

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

3
4 Andrew Whiten^{a*} and Erica van de Waal^b

5
6 ^a Centre for Social Learning and Cognitive Evolution, School of Psychology and
7 Neuroscience, University of St Andrews, St Andrews, KY16 9JP, UK.

8 ^b Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190,
9 Zurich 8057, Switzerland.

10
11 * Corresponding author: Tel.: 44 1334 462073

12 E-mail addresses: a.whiten@st-andrews.ac.uk (A. Whiten), erica.vandewaal@uzh.ch
13 (E. van de Waal).

14
15 *Neurosci. Biobehav. Rev. acc Dec 2016. Theme issue on Primate Social Cognition*

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
36	Imitation
37	Culture
38	Primates
39	Vervet monkeys
40	Chimpanzees
41	Social brain
42	Social intelligence
43	Cultural intelligence hypothesis
44	Mirror neurons
45	Autism
46	
47	
48	Contents
49	
50	1. Introduction
51	2. Social intelligence and the ‘social brain’ of primates
52	2.1 Social and Machiavellian intelligence hypotheses
53	2.2 Social intelligence and encephalization
54	3. Cultural intelligence and the ‘cultural brain’
55	3.1 The scope of culture in primates
56	3.2 The cultural intelligence hypothesis
57	3.3 Vygotskian and cultural intelligence hypotheses
58	4. Social learning, mirror neuron systems and neural networks
59	4.1 Primate social learning: imitation, emulation and transmission fidelity
60	4.2 Social learning, imitation and the function of mirror neurons
61	4.2.1 Imitation and the scope of social learning in apes
62	4.2.2 Imitation and the scope of social learning in monkeys
63	4.2.3 Neural circuits, mirror neurons and social learning in primates
64	4.3 Imitation, autism and the human mirror neuron system
65	5. Concluding Discussion
66	
67	

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 < insert figure 1 about here >

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 20th 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 < insert figure 3 about here >

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 < insert figure 4 about here >

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; Frigaszy,
776 Deputte et al. unpublished, cited in Visalberghi and Frigaszy, 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 Frigaszy, 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

1095 Acknowledgements

1096 AW was supported during the writing of this review by the John Templeton Foundation
1097 (grant number ID40128). EvdW was supported by the Swiss National Science
1098 Foundation (grant number P300P3-151187) and Society in Science - Branco Weiss
1099 Fellowship.

1100

1101

1102 References

1103

- 1104 Arbib, M.A. 2010. Mirror system activity for action and language is embedded in the
1105 integration of dorsal and ventral pathways. *Brain Lang.* 112, 12-24.
- 1106 Barton, R.A. 2006. Primate brain evolution: integrating comparative,
1107 neurophysiological and ethological data. *Evol. Anthropol.* 15, 224-236.
- 1108 Barton, R.A., Harvey, P.H. 2000. Mosaic evolution of brain structure in mammals.
1109 *Nature* 405, 1055-1058.
- 1110 Barton, R.A., Venditti, C. 2014. Rapid evolution of the cerebellum in humans and other
1111 great apes. *Curr. Biol.* 24, 2440-2444.
- 1112 Bickart, K.C., Wright, C.I., Dautoff, R.J., Dickerson, B.C., Barrett, L.F. 2011.
1113 Amygdala volume and social network size in humans. *Nat. Neurosci.*, 14, 163-164.
- 1114 Boesch, C., Tomasello, M. 1998. Chimpanzee and human cultures. *Curr. Anthropol.*
1115 39:591-614
- 1116 Brothers, L. 1990. The social brain: a project for integrating primate behaviour and
1117 neurophysiology in a new domain. *Conc. Neurosci.* 1, 27-51.
- 1118 Burkart, J., Schübiger, M. N., van Schaik, C. P. 2017. The evolution of general
1119 intelligence. *Behav. Brain Sci.* in press.
- 1120 Buttelmann, D., Carpenter, M., Call, J, Tomasello, M. 2007. Enculturated chimpanzees
1121 imitate rationally. *Dev. Sci.*, 10: 31-38
- 1122 Byrne, R.W., Corp, N. 2004. Neocortex size predicts deception rate in primates. *Proc.*
1123 *R. Soc. B*, 271, 1693-1699.
- 1124 Byrne, R.W., Russon, A.E. 1998. Learning by imitation: a hierarchical approach.
1125 *Behav. Brain Sci.* 21, 667-721.
- 1126 Byrne, R.W., Whiten, A. (Eds.) 1988. Machiavellian Intelligence: Social Complexity
1127 and the Evolution of Intellect in Monkeys, Apes and Humans. Oxford, Oxford
1128 University Press.
- 1129 Call, J. 2001. Body imitation in an enculturated orangutan (*Pongo pygmaeus*).
1130 *Cybernet. Syst.* 32: 97-119
- 1131 Call, J., Santos, L.R. 2012. Understanding other minds. In Mitani, J., Call, J., Kappeler,
1132 P., Palombit, R., Silk, J. (Eds), *The Evolution of Primate Societies*. Chicago
1133 University Press, Chicago, pp. 514-530.
- 1134 Call, J., Tomasello, M. 1994. The social learning of tool use by orangutans. *Hum.Evol.*,
1135 9: 297-313.
- 1136 Cheney, D., Seyfarth, R., Smuts, B. 1986. Social relationships and social cognition in
1137 nonhuman primates. *Science* 234, 1361-1366.
- 1138 Claidiere, N., Messer, E.J.E., Hoppitt, W., Whiten, A. 2013. Diffusion dynamics of
1139 socially learned foraging techniques in squirrel monkeys. *Curr. Biol.* 23, 1251-
1140 1255.
- 1141 Claidiere, N., Smith, K., Kirby, S., Fagot, J. 2014. Cultural evolution of systematically
1142 structured behaviour in a non-human primate. *Proc. Biol. Sci.* 281, 20141541
- 1143 Claidière, N., Whiten, A. 2012. Integrating the study of conformity and culture in
1144 humans and non-human animals. *Psych. Bull.* 138, 126-145.
- 1145 Crockford, C., Herbinger, I., Vigilant, L., Boesch, C. 2004. Wild chimpanzees produce
1146 group-specific calls: a case for vocal learning? *Ethology* 10, 221-243.
- 1147 Custance, D.M., Whiten, A., Bard, K.A. 1995. Can young chimpanzees (*Pan*
1148 *troglodytes*) imitate arbitrary actions? Hayes and Hayes (1952). revisited.
1149 *Behaviour* 132, 837-859.

- 1150 Davila-Ross, M., Hutchinsinon, J., Russell, J.L., Schaeffer, J., Billard, A., Hopkins,
 1151 W.D., Bard, K.A. 2014. Triggering social interactions: chimpanzees respond to
 1152 imitation by a humanoid robot and request responses from it. *Anim. Cogn.* 17, 589-
 1153 595.
- 1154 Dean, L.G., Kendal, R.L., Schapiro, S.J., Thierry, B., Laland, K.N. 2012. Identification
 1155 of the social and cognitive processes underlying human cumulative culture. *Science*
 1156 335, 1114–8
- 1157 Deaner, R.O., Isler, K., Burkart, J., van Schaik, C. 2006. Overall brain size, and not
 1158 encephalization quotient, best predicts cognitive ability across non-human primates.
 1159 *Brain Behav. Evol.* 70, 115-124.
- 1160 de Waal, F.B.M. 1982. *Chimpanzee Politics*. Jonathan Cape, London.
- 1161 de Waal, F.B.M. 2001. *The Ape and the Sushi Master: Cultural reflections of a*
 1162 *primatologist*. London: Allen Lane.
- 1163 de Waal, F.B.M., Ferrari, P. F. (Eds.) 2012. *The Primate Mind: Built to Connect With*
 1164 *Other Minds*. Harvard University Press, Cambridge, MA.
- 1165 de Waal, F.B.M., Tyack, P.L. (Eds.) 2005. *Animal Social Complexity: Intelligence,*
 1166 *Culture and Individualised Societies*. Harvard University Press, Cambridge, MA.
- 1167 Dindo, M., Thierry, B., Whiten, A. 2008. Social diffusion of novel foraging methods in
 1168 brown capuchin monkeys (*Cebus apella*). *Proc. R. Soc. Lond. B* 275, 187-193.
- 1169 Dindo, M., de Waal, F.B.M., Whiten, A. 2009. In-group conformity sustains different
 1170 foraging traditions in capuchin monkeys (*Cebus apella*). *PLoS One* 4, e7858.
- 1171 Dindo, M., Stoinski, T., Whiten, A. 2011. Observational learning in orangutan cultural
 1172 transmission chains. *Biol Lett.* 7, 181-183.
- 1173 Dunbar, R.I.M. 1995. Neocortex size and group size in primates: a test of the
 1174 hypothesis. *J. Hum. Evol.* 28, 287-296.
- 1175 Dunbar, R.I.M. 1998. The social brain hypothesis. *Evol. Anthropol.* 6, 178-190.
- 1176 Dunbar, R.I.M., Shultz, S. 2007. Evolution in the social brain. *Science*, 317, 1344-1347.
- 1177 Emery, N.J., Clayton, N.S., Frith, C.D. 2007. Social intelligence: from brain to culture.
 1178 *Phil. Trans. R. Soc. B*, 362, 485-488.
- 1179 Emery, N.J., Seed, A.M., von Bayern, A.M.P., Clayton, N.S. 2005. Cognitive
 1180 adaptations for bonding in birds. *Phil. Trans. R. Soc. B*, 362, 489-505.
- 1181 Ferrari, P. F., Rizzolatti, G. (Eds.) 2014. *Mirror neurons: fundamental discoveries,*
 1182 *theoretic perspectives and clinical applications*. *Phil. Trans. R. Soc. B* 369, whole
 1183 issue 1644.
- 1184 Forss, S. I. F., Willems, E., Call, J., van Schaik, C.P. 2016. Cognitive differences
 1185 between orangutan species: a test of the cultural intelligence hypothesis. *Sci. Rep.*
 1186 6, 30516.
- 1187 Fragaszy, D.M., Perry, S. (Eds.) 2003. *The Biology of Traditions: Models and*
 1188 *Evidence*. Cambridge University Press, Cambridge, UK.
- 1189 Frith, U., Hill, E. 2003. *Autism: Mind and Brain*. Oxford University Press, Oxford.
- 1190 Frey, S.H. 2007. What puts the how in where? Tool use and the divided visual streams
 1191 hypothesis. *Cortex* 43, 368-375.
- 1192 Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., Whiten, A. 2014. Synchrony and
 1193 motor mimicking in chimpanzee observational learning. *Sci. Rep.* 4: 5283. DOI:
 1194 10.1038/srep05383
- 1195 Galef, B.G. 1992. The question of animal culture. *Hum. Nat.* 3, 157-178.

- 1196 Galef, B.G., Whiten, A. (in press). The comparative psychology of social learning. In J.
 1197 Call (Ed.), *APA Handbook of Comparative Psychology*. American Psychological
 1198 Association, Washington.
- 1199 Gallese, V., Goldman, A. 1998. Mirror neurons and the simulation theory of mind-
 1200 reading. *Tr. Cog. Sci.* 2, 493-501.
- 1201 Goodall, J. 1986. *The Chimpanzees of Gombe*. Belknap Press, Cambridge, MA.
- 1202 Gruber, T., Muller, M.N, Reynolds, V., Wrangham, R., Zuberbuhler, K. 2011.
 1203 Community-specific evaluation of tool affordances in wild chimpanzees. *Sci. Rep.*
 1204 1, 1038/srep00128.
- 1205 Gunhold, T., Massen, J.J.M., Schiel, N., Souto, A., Bugnyar, T. 2014. Memory,
 1206 transmission and persistence of alternative foraging techniques in wild common
 1207 marmosets. *Anim Behav.* 91,79-91.
- 1208 Gunhold, T., Whiten, A., Bugnyar, T. 2014. Video demonstrations seed alternative
 1209 problem-solving techniques in wild common marmosets. *Biol Lett.* 10, 20140439.
- 1210 Haun, D.B., Rekers, Y., Tomasello, M. 2012. Majority-biased transmission in
 1211 chimpanzees and human children, but not orangutans. *Curr Biol* 22, 727-731.
- 1212 Hayes, K.J., Hayes, C. 1952. Imitation in a home-reared chimpanzee. *J. Comp. Physiol.*
 1213 *Psychol.* 45, 450-459.
- 1214 Hecht, E. E., Gutman, D. A., Preuss, T. M., Sanchez, M. M., Parr, L. A., Rilling, J. K.
 1215 2013a. Process versus product in social learning : comparative diffusion tensor
 1216 imaging of neural systems for action execution-observation matching in macaques,
 1217 chimpanzees, and humans. *Cereb. Cortex* 23, 1014-1024.
- 1218 Hecht, E. E., Murphy, L. E., Gutman, D. A., Schuster, D. M., Preuss, T. D., Orban, G.
 1219 A., Stout, D., Parr, L. A. 2013b. Differences in neural activation for object-directed
 1220 grasping in chimpanzees and humans. *J. Neurosci.* 33, 14177-141117.
- 1221 Hecht, E. E., Gutman, D. A., Khreisheh, N., Taylor, S. V., Kilner, J., Faisal, A. A.,
 1222 Bradley, B. A., Chaminade, T., Stout, D. 2015. Acquisition of tool-making abilities
 1223 involves structural remodelling to inferior frontparietal regions. *Brain Struct. Funct.*
 1224 220, 2315-2331.
- 1225 Herrmann, E., Call, J., Hernandez-Loreda, M.V., Hare, B., Tomasello, M. 2007.
 1226 Humans have evolved specialized skills of social cognition: the cultural intelligence
 1227 hypothesis. *Science* 317, 1360-1366.
- 1228 Heyes, C.M. 1994. Social learning in animals: Categories and mechanisms. *Biol. Rev.*
 1229 69, 207-231.
- 1230 Hirata, S. Watanabe, S., Kawai, M. 2001. "Sweet-potato washing" revisited. In T.
 1231 Matsuzawa (Ed.), *Primate Origins of Human Behavior and Cognition*, Springer-
 1232 Verlag, Tokyo, pp. 487-508.
- 1233 Hobaiter, C., Poiso, T., Zuberbühler, K., Hoppit, W., Gruber, T. 2014. Social network
 1234 analysis shows direct evidence for social learning of tool use in wild chimpanzees.
 1235 *PLoS Biol.* 12, e1001960 (doi: 10.1371/journal.pbio.1001960)
- 1236 Hohmann, G. & Fruth, B. 2003. Culture in Bonobos? Between-species and within-
 1237 species variation in behavior. *Curr. Anthropol.* 44, 563-571.
- 1238 Hopper, L.M., Holmes, A., Williams, L., Brosnan, S. 2013. Dissecting the mechanisms
 1239 of squirrel monkey (*Saimiri boliviensis*) social learning. *PeerJ* 1, e13.
- 1240 Hopper, L.M., Schapiro, S. J., Lambeth, S.P., Brosnan S.F. 2011. Chimpanzees'
 1241 socially maintained food preferences indicate both conservatism and conformity.
 1242 *Anim. Behav.* 81, 1195-1202.

- 1243 Hopper, L.M., Spiteri, A., Lambeth, S.P., Schapiro, S.J., Horner, V., Whiten, A. 2007.
 1244 Experimental studies of traditions and underlying transmission processes in
 1245 chimpanzees. *Anim. Behav.* 73, 1021-1032.
- 1246 Hopper, L.M., Lambeth, S.P., Schapiro, S.J., Whiten, A. 2008. Observational learning
 1247 in chimpanzees and children studied through ‘ghost’ conditions. *Proc. R. Soc.*
 1248 *Lond. B*, 275, 835-840.
- 1249 Hopper, L.M., Lambeth, S.P., Schapiro, S.J., Whiten, A. 2015. The importance of
 1250 witnessed agency in chimpanzee social learning of tool use. *Behav. Proc.* 112: 120-
 1251 129.
- 1252 Hoppitt, W.J.E., Brown, G.E., Kendal, R., Rendell, L., Thornton, A., Webster, M.M.,
 1253 Laland, K.N. 2008. Lessons from animal teaching. *Tr. Ecol. Evol.* 23, 486-93
- 1254 Hoppitt, W.J.E., Laland, K.N. (Eds.) 2013. *Social Learning: An Introduction to*
 1255 *Mechanisms, Methods and Models.* Princeton University Press, Princeton.
- 1256 Hoppitt, W.J.E., Laland, K.N. 2008. Social processes influencing social learning in
 1257 animals: a review of the evidence. *Adv. Stud. Behav.* 38, 1-5-165.
- 1258 Horner, V., Proctor, D., Bonnie, K.E., Whiten, A., de Waal F.B.M. 2010. Prestige
 1259 affects cultural learning in chimpanzees. *PLoS ONE*, 5, e10625
- 1260 Horner, V., Whiten, A. 2005. Causal knowledge and imitation/emulation switching in
 1261 chimpanzees (*Pan troglodytes*) and children. *Anim. Cogn.* 8, 164-181
- 1262 Huffman, M. A. 1996. Acquisition of innovative cultural behaviours in nonhuman
 1263 primates: a case study of stone handling, a socially transmitted behavior in Japanese
 1264 macaques. In C. M Heyes & B. G Galef, Jr. (Eds.), *Social Learning in Animals:*
 1265 *The roots of culture* Academic Press, London, pp. 267-289.
- 1266 Humphrey, N.K. 1976. The Social Function of Intellect. In Bateson, P. P. G., Hinde, R.
 1267 A. (Eds) *Growing Points in Ethology.* Cambridge University Press, Cambridge, pp.
 1268 303-317.
- 1269 Iacoboni, M., Woods, R.P., Brass, H., Bekkering, H., Mazziotta, J.C., Rizzolatti, G.
 1270 1999. Cortical mechanisms of imitation. *Science* 286, 2526-2528.
- 1271 Iacoboni, M. 2012. The human mirror neuron system and its role in imitation and
 1272 empathy. In de Waal, F. B. M., Ferrari, P. F. (Eds). *The Primate Mind: Built to*
 1273 *Connect with Other Minds.* Harvard University Press, Cambridge, MA., pp. 32-47.
- 1274 Isler, K, van Schaik, C. P. 2014. How humans evolved large brains: comparative
 1275 evidence. *Evol. Anthropol.* 23, 65-75.
- 1276 Jolly, A. 1966. Lemur social behavior and primate intelligence. *Science*, 153, 501-506.
- 1277 Kanai, R., Bahrami, B., Roylance, R., Rees, G. 2012. Online social network size is
 1278 reflected in human brain structure. *Proc. R. Soc. B*, 279, 1327-1334.
- 1279 Kendal, R.L., Custance, D.M., Kendal, J.R., Vale, G., Stoinski, T.S., Rakotomalala,
 1280 N.L., Rasamimanana, H. 2010. Evidence for social learning in wild lemurs (*Lemur*
 1281 *catta*). *Learn. Behav.* 38, 220-234.
- 1282 Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J.,
 1283 Hoppitt, W. 2015. Chimpanzees copy dominant and knowledgeable individuals:
 1284 implications for cultural diversity. *Evol. Hum. Behav.* 36, 65-72.
- 1285 Krupenye, C., Kano, F., Hirata, S., Call, J, Tomasello, M. 2016. Great apes anticipate
 1286 that other individuals will act according to false beliefs. *Science* 354, 110-114.
- 1287 Krützen, M., Willems, E.P., van Schaik, C.P. 2011. Culture and geographic variation in
 1288 orang-utan behaviour. *Curr Biol.* 21, 1808-1812
- 1289 Kudo, H., Dunbar, R.I.M. 2001. Neocortex size and social network size in primates.
 1290 *Anim. Behav.* 62, 711-722.

- 1291 Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D’Auvergne, L. et al. (2016).
 1292 Chimpanzee accumulative stone throwing. *Scientific Reports* 6, 22219, DOI:
 1293 10.1038/srep22219.
- 1294 Leca, J.-B., Gunst, N., Huffman, M. A. 2007. Japanese macaque cultures: Inter- and
 1295 intra-troop behavioral variability of stone-handling patterns across 10 groups.
 1296 *Behaviour* 144, 251-81.
- 1297 Lefebvre, L. 2013. Brains, innovations, tools and cultural transmission in birds, non-
 1298 human primates and fossil hominins. *Front. Hum. Neurosci.* 7, 245.
- 1299 Lewis, P.A., Rezaie, R., Brown, R., Roberts, N., Dunbar, R.I.M. 2011. Ventromedial
 1300 prefrontal volume predicts understanding of others and social network size.
 1301 *Neuroim.* 57, 1624-1629.
- 1302 Lonsdorf, E.V., Pusey, E.A., Eberly, L. 2004. Sex differences in learning in
 1303 chimpanzees. *Nature* 428, 715-716.
- 1304 Luncz, L.V., Boesch, C. 2014. Tradition over trend: Neighboring chimpanzee
 1305 communities maintain differences in cultural behaviour despite frequent
 1306 immigration of adult females. *Am. J. Primatol.* 76: 649–657
- 1307 Luncz, L., Wittig, R.M., Boesch, C. 2015. Primate archaeology reveals cultural
 1308 transmission patterns in wild chimpanzees (*Pan troglodytes verus*). *Phil. Trans. R.*
 1309 *Soc. B.* 370, 20140348
- 1310 Lyons, D.E., Young, A.G., Keil, F.C. 2007. The hidden structure of overimitation. *Proc.*
 1311 *Natl. Acad. Sci. USA* 104, 19751-19756.
- 1312 Machiavelli, N. 1513/1961. *The Prince*. Penguin, Harmondsworth, UK (translated from
 1313 the Italian by G. Bull).
- 1314 Marlowe, F.W. 2005. Hunter-gatherers and human evolution. *Evol. Anthropol.* 14, 54-
 1315 67.
- 1316 Marshall-Pescini, S., Whiten, A. 2008a. Social learning of nut-cracking behaviour in
 1317 East African sanctuary-living chimpanzees (*Pan troglodytes schweinfurthii*). *J.*
 1318 *Comp. Psychol.*, 122, 186-194.
- 1319 Marshall-Pescini, S., Whiten, A. 2008b. Chimpanzees (*Pan troglodytes*) and the
 1320 question of cumulative culture: an experimental approach. *Anim. Cog*, 11, 449-456
- 1321 Martineau, J., Andersson, F., Barthelemy, C., Cottier, J.P., Destrieux, C. 2010. Atypical
 1322 activation of the mirror neuron system during perception of hand motion in autism.
 1323 *Brain Res.* 1320, 168-175.
- 1324 McGrew, W.C. 1992. *Chimpanzee Material Culture*. Cambridge University Press,
 1325 Cambridge.
- 1326 McGrew, W.C., Marchant, L.F., Scott, S.E., Tutin, C.E.G. 2001. Intergroup differences
 1327 in a social custom in wild chimpanzees: the grooming handclasp of the Mahale
 1328 Mountains. *Curr. Anthropol.* 42, 148-153.
- 1330 Meltzoff, A. 2005. Imitation and other minds: the “like me” hypothesis. In Hurly, S.,
 1331 Chater, N. (Eds.) *Perspectives on Imitation Volume 2, Imitation, Human*
 1332 *Development and Culture*. MIT Press, Cambridge, MA, pp. 55-77..
- 1333 Meltzoff, A., Moore, J. 1983. Newborn infants imitate adult facial gestures. *Child Dev.*
 1334 54, 702-709.
- 1335 Meunier, H. (in press). Do monkeys have a theory of mind? How to answer the
 1336 question. *Neurosci. Biobehav. Rev.* in press (this Issue).
- 1337 Milner, A. D., Goodale, M. A., 2008. Two visual systems re-viewed. *Neuropsychologia*
 46, 774-785.

- 1338
1339 Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A., Silk, J.B. (Eds.) 2012. The
Evolution of Primate Societies. University of Chicago Press, Chicago.
- 1340 Mitchell, R.W., Anderson, J.R. 1993. Discrimination learning of scratching, but failure
1341 to obtain imitation and self-recognition in a long-tailed macaque. *Primates* 34, 301-
1342 309.
- 1343 Möbius, Y., Boesch, C., Koops, K., Matsuzawa, T., Humle, T. 2008. Cultural
1344 differences in army ant predation by West African chimpanzees? A comparative
1345 study of microecological variables. *Anim. Behav.* 76, 37-45.
- 1346 Molenberghs P., Cunnington R., Mattingly, J.B. 2009. Is the mirror neuron system
1347 involved in imitation? A short review and meta-analysis. *Neurosci. Behav. Rev.* 33,
~~1348~~ 975-980.
- 1350 Moll, H., Tomasello, M. 2007. Cooperation and human cognition: the Vygotskian
1351 intelligence hypothesis. *Phil. Trans. R. Soc. B* 362, 639-648.
- 1352 Mooney, R. Auditory-vocal mirroring in songbirds. *Phil. Trans. R. Soc. B.* 369,
20130179.
- 1353 Nagell, K., Olguin, R.S., Tomasello, M. 1993. Processes of social learning in the tool
1354 use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J.*
1355 *Comp. Psychol.* 107, 174-186.
- 1356 Navarrete, A.F., Reader, S.M., Street, S.E., Whalen, A., Laland, K.N. 2016. The
1357 coevolution of innovation and technical intelligence in primates. *Phil. Trans. R.*
1358 *Soc. B.* 371, 20150186.
- 1359 Nielsen, M., Collier-Baker, E., Davis, J.M., Suddendorf, T. 2005. Imitation recognition
1360 in a captive chimpanzee (*Pan troglodytes*). *Anim. Cogn.* 8, 31-36.
- 1361 Nielsen, M., Mushin, I., Tomaselli, K., Whiten, A. 2014. Where culture takes hold:
1362 'overimitation' and its flexible deployment in Western, Aboriginal and Bushmen
1363 children. *Child Dev.* 85, 2169-2184.
- 1364 Oostenbroek, J., Slaughter, V., Nielsen, M., Suddendorf, T. 2013. Why the confusion
1365 around neonatal imitation? A review. *J. Reprod. Inf. Psychol.* 31, 328-341.
- 1366 Oostenbroek, J., Suddendorf, T., Nielsen, M., Redshaw, A., Kennedy-Constantini, S.,
1367 Davis, J., Clark, S., Slaughter, V. 2016. Comprehensive longitudinal study
1368 challenges the existence of neonatal imitation in humans. *Curr. Biol.* 26, 1334-
1369 1338.
- 1370 Ottoni, E.B., Dogo de Resende, B., Isar, P. 2005. Watching the best nutcrackers: what
1371 capuchin monkeys (*Cebus paella*) know about others' tool-using skills. *Anim.*
1372 *Cogn.* 24, 215-219.
- 1373 Panger, M.A., Perry, S., Rose, L., Gros-Luis, J., Vogel, E., Mackinnon, K.C., Baker,
1374 M. 2002. Cross-site differences in foraging behavior of white-faced capuchins
1375 (*Cebus capuchinus*). *Amer. J. Phys. Anthropol.* 119, 52-56.
- 1376 Paukner, A., Anderson, J.R., Borelli, E., Visalberghi, E., Ferrari, P.F. 2005. Macaques
1377 (*Macaca nemestrina*) recognise when they are being imitated. *Biol. Lett.* 1, 219-
1378 222.
- 1379 Paukner, A., Suomi, S.J., Visalberghi, E., Ferrari, P.F. 2009. Capuchin monkeys display
1380 affiliation toward humans who imitate them. *Science* 325, 880-883.
- 1381 Perkins, T., Stokes, M., McGillivray, J., Bittar, R. 2010. Mirror neuron dysfunction in
1382 autism spectrum disorders. *J. Clin. Neurosci.* 17, 1239-1243.
- 1383 Perry, S. 2009. Conformism in the food-processing techniques of white-faced capuchin
1384 monkeys (*Cebus capucinus*). *Anim. Cogn.*, 12, 705-716.

- 1385 Perry, S., Baker, M., Fedigan, L., Gros-Luis, J., Jack, K., Mackinnon, K.C., Manson, J.,
 1386 Panger, M., Pyle, K., Rose, L.M. 2003. Social conventions in white-face capuchins
 1387 monkeys: evidence for behavioral traditions in a neotropical primate. *Curr.*
 1388 *Anthropol.* 44, 241-268.
- 1389 Platt, M.L., Seyfarth, R.M., Cheney, D.L. 2016. Adaptations for social cognition in the
 1390 primate brain. *Phil. Trans. R. Soc. B* 371, 200150096.
- 1391 Pope, S.M., Russell, J.M., Hopkins, W. 2015. The association between imitation
 1392 recognition and socio-communicative competencies in chimpanzees (*Pan*
 1393 *trogodytes*). *Front. Psychol.* 6, 188.doi: 10.3389/fpsyg.2015.00188.
- 1394 Powell, J., Lewis, P.A., Roberts, N., Garcia-Finana, M., Dunbar, R.I. 2012. Orbital
 1395 prefrontal cortex volume predicts social network size: an imaging study of
 1396 individual differences in humans. *Proc. R. Soc. B* 279, 2157-2162.
- 1397 Price, E.E., Wood., L.A., Whiten, A. in press. Adaptive cultural transmission biases in
 1398 children and nonhuman primates. *Inf. Behav. Dev.* in press.
- 1399 Reader, S., Laland, K. 2002. Social intelligence, innovation, and enhanced brain size in
 1400 primates. *Proc. Natl. Acad. Sci. USA* 99, 4436-4441.
- 1401 Rendell, L., Whitehead, H. 2001. Cultures in whales and dolphins. *Behav. Brain Sci.*, 24,
 1402 309-324.
- 1403 Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L. 1996. Premotor cortex and the
 1404 recognition of motor actions. *Cog. Brain Res.* 3, 131-141.
- 1405 Rizzolatti, G., Fogassi, L., 2014. The mirror mechanism: recent finding and
 1406 perspectives. *Phil. Trans. R. Soc. B* 369, 20130169.
- 1407 Rizzolatti, G., Fogassi, L., Gallese, V. 2001. Neurophysiological mechanisms
 1408 underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661-
 1409 670.
- 1410 Robbins, M. M., Ando, C., Fawcett, K. A., Gruiter, C. C., Hedwig, D., Iwata, Y.,
 1411 Lodwick, J.L., Masi, S., Salmi, R., et al. 2016. Behavioural variation in gorillas:
 1412 evidence of potential cultural traits. *PLOS ONE* 11, e0160483.
- 1413 Rogers, S.J., Pennington, B.F. 1991. A theoretical approach to the deficits in infantile
 1414 autism. *Dev. Psychopathol.* 3, 137-162.
- 1415 Rose, L.M., Perry, S., Panger, M., Jack, K., Manson, J., Gros-Luis, J., Mackinnon, K.C.,
 1416 Vogel, E. 2003. Interspecific interactions between *Cebus capuchinus* and other
 1417 species in Costa Rican sites. *Int. J. Primatol.* 24, 759-796.
- 1418 Sapolsky, R. M., Share, L. J. 2004. A pacific culture among wild baboons: its
 1419 emergence and transmission. *PLoS Biol.* 2, 294-304.
- 1420 Santorelli, C.J., Schaffner, C.M., Campbell, C.J., Notman, H., Pavelka, M.S., Weghorst,
 1421 J.A., Aureli, F. 2011. Traditions in spider monkeys are biased towards the social
 1422 domain. *PLoS ONE* 6, e16863.
- 1423 Santorelli, C.J., Schaffner, C.M., Aureli, F. 2011. Universal behaviours as candidate
 1424 traditions in wild spider monkeys. *PLoS ONE* 6, e24400.
- 1425 Schnoell, A.V., Dittmann, M.T., Fichtel, C. 2014. Human-introduced long-term
 1426 traditions in wild redfronted lemurs? *Anim Cogn.* 17, 45-54.
- 1427 Schnoell, A.V., Fichtel, C. 2012. Wild redfronted lemurs (*Eulemur rufifrons*) use social
 1428 information to learn new foraging techniques. *Anim Cogn.*, 15, 505-516.
- 1429 Schuppli, C., Meulman, E. J. M., Forss, S. I. M., Aprilinayati, F., van Noordwijk, M.A.,
 1430 van Schaik, C. P. 2016. Observational learning and socially induced practice of
 1431 routine skills in immature orangutans. *Anim. Behav.* 119, 87-98.

- 1432 Seyfarth, R.M., Cheney, D.L. 2015a. How sociality shapes the brain, behaviour and
1433 cognition. *Anim. Behav.* 103, 187-190.
- 1434 Seyfarth, R.M., Cheney, D.L. 2015b. Social cognition. *Anim. Behav.* 103, 191-202.
- 1435 Shöning, C., Humle, T., Möbius, Y., McGrew, W. C. 2008. The nature of culture:
1436 technological variation in chimpanzee predation on army ants revisited. *J.Hum.*
1437 *Evol.* 55, 48-59.
- 1438 Shultz, S., Dunbar, R.I.M. 2007. The evolution of the social brain: anthropoid primates
1439 contrast with other vertebrates. *Proc. R. Soc. B* 274, 2429-2436.
- 1440 Shultz, S., Dunbar, R.I.M. 2010. Encephalization is not a universal macroevolutionary
1441 phenomenon in mammals but is associated with sociality. *Proc. Natl. Acad. Sci.*
1442 *USA* 107, 21582-21586.
- 1443 Simpson, E.A, Murray, L., Paukner, A., Ferrari, P.F. 2014. The mirror neuron system as
1444 revealed through neonatal imitation: presence from birth, predictive power and
1445 evidence of plasticity. *Phil. Trans. R. Soc. B* 369, 20130180.
- 1446 Southgate, V., Hamilton, A.F.D. 2008. Unbroken mirrors: challenging a theory of
1447 Autism. *Tr. Cog. Sci.* 12, 225-229.
- 1448 Stout, D., Toth, N., Schick, K, Chaminade, T. 2008. Neural correlates of Early Stone
1449 Age toolmaking: technology, language and cognition in human evolution. *Phil.*
1450 *Trans. R. Soc. B.* 363, 1939-1949.
- 1451 Subiaul, F. 2007. The imitation faculty in monkeys: evaluating its features, distribution
1452 and evolution. *J. Anthropol. Sci.* 85: 35-62.
- 1453 Subiaul, F., Cantlon, J.F., Holloway, R.L., Terrace, H.S. 2004. Cognitive imitation in
1454 rhesus macaques. *Science* 305, 407-410.
- 1455 Tennie, C., Call, J., Tomasello, M. 2009. Ratchetting up the ratchet: on the evolution of
1456 cumulative culture. *Phil Trans. R. Soc. B* 364, 2405-2415.
- 1457 Tennie, C., Call, J., Tomasello, M. 2010. Evidence for emulation in chimpanzees in
1458 social settings using the floating peanut task. *PLoS ONE* 5, e10544
- 1459 Tomasello, M. 1990. Cultural transmission in the tool use and communicatory signaling
1460 of chimpanzees? In Parker, S.T., Gibson, K. (Eds.) "Language" and intelligence in
1461 monkeys and apes: Comparative developmental perspectives. Cambridge
1462 University Press, Cambridge, UK, pp. 274-311.
- 1463 Tomasello, M., Call, J. 1997. *Primate Cognition*. Oxford University Press, Oxford.
- 1464 Tomasello, M., Call, J. 2004. The role of humans in the cognitive development of apes
1465 revisited. *Anim. Cogn.* 7, 213-215.
- 1466 Tomasello, M., Carpenter, M. 2005. The emergence of social cognition in three young
1467 chimpanzees. *Monog. Soc. Res. Child Dev.* 70 (1, Ser. No. 279).
- 1468 Tomasello, M., Davis-Dasilva, M., Camak, L., Bard, K. 1987. Observational learning of
1469 tool-use by young chimpanzees. *Hum. Evol* 2, 175-183
- 1470 Tomasello, M., Kruger, A.E., Ratner, H. 1993a. Cultural learning. *Behav. Brain Sci.* 16,
1471 595-652.
- 1472 ~~1471~~ Tomasello, M., Savage-Rumbaugh, S., Kruger, A. C. 1993b. Imitative learning of
1473 actions on objects by children, chimpanzees and enculturated chimpanzees. *Child*
1474 *Dev.* 64, 1688-1705.
- 1475 Tournier, E., Tournier, V., van de Waal, E., Barrett, A., Brown, L. , Bshary, R. 2014.
1476 Differences in diet between six neighbouring groups of vervet monkeys. *Ethology*
1477 120, 1-12.

- 1478 Tramacere, A., Pievani, T., Ferrari, P. F. 2016. Mirror neurons in the tree of life: mosaic
1479 evolution, plasticity and exaptation of sensorimotor matching responses. *Biol. Rev.*
1480 in press. Doi:10.1111/brv.12310.
- 1481 van de Waal, E., Borgeaud, C., Whiten, A. 2013a. Potent social learning and conformity
1482 shape a wild primate's foraging decisions. *Science*, 6131, 483-5.
- 1483 van de Waal, E., Bshary, R., Whiten, A. 2014. Wild vervet monkey infants acquire the
1484 food-processing variants of their mothers. *Anim. Behav.* 90, 41-45.
- 1485 van de Waal, E., Claidière, N., Whiten, A. 2013b. Social learning and spread of
1486 alternative means of opening an artificial fruit in four groups of vervet monkeys.
1487 *Anim. Behav.* 85, 71-76.
- 1488 van de Waal, E., Claidière, N., Whiten, A. 2015. Wild vervet monkeys copy alternative
1489 methods for opening an artificial fruit. *Anim. Cogn.* 18, 617-627.
- 1490 van de Waal, E., Renevey, N., Favre, C.M., Bshary, R. 2010. Selective attention to
1491 philopatric models causes directed social learning in wild vervet monkeys. *Proc.*
1492 *Biol. Sci.* 277, 2105-2111.
- 1493 van de Waal, E., Whiten, A. 2012. Spontaneous emergence, imitation and spread of
1494 alternative foraging techniques among groups of vervet monkeys. *PLoS ONE* 7,
1495 e47008. doi:10.1371/journal.pone.0047008
- 1496 van Leeuwen, E.J., Cronin, K.A., Schutte, S., Call, J., Haun, D.B. 2013. Chimpanzees
1497 (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not
1498 to conform to majorities. *PLoS ONE* 8, e80945.
- 1499 van Leeuwen, E.J.C., Haun, D.B.M. 2014. Conformity without majority? The case for
1500 demarcating social from majority influences. *Anim. Behav.*, 96, 187-194.
- 1501 van Leeuwen, E.J.C., Acerbi, A., Kendal, R.L., Tennie, C. 2016. A reappraisal of
1502 'conformity'. *Anim Behav.* 122, e 5-10.
- 1503 van Schaik, C.P. 2006. Why are some animals so smart? *Sci. Amer.* 294, 64-71.
- 1504 van Schaik, C. P. 2009. Geographic variation in the behavior of wild great apes:
1505 is it really cultural? In K. N. Laland, B. G. Galef (Eds.) *The Question of*
1506 *Animal Culture*. Harvard University Press, Cambridge, MA., pp. 70-98.
- 1507 van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I.,
1508 Suzuki, A., Utami, S.S., Merrill, M. 2003. Orangutan cultures and the evolution of
1509 material culture. *Science*. 299, 102-105.
- 1510 van Schaik, C.P., Burkart, J.M. 2011. Social learning and evolution: the cultural
1511 intelligence hypothesis. *Phil. Trans. R. Soc. B*, 366, 1008-1016.
- 1512 Vanvuchlene, M., van Schuerbeeck, L., Roeyers, H., deWeerd, W. 2013.
1513 Understanding the mechanisms behind deficits in imitation: Do individuals with
1514 autism know 'what' to imitate and do they 'how' to imitate? *Res. Dev. Dis.* 34,
1515 538-545.
- 1516 Visalberghi, E., Fragaszy, D.M. 2002. Do monkeys ape? - Ten years after. In
1517 Dautenhahn, K., Nehaniv, C.L. (Eds.) *Imitation in animals and artifacts*. MIT Press,
1518 Cambridge, MA., pp. 471-499.
- 1519 Voelkl, B., Huber, L. 2000. True imitation in marmosets. *Anim. Behav.* 60, 195-202.
- 1520 Voelkl, B., Huber, L. 2007. Imitation as faithful copying of a novel technique in
1521 marmoset monkeys. *PLoS ONE* 2, e611.
- 1522 Watson, S.J., Botting, J., Whiten, A., van de Waal, E. in press. Culture and selective
1523 social learning: complementary studies of wild and captive primates. In Di Paolo,
1524 L.D., d'Almeida, A.F.A., Vincenzo, F.D. (Eds.) *Social cognition in non-human*
1525 *primates and early Homo*. Springer, Berlin, in press.

- 1526 Whitehead, H., Rendell, L. 2015. *The Cultural Lives of Whales and Dolphins*.
 1527 University of Chicago Press, Chicago.
- 1528 Whiten, A. 1998. Imitation of the sequential structure of actions by chimpanzees (Pan
 1529 troglodytes). *J. Comp. Psychol.* 112, 270-281.
- 1530 Whiten A. 2005. The second inheritance system of chimpanzees and humans. *Nature*,
 1531 437: 52-55.
- 1532 Whiten, A. 2006. The significance of socially transmitted information for nutrition and
 1533 health in the great ape clade. In Wells, J .C. K., Laland, K., Strickland, S.S. (Eds.)
 1534 *Social Information Transmission and Human Biology*, CRC Press, London. pp.
 1535 118-134.
- 1536 Whiten, A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. *Phil.*
 1537 *Trans. R. Soc. B*, 366, 997-1007.
- 1538 Whiten A. 2012. Primate social learning, traditions and culture. In Mitani, J., Call, J.,
 1539 Kappeler, P., Palombit, R., Silk, J. (Eds.). *The Evolution of Primate Societies*.
 1540 Chicago University Press, Chicago, pp. 681-699.
- 1541 Whiten, A. 2013. Humans are not alone in computing how others see the world. *Anim.*
 1542 *Behav.* 86, 213-221.
- 1543 Whiten, A. 2015. Experimental studies illuminate the cultural transmission of
 1544 percussive technology in *Homo* and *Pan*. *Phil. Trans. R. Soc. B* 370, 20140359.
- 1545 Whiten, A. 2017a. Social learning and culture in child and chimpanzee. *Ann. Rev.*
 1546 *Psychol.* 68, 129-154.
- 1547 Whiten, A. 2017b. The evolution and ontogeny of ‘Deep Social Mind’ and the social
 1548 brain. In *Minnesota Symposia in Child Development*, Vol. 39: ‘Development of the
 1549 Social Brain’ (Eds. Ellison, J., Serra, M.). Hoboken, New Jersey: John Wiley &
 1550 Sons Inc.
- 1551 Whiten, A., Caldwell, C.A., Mesoudi, A. 2016. Cultural diffusion in humans and other
 1552 animals. *Curr. Op. Psychol.* 8, 15-21.
- 1553 Whiten, A., Byrne, R.W. 1988a. The Machiavellian intelligence hypotheses. In Byrne
 1554 R.W., Whiten, A. (Eds), *Machiavellian Intelligence: Social Complexity and the*
 1555 *Evolution of Intellect in Monkeys, Apes and Humans*. Oxford University Press,
 1556 Oxford, pp. 1-9.
- 1557 Whiten, A., Byrne, R.W. 1988b. Tactical deception in primates. *Behav. Brain Sci.* 11,
 1558 233-273.
- 1559 Whiten, A., Cusance, D. 1996. Studies of imitation in chimpanzees and children. In
 1560 Heyes, C.M., Galef, B.G. Jr. (Eds), *Social Learning in Animals: The roots of*
 1561 *culture*. Academic Press, London, pp. 291-318.
- 1562 Whiten, A., Erdal, D. 2012. The human socio-cognitive niche and its evolutionary
 1563 origins. *Phil. Trans. R. Soc. B* 367, 2119-2129.
- 1564 Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y.,
 1565 Tutin, C.E.G., Wrangham, R.W., Boesch, C. 1999. Cultures in chimpanzees.
 1566 *Nature* 399, 682-685.
- 1567 Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., et al. 2001. Charting
 1568 cultural variation in chimpanzees. *Behaviour* 138, 1489-1525.
- 1569 Whiten, A., Ham, R. 1992. On the nature and evolution of imitation in the animal
 1570 kingdom: Reappraisal of a century of research. *Advances in the Study of*
 1571 *Behaviour* 21, 239-83.
- 1572 Whiten, A., Hinde, R. A., Stringer, C. B. & Laland, K. N. 2011. Culture Evolves. *Phil.*
 1573 *Trans. R. Soc. B* 366, 938-948.

- 1574 Whiten, A., Horner, V., de Waal, F.B.M. 2005 Conformity to cultural norms of tool use
1575 in chimpanzees. *Nature* 437, 737-740.
- 1576 Whiten, A., Horner, V., Litchfield, C.A., Marshall-Pescini, S., 2004. How do apes ape?
1577 *Learn. Behav.* 32, 36-52.
- 1578 Whiten, A., Horner, V., Marshall-Pescini, S. 2003. Cultural panthropology. *Evol.*
1579 *Anthropol.* 12, 92-105.
- 1580 Whiten, A., McGuigan, H., Hopper, L.M., Marshall-Pescini, S. 2009. Imitation, over-
1581 imitation, emulation and the scope of culture for child and chimpanzee. *Phil. Trans.*
1582 *R. Soc. B* 364, 2417-28.
- 1583 Whiten, A., Mesoudi, A. 2008. An experimental science of culture: animal social
1584 diffusion experiments. *Phil. Trans. R. Soc. B* 363, 3477-3488.
- 1585 Whiten, A., Spiteri, A., Horner, V., Bonnie, K.E., Lambeth, S.P., Schapiro, S.J., de
1586 Waal, F.B.M. 2007 Transmission of multiple traditions within and between
1587 chimpanzee groups. *Curr. Biol.* 17, 1038-1043.
- 1588 Whiten, A., van de Waal, E. (2016). Identifying and dissecting conformity in animals in
1589 the wild: further analysis of primate data. *Anim. Behav.* 122, e1-e4.
- 1590 Whiten, A., van Schaik, C.P. 2007. The evolution of animal ‘cultures’ and social
1591 intelligence. *Phil. Trans. R. Soc. B*, 362, 603-620.
- 1592 Williams, J.H.G., Whiten, A., Singh, T. 2004. A systematic review of action imitation
1593 in autistic spectrum disorder. *J. Aut. Dev. Dis.* 34, 285-299.
- 1594 Williams, J.H.G., Whiten, A., Suddendorf, T., Perrett, D.I. 2001. Imitation, mirror
1595 neurons and autism. *Neurosci. Biobehav. Rev.* 25, 287-295.
- 1596 Williams, J.H.G., Whiten, A., Waiter, G. D., Pechey, S., Perrett, D. I. 2007. Cortical and
1597 sub-cortical mechanisms at the heart of imitation. *Soc. Neurosci.*, 2, 66-78.
- 1598 Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou,
1599 Guinea: Possible implications for ecological importance of tool use. *Am. J. Phys.*
1600 *Anthropol.* 106, 283-295.
- 1601 Yoshida, K., Saito, N., Iriki, A., Isoda, M. 2011. Representation of other’s action by
1602 neurons in monkey medial frontal cortex. *Curr. Biol.* 21, 249-253.
- 1603 Zentall, T.R., Sutton, J.E., Sherburne, L.M. 1996. True imitative learning in pigeons.
1604 *Psychon. Sci.* 7, 343-346.

1605

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.

1647

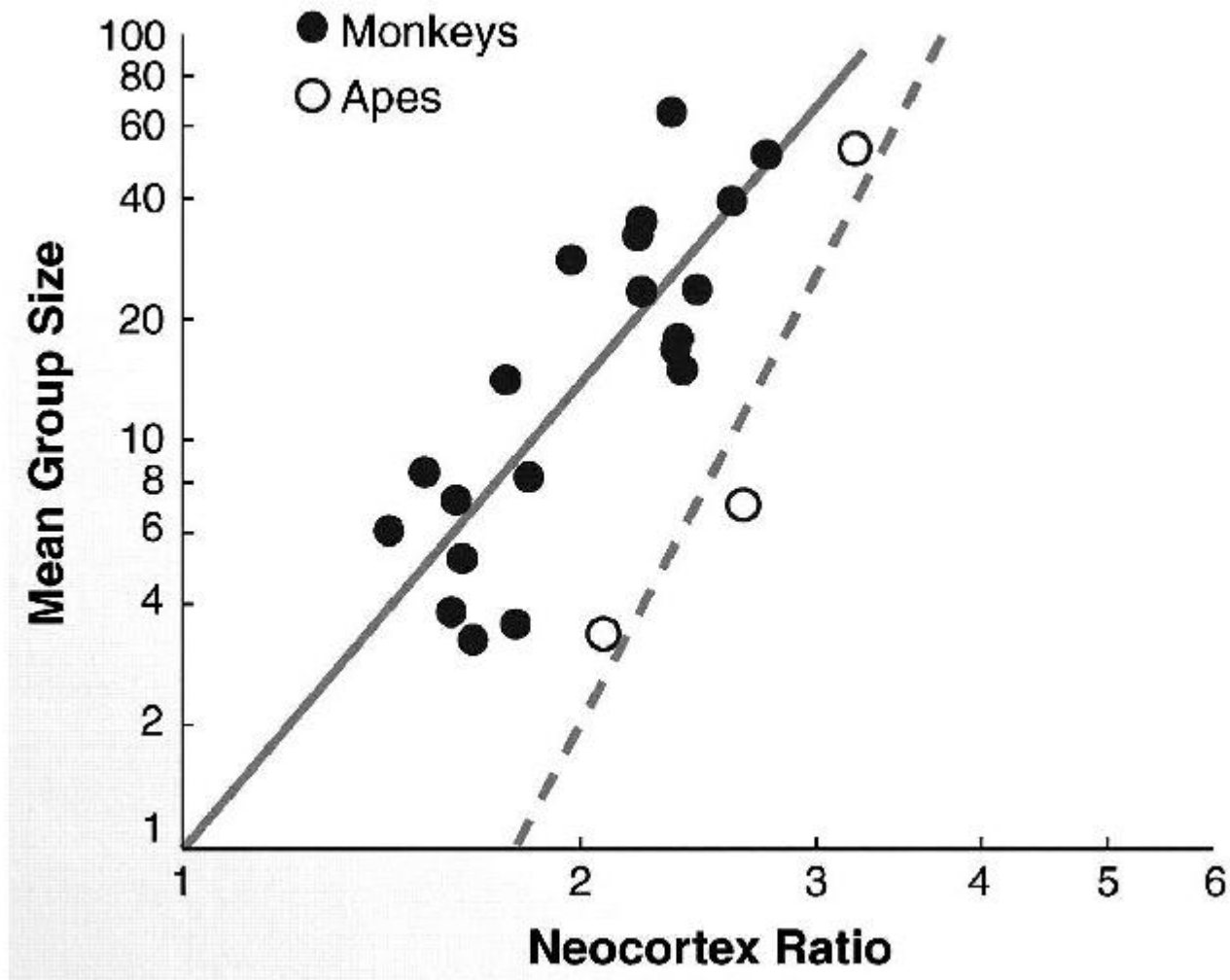
1648 Table 2. Cultural diffusion experiments with non-human primates since the first field
1649 experiments (2010).

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.

1650
1651
1652
1653

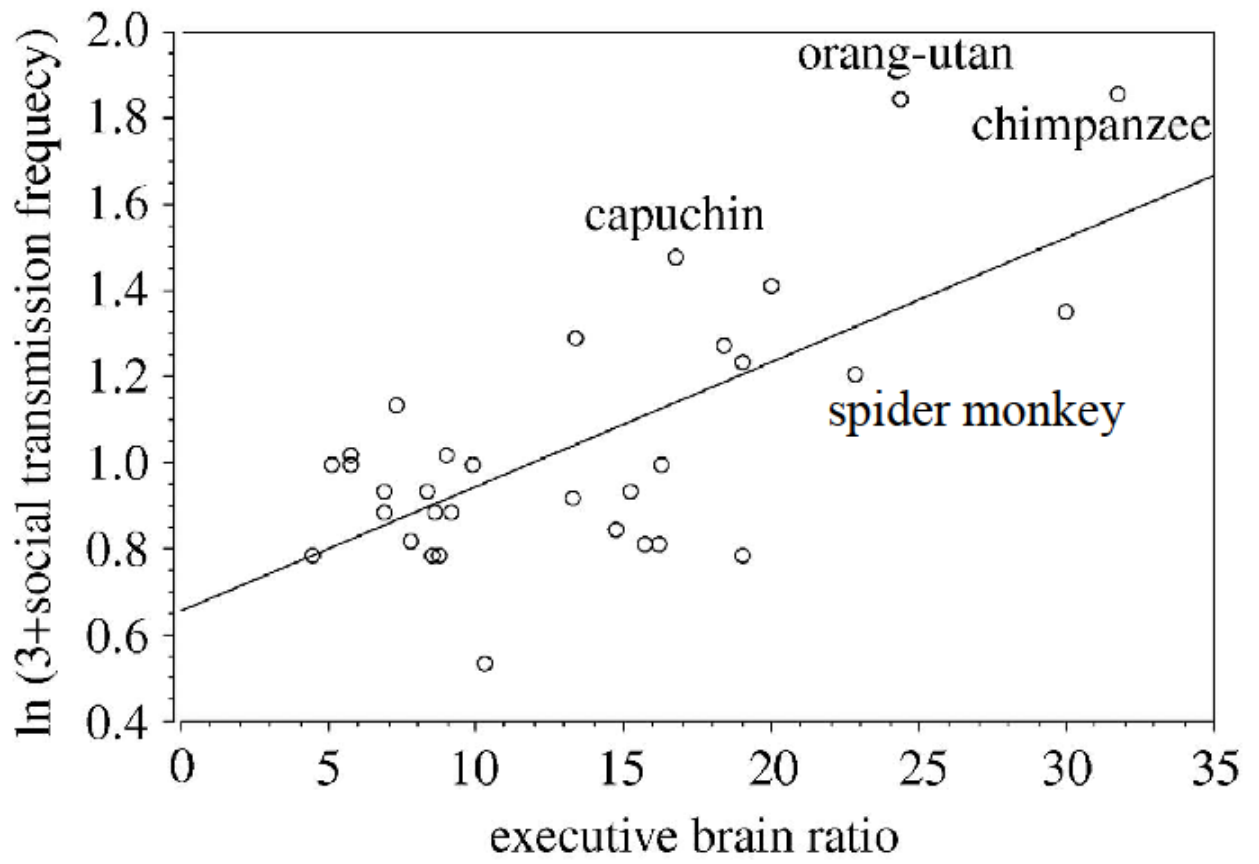
Primate diffusion studies 2010-2015 (n = 19) from within a set of 30 for all animal species listed in Whiten et al. 2016. * = field study of wild subjects (n = 8); 'group seeded' = open diffusion with trained model(s) seeded in group(s); 'chain' = diffusion chain. Effects are reported when statistically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



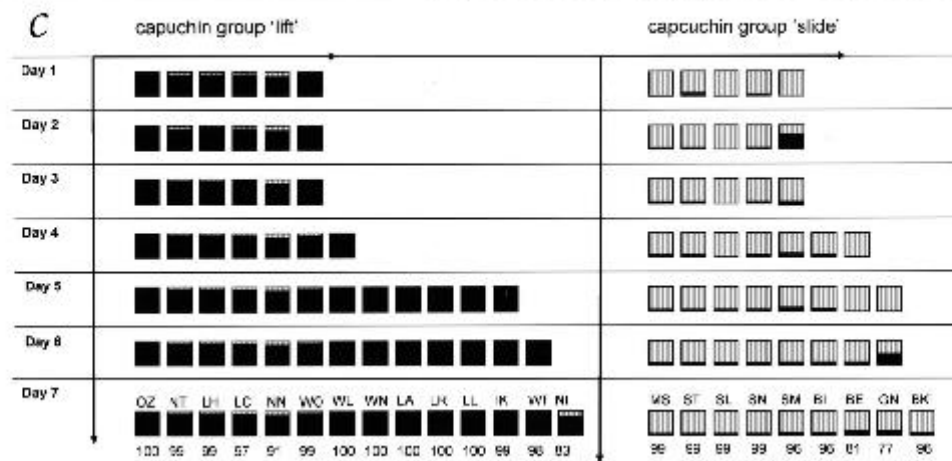
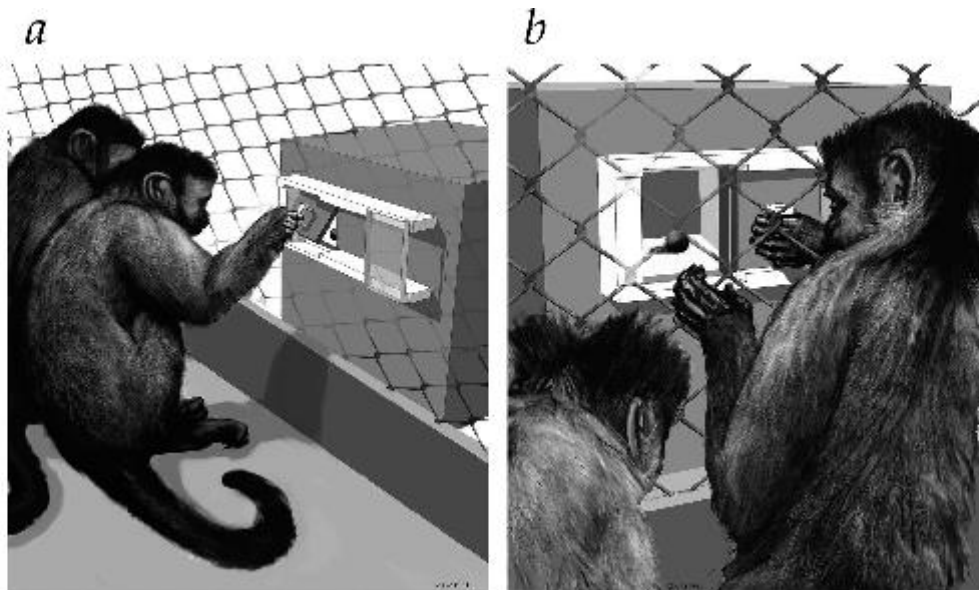
1654
1655

1656 Figure 1

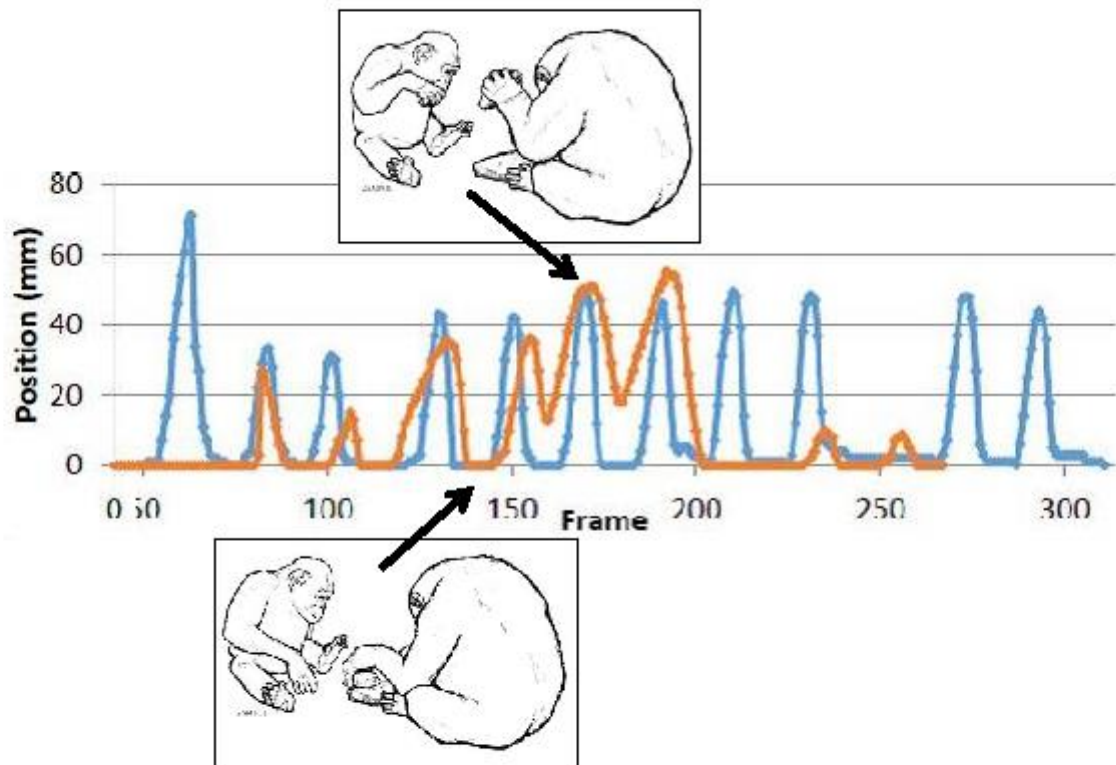
1657



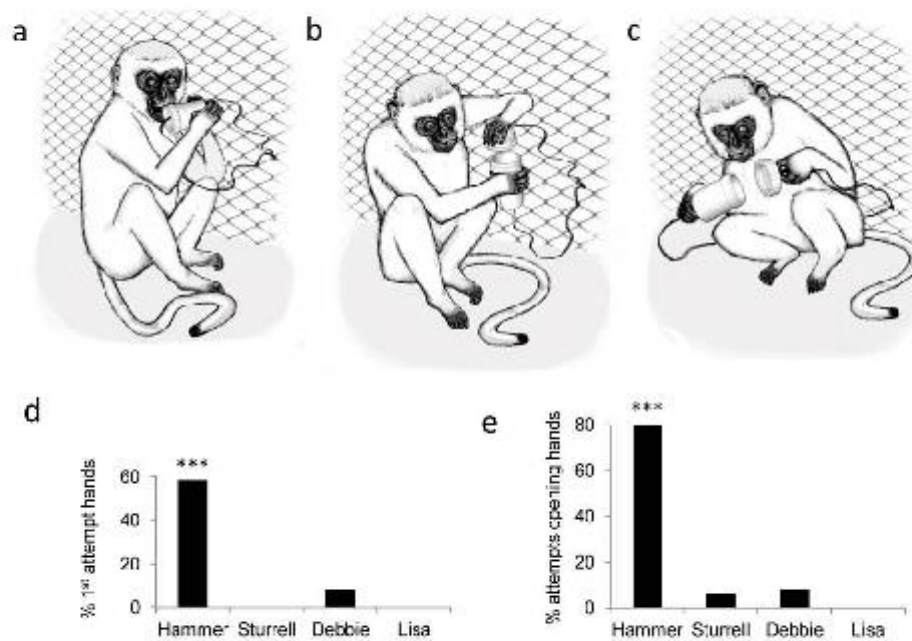
1658
1659 figure 2
1660



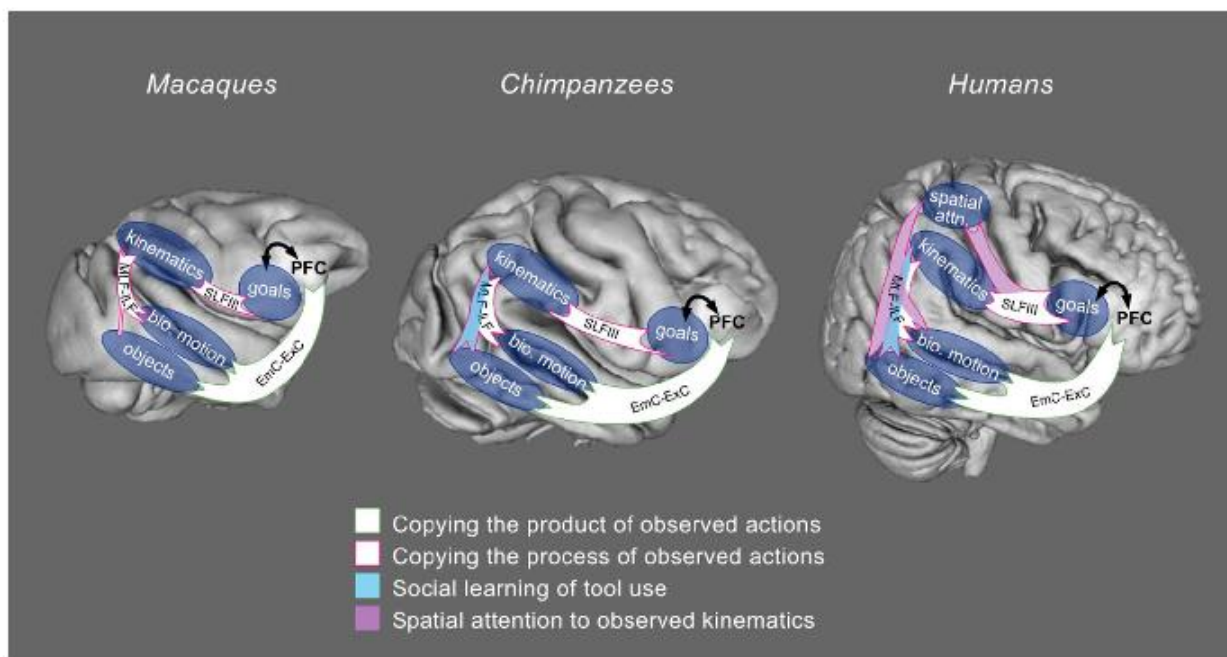
1661
1662 figure 3
1663



1664
1665 figure 4
1666



1667
1668 figure 5
1669



1670
1671 figure 6