 1999, 2001). Starting with 65 candidate behaviour patterns, 39 were identified as  
285 putative cultural variants (traditions) because they were common in at least one  
286 community yet absent in at least one other, with no apparent genetic or environmental  
287 explanations (such as being determined by the availability of key resources). This  
288 number of traditions was unprecedented in comparison to existing reports for other  
289 animals, that typically reported just one or a handful of such variants; moreover they  
290 spanned much of chimpanzees’ repertoires, with examples from tool use for foraging,  
291 comfort and hygiene purposes, grooming, communication and sexual behaviour. Each

292 community was found to exhibit a unique array of such variants so that a chimpanzees'  
293 behavioural profile could be sufficient to allocate it to the region in which it lived; a  
294 cultural 'quilt' diagram illustrating such patterning, after Whiten et al. (1999) is  
295 illustrated in electronic supplementary information in Figure S1 along with a later, more  
296 fine-grained one.

297       Although these findings did not discriminate between specific potential social  
298 learning mechanisms responsible, they nevertheless have profound implications for  
299 primate social cognition, because they imply that these apes live in a cognitive world  
300 that is shaped by the cultural variants of their parents or parental generation in a  
301 significantly rich way.

302       An extensive range of supplementary chimpanzee studies followed, illustrated by  
303 selected examples in Table 1, and other fieldworkers applied what came to be called the  
304 'method of exclusion' (inferring cultural transmission where environmental and genetic  
305 explanations were judged implausible) to other species. Thus orangutans were reported  
306 to display over 20 (later, over 30) cultural variants (van Schaik et al. 2003; for follow up  
307 studies see Table 1), leading to the inference that this degree of cultural complexity  
308 would likely have characterized the common ancestor of all the great apes, around 14  
309 million years ago (van Schaik et al. 2003; Whiten and van Schaik, 2007). Likewise, a  
310 consortium of gorilla researchers have recently produced a similar analysis reporting 23  
311 different cultural variants (Robbins et al. 2006).

312

313       < Insert Table 1 about here >

314

315       Other primates have since been reported to sustain cultures constituted by multiple  
316 traditions of different kinds, notably spider and capuchin monkeys (Santorelli et al.  
317 2011a; Perry et al. 2003; Table 1 and Figure S1 c). Interestingly, these species exploit  
318 ecological niches in the New World that share some commonalities with those favored  
319 by chimpanzees in the Old World, and they are also large-brained; spider monkeys have  
320 the largest brains amongst New World primates and capuchins have the highest  
321 encephalization quotient (brain size corrected for body size) of any monkey. Such  
322 features are consistent with the cultural intelligence hypothesis that we discuss next,

323 which proposes an adaptive linkage between encephalization and the complexity of  
324 cultural transmission on which a species relies.

325       However, we note that the number of species for which serious investigations on  
326 the scope of culture have been published remains regrettably small, as Table 1  
327 demonstrates. This may be due in part to the demanding requirement for long-term  
328 studies of multiple groups of the same species, of which there are still all too few. This  
329 means that we must be correspondingly cautious about the significance of those species  
330 mentioned above, that are prominent in the table so far – an issue we return to in the  
331 section that follows.

332

### 333 *3.2 The cultural intelligence hypothesis*

334

335 Measures of encephalization and social complexity exhibit a good fit across primates as  
336 a whole, but the fit is better if the great apes are considered separately, because as a  
337 family they are even more encephalized (Fig. 1). This difference is not well explained  
338 by the social intellect/brain hypotheses, because aside from chimpanzees' distinctive  
339 fission-fusion communities, the apes cannot be claimed to exhibit greater social  
340 complexity. Noting the complexity of culture attributed to the great ape family on the  
341 basis of the chimpanzee and orangutan field data outlined above, van Schaik (2006) and  
342 Whiten and van Schaik (2007) developed a 'cultural intelligence hypothesis' (CIH),  
343 proposing that the complexity of culture may help explain the enlarged brains of the  
344 apes. Like the MIH, the CIH is not inherently restricted to primates but could apply to  
345 any animals that display these characteristics, so other potential candidates might  
346 include large-brained cetaceans that evidence cultural complexity, spanning both vocal  
347 and behavioural domains (Rendell and Whitehead 2001; Whitehead and Rendell 2015).

348       The CIH is in one sense a competitor to the MIH insofar as its potential to explain  
349 encephalization is concerned, but equally it can be seen as a particular version of the  
350 social intellect hypotheses, emphasizing one particular component of an animal's social  
351 life concerned with the transmission of culture. The CIH in turn embodies multiple  
352 strands. One is the proposition that 'culture makes you smart'; that what a child or  
353 juvenile primate acquires from its cultural heritage gives it a greater competence in  
354 varied but important aspects of its daily life, ultimately enhancing reproductive

355 potential. In turn, the importance of culture to the species concerned is expected to  
356 shape and enhance the cognitive underpinnings of key cultural processes, and thus the  
357 corresponding structures in the social/cultural brain. This includes multiple capacities  
358 for (i) cultural transmission such as imitation, emulation and teaching, (ii) storage of an  
359 expanding cultural repertoire, and (iii) the intermittent creation of the innovations that  
360 feed cultural change. The hypothesis that ‘culture makes you smart’ is thus proposed to  
361 operate both on ontogenetic-developmental timescales and on the long-term evolution  
362 of species’ brains and culture-related cognitive capacities (van Schaik and Burkart  
363 2011).

364 Evidence supportive of these hypotheses comes from a variety of sources across  
365 humans, apes, other primates and non-primates, explored by Whiten and van Schaik  
366 (2007) and van Schaik and Burkart (2011). In humans, of course, the proposition that  
367 ‘culture makes you smart’ is uncontentious; indeed, it is the basis of our educational  
368 systems. For the non-human primates the hypothesis was originally developed to  
369 explain the particular enhanced encephalization of the great apes, and the evidence is  
370 arguably strongest for them. In chimpanzees, one particularly relevant study in the wild  
371 showed that juvenile females invested more time than did their male peers in closely  
372 observing their mother skilfully apply stem tools to extract prey from termite mounds  
373 (Lonsdorf et al. 2003). Most significantly, these females became ‘smarter’ in their  
374 mastery of the technique a whole year ahead of the males, also showing some matching  
375 to differences in mothers’ techniques (length of tool and depth of probing) than did the  
376 males. Such mastery is particularly important for females, who as adults spend more  
377 time in tool use for gaining invertebrate prey than males, who are able to gain more  
378 vertebrate prey through hunting (Whiten, 2006). More generally, most of the behaviour  
379 patterns in the corpus of putative chimpanzee traditions concern tool-aided or other  
380 forms of foraging technique. Becoming culturally competent in these techniques can  
381 significantly extend these animals’ lifetime success, as in helping them through dry-  
382 season bottlenecks in fruit availability, where technology has been shown to provide  
383 critical access to other food sources such as nuts and otherwise resistant embedded food  
384 sources not available to other species (Yamakoshi, 1998).

385 Orangutan culture also incorporates such life-skills. Forss et al. (2016) and Burkart  
386 et al. (2017) suggest that in a species that depends significantly on cultural transmission,

387 there will be correlated selection on individual intelligence. Forss et al. (2016) provide  
388 evidence in support of this insofar as Sumatran orangutans, which display a more  
389 extensive and complex cultural repertoire than their Bornean cousins, achieve more in  
390 zoo-based tests of ‘general intelligence’ and have marginally but significantly larger (by  
391 2-12%) brains.

392 Experimental studies complement and reinforce these findings from the field  
393 (Whiten, 2015). Multiple studies show that chimpanzee tool use is socially learned,  
394 through both dyadic experiments involving a single model and single observer (Whiten  
395 et al., 2004) and diffusion experiments in which different forms of tool use, seeded in  
396 different groups, pass from individual to individual, creating incipient traditions that  
397 deliver access to a food source otherwise unavailable (Whiten et al., 2007). Relevant  
398 examples of each are that East African chimpanzees who do not nut-crack in the wild  
399 learned to do so through observation of a skilled nutcracker (Marshall-Pescini &  
400 Whiten, 2008a); and that alternative forms of stick-tool use to solve an artificial  
401 foraging task spread further in the groups into which they were seeded (Whiten et al.,  
402 2005).

403 A different kind of evidence supporting the CIH is that for both chimpanzees and  
404 orangutans, Whiten & van Schaik (2007) showed that greater opportunities to learn  
405 from others, deriving from more extended times in association with groupmates in some  
406 communities, predicted the acquisition of the more complex techniques of each ape’s  
407 cultures. In a more fine-grained study, Schuppli et al. (2016) recorded the intense  
408 ‘peering’ behaviour of wild juvenile orangutans, finding its occurrence confirmed a  
409 suite of predictions concerning its role in skill acquisition, such as that relevant  
410 exploration was enhanced following close peering events of events like nest-building  
411 and tool use. A further, complementary kind of evidence is that the ‘enculturation’ of  
412 young apes raised in intimate relationships with human culture tends to create an  
413 enhanced capacity to learn by imitation and a corresponding repertoire of competences  
414 in aspects of the surrounding culture, from symbolic communication to use of artefacts  
415 ranging from cups to toothbrushes (Tomasello et al. 1993a; Tomasello and Call, 2004;  
416 Whiten, 2011).

417 The sophistication of social learning in the apes is also relevant and further  
418 reviewed in the following section. As noted above, the findings indicated in Table 1

419 together with their encephalization status suggests that both capuchins and spider  
420 monkeys may also fit the predictions of the CIH, even if the linkages are less robust for  
421 them. Supplementary experimental evidence is more lacking for these monkeys, but for  
422 capuchins at least, there is some evidence of social learning effects strong enough to  
423 sustain laboratory traditions (Dindo et al. 2008, 2009), and evidence for selective  
424 attention to the most proficient nut-cracking adult models has been documented in free-  
425 ranging capuchins (Ottoni et al. 2005). By contrast we are not aware of any such  
426 experimental studies of social learning in spider monkeys, and the survival value of  
427 many of the cultural variants identified in the wild for this species (Santorelli et al.  
428 2011a) beg further study.

429 More broadly based evidence that social transmission is associated with enhanced  
430 cognition comes from a study that identified correlations between a measure of  
431 encephalization ('executive brain ratio' – the volume of the cortex plus striatum,  
432 relative to brain stem) and the prevalence of social learning in a species, based on  
433 reports in the research literature (Reader & Laland, 2002). Social learning explained  
434 more of the variance than any of the other variables analysed in this study, with an  $r^2$  of  
435 0.48 (Fig. 2). Reader and Laland (p. 4440) concluded their results "suggest an  
436 alternative social intelligence hypothesis to those stressing the Machiavellian  
437 characteristics of mind-reading, manipulation and deception"; instead, "individuals  
438 capable of inventing new solutions to ecological challenges, or exploiting the  
439 discoveries or inventions of others, may have had a selective advantage over less able  
440 conspecifics, which generated selection for those brain regions that facilitate complex  
441 technical and social behaviour".

442

443 < insert figure 2 about here >

444

445 This conclusion is clearly consistent with the cultural intellect/brain hypothesis.  
446 However, research particularly by Barton (2006; Barton and Harvey, 2000) has shown  
447 that many brain components coevolve as a network, so that more recent studies of this  
448 kind have tended to retreat to examining cognitive correlations with absolute brain size,  
449 or total brain size corrected for body size (see also Deaner et al., 2006). The most recent  
450 study in this line (Navarrete et al., 2016) was focused on primate innovation and tool

451 use, but also included the measure of social learning frequency employed by Reader and  
452 Laland (2002); it confirmed and extended their findings, concluding from the  
453 relationships between them that encephalization and capacities for both innovation,  
454 especially innovation involving tool use, and social learning coevolved. Inference of  
455 any simple directional causality between these cannot be established - most probably  
456 they influenced each other over their evolutionary history. Nevertheless, Navarrete et al.  
457 (2016) suggest that one plausible interpretation of their findings is that “through social  
458 transmission many primates learn to exploit novel foods, and the resources so gained  
459 both aid survival and fuel brain growth” (p. 8). Moreover, in relation to the discussion  
460 of social intelligence further above, these authors note that the consistent linkage they  
461 find between “social group size and brain size support the established finding that social  
462 intelligence is an important driver of brain evolution” (p. 8).

463         Nevertheless, caution seems in order in relation to social learning in these studies,  
464 for the data used were simply those reported in the primate literature. They may thus be  
465 subject to several forms of bias, such as that certain researchers interested in topics like  
466 intelligence and culture selectively target what they anticipate are promising species,  
467 and these researchers may then be more likely to be motivated to put observations of  
468 corresponding behaviour into print for these species. Lefebvre (2013) discusses a  
469 variety of potential biases of this kind and how corrective measures may be  
470 implemented.

471         An intriguing complication in the picture is the discovery by Barton and Venditti  
472 (2014) that it is the cerebellum that has expanded fastest in the great ape family, a trend  
473 carried further in humans. It has been common to focus on the neocortex as the seat of  
474 ape, and particularly human intelligence, no less so than for social intelligence, yet as  
475 Barton and Venditti point out, the human cerebellum contains four times as many  
476 neurons as the neocortex and it has expanded at several times the rate of the neocortex  
477 amongst the apes. These authors calculate that as a result, in human evolution  
478 approximately 16 billion more cerebellar neurons have been added beyond expectations  
479 for our brain size, equivalent to all the neurons in the neocortex! Yet the cerebellum is  
480 the relative ‘Cinderella’ of the pair (in fMRI work, it is often even omitted from the  
481 image!) and its functions are less well understood. Barton and Venditti suggest that key  
482 functions in relation to their analysis are likely to include “learning of sensory-motor

483 skills, imitation, and production of complex sequences of behaviours” (p. 2442) and the  
484 cerebellum is in any case massively inter-connected with the neocortex.

485

### 486 *3.3 ‘Vygotskian’ and ‘cultural intelligence’ hypotheses*

487

488 The cultural inheritance hypothesis discussed above was developed to explain variance  
489 amongst non-human primates, and great ape encephalization and social learning in  
490 particular. It is important to recognize that Moll and Tomasello (2007) instead offered a  
491 potentially complementary, human-focused ‘Vygotskian intelligence hypothesis’,  
492 proposing that “primate cognition in general was driven mainly by social competition,  
493 but beyond that the unique aspects of human cognition were driven by, or even  
494 constituted by, social cooperation” and that “regular participation in cooperative,  
495 cultural interactions during ontogeny leads children to construct uniquely powerful  
496 forms of perspectival cognitive representation”. (p. 639). Lev Vygotsky’s name was an  
497 appropriate one to adopt for this, given his classic writings on culture and collaboration  
498 in cognitive development, and the hypothesis nicely complemented the broader CIH  
499 that Whiten and van Schaik contributed in the same themed journal issue (“Social  
500 intelligence: from brain to culture”; Emery et al. 2007). However, in presenting data  
501 supportive of these ideas from comparisons between children and other apes in social  
502 versus physical cognition, an article by Herrmann et al. (2007) now referred to the  
503 Vygotskian version as the “cultural intelligence hypothesis” - a potentially confusing  
504 step because this hypothesis, seeking to explain ape/human differences, has a different  
505 focus to the CIH which is about differences across primates and even broader classes of  
506 animal. Accordingly we advocate that either there be a reversion to the label of  
507 ‘Vygotskian intelligence hypothesis’ to mark the specific scope explicated by Moll and  
508 Tomasello, or alternatively the two hypotheses may be harmonized with each other,  
509 each essentially representing different points along a continuum of complexities in  
510 cultural cognition on the one hand, and encephalization on the other. We advocate  
511 exploring the latter as an interesting option for future development.

512

## 513 **4. Social learning, brain circuits and the mirror neuron system**

514



515 Primate social learning has been studied for over a century (Whiten and Ham, 1992;  
516 Tomasello and Call, 1997) and has been yet more intensely researched in recent decades  
517 (Whiten, 2012). Much of this work in the last century focused on the question of what  
518 kinds of social learning processes were at work, but in recent years new perspectives  
519 have emerged. Notable amongst these has been an extension of experimental designs  
520 beyond the common ‘what does primate B learn from primate A?’ to social diffusion  
521 experiments in which the spread of socially learned information is tracked across and  
522 between groups, linking more directly with research on primate cultures at large,  
523 outlined above. A further new focus has been on adaptive, contextual selectivity in  
524 social learning, for example in relation to preferential learning from certain classes of  
525 individual, such as those most skilled (Price et al. 2017; Watson et al. in press). As a  
526 result, we now know an enormous amount about social learning in a widening array of  
527 primates, less about the enormously complex underlying neuroscience of such learning.  
528 Further below we focus on potential links between aspects of our findings in primate  
529 social learning and some new discoveries about relevant neural circuits and the  
530 functioning of what has come to be called the mirror neuron system.

531

#### 532 *4.1 Primate social learning: imitation, emulation and cultural diffusion*

533

534 As animal social learning theory has developed, increasingly complex taxonomies  
535 dissecting the diverse psychological processes involved have been developed (Whiten et  
536 al. 2004; Hoppitt and Laland, 2008). However, three broad categories have dominated  
537 this research area: imitation, emulation and stimulus/local enhancement.

538 The distinction between emulation and imitation emerged when, in a study of  
539 chimpanzees’ social learning of using a rake to acquire food, Tomasello et al. (1987)  
540 observed that, although most chimpanzees did not copy the particular motor act a model  
541 used to acquire food, they did apply the tool more successfully than could be accounted  
542 for by mere ‘stimulus enhancement’, in which social learning involves only the drawing  
543 of attention to a particular object. Tomasello et al. suggested that the chimpanzees had  
544 observed “the relation between the tool and the goal” (p. 182) and learned “to use the  
545 tool in its function as a tool” (p.182), a type of social learning that Tomasello (1990)  
546 later labelled ‘emulation’. Tomasello noted that in emulation the observer may act “in

547 any way it may devise” (p. 284) to achieve the goal or result it had seen attained, thus  
548 contrasting with imitation, which is defined by matching to the actions of the model  
549 observed. Accordingly, to a first approximation, imitation is copying the actions of  
550 another individual, whereas emulation is copying only the results the model achieves.

551 A series of experiments comparing children’s social learning with that of  
552 chimpanzees and focused on emulation followed. In the first, children copied a human  
553 model’s trick of flipping over a pronged rake to pull in a reward and were described as  
554 imitating, unlike chimpanzees who used the tool without replicating the flip action and  
555 were therefore described as emulating (Nagell et al. 1993). Call and Tomasello (1994)  
556 found similar copying in orangutans. On the basis of such studies, Tomasello, Kruger et  
557 al. (1993a) argued that the earlier assumption that chimpanzees (and other primates)  
558 were capable of imitation was not supported; instead, they emulate, and the only true  
559 imitators are humans, who display high fidelity copying in childhood. The case for this  
560 dichotomy between non-human primate emulation and human imitation has been  
561 supported by a growing set of studies over the years, and hypothesized to be key in  
562 explaining the gulf between the richness of human culture and particularly its  
563 cumulative nature, contrasting with the limited cultures of other primates (Tomasello et  
564 al. 1993a; Tennie et al. 2009).

565 However, results have also emerged in our own studies and those of others that  
566 indicate a measure of imitative capacity in both apes and monkeys. We review these  
567 studies below and suggest their relevance to the function of mirror neurons. Mirror  
568 neurons are a class of neurons identified in the premotor cortex of macaque monkeys,  
569 that fire not only when the monkey performs a certain action such as grasping a food  
570 item, but also when it sees another monkey do this (Rizzolatti and Fogassi, 2014). In  
571 discussing the potential function of these neurons in primates, the researchers involved  
572 initially dismissed what might seem the most obvious – imitation – because they did not  
573 see evidence of imitation in their monkeys and they noted a current scepticism about the  
574 occurrence of imitation in monkeys generally, as noted above (see also Visalberghi and  
575 Frigaszy, 2002). Instead they proposed that the function of these neurons was in effect  
576 to ‘stand in the shoes of the other’ and through this mirroring, recognize the goals  
577 inherent in the actions of others (Rizzolatti et al. 1996; Gallese and Goldman, 1998).

578 Our results concerning bodily imitation in monkeys and apes, reviewed further  
579 below, moderate this view that non-human primates lack the capacity for matching and  
580 replicating the actions of others apparent in human imitation. However there is another  
581 set of studies to which we draw attention, that demonstrate matching and replication on  
582 a scale relevant to the larger question of cultural transmission. These are cultural  
583 ‘diffusion experiments’, that go beyond the classic, dyadic ‘does B copy A?’ design of  
584 most 20<sup>th</sup> century research, instead tracking the outcome of an initial seeding of a novel  
585 behaviour as it spreads (or not), across multiple individuals. By 2008, Whiten and  
586 Mesoudi were able to review 33 such studies in animals, including 17 on primates.  
587 Whiten et al. (2016) have reviewed 30 further diffusion studies published since, of  
588 which as many as 20 were on primates and these are summarized in Table 2. The  
589 resilience of replication shown in these studies is very variable, which in itself is  
590 consistent with the relatively negative conclusions drawn about primates’ powers of  
591 copying outlined above. However, this corpus of studies includes some that do show  
592 considerable resilience. For example amongst the ape studies, Whiten et al. (2007)  
593 found that alternative foraging techniques (both with tool-use, and not) seeded in  
594 separate groups of chimpanzees spread with significant fidelity across these groups, and  
595 then to a second group who watched the first one, and in the same way to a third.  
596 Interestingly, some ‘corruption’ that occurred along the way, in which a few individuals  
597 discovered the technique used by the other group, were over-ridden such that the third  
598 group expressed good conformity to the technique originally seeded in the first group.  
599 Amongst the monkey studies we find a similar phenomenon, as alternative seeded  
600 foraging techniques spread across two groups of capuchin monkeys, showing occasional  
601 corruptions but nevertheless maintaining resilience of the alternative incipient traditions  
602 (Fig. 3; Dindo et al. 2009).

603

604 &lt; insert figure 3 about here &gt;

605

606 We highlight these studies here to emphasize that non-human primate social  
607 learning can be capable of significant copying fidelity, sufficiently potent to sustain  
608 alternative traditions. However such effects can also be fragile, with several studies in  
609 Table 2 reporting weak fidelity. Moreover, these studies do not discriminate whether

610 fidelity is maintained by imitation of the actions involved, or emulation of the results of  
611 actions (e.g. in Fig. 3, door rises versus door slides). This is an issue we consider in the  
612 two sections to follow and is a significant issue in the neuroscientific analyses of Hecht  
613 et al. (2013a,b) we shall discuss there.

614  
615 *4.2 Forms of social learning in apes and monkeys; neural circuits and mirror neurons*

616 Much more research on social learning has been undertaken with chimpanzees and  
617 other apes than with any species of monkey, and several of the methodological  
618 approaches have not been replicated for both monkeys and apes, so here we discuss  
619 apes (principally chimpanzees) first, and monkeys separately.

620

621 *4.2.1 Imitation, emulation and the scope of social learning in apes*

622

623 Soon after setting out the basic ‘chimpanzee-emulators versus child imitators’  
624 hypothesis, Tomasello and colleagues provided one particular exception. Savage-  
625 Rumbaugh had remarked that chimpanzees and bonobos participating in her  
626 explorations of language-like abilities, which involved highly enriched learning  
627 contexts, displayed spontaneous imitation; accordingly, Tomasello, Savage-Rumbaugh  
628 et al. (1993b) conducted a battery of formal tests inviting the apes to copy a wide range  
629 of novel actions on objects, such as squeezing the bristles on a brush, or instead using it  
630 to paint some foam on the floor. Three chimpanzees with the most intense  
631 ‘enculturation’ into human daily life displayed recognizable imitation in nearly half  
632 these cases, as did two year old children tested similarly, whereas other, mother-reared  
633 chimpanzees showed very little. Thus, here was evidence both that quite high fidelity  
634 copying is within the grasp of at least some non-human apes; and (ii) that it is  
635 significantly enhanced during development by an appropriate social environment. We  
636 suggest it is unlikely the latter conjures imitative ability out of the blue.

637 In this 1993 study chimpanzees were verbally invited to “Do what I do”, an  
638 approach that shared some methodological overlap with an earlier study by Hayes and  
639 Hayes (1952) in which a home-raised chimpanzee was first trained to imitate a series of  
640 actions on the invitation to “Do this”, then tested on a battery of more novel actions,  
641 many of which the chimp, Viki, was reported to copy. The basic approach was  
642 replicated by Custance et al. (1995) with two young non-enculturated chimpanzees,

643 with the important added rigor of responses being classified by coders blind to what  
644 action the chimpanzee had seen. This was also replicated by Call (2001) with an  
645 enculturated orangutan. In both studies response matches to each of the 48 test items  
646 could be identified at significant levels by the coders. The orangutan was reported to  
647 fully imitate 58% and partially imitate another 36% of the target items.

648       Such studies are important in relation to those definitions of imitation in which  
649 some authors require bodily matching between what the model does and what the  
650 observer does, to discriminate imitation of actions from emulation. All the target items  
651 of Tomasello et al. (1993b) employed objects, so it is difficult to rule out the possibility  
652 that the chimpanzees were replicating what the objects did, rather than actions of the  
653 model. By contrast the battery employed by both Custance et al. and Call included  
654 many purely bodily actions, including whole body ones like hugging oneself, and finer  
655 facial and manual actions, like ‘clap back of hand’. These studies thus demonstrate a  
656 mapping in these apes of body-part, model-to-self correspondence, a finding that is  
657 further complemented by a study by Buttelmann et al. (2007) in which chimpanzees  
658 copied some bizarre uses of body parts such as a head touch to switch on a light.

659       Such bodily correspondence is what is coded in the firing of certain mirror neurons  
660 identified in the research program of Rizzolatti and colleagues cited above. Mirror  
661 neurons were discovered in, and have principally been further studied in, macaque  
662 monkeys rather than apes, but brain imaging with humans has identified regions  
663 homologous to those where mirror neurons are recorded in monkeys, that respond to  
664 observed actions of others in similar ways, and the network of these regions is referred  
665 to as the ‘mirror system’. Accordingly it is likely that mirror neurons are to be found in  
666 other primates including apes (indeed, mirror neurons for vocalization have also been  
667 reported in songbirds, that typically learn their song by copying others: Mooney, 2014).  
668 Moreover, through further fMRI studies, the human mirror system has been implicated  
669 in imitation, among other functions (Iacoboni et al. 2001; Iacoboni, 2012; Rizzolatti et al.  
670 2001). Putting all these findings together, the demonstration of significant bodily  
671 imitation in chimpanzees now makes it a plausible hypothesis that mirror neurons  
672 support imitative functions in our closest ape relatives, that are capable of the degree of  
673 matching shown in the Custance et al. and Call studies.

674 One fine-grained analysis within a chimpanzee social learning study appears  
675 particularly relevant to this likelihood. In a study of the social learning of nut-cracking  
676 in East-African chimpanzees, Marshall-Pescini and Whiten (2008b) reported that when  
677 naïve young recruits watched an older, skilled nut-cracking model, they would  
678 sometimes show some entrainment (even synchrony) of downward striking actions like  
679 those of the hammering model. This cannot be emulation because the recruit is holding  
680 no hammer stone and has no nut – it is pure bodily mimicry. Fuhrmann et al. (2014)  
681 have since analysed the relevant video records frame by frame, as shown in Fig. 4 (and  
682 see video clips in the electronic supplements to these two papers), allowing  
683 sophisticated time-series analyses to objectively confirm significant motor matching and  
684 entrainment, even though such phenomena appeared to repeatedly ‘spill over’ in the  
685 actions of only one youngster in particular. This kind of entrainment, linking visual  
686 perceptions of another’s actions with motor correspondences in oneself, is just the kind  
687 of linkage that is signalled by the firing of mirror neurons.

688

689 &lt; insert figure 4 about here &gt;

690

691 The same can be said for the reverse process of recognizing when another  
692 individual is imitating one’s own actions, which was first demonstrated in an  
693 experiment by Nielsen et al. (2005). In this study, after a period in which humans  
694 copied the spontaneous actions of a chimpanzee, the ape started to vary its actions with  
695 apparent intent, monitoring the imitative efforts of the human, and did so more than in a  
696 series of control conditions such as contingent but non-imitative responses. More recent  
697 studies have replicated the phenomenon, reporting it to be elicited by the imitative  
698 actions of a humanoid robot (Davilla-Ross et al., 2014) and to be correlated with  
699 variation in other social and communicative competencies (Pope et al., 2015). Such  
700 imitation recognition calls on neural mechanisms that code the correspondence between  
701 another’s actions and one’s own, just as the primary process of imitation does.

702 However, we note that bodily matching is not the only way imitation has been  
703 defined. Byrne and Russon (1998), in an influential theoretical analysis, suggested that  
704 alternatively one might see imitation in the overall sequential or hierarchical structure of  
705 complex actions like nut-cracking, a phenomenon they called program-level imitation.

706 Accordingly, Whiten (1998) demonstrated that chimpanzees a convergence, over a  
707 series of trials, on whichever of two alternative sequences of disabling defences of an  
708 ‘artificial fruit’ they witnessed a model perform. An experiment by Horner and Whiten  
709 (2005) was in line with such conceptions but explored imitation versus emulation  
710 conceptualized as different ends of a continuum. In this study, when participant juvenile  
711 chimpanzees witnessed a model perform a sequence of tool-based actions on an opaque  
712 foraging task, it was predicted that a more complete imitative copy of the sequence  
713 would be seen than when the same task was transparent and the first segment of the  
714 action sequence could be seen to be causally unnecessary. This prediction was  
715 confirmed in the case of the chimpanzees, who thus produced a more ‘emulative’  
716 response in the transparency condition. Surprisingly, in this study young children copied  
717 all segments of the sequence even in the transparent condition where causal irrelevance  
718 appeared visibly obvious, a disposition later dubbed ‘over-imitation’ (Lyons et al.,  
719 2007). Such over-imitation has since become a vigorous field of research particularly in  
720 developmental psychology (Whiten et al. 2009; Nielsen et al., 2014).

721 A different way in which the emulation/imitation distinction has been approached  
722 is via a ‘ghost experiment’ in which there is no model visible to imitate, and all an  
723 observer can watch is the movement of the objects normally caused by a model. This  
724 can be achieved in various ways, such as mechanically or by appropriate video  
725 manipulation. Hopper et al. (2007, 2015) found that chimpanzees learned nothing from  
726 such scenarios in a complex tool use task; instead chimpanzees seem to need to see  
727 another chimpanzee acting on the objects, implicating at least some basic level of  
728 imitation. However, in a much simpler task Hopper et al. (2008) did find evidence for  
729 emulation in a ghost condition. Tennie et al. (2010) went further, showing that when  
730 chimpanzees could not copy how they saw a human pour water into a tube to make a  
731 desirable peanut float up to be grasped, because the chimpanzees did not have the bottle  
732 the human had used, some chimpanzees collected water from their drinker and spat it  
733 into the tube instead – an impressive display of imaginative emulation!

734 Taking account of this array of findings and others, Whiten et al. (2009) rejected  
735 the simple dichotomy of emulating apes versus imitative children, and instead  
736 concluded that all these species have a ‘portfolio’ of social learning processes that  
737 include imitative, emulative and other, simpler forms, applying these in often adaptive

738 ways, selectivity according to context. Such selectivity may take a variety of forms; one  
739 has already been outlined in the differential response of young chimpanzees to the  
740 transparent and opaque test boxes of Horner and Whiten (2005). Other forms include  
741 choices between alternative models to copy, such as ‘copy the most successful’ (Watson  
742 et al. in press; Price et al. 2017).

743 Another form of selectivity is to copy the majority, thus potentially benefitting from  
744 what many of one’s groupmates have found to be a preferred option to choose. Whiten  
745 et al. (2005) found evidence suggesting conformity to the majority in a diffusion  
746 experiment in which alternative tool-use techniques were seeded in two groups and  
747 spread further in them, creating incipient traditions. Several individuals subsequently  
748 discovered the technique used by the other group, but by two months later they tended  
749 to have converged again on the technique favoured in their own group. However, this  
750 was a post-hoc finding and not one explicitly tested by an experiment. This was done by  
751 Haun et al. (2012), who showed that chimpanzees preferred to copy the choices of three  
752 chimpanzees over a single one, demonstrating a ‘copy the majority’ rule of conformity.  
753 Results consistent with this have been reported from the wild by Luncz and Boesch  
754 (2012, 2014), who discovered different preferences for seasonal nut-cracking tools in  
755 neighbouring communities and that females, who transfer between communities, came  
756 to display the same preference as residents, implying that these immigrants conform to  
757 the local norms they experience after transferring communities. The phenomenon of  
758 conformity has become a topic of much interest, and also contention, in the field of  
759 animal social learning (Claidière and Whiten, 2012; van Leeuwen and Haun, 2014; van  
760 Leeuwen et al., 2016; Whiten and van de Waal, 2016.).

761 As will be apparent, the research literature on ape social learning has become huge,  
762 particularly for our closest living relative, the chimpanzee, and we have been forced to  
763 be highly selective in the above review. Topics not covered here for want of space  
764 include so-called ‘rational’ imitation (Buttelmann et al. 2007), the selective copying of  
765 intentional acts (Tomasello and Carpenter, 2005), teaching (Hoppitt et al. 2008) and  
766 cumulative culture (Dean et al. 2012). For complementary reviews that address these  
767 and other current issues in this area, readers may wish to consult Whiten and Erdal  
768 (2012), Galef and Whiten (2017), Whiten (2017, a, b) and Watson et al. (in press) as  
769 appropriate.



770

771 *4.2.2 Imitation, emulation and the scope of social learning in monkeys*

772

773 Several of the complementary approaches to imitation that have been brought to  
774 bear on apes are not available for monkeys. For example, efforts to train monkeys to  
775 ‘Do-as-I-do’ have met with no success (Mitchell and Anderson, 1993; Fragaszy,  
776 Deputte et al. unpublished, cited in Visalberghi and Fragaszy, 2002). This in itself  
777 suggests an intriguing difference between apes and monkeys, with the former appearing  
778 to be able to recognize the act of imitation itself, unlike the monkeys tested. To our  
779 knowledge, episodes of model-observer ‘entrainment’ like that outlined above for nut-  
780 cracking chimpanzees have also not been recorded in monkeys, and equivalent ‘ghost  
781 experiments’ have not been completed (although see further below for a novel variant  
782 employed by Subiaul et al., 2004). These contrasts suggest a lesser facility in imitation  
783 in monkeys compared to apes, and it is not uncommon for authors to state baldly that  
784 monkeys do not imitate (Visalberghi and Fragaszy, 2002).

785 Limited evidence for bodily imitation has nevertheless been published, employing  
786 an approach applied in avian studies, where observer birds who witnessed a model  
787 stepping on a treadle to obtain food as opposed to a model using their beak to depress  
788 the treadle, showed a significant tendency to use the same body part (Zentall et al.,  
789 1996). Similarly, in a study of marmoset social learning of how to open a lidded food  
790 canister, those who watched a model using their hand to do so, as opposed to a model  
791 using their mouth, likewise showed a significant degree of using the same body part  
792 they had witnessed (Voelkl and Huber, 2000). This cannot be emulation because the  
793 result is the same in both cases: what is different is the action, which is what must be  
794 being replicated. The same authors later took a different approach to the question of  
795 imitation in their marmosets, performing a painstaking frame-by-frame analysis of the  
796 trajectory of a socially learned action that demonstrated a precision of matching to the  
797 model witnessed that departed significantly from chance (Voelkl and Huber, 2007).

798 Echoing the first marmoset study, van de Waal and Whiten (2012) offered similar  
799 food canisters with lids that could be popped off (‘aethipops’) to four groups of vervet  
800 monkeys in African sanctuaries. Most models and indeed most monkeys used their  
801 mouth to remove the lid, but in one group a model used her hands, and this method then  
802 spread significantly in her group (Fig. 5). Similarly in one group an individual grasped

803 the cords at the ends of the aethipop and pulled it apart like a Christmas cracker, a  
804 different approach that again spread significantly in this monkey's group. As in the  
805 studies summarized above, differential matching of body parts cannot be explained by  
806 emulation but only by action imitation.

807

808 < insert figure 5 about here >

809

810 Such cases of matching are again consistent with the operation of mirror neurons,  
811 as is complementary evidence that monkeys may recognize when another individual -  
812 even a human - is copying them (Paukner et al., 2005). Paukner et al. (2009) showed the  
813 macaques who were imitated looked longer at the person than in non-imitative control  
814 conditions, and moreover, were more prepared to engage in social interaction (object  
815 exchanges) with the person. Accordingly, putting these studies alongside those in apes  
816 summarized above, we propose that it was premature to demote imitative learning as an  
817 important potential function supported by this neuronal system in primates.

818 As was also the case for the ape research reviewed above, bodily imitation is far  
819 from the only topic being actively tackled with respect to social learning in other  
820 primates. An extensive range of studies has demonstrated social learning and cultural  
821 transmission in several species of monkeys and lemurs, even where these do not  
822 necessarily discriminate whether imitation or other processes are responsible. Several  
823 are included in the recent illustrations of diffusion experiments listed in Table 2 and  
824 others are reviewed by Subiaul (2007) and Whiten (2012). An innovative approach with  
825 macaque monkeys was described by Subiaul et al. (2004), in which a model received a  
826 reward after touching a series of images on a screen in a particular sequence  
827 independent of their (changing) locations in an array, while an observer monkey  
828 watched. The observer monkey was then later shown to learn such sequences faster  
829 themselves, implicating observational learning. Merely seeing the sequence occur  
830 without monkey actions, a kind of ghost condition, did not have the same effect. Subiaul  
831 et al. called the monkeys' achievement 'cognitive imitation', to stress that this is a form  
832 of copying what others do that unlike in most studies in this area, does not involve the  
833 acquisition of a manipulative skill. However, we think the term rather unfortunate

834 insofar as it may imply that instances of skill learning are not cognitive, which seems  
835 misleading.

836

837 < insert Table 2 about here >

838

839 A different kind of evidence for imitation concerns neonates. Meltzoff and Moore  
840 (1983) reported that human new-borns showed evidence of mimicking facial  
841 movements, discriminating tongue protrusion from mouth opening, for example.  
842 Meltzoff (2005) later linked the primordial bodily mapping implicated in neonatal  
843 imitation to the mirror neuron system, proposing both nativist and developmental  
844 elements. This work has been controversial, both with respect to whether such an  
845 infantile imitative capacity truly exists, and its relationship to later undisputed imitative  
846 competences (Oostenbroek et al., 2013, 2016), topics beyond the scope of this review.  
847 However, more surprisingly given the earlier, widespread dismissal of imitation in  
848 monkeys noted above, evidence for neonatal imitation in macaque monkeys has been  
849 offered by Ferrari and colleagues and again linked to the mirror system (Simpson et al.,  
850 2014). However, the suite of publications reporting these findings emanate from one  
851 research group and remain to be replicated by others, so that given the controversial  
852 nature of the parallel human neonatal imitation evidence, we highlight these results as  
853 providing a convergent source of evidence on imitation in monkeys, but remain cautious  
854 about interpreting them further.

855 Selectivity in monkeys' social learning has been shown in a number of studies. As  
856 for apes, these include biases about whom to learn from. Here questions shift from the  
857 cognitive abilities underlying different capacities for social learning to what motivates  
858 individuals to learn. De Waal (2001) conceptualised the latter in terms of what he called  
859 Bonding and Identification-based Observational Learning (BIOL), a motivation to be  
860 like others, such as one's mother or peers, as opposed to being dependent on physical  
861 rewards to copying, such as gaining food items. An example comes from the vervet  
862 monkeys we study, where we have identified an initial bias to learn from one's mother  
863 (van de Waal et al. 2013a, 2014). In the latter study this was revealed when the  
864 monkeys were supplied with sandy grapes, that mothers cleaned using one or more of  
865 several alternative techniques, which tended then to be adopted by their infants. Seeding

866 alternative ways to open an artificial fruit in different groups either in a sanctuary (van  
867 de Waal 2013b) or in the wild (van de Waal et al. 2010, 2015) demonstrated the spread  
868 of these alternatives via social learning, but the 2010 study revealed that this occurred  
869 only if the model was an adult female, not a male. This could make adaptive sense  
870 because females are the philopatric sex and are thus likely to provide the better models  
871 to copy than the males, who have immigrated into the group at some point and so have  
872 less experience about the optimal ways to behave in the local conditions pertaining.

873       Such migrant males, however, have provided evidence of conformity to majority  
874 preferences. In a study originally designed to examine the relative roles of social and  
875 individual learning in infants, two containers offering pink versus blue coloured corn  
876 were provisioned monthly, one made highly distasteful by soaking along with aloe  
877 leaves (van de Waal et al. 2013a). Two groups were in this way trained to avoid pink  
878 and two blue, while a new cohort of infants were suckling and taking no solid food.  
879 Several months later, when the corn options were offered again with no distasteful  
880 additive, adults maintained their bias and it was found that infants acquired this socially,  
881 adopting the preferences of their mothers and her group. Fortunately, in their migrations  
882 from pink to blue preference groups or vice versa, adult males provided a different class  
883 of individuals naïve to the local colour norm. Surprisingly, after watching the local  
884 monkeys eating, as many as nine of these ten males switched preferences already in  
885 their first choices, once they were not outranked by residents and could freely choose,  
886 demonstrating a remarkable degree of conformity. A different kind of evidence for the  
887 potential potency of social learning was offered by Perry (2009), who showed that  
888 despite young white-faced capuchins' experience with two alternative ways to open a  
889 difficult fruit, they eventually tended to settle on the one they had witnessed most.

890

#### 891 *4.2.3 Neural circuits, mirror neurons and social learning in primates*

892

893 By contrast with all that has been learned about social learning and cultural transmission  
894 in many species of primate over the last century, neuroscience is only in the early stages  
895 of beginning to address these phenomena. Neuroscience, including that focused on  
896 mirror neurons, has tended to dismiss monkeys as simply not imitating. In part this may  
897 reflect the dispositions of the macaque monkeys studied in the neuroscience laboratories

898 concerned, and in part a limited reading of the literature. As reviewed above, there are  
899 reports of imitation in monkeys, that have perhaps not yet come to the attention of many  
900 neuroscientists. Similarly for apes, neuroscientists often cite conclusions from research  
901 groups who argue that apes emulate rather than imitating (Tennie et al. 2009), and in  
902 any case apes have been spared invasive neuroscience such as the single unit recording  
903 that identified mirror neurons.

904       However, some recent neuroscientific investigations have begun to interdigitate in  
905 interesting ways with the findings of comparative psychology concerning social  
906 learning. Hecht et al. (2013b) used positron emission tomography (PET) functional  
907 neuroimaging to record regions showing overlapping ‘mirror’ activation in relation to  
908 ‘transitive’ actions defined by having an object as their target, in both humans and  
909 chimpanzees, the latter being understudied in this respect, as we noted earlier. As  
910 predicted, such activation was recorded in chimpanzees in a distributed front-oparietal  
911 network homologous with that identified in earlier studies of the mirror systems of both  
912 macaque monkeys and humans. However whereas macaques characteristically show  
913 mirror responses *only* to goal-oriented, object-directed (transitive) actions (Rizzolatti et  
914 al. 1996), chimpanzees were found to resemble humans in also showing activation to  
915 transitive actions; indeed, transitive and intransitive activations were similar across  
916 regions homologous with those in which mirror neurons have been recorded in  
917 macaques.

918       Accordingly, the authors propose that the striking pattern of similarities and  
919 differences they report “suggests that chimpanzees map not only the results but also the  
920 movements of observed actions to the same brain regions that produce those actions.  
921 This may be a correlate of, and a prerequisite to, the ability to copy specific  
922 movements.” (Hecht et al. 2013b, p. 14129). This discovery appears entirely consistent  
923 with the conclusion of our review above, that chimpanzees are not limited only to  
924 emulative learning about the results of their actions, but also have in their social  
925 learning ‘portfolio’ an imitative capacity. These neuroscientific results are consistent  
926 with and may help explain the capacity of chimpanzees to learn, and show some facility  
927 in, ‘Do-as-I-do’ games, which are largely based on a battery of intransitive actions like  
928 ‘grab thumb’ (Table S1 in supplementary information) (Whiten and Custance, 1996), as  
929 well as monkeys’ repeated failure to master this game (Whiten et al., 2004). Nor are the

930 results inconsistent with our conclusions above concerning evidence of imitation in  
931 monkeys, because this derived from transitive actions on object where there was match  
932 to what was observed (e.g. oral versus manual foraging actions).

933         Complementary convergences between neuroscience and our behavioural  
934 findings also emerged through a related study by Hecht et al. (2013a) which applied the  
935 technique of diffusion tensor imaging to trace neural connections within mirror  
936 networks in macaques, chimpanzees and humans. The principal result of most interest  
937 in the present context concerns contrasts between ventral and dorsal streams of visual  
938 information processing, the existence of which have been important topics in  
939 neuropsychology for some time (see Milner and Goodale, 2008, for a recent ‘re-view’).  
940 In the present context the important findings were that on the one hand, a ventral stream  
941 was found to be robust in all three species, indicating a route of information between  
942 temporal areas (superior temporal sulcus) initially processing biological motion, inferior  
943 temporal cortex processing objects (that may include tools) and frontal areas processing  
944 actions goals. The authors suggest this stream will support extraction of action end-  
945 results or goals, the focus of emulative responses shown by all these species. However,  
946 dorsal streams contrast with the ventral streams along a continuum, being most robust in  
947 humans and least so in the macaques, with chimpanzees showing an intermediate state  
948 of development. Since these dorsal streams from temporal sensory areas to frontal areas  
949 link in inferior parietal cortex that is involved in the more fine-grained mapping of  
950 movements, the authors suggest this corresponds to the continuum from monkey to  
951 chimpanzee to human in their facility in discriminating and copying finer motor  
952 patterns. The authors’ schematic interpretation of these findings is illustrated in figure 6,  
953 which also indicates both (i) connections between parietal mirror regions and inferior  
954 temporal cortex, important in processing of tool characteristics, that are stronger in the  
955 tool-using chimpanzees than the monkeys, and yet stronger in humans; and (ii)  
956 connections between frontal and parietal regions extended further into superior parietal  
957 cortex in humans, an area associated with spatial awareness and attention. The authors  
958 speculate that the latter may support enhanced awareness of the trajectories of other’s  
959 actions, and these areas are activated during re-creation of humans’ early lithic tool-  
960 making (Stout et al. 2008; Hecht et al. 2015; and see Frey (2007) and Arbib (2010) for

961 further exploration of dorsal and ventral streams in relation to tool use, tool making and  
962 language).

963         The mirror system may encode others' actions in the frame of one's own motor  
964 system, but this also requires that the distinction be recognised between the actions of  
965 self and other. Using an ingenious approach in which two macaque monkeys monitored  
966 each other's actions, Yoshida et al. (2011) identified neurons in medial frontal cortex  
967 that selectively encode actions that are taken by the other.

968

969         < insert figure 6 about here >

970

971         The neural processing models portrayed in figure 6 appear highly consistent with  
972 the more detailed review of ape and social learning capacities we reviewed earlier. The  
973 consistency is perhaps most obvious in the case of the social learning portfolio we  
974 described for chimpanzees. The only real difference is that while Hecht et al. adopt the  
975 common view in neuroscientific works (e.g. Tramacere et al. 2016), we have  
976 summarized the evidence that imitation is shown by at least some monkeys. However,  
977 we suggest that in fact there is no real disagreement here, because (i) the monkey cases  
978 all involve transitive actions, as noted above; and (ii) the dorsal stream is not absent in  
979 the monkey brains; rather, the proportion of dorsal to ventral white matter is simply  
980 less. This fits entirely with our portrayal of the current picture of social learning in  
981 monkeys, apes and humans.

982

#### 983 *4.3 Imitation, autism and the human mirror neuron system*

984

985         An autistic spectrum disorder (ASD) is a condition marked by often quite severe  
986 disturbances in relating socially to others. Through the last several decades, ASD has  
987 been attributed to deficits and delays in social cognition, notably mindreading or theory  
988 of mind, which has become a dominant explanatory factor (Frith and Hill, 2003).

989         However others noted early difficulties in imitation too, and developed a theory that  
990 such deviations from normal development may represent the first stages in difficulties  
991 in translating between the perspectives of others and oneself, a fundamental process that  
992 underlies both imitation in its earliest stages, and theory of mind as it becomes  
993 elaborated through the childhood years (Rogers and Pennington, 1991).

994 As noted earlier, studies from Iacoboni et al. (2001) onwards have identified  
995 imitation as one of the functions served by the mirror neuron system in humans. Noting  
996 this and the evidence of early problems in imitation in autism, Williams et al. (2001) put  
997 these findings together and suggested that at the core of ASD might be some non-  
998 normal developments in the mirror system, possibly including the inhibitory controls  
999 implicit in it. The latter is emphasized because on the one hand, the downstream effects  
1000 of premotor mirror neurons firing need to be inhibited, or we should all be constantly  
1001 mimicking the actions of those we are watching; and on the other hand, although  
1002 children on the autism spectrum may show deficits in imitation, they also often display  
1003 behavior like echolalia, where they simply echo back things that are said to them in an  
1004 uninhibited fashion.

1005 This theory was suggested as a prospect to explore. It has been contentious, with  
1006 disputes about both the reality of imitation deficits and delays in autism (Williams et al.  
1007 2004; Vanvuchelen et al. 2013) and the explanatory role of the mirror neuron system  
1008 (Williams et al. 2007; Southgate and Hamilton, 2008). However a recent review by  
1009 Perkins et al. (2010) concluded that “evidence from functional MRI, transcranial  
1010 magnetic stimulation, and an electro-encephalic component call the *mu* rhythm suggests  
1011 MNs are dysfunctional in subjects with ASD” (p. 1239). Problems may entail not so  
1012 much the basic function of mirroring as the control of such processes, as alluded to  
1013 above. For example, Martineau et al. (2010) concluded that “hyperactivation of the pars  
1014 opercularis (belonging to the MNS) during observation of human motion in autistic  
1015 subjects provides strong support for the hypothesis of atypical activity of the MNS that  
1016 may be at the core of the social deficits in autism” (p. 168).

1017

## 1018 **5. Concluding Discussion**

1019

1020 We have offered a review of progress in the study of primate social learning at  
1021 several levels the phenomena span, from the underlying mechanisms to the scope of  
1022 traditions and cultures in wild populations. As we hope to have demonstrated, the  
1023 research literature has burgeoned in all these domains in recent years and we now know  
1024 a great deal about each of them, even though in many cases we have extensive  
1025 knowledge for a handful of favoured species but know little concerning a majority of



1026 primates. Nevertheless, we have accumulated much secure knowledge based on solid  
1027 and rigorously researched studies, whether from purely observational approaches, or  
1028 tightly designed experiments. Neuroscientific analysis of social learning and cultural  
1029 transmission are much younger sciences and still in their early stages. On the one hand,  
1030 the ‘macro’ analyses of the correlates of encephalization appears to remain highly  
1031 contentious and difficult to interpret; while at the more detailed level of neural networks  
1032 and mirror neurons, the empirical literature remains small, particularly for apes (Hecht  
1033 et al. 2013a,b; Tramacere et al. 2016).

1034 Mindful of the latter, we have focused our review of social learning on relatively  
1035 complex levels of social cognition that cover imitation and emulation, in part because of  
1036 the theme of the current issue of the journal and in part because of the neuroscientific  
1037 relevance of ‘mirroring’ others. In relation to our highlighting here of the topic of bodily  
1038 imitation, we note that our review suggests that the methodological and evidence base  
1039 for apes is often different to that for monkeys.

1040 Thus, for apes we have a cluster of ‘Do-as-I-do’ studies that are important in  
1041 exploring the range of bodily matches that apes can register. This approach, not so far  
1042 achieved for monkeys, allowed an extensive range of action matchings to be  
1043 systematically tested, demonstrating, for example that touches to non-visible body parts  
1044 like the back of the head can be copied, and that apes often begin their copying attempt  
1045 by repeating one of the approximating training actions, then adjusting it to generate a  
1046 better match (Custance et al. 1995). Similarly, the motor mimicry subjected to micro-  
1047 analysis in the case of chimpanzees learning to nut-crack has no counterpart we are  
1048 aware of in monkeys. Nor have the ‘ghost’ conditions applied in several ape studies  
1049 been applied in monkey experiments, although the condition in Subiaul et al. (2004) in  
1050 which a sequential pattern of images was displayed without a monkey touching them  
1051 may be regarded as formally similar even if physically quite different approach. Finally,  
1052 ape experiments in which the sequential or hierarchical structure of complex actions has  
1053 been manipulated (Whiten et al. 2003) appear to have no counterpart in monkey studies,  
1054 although this takes us beyond bodily matching.

1055 However, monkey studies also include approaches yet to be replicated for apes.  
1056 Arguably the key method is two-action studies where the two alternatives involve  
1057 differences at a bodily level, such as completing an action using one’s hands versus a

1058 different effector, like mouth or head. As noted earlier, this approach has been used  
1059 more generally in comparative psychology but, perhaps strangely, not with apes. Of  
1060 course the Do-as-I-do method involves all kinds of body-part matching, but it is a test of  
1061 what apes *can* do, rather than what they spontaneously *do*, which is what has been  
1062 tested in monkeys and other animals. The precise bodily trajectory matching identified  
1063 by Voelkl and Huber (2007) also has no apparent counterpart in ape studies and indeed  
1064 may be a unique application of this approach. The same may be said of the method used  
1065 by Subiaul et al. (2004) to identify what they called ‘cognitive imitation’ in macaques,  
1066 but this was expressly not concerned with bodily imitation.

1067       One of the few methods that have been applied to both monkeys and apes is  
1068 assessing their recognition of being copied by others, and such recognition has been  
1069 demonstrated for both. However in this case, apes and monkeys still appear to respond  
1070 differently. Apes have demonstrated this recognition in what we may regard as an  
1071 explicit fashion, appearing to be intrigued by the bodily matching of their imitator, and  
1072 experimenting with their own actions to see what copies the other (human) individual  
1073 delivers. Monkeys have not shown such responses, and their recognition of being  
1074 copied has been assessed more indirectly, by their visual attention and subsequent  
1075 affiliative behaviour. Perhaps apes’ explicit responses reflect the same underlying  
1076 representation of the act of imitation that underlies their capacity to learn the Do-as-I-do  
1077 game.

1078       Despite the differences in how imitation has been investigated in apes and  
1079 monkeys, in each case multiple methods have been applied, providing some degree of  
1080 convergent evidence on the reality of the imitative capacity of interest, and as discussed  
1081 in section 4.2.3, there is some recent exciting convergence with non-invasive  
1082 neuroscientific studies with apes, as well as monkeys. Some of the experimental  
1083 methods, such as Do-as-I-do, have been applied to both apes and monkey but found not  
1084 to be workable. Others, such as two-bodily-action experiments, should in principle be  
1085 applicable to both. We hope that some of the varied and ingenious behavioural and  
1086 neuroscientific approaches we have reviewed, not only with respect to imitation but to  
1087 the many other aspects of social learning traditions and culture, will be applied more  
1088 broadly in future and help build a more comprehensive comparative analysis of primate  
1089 social learning. We close by noting that the subtitle of ‘The Primate Mind’, edited by de

1090 Waal and Ferrari (2012) – ‘Built to Connect with Other Minds’ - is apt to our topic, but  
1091 also reminds us that this umbrella term covers several related topics beyond the scope of  
1092 our review, such as empathy and the recognition of states of mind in others. Such topics  
1093 are also, of course, the focus of other contributions to this special issue.

1094

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1606

1607 Figure Captions

1608

1609 Fig. 1. Group size and encephalization (here, executive brain ratio = volume of cortex over rest  
1610 of brain) in primates (based on Dunbar and Shultz, 2007).

1611

1612 Fig. 2. Social learning and encephalization in primates. Frequency of social learning based on  
1613 the survey of Reader and Laland (2002) is plotted against executive brain ratio (see text for  
1614 further explanation). Added labels refer to three species with complex cultures discussed in the  
1615 text.

1616

1617 Fig. 3. An ‘open diffusion’ study with capuchin monkeys: (a) capuchin performing ‘lift’  
1618 technique on artificial doorian fruit; (b) capuchin performing alternative ‘slide’ technique to  
1619 gain reward; (c) spread of each technique in groups where one male was first taught to use  
1620 either the lift or slide technique (data from Dindo et al. 2009). Each symbol represents the  
1621 proportion of each technique performed by each individual on consecutive days. Dark = slide,  
1622 light = lift. Numbers indicate the percentage of actions performed on day 7, corresponding to  
1623 that seeded in the group on day 1.

1624

1625 Fig. 4. Entrainment of nut-cracking between observer and model. Example of frame-by-frame  
1626 measures of the height of the hand shown for model (blue) and younger observer (red). Time  
1627 series analyses of such episodes confirmed matching and even synchronic entrainment of hitting  
1628 actions (based on Fuhrmann et al., 2014).

1629

1630 Fig. 5. Bodily imitation of manual versus oral opening of ‘aethipop’ artificial fruit by vervet  
1631 monkeys. Most monkeys, and most models, opened aethipops orally (a). In Hammer group, the  
1632 model opened it with her hands (b) and graphs show corresponding behavior of other group  
1633 members (d: first attempts with hands, e: all attempts with hands, based on van de Waal et al.,  
1634 2012). In a further group, an individual opened aethipops using a third method (c) that also  
1635 spread: see van de Waal et al. (2012) for details.

1636

1637 Fig. 6. Model linking species differences in mirror system circuitry, mirror system functional  
1638 responses, and social learning, after Hecht et al. (2013a) with permission. PFC: Prefrontal  
1639 cortex; MLF-ILF: Middle and inferior longitudinal fasciculi; SLFIII: Third branch of the  
1640 superior longitudinal fasciculus; EmC-ExC: Extreme capsule and external capsule. For further  
1641 explanation and discussion, see text.

1642

1643 Table 1. Core studies reporting evidence for primate cultural variation in behaviour in the wild.  
1644

Species and Year	Studies and outline of evidence	References
Chimpanzee 1999	Building on earlier cited foundational studies, consortium of research leaders at 9 long term study sites completed first collaborative and systematic study, identifying 39 behaviours as cultural variants, common at some sites yet absent at others without apparent environmental or genetic explanation, (1,2). Further detailed studies of specific behaviours and ecological variables, including neighbouring communities, added finer supportive evidence (e.g. 3-7). Experiments highlighted local differences in cultural cognition (8-9).	1. Whiten et al. 1999 2. Whiten et al. 2001 3. McGrew et al. 2001 4. Crockford et al. 2004 5. Möbius et al. 2008 6. Schöning et al. 2008 7. Luncz & Boesch 2014 8. Gruber et al. 2011 9. Kuhl et al. 2016
White faced capuchin 2002	Comparison of different groups recorded the emergence, spread and loss of social customs involving intimate finger poking in nose and eyes (1), plus differences in foraging habits (2) and interspecies interactions (3).	1. Perry et al. 2003 2. Panger et al. 2002 3. Rose et al. 2002
Orangutan 2003	Replication of the chimpanzee methodology (1,2 above) identified 19-24 cultural variants (1) with more reported later (2). More detailed analyses of genetic and habitat variables identified some variants to be linked to environmental differences but strengthened conclusions about a cultural subset (3).	1. van Schaik et al. 2003 2. van Schaik 2009 3. Kruzen et al. 2011
Bonobo 2003	Application of the chimpanzee methodology identified a small set of cultural variants including few forms of tool use, unlike chimpanzees, but range of bonobos much smaller.	Hohmann & Fruth 2003
Olive baboon 2004	Death of dominant males through disease led to peaceful forms of social interaction that continued to reign as new males populated the group, leading to inference of local 'pacific culture'.	Sapolsky & Share 2004
Japanese macaque 2007	34 styles of 'stone handling', an apparently functionless behaviour among provisioned monkeys, were identified, with different ones common or absent at different locations (1). Origin and spread of stone handling was earlier documented (2). Early reports of 'protocultural' behaviours like wheat sluicing are debated (3).	1. Leca et al. 2007 2. Huffman 1996 3. Hirata et al. 2001
Spider monkey 2011	Following chimpanzee methodology (1,2 above) 22 variants identified between different groups, a majority social (1). Further study identified 14 additional behaviours differentially locally preferred, 6 of them inferred to be socially learned (2).	1. Santorelli et al. 2011a 2. Santorelli et al. 2011b
Vervet monkey 2014	Differences in dietary preferences were identified between neighbouring groups that were not explicable by habitat and availability variables measured.	Tournier et al. 2014
Gorilla 2016	Following chimpanzee methodology (1,2 above) 23 putative cultural variants identified between different groups.	Robbins et al. 2016

1645 Studies are listed chronologically by year of foundational paper; for well-studied species, other references  
1646 listed are selective rather than comprehensive.

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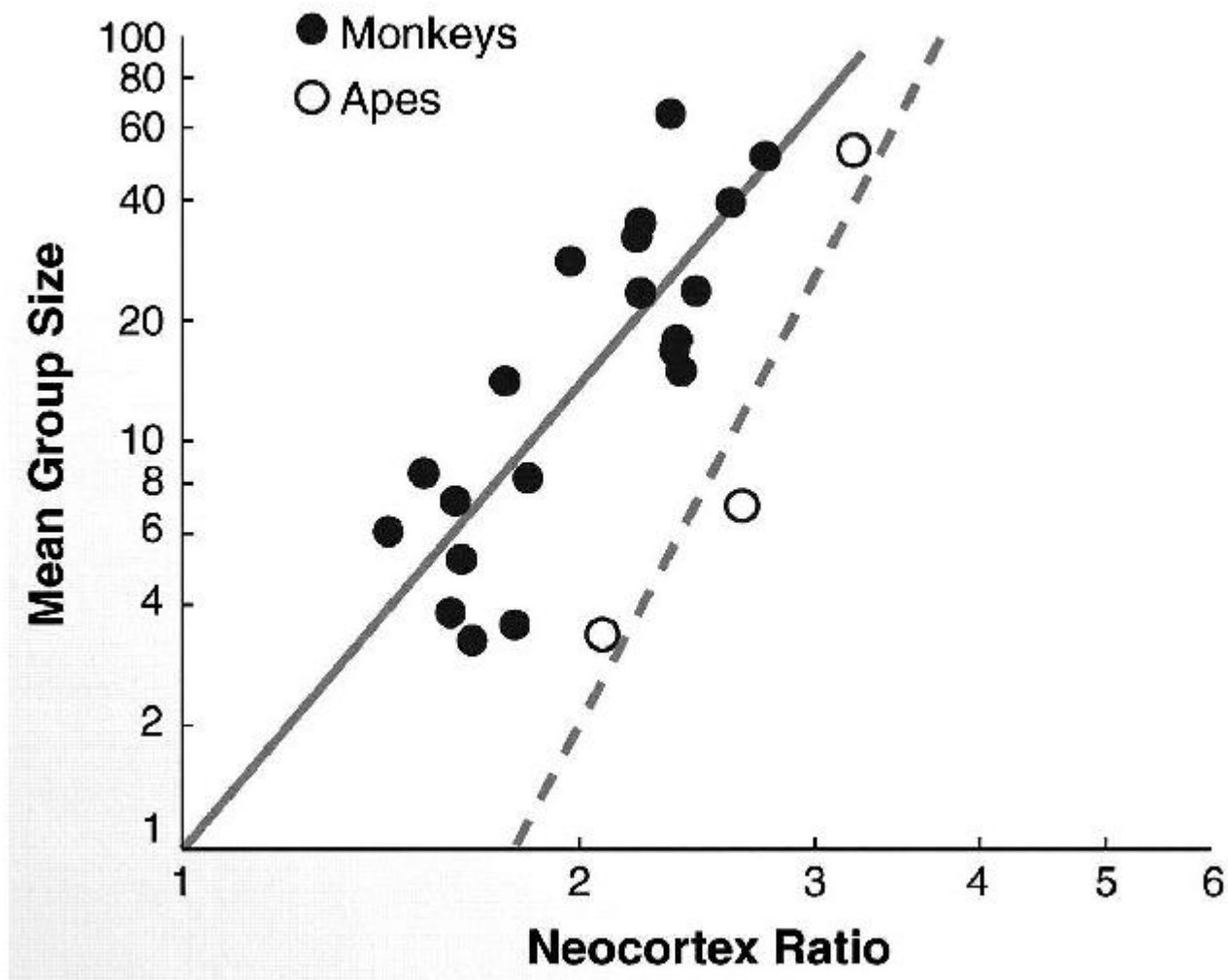
Table 2. Cultural diffusion experiments with non-human primates since the first field experiments (2010).

authors	species	design	content and findings
van de Waal 2010	vervet monkey *	group seeded	Trained opening of an artificial fruit by models either lifting one door or sliding another spread to others in the groups so long as the model was a resident female.
Kendal et al. 2010	ring-tailed lemur *	group seeded	An idiosyncratic technique to obtain food from an artificial fruit emerged in a subset of lemurs that were close associates, implicating social learning.
Horner et al. 2010	chimpanzee	group seeded	Trained posting of tokens in two different receptacles to obtain food by reliable high ranking models spread to others in preference to those posted by low ranking models.
Hopper et al. 2011	chimpanzee	group seeded	Trained trading of either of two types of tokens to obtain food spread to others even when the option shown gained less quality rewards.
Dindo et al. 2011	orangutan	chain	Each of two different methods to open an artificial fruit (lift door versus slide door) spread preferentially along chains of five and six individuals respectively.
Schnoell et al. 2012	red-fronted lemur *	group seeded	Individuals preferred whichever of two alternative techniques to open an artificial fruit was shown by a trained model in their group and in one of two unseeded groups a stable tradition focused on one technique emerged.
van de Waal et al. 2012	vervet monkey	group seeded	Four groups with model trained to open artificial fruit in each. Most used mouth to open fruit, but in group with model showing manual opening, this method spread to be more common; in group using cord to pull fruit apart, this likewise spread.
Dean et al. 2012	chimpanzee, capuchin monkey	group seeded	An artificial fruit with three escalating levels of difficulty and reward was made available. In conditions where models proficient in the highest level were introduced, these did not spread, unlike in children in parallel experiments.
Hopper et al. 2013	squirrel monkey	group seeded	Groups seeded with trained models pushing a door left or right to obtain food tended to adopt the method witnessed. Monkeys exposed instead to a 'ghost control' in which the door moved without an agent did not succeed in gaining rewards.
Claidiere et al. 2013	squirrel monkey	group seeded	Two groups with model trained to open artificial fruit by lift versus swing door. These methods spread differentially with a bias for those well connected in the social network to open the fruit earlier and use the method they witnessed.
van de Waal et al. 2013a	vervet monkey	group seeded	Four groups with model trained to open artificial fruit in each. Methods of lifting door versus sliding left or right spread more commonly in the group corresponding to seeded model.
van de Waal et al. 2013b	vervet monkey *	group seeded	Whole groups were trained to avoid either pink or blue coloured maize corn made bitter. Naïve infants later tested with no bitter additive nevertheless copied maternal preference. Immigrant males switched quickly, conforming to new group preference.
van Leeuwen et al.	chimpanzee	group	Chimpanzees that had individually learned to use

2013		seeded	either of two alternative tokens to gain rewards, or in other experiments use either of two targets for tokens, did not change their token use when exposed to a majority using the other option (they did not conform to a majority) but did switch when the alternative yielded a great payoff.
Schnoell et al. 2014	red-fronted lemur *	group seeded	Some individuals in groups seeded with either of two methods to obtain food from an artificial fruit maintained the seeded preference over two years, others fluctuated in showing a preference or none, but none switched between preferences.
Gunhold et al. 2014a	marmoset *	group seeded	Naïve individuals tended to adopt whichever of two alternative techniques to open an artificial fruit that the remainder of the whole group had learned X months earlier and maintained the preferences Y months later.
Gunhold et al. 2014b	marmoset *	group seeded	Groups seeded with alternative foraging techniques through video displays in the forest exhibited associated bias in spread of these.
Claidiere et al. 2014	Guinea baboon	chain	Patterns of pixels on a screen remembered by subjects became the stimuli for next animal in chain. Patterns became progressively structured, described as cumulative cultural transmission. Different lineages developed different regular patterns.
Kendal et al. 2015	chimpanzee	group seeded	Statistical models fitted to the results of open diffusion experiments with two alternative techniques to obtain food seeded from trained models
van de Waal et al. 2015	vervet monkey *	group seeded	Replication of 2013 van de Waal et al. paper with wild vervet monkeys. Lift door and slide door methods spread preferentially in groups seeded with these methods.

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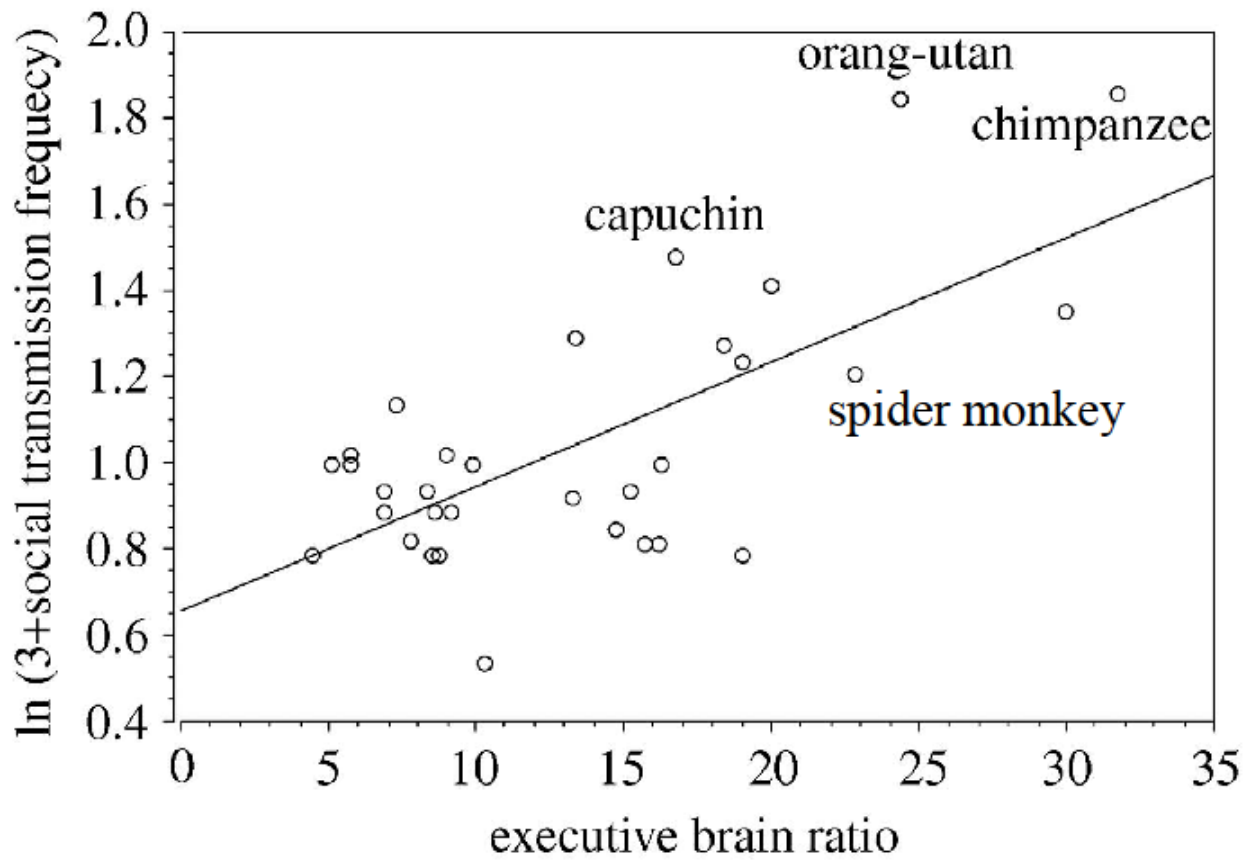
Primate diffusion studies 2010-2015 (n = 19) from within a set of 30 for all animal species listed in Whiten et al. 2016. \* = field study of wild subjects (n = 8); 'group seeded' = open diffusion with trained model(s) seeded in group(s); 'chain' = diffusion chain. Effects are reported when statistically significant.



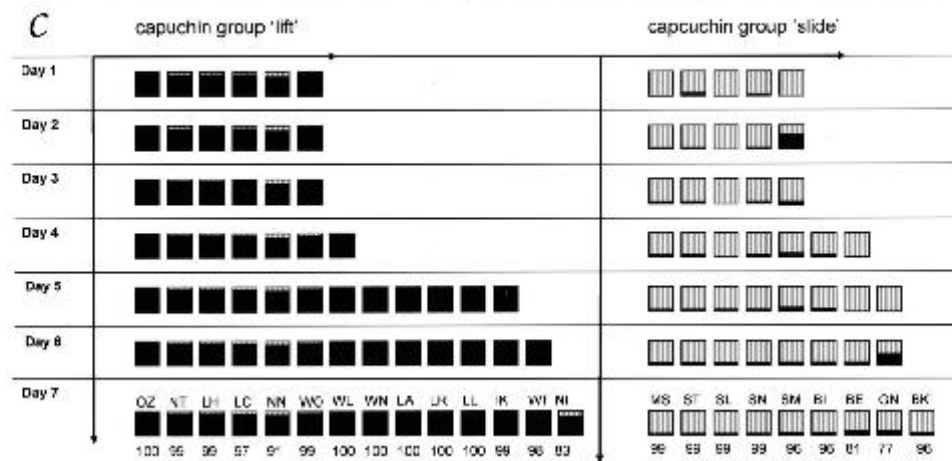
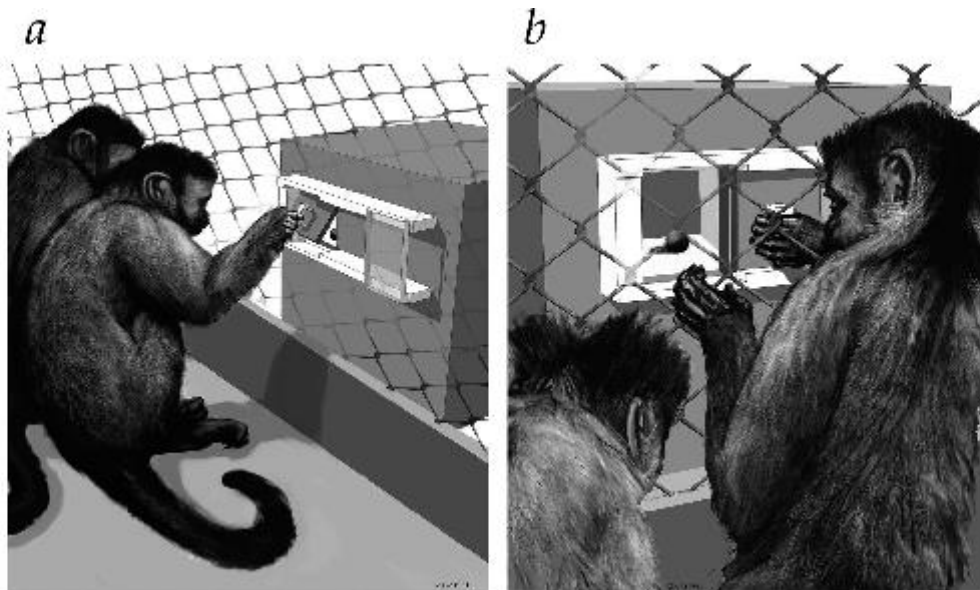
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1656 Figure 1

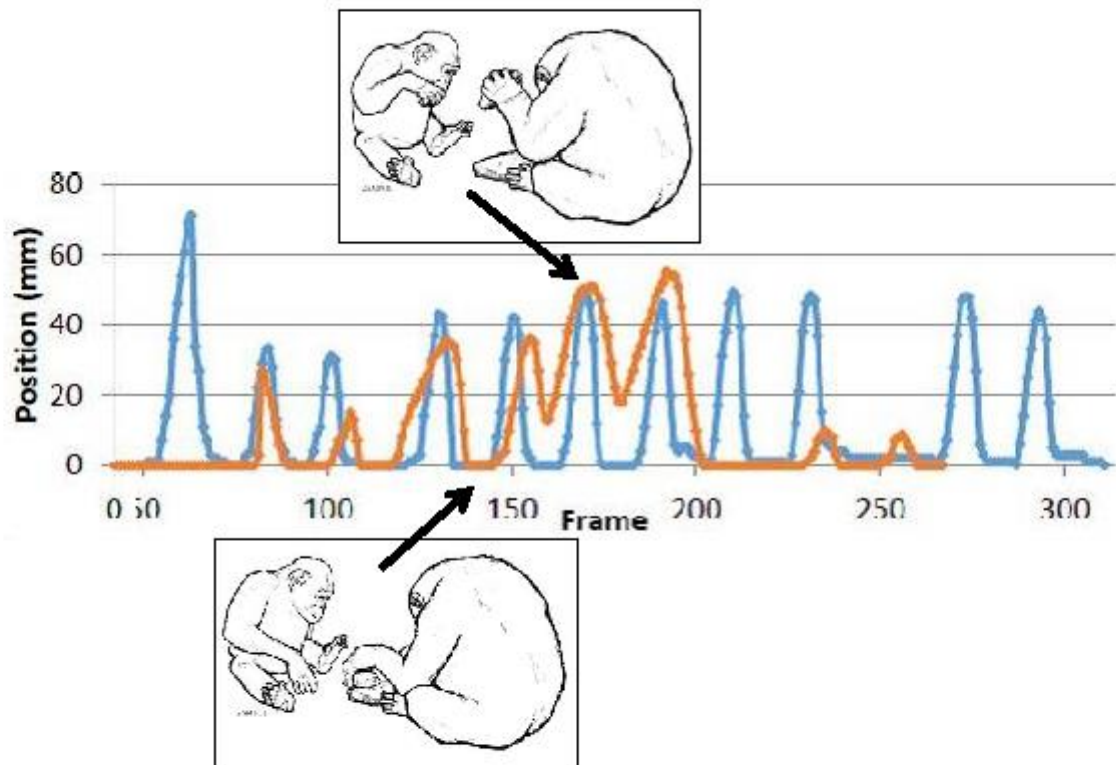
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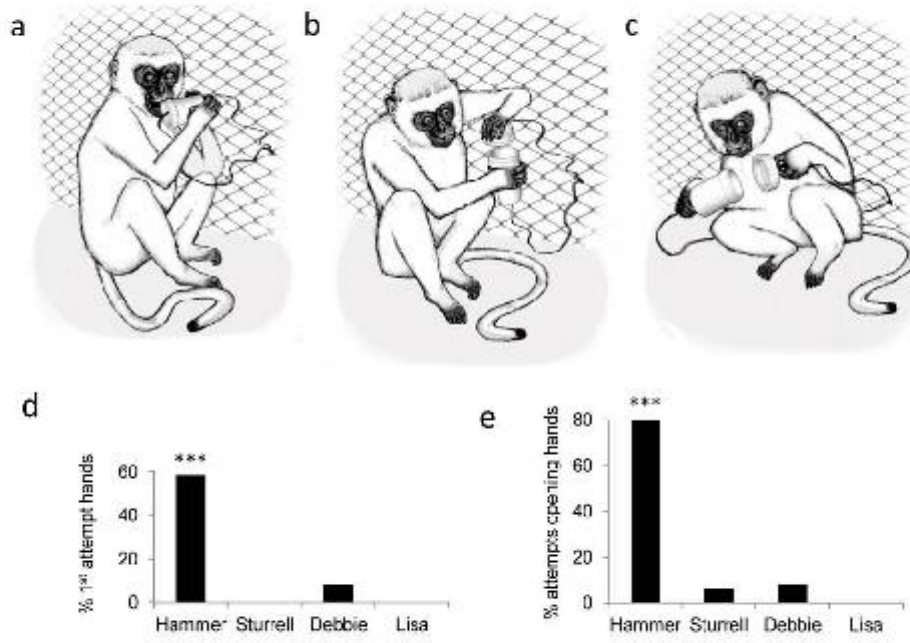
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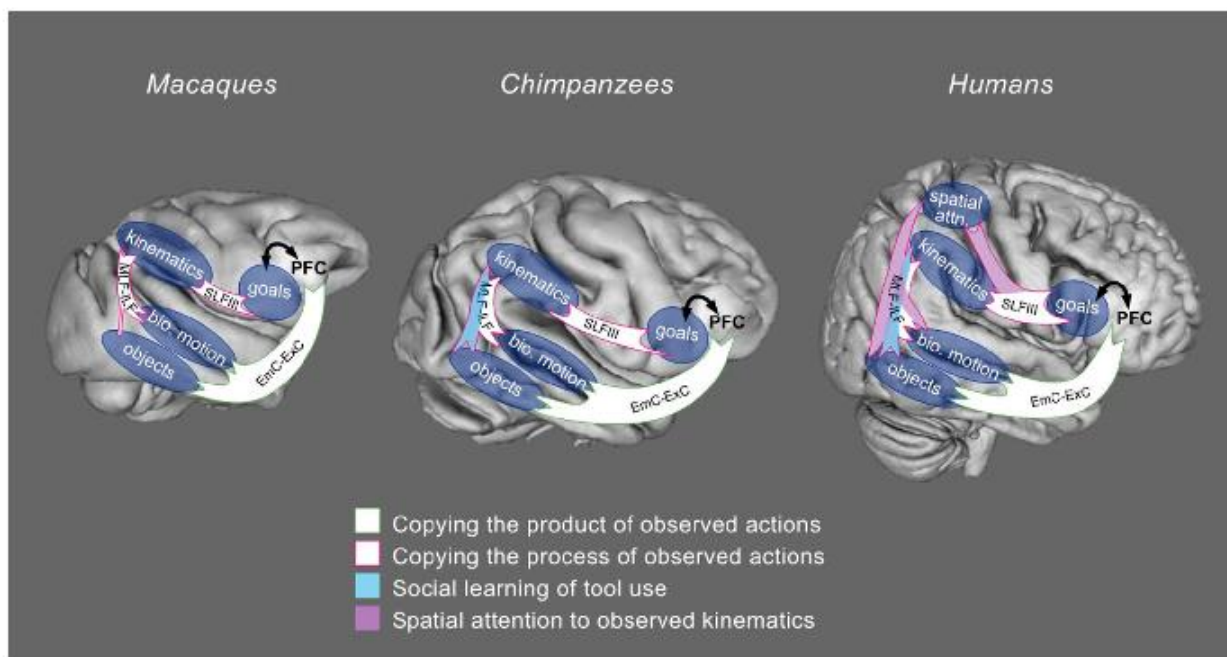
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