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# The co-evolution of innovation and technical intelligence in primates

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# The co-evolution of innovation and technical intelligence in primates

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## Summary

In birds and primates the frequency of behavioural innovation has been shown to covary with absolute and relative brain size, leading to the suggestion that large brains allow animals to innovate, and/or that selection for innovativeness, together with social learning, may have driven brain enlargement. We examined the relationship between primate brain size and both technical (i.e. tool using) and non-technical innovation, deploying a combination of phylogenetically informed regression and exploratory causal graph analyses. Regression analyses revealed that absolute and relative brain size correlated positively with technical innovation, and exhibited consistently weaker, but still positive, relationships with non-technical innovation. These findings mirror similar results in birds. Our exploratory causal graph analyses suggested that technical innovation shares strong direct relationships with brain size, body size, social learning rate and social group size, while non-technical innovation did not exhibit a direct relationship with brain size. Nonetheless, non-technical innovation was linked to brain size indirectly via diet and life-history variables. Our findings support 'technical intelligence' hypotheses in linking technical innovation to encephalization, in the restricted set of primate lineages where technical innovation has been reported. Our findings also provide support for a broad co-evolving complex of brain, behaviour, life history, social and dietary variables, providing secondary support for social and ecological intelligence hypotheses. The ability to gain access to difficult-to-extract, but potentially nutrient-rich, resources through tool use may have conferred on some primates adaptive advantages, leading to selection for brain circuitry that underlies technical proficiency.

## 1. Introduction

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The extraordinary ecological and demographic success of humanity is commonly linked to our capacity for innovation. We humans would appear to possess an unprecedented capability to devise novel solutions to life's challenges, to express these solutions in our behaviour, tools and technology, and to propagate innovation through social learning. Our engineering and technology have allowed us to inhabit even the most hostile environments. Genetic studies suggest that this capability is longstanding, with hundreds, possibly thousands, of human genes subject to positive selection over the last 100kyr, with a primary hypothesis for why many of these alleles spread being adaptive responses to human learning and cultural activities [1-3]. For instance, the domestication of plants and animals and associated consumption of novel foods seemingly selected for alleles expressed in human digestion, as well as in resistance to animal-borne diseases [1-3].

While humans may be exceptional innovators, we are far from the only species that devises novel behaviour patterns. Recent research reveals that many animals will invent new behaviours or modify existing behaviours (e.g. devise more efficient foraging techniques), that such innovation is taxonomically widespread, and that there is considerable inter- and intra-specific variation in innovation rates [4]. Innovation has been hypothesized to be an important influence on the success and evolution of many nonhuman animals, particularly in populations faced with novel challenges such as anthropogenic change [4-6]. Evidence from comparative and experimental studies supports this contention. For example, comparative studies of birds have linked rates of behavioural innovation with range expansion [7-9], with rates of evolutionary diversification [10, 11], and with dietary and habitat generalism [12, 13]. Experimental studies have associated novel problem solving with fitness components such as mating success and offspring survival [14-16].

These observations raise a number of questions: How did the ability to innovate evolve? How are the aforementioned relationships between innovation and variables such as invasion success, fitness, and speciosity causally related? What neurocognitive processes underpin innovation? And to what extent can innovation be treated as a unitary phenomenon [4]? Might it, for instance, make better sense to subdivide innovation into different categories, perhaps controlled by different neurocognitive processes, or to recognize that different aspects of innovation may have quite distinctive evolutionary histories and taxonomic distributions?

To date, both theoretical arguments and empirical evidence have supported the idea that innovation will be largely the product of domain-general cognitive abilities [4, 17, 18]. For example, comparative analysis of observational reports of innovation across primate species reveal that innovation rate covaries together with other observational measures thought to indicate general cognitive ability, such as rates of social learning, tool use, and tactical deception [18, 19], as well as with experimental tests of learning and problem-solving [20-22]. Similarly, experimentally induced and other novel behaviour in corvids (e.g. [23, 24]) supports the idea that innovations appear when existing, domain-general abilities are applied to a novel problem. However, there is some evidence that innovation may carry specific costs, such as exposure to environmentally-transmitted parasites [19]. Behaviour patterns described as innovations encompass a huge range of behaviour, likely involving multiple psychological processes [25; 26]. A potentially useful approach is to subdivide innovation into different categories and to examine to what extent the same processes predict these different categories of innovation.

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72        Here, we present comparative analyses based on an observational database of primate innovation
73 used in several previous studies (e.g. [18-21, 27, 28]). Innovation rates for different primate species are
74 estimated by surveying published literature for reports of innovation, an approach pioneered in studies of
75 foraging innovation in birds [22, 28-31]. The major advantage of this approach is that it provides quantitative
76 data on a large number of species, circumventing the longstanding challenge of designing experimental tests
77 that are fair to all species [18, 25, 32]. Multiple potentially confounding variables have been examined, with
78 little support for the method being subject to persistent or sizable biases over-and-above those that are readily
79 controlled for (e.g. research effort) [22]. The fact that similar patterns have been uncovered in both birds and
80 primates [22], and between this quantitative measure of innovativeness and performance in experimental tests
81 [18], enhances the validity of the approach. The method, interpreted appropriately, thus provides a useful
82 broad-scale complement to the in-depth data that can be obtained by experimental or observational study of
83 one or a few species [18, 20, 25, 33].

84        A long-held assumption is that innovation is a marker of intelligence, and more extensive or complex
85 innovation is thought to be facilitated by brain enlargement, particularly expansion of forebrain regions such
86 as the primate prefrontal cortex that are linked to creativity and problem solving [34]. Innovation has long
87 been proposed as a driver of brain evolution [5, 20, 35]. Examination of the links between innovation and brain
88 evolution provide a first step into understanding the neural underpinnings of innovation, and whether neural
89 changes accompany enhanced innovative propensities. Above we raised the question as to whether it would
90 be informative to divide innovation into different subcategories, potentially controlled by different
91 neurocognitive processes and driven by different selection pressures. One observation that prompts this
92 question is a recent analysis of avian foraging innovation [36], which divided foraging innovations into
93 'technical' innovations and 'food-type' innovations. Overington *et al.* [36] characterised 'technical' innovations
94 as those involving novel foraging techniques, such as innovative predatory techniques, commensal foraging,
95 tool use, and extractive foraging, and hence might be regarded as exerting some additional demands on the
96 cognitive capabilities of the animal associated with the extraction and exploitation of the novel resource.
97 Conversely, in birds, non-technical innovations are those where a novel food source is exploited without the
98 use of any novel technique ('food type' innovations), typically deploying established feeding methods that
99 seemingly exert few additional cognitive demands on the innovator over-and-above the recognition of the
100 novel resource as food. While both technical and food-type innovations covaried with brain size, Overington
101 *et al.* found that technical innovations exhibited a far stronger relationship with brain size, and explained a
102 greater proportion of variance in residual brain size than food-type innovations. These authors suggested that
103 the ability to extract valuable resources through novel technical foraging skills may require more advanced
104 cognition than merely introducing novel food items into their diet, and argued that technical innovation may
105 have driven brain evolution through selection for the neural underpinnings of technical proficiency. Thus
106 Overington *et al.'s* results were interpreted as supporting a technical intelligence hypothesis, suggesting that
107 increased brain size allows individuals to use innovation to modify their technical skills.

108        Here we explore the generality and robustness of Overington *et al.'s* [36] conclusions by investigating
109 whether similar relationships between innovation and brain evolution are observed in nonhuman primates.

110    We take a broadly similar approach by subdividing our primate innovation dataset into technical innovations

111    and non-technical innovations. We focus particularly on innovations that require tool use as this is a core

112    element of technical intelligence hypotheses [37], one of several hypotheses put forward to explain the

113    evolution of enhanced cognition and brain enlargement [20, 38-41]. In a second set of analyses, we examine a

114    broader definition of technical innovation, including both innovative tool use and innovative extractive

115    foraging, reflecting arguments that extractive foraging played a role in primate cognitive evolution [42, 43].

116         Our analyses examine the relationship between technical innovation, non-technical innovation, and

117    both absolute and relative brain size, as well as several factors that have been shown to covary with brain size

118    and/or innovation rate, including body size, life history variables, social group size, diet breadth and rates of

119    social learning. While there is potential utility in examining individual brain components and their relation to

120    behavioural innovation, currently insufficient data are available when innovation is sub-divided. Moreover,

121    recent work on the co-evolution of different brain areas suggests that many components change in volume

122    together as a network [44, 45]. This suggests that a focus on large brain areas or the entire brain may be

123    appropriate, particularly for broad categories of behaviour such as innovation that are plausibly reliant on

124    domain-general capabilities, and involve many cognitive and other processes and many parts of the brain.

125         Our objectives are twofold: (*i*) to determine the extent to which different classes of innovation covary

126    with brain size in primates, and (*ii*) to examine how technical and non-technical innovation co-evolve with

127    other behavioural and socioecological traits. We address these objectives deploying a powerful combination of

128    comparative phylogenetic analyses [46], phylogenetically-informed causal graphs [47] and non-linear

129    statistical approaches, to examine potential evolutionary drivers and infer causal relations. We conduct

130    analyses on datasets including all primate innovations recorded and also, to facilitate more precise

131    comparison with Overington *et al.* [36], who examined foraging innovation, on datasets limited to foraging

132    behaviour. The analyses shed new light on how and why innovative propensities evolved.

133

## 2. Methods

135
136    *2.1. Brain data*

137    Species means for brain size and body mass were obtained from Isler *et al.* [48]. Isler *et al.* compiled

138    endocranial volumes for 3813 museum specimens, at least 88% wild-caught, for 167 primate species.

139    Endocranial volume (ECV) provides a good estimate of brain volume which is easily convertible into brain

140    mass [49]. We complemented the dataset with body mass and brain mass for four additional species: *Callicebus*

141    *moloch*, *Cercopithecus talapoin* (from [50]), *Saguinus imperator* and *Callithrix geoffroyi* (from [51]). Brain mass in

142    these species was converted into ECV [49] before being added to the dataset. Endocranial volume (ECV) and

143    body mass were natural log-transformed prior to analysis to normalise distributions. Below we refer to ECV

144    as 'brain size' and to body mass as 'body size'.

145

146    *2.2. Behavioural data*

147    Behavioural data were drawn from Reader *et al.* [18]. Reader *et al.* surveyed over 4000 published articles for

148    examples of innovation, social learning, tool use, and extractive foraging in living non-human primates, using

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149 keywords (e.g. 'novel' or 'traditional') to classify behaviour patterns (e.g. as 'innovation' or 'social learning').

150 Full details of the database and discussion of its merits, disadvantages, reliability and validity are given in

151 Reader *et al.* [18] and the papers cited therein. The observation frequencies for each of the four behavioural

152 measures were calculated as the total number of reported examples of each class. Initially, we examined each

153 innovation report and categorized it as a 'technical' innovation (involving tool use) or a 'non-technical'

154 innovation (not involving tool use; data will be archived online in the Dryad depository). We go on to conduct

155 further analyses in which 'technical innovation' is broadened to include both innovative tool use and

156 innovative extractive foraging. We also restricted a subset of analyses to foraging innovations only (strictly,

157 innovations that occur in a foraging context), deploying the classification in Reader & Laland [27]. We used

158 the number of published articles on each species in the *Zoological Record* (taken from [18]) as a measure of

159 research effort. We corrected the behavioural measures for differences in research effort by including research

160 effort as an independent variable in statistical analyses [52].

161

162 *2.3. Diet breadth, life history and social group size*

163 Data on diet breadth (the number of food types typically eaten, out of a maximum of 13 different categories)

164 were obtained from Reader *et al.* [18]. Social group size and six life-history variables (gestation length,

165 interbirth interval, weaning age, age of sexual maturity, age at first birth and maximum longevity) were

166 extracted from the PanTheria dataset for the 167 species with brain data, with these measures available and

167 complete for 71 species [53]. In pairwise PGLS analyses, the six life-history variables were found to be

168 significantly positively correlated (p<0.05). In order to extract a single dimension of life-history to use later as

169 a predictor in an exploratory analysis of causality, these six variables were natural log-transformed and used

170 to create a composite 'life-history' variable using phylogenetically controlled principal components analysis

171 (PPCA; [54]). The PPCA extracted a single component, which explained 78% of the variance in the data, and

172 all variables loaded positivity on this component, with loadings from 0.58 to 0.90 ($\lambda$= 0.84). This composite

173 life-history variable was used in subsequent analyses. Social group size was natural log-transformed for

174 normalization. Diet breadth did not require transformation.

175

176 *2.4. Phylogeny*

177 For the phylogenetic analyses, we used the 10k Trees project dated consensus tree (version 3) [55], and

178 matched primate species from the brain dataset and the behavioural dataset with species in the tree, taking

179 into consideration changes in nomenclature (ESM).

180

181 *2.5. Data analyses*

182 A total of 167 primate species were represented in the phylogenetic tree and had published brain and

183 innovation data (strepsirrhines: 39 species, tarsids: 3 species, platyrrhines: 49 species, catarrhines: 76 species).

184 Data on life history, social group size and diet breadth were only available for 71 species in the innovation and

185 brain dataset (19 strepsirrhines, 1 tarsid, 21 platyrrhines and 30 catarrhines), and thus analyses involving these

186 variables were restricted to these 71 species. A substantial number of the 167 species had no recorded

187  innovations. The fact that a species has zero recorded innovations when this is unexpected for a given research

188  effort may be informative, but it is also possible that species with no innovation reports have been studied

189  differently to those with innovation reports [25]. Thus, we also conducted analyses excluding those species

190  with zero innovation reports in our database. This "innovators" sample covered 48 species with available

191  brain data.

192      To account for non-independence of species-level data, we used phylogenetic generalized least square

193  regressions (PGLS), with phylogenetic signal (Pagel's λ) estimated by maximum likelihood (henceforth

194  λ=ML). Analyses were run in R version 3.0.2 [56] using the "caper" [57] and "phytools" packages [58]. Models

195  explored the relationship between brain size and innovation, treating innovation rates as response variables,

196  and including research effort as a covariate. Analyses that examined the relationship between relative brain

197  size and innovation included body mass. We also ran analyses examining absolute brain size, without body

198  mass as a covariate, to allow comparison of absolute versus relative brain measures of brain size as predictors

199  of cognitive differences, an open question in the field [21].

200      We ran additional analyses (ESM) to take into account the fact that a large number of species in our

201  database had zero recorded innovations. We ran a binomial regression predicting the probability that an

202  innovation is observed in each paper based on research effort (conducted using the method "glm" in R [56]).

203  We also present the results of using a zero-inflated Poisson (ZIP) model, which provides an alternative

204  method for controlling for the large number of species with zero recorded innovations [59]. However, the ZIP

205  model may not be suitable when there are a small number of observations for some entries (over 58% of the

206  species had under 20 papers recorded in the *Zoological Record* survey), meaning that the results of these models

207  should be interpreted with caution. Both the binomial model and the zero-inflated Poisson models also help

208  control for the observed heteroscedasticity in the data (if the number of observations for a species is large, we

209  should expect greater absolute variance in the number of reported innovations). However, binomial and ZIP

210  models that incorporate phylogenetic information are not well-established methodologies. Thus we used non-

211  phylogenetic methods for these analyses.

212      Exploratory causal graphs were used to further examine interrelationships between variables. Causal

213  graphs were generated by examining the phylogenetic partial correlation between variables, taking into

214  account the remaining variables (using PGLS). For a set of variables A = {$A_1$,…,$A_n$}, this method assesses the

215  relationship between $A_i$ and $A_j$, by examining the correlation between the residuals of a phylogenetic linear

216  model of Ai predicted by the remaining variables (i.e. $A_k$ for all *k* except for $A_i$ and $A_j$) and $A_j$ predicted by the

217  remaining variables. In order to guard against the premature rejection of causal relations between variables

218  we take the conservative stance of treating the correlation as potentially significant if p<0.1, in which case an

219  edge between $A_i$ and $A_j$ is added to the causal graph. This method allows us to visualize the significant

220  relationships between variables when taking into account the presence of other variables, similar to other path

221  analysis methods [47, 60]. Edges were not oriented (i.e. directed) as we reasoned that biological evolution in

222  this domain frequently encompasses feedback processes between traits [18, 61].

223      Although this method uses the full set of covariates (all $A_k$) to assess independence, which may

224  reduce statistical power, we find that the results of this procedure are the same as a more complex algorithm

225   (Whalen *et al.*, in preparation) which uses only connected variables. Our new method can be seen as an
226   exploratory automation of von Hardenberg and González-Voyer [62], building on Pearl's PC algorithm [63].
227   For PGLS models within a given causal graph, λ is estimated by maximum likelihood, in order to account for
228   differing levels of phylogenetic signal across each linear model. . However, given that previous approaches
229   have assumed a fixed common value for λ for all paths [62], we also analyse graphs with λ fixed at 0 or 1,
230   which represent the extreme values of λ, and thereby provide a strong check as to whether our conclusions are
231   robust to different values of phylogenetic signal. The values on the edge of each graph represent the p-value,
232   i.e. the significance of the relationship between variables when taking into account the influence of only
233   connected variables.

234

## 235   3. Results

236
237   Where technical innovation was restricted to tool use, of the 584 reports of innovation, 45% were classified as
238   technical innovations and 55% as non-technical innovations (Figure 1). In the broader categorization of
239   technical innovation that included novel extractive-foraging behaviour patterns, 60% were classified as
240   technical innovations and 40% as non-technical innovations.

241

242   *3.1. Comparative phylogenetic analyses for all species*
243   Total innovation rate (i.e., technical and non-technical combined) was found to be positively correlated with
244   absolute but not relative brain size in primates (Table 1). That is, there was a significant positive correlation
245   between innovation rate and brain volume, but this relationship was no longer significant when body mass
246   was taken into account.

247          Technical (i.e. involving tool use) and non-technical innovation rates correlated positively with each
248   other (PGLS: λ=0, r=0.61, β=0.49±0.09, p<0.0001). A similar correlation was observed using a broader
249   classification of technical innovation, including innovative extractive foraging (PGLS: λ=0.06, r=0.53,
250   β=0.44±0.10, p<0.0001). However, despite this positive correlation, different relationships were observed
251   between brain size and technical versus non-technical innovation rates. Technical innovation rate was
252   significantly correlated with absolute but not relative brain size, and we observed a stronger relationship with
253   brain size than that observed for total innovation rate. Similar results were found for technical innovation
254   including extractive foraging (Table 1). In contrast, non-technical innovation rate was not significantly
255   correlated with either absolute brain size or relative brain size (Table 1). The model including brain size as a
256   predictor of technical innovation, with research effort as a covariate, showed a higher correlation coefficient
257   (r=0.13) than the model predicting non-technical innovation (r=0.07), with a similar pattern observed using the
258   broader classification of technical innovation including extractive foraging (r=0.14 vs r=0.08).

259

260   *3.2. Controlling for zero-inflation*
261   To address the concern that our PGLS results were biased by the large number of primate species with no
262   innovations (zero inflation), we conducted ZIP and binomial analyses. ZIP models on our 167-species sample
263   confirmed that zero scores on all measures of innovation were more likely in those species where research

264    effort was low (Table S1). We found that the number of innovations observed correlated significantly with

265    research effort, body mass, and relative brain size using all innovation classifications. In contrast, absolute

266    brain size correlated with only two innovation measures, total innovation rate and technical innovation

267    including extractive foraging. Technical innovation was more strongly related to brain size than was non-

268    technical innovation, using both absolute and relative brain size measures and for all classifications of

269    technical innovation (see Block A in Table S1). Comparison of AIC values between models with and without

270    body size found better support for models that included body size (i.e., relative brain size models).

271         We also ran a set of analyses using a binomial model, which predicted the likelihood that a given

272    paper in the data set contained an innovation. Binomial models for all species showed that all innovation rates

273    (including total innovations, technical innovations and non-technical innovations) exhibited strong positive

274    correlations with both absolute and relative brain size (p<0.0001, Table S2). Technical innovation was more

275    strongly related to both absolute and relative brain size than was non-technical innovation. These results are

276    consistent with the results of the ZIP model, and again, comparison of AIC values between models with and

277    without body size found better support for models that included body size.

278

279    *3.3 Innovators only analyses*

280    Confirmation of zero inflation in the full species dataset provides further justification for repeating the

281    analysis using the reduced dataset of innovators (see Table 1). Amongst our sample of innovators (48 species),

282    we found strong correlations between total innovation rate and both absolute and relative brain size.

283    Technical innovation also exhibited strong correlations with both absolute and relative brain size, and these

284    relationships were stronger than those for total innovations. Non-technical innovation correlated significantly

285    with absolute brain size only, and this correlation was weaker than the one observed between technical

286    innovations and absolute brain size. Brain size was a better predictor of technical innovation than a predictor

287    of non-technical innovation (technical innovation: r=0.14; non-technical innovation: r=0.10; technical

288    innovation with extractive foraging: r=0.26, non-technical innovation without extractive foraging: r=0.05).

289    Using the binomial models, we again observed strong and significant correlations between all innovation rates

290    and absolute and relative brain size (see Table S2), and stronger relationships were observed between

291    technical innovation rates and brain size measures than between non-technical innovation rates and brain size.

292

293    *3.4 Comparisons with Overington et al.: Foraging innovations*

294    To facilitate a closer comparison with Overington *et al.* [36], extractive foraging innovations were included in

295    technical innovation, and PGLS analyses were restricted to foraging innovations only. This reduced the

296    available pool of innovations considerably, and because of the aforementioned problems with zero-innovation

297    scores, the 167-species analysis was not appropriate. In the innovators only sample, technical innovation

298    correlated significantly with both absolute and relative brain size, but non-technical innovation did not

299    correlate with either (Table 1). In the ZIP and binomial models, technical innovation was again more strongly

300    correlated with brain size measures than was non-technical innovation (Tables S1, S2).

301

302    *3.5 Causal graphs*

303    We constructed three phylogenetically informed causal graphs, using total innovations, technical innovations

304    and non-technical innovations. In all sets of causal graphs, the findings for total innovations resemble those

305    for non-technical innovations, and can be contrasted with those for technical innovation. Also, in all of our

306    analyses, brain size, body size, the life-history composite measure and social group size shared multiple direct

307    connections ("edges") with each other, suggesting that these variables have evolved together (Figure 2).

308    Technical innovation rate shared direct edges with brain size in the best-supported graphs (λ=ML:

309    p=0.043, Fig. 2a; λ=0: p=0.014, λ=1: p=0.009, see Fig. S1), which indicates that these two variables are directly

310    correlated even when the other variables are taken into account. Technical innovation rate also was directly

311    related to social learning rate (p<0.0001), body size (p=0.039) and social group size (p<0.0001). PGLS analyses

312    showed that these associations were all positive (brain size: λ=0.84, r=0.27, p=0.014; body size: λ=0.85, r=0.20,

313    p=0.050; social learning: λ=0, r=0.77, p<0.0001; Table S3). However, the relationship between technical

314    innovation and social group size was not statistically significant in the PGLS model (λ=0.91, r=0.02, p=0.88).

315    These edges are also strong when λ was set to 0 or 1 (λ=0: social learning rate: p<0.0001, body size: p=0.041,

316    social group size: p<0.0001; λ=1: social learning rate: p<0.0001, body size: p=0.007, social group size: p<0.0001,

317    see Figure S1a).

318    Non-technical innovation shared a direct edge with social learning rate alone (λ=ML: p<0.0001, Fig.

319    2b; λ=0: p<0.0001, λ=1: p<0.0001, Fig. S1b). PGLS analysis showed that the correlation between these two

320    variables was positive (λ=0, r=0.66, p<0.0001). Any relationships between non-technical innovation rates with

321    other variables in the graph, including brain size, were mediated by social learning and diet breadth.

322    Technical innovation rate including extractive foraging shared direct edges with social learning rate

323    (p<0.0001), and social group size (p=0.020) in the graphs with λ=ML (Fig. 2c), as well as in the graphs with λ=0

324    and λ=1 (Fig. S1c), but the direct relationship with brain size was lost (p>0.1). PGLS analyses showed that the

325    correlation of this measure of technical innovation with social learning was positive (λ=0, r=0.76, p<0.0001),

326    but the relationship with social group size was not significant (λ=0.728, r=0.11, p=0.17).

327

328    ## 4. Discussion

329    The innovativeness of a species, defined as the frequency with which novel behaviour patterns are generated

330    (controlling for research effort) covaries with diverse measures of absolute and relative brain size in both birds

331    and primates [18, 22]. In birds, brain size covaries more strongly with technical than with non-technical

332    innovation [36], suggesting a potentially important distinction between these types of novel behaviour. Our

333    findings in nonhuman primates were broadly consistent with those of Overington *et al.* [36]. Phylogenetic

334    analyses comprising all primate innovations found that absolute (but not relative) brain size correlated

335    positively and strongly with both technical innovation and total innovations but showed a non-significant

336    relationship with non-technical innovation. However, PGLS analyses do not account for the zero-inflated

337    distribution of innovation counts across species. When this is controlled for, either by deploying zero-inflated

338    Poisson or binomial models, or by reducing the sample to 'innovator' species, we find that total innovation

339    measures covary significantly with absolute and relative brain size, and that technical innovation always

340    exhibits a stronger relationship with brain size than non-technical innovation.

341      Exploratory causal graph analyses painted a similar picture, where technical innovation shared a
342  direct edge with brain size (Fig. 2a), whilst the number of non-technical innovations did not. Rather, non-
343  technical innovation was linked to brain size via social learning, diet and life-history variables (Fig. 2b).
344  Technical innovation also shared very strong direct edges with social learning, body size and social group
345  size. However, when we add extractive foraging to technical innovation the direct relationship with brain size
346  was lost (Fig. 2c). This implies that tool use, more so than extractive foraging, may be the relevant factor
347  underlying the direct relationship between technical innovation and brain size.

348      This direct connection between technical innovation and brain size provides support for 'technical
349  intelligence' hypotheses (e.g. [37]) in suggesting that in some primate lineages the ability to invent novel
350  technical behaviours, specifically those involving tools, may have favoured encephalization, more than the
351  ability to generate novel behaviours per se. Overington *et al.* [36] restrict their analyses to foraging innovations
352  alone, and used a somewhat broader definition of technical innovations, with technical innovations referring
353  to novel foraging techniques, not just tool use. Our analyses tell a similar story to those of Overington *et al*. As
354  in birds, the ability to gain access to difficult-to-extract, but potentially nutrient-rich, resources through tool
355  use and technical skill may have conferred adaptive advantages, leading to selection for brain regions and
356  circuitry that underlie technical flexibility and proficiency in some primate lineages. This pattern holds when
357  our PGLS analyses were restricted to foraging innovations.

358      We also observed strong connections in causal graph analyses between primate technical innovation
359  and both social learning and social group size (although the group size-technical innovation link was not
360  significant in a PGLS analysis), suggesting co-evolution of elements of social, technical and ecological
361  intelligence, as has been previously argued (e.g. [64]). Those primates that score highly for innovation and tool
362  use (e.g. the great apes, capuchins, macaques) are also renowned for their social learning [18, 64], and there is
363  now extensive experimental evidence demonstrating that primates can acquire many tool using methods
364  through social learning [61]. Indeed, a robust finding of both our causal graph analyses and our previous
365  work [18, 19] is that innovation and social learning evolve together, a conclusion that holds here for both
366  technical and non-technical innovation.

367      The direct connections between technical innovation and social group size, as well as between social
368  learning and social group size, conflict with previous analyses that found no relation between social group
369  size and total innovation rate or social learning rate [18, 65]. This could reflect the effect of examining technical
370  innovations alone, additional power in the current analyses or sample, or the effect of the additional variables
371  incorporated in the present analyses. Theoretical work, however, suggests that the observed relationships of
372  group size with reported technical innovation rates may be no artefact. A wide variety of theoretical studies
373  now link the size of cultural repertoires with social group size, as larger populations provide a more stable
374  repository for the retention of innovations than do smaller groups, as well as more potential innovators [66-
375  69]. These links between technical innovation and both social learning incidence and social group size are, of
376  course, consistent with several social intelligence hypotheses [20, 38-41], which supports the suggestion that
377  these explanations are not mutually exclusive [18, 66]. The consistently observed edge in our path analyses

378 linking social group size and brain size supports the established finding that social intelligence is an important

379 driver of brain evolution [20, 38-41].

380  Our causal graph analyses linked non-technical innovation to measures of diet breadth via social

381 learning, a finding that evokes ecological intelligence explanations, in which primate intelligence is favoured

382 by the challenge of locating and extracting diverse and constantly changing foods (e.g. [42, 43, 71, 72]).

383 However, as Overington *et al.* [36] reported for birds, while larger-brained, innovative primate species may be

384 more likely to incorporate novel foods into their diets, and while this ability may be ecologically important,

385 our findings imply that the relationship between innovativeness and brain size in primates is more likely to be

386 primarily driven by technical innovations.

387  Although the absence of an edge between non-technical innovation and brain size in the best-

388 supported causal graph ostensibly rules out a direct coevolutionary relationship between these variables, it

389 does not preclude a more diffuse coevolutionary interaction. What the causal graph analysis implies is that if

390 there is a causal influence of non-technical innovation on brain evolution it occurs through changes in social

391 learning, diet and life-history. One plausible interpretation of these findings is that through social

392 transmission many primates learn to exploit novel foods, and the resources so gleaned both aid survival and

393 fuel brain growth. Cultural drive explanations [5, 20, 35, 41, 73] are relevant here, as they propose that

394 selection for innovativeness and/or efficient social learning drove the evolution of encephalization in

395 primates. However, given that most primate species in our sample exhibited zero innovations, we emphasize

396 that any causal role for innovation, be it technical or non-technical, in driving encephalization is likely to be,

397 only part of the story, and restricted to a subset of primate lineages.

398  We emphasize that our causal graph analyses merely establish significant direct versus diffuse

399 coevolutionary relationships between variables, and we explicitly avoid attempting to infer the directionality

400 of edges. We adopt this conservative stance as we anticipate that feedback between coevolving traits is highly

401 likely, indeed at least as likely as the unidirectional evolution of one trait in response to changes in the other.

402 Hence, while our analyses are consistent with the interpretations that in some primate lineages (i) technical

403 innovation drove brain enlargement, or (ii) that large brains (which evolved for reasons unconnected to

404 innovation) are facultatively expressed in innovative behaviour, we suggest (iii) that technical innovation and

405 brain size coevolved in certain taxa, with each driving enhancements in the other. In addition, while it is likely

406 that technical innovation is more cognitively complex than non-technical innovation, a suggestion that our

407 findings may appear to support, there are reasons to be cautious in drawing this conclusion as technical

408 innovations may differ from other innovations in ways other than tool use.

409  Given the fact that both brains and innovations can perform many functions, a complete analysis

410 would require numerous interacting variables to be investigated. Moreover, it remains an open question as to

411 whether innovation is a driving causal factor in our evolutionary analyses, or whether the innovations

412 observed in our survey are simply the by-products of broader psychological processes. Reports of technical

413 innovation are relatively sparsely distributed across the primates, and close relatives often differ considerably

414 in innovation rates. This could reflect the difficulty in gathering a comprehensive sample of primate

415 innovation, but also points to technical innovation being just a part of a larger story. Even focused on the

416 restricted set of variables considered in our analyses, the emergent picture is one in which there are multiple

417 drivers of the evolution of the primate brain and intelligence that feed back on each other in complex,

418 nonlinear ways. It would seem that innovativeness in primates, like intelligence and cognition more generally,

419 is not to be explained by a single prime mover, but rather by a complex of factors that encompass technical,

420 social and ecological intelligence.

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423 # Additional Information

428 **Data Accessibility**

429 The datasets supporting this article have been uploaded as part of the Supplementary Material and will be available via

430 the Dryad depositary.

431

432 **Authors' Contributions**

433 AN and SMR compiled the data; AN. AW and SES analysed the data; AN, SMR and KNL took the lead in writing the

434 article, with contributions from AW and SES. All authors gave final approval for publication.

435

436 **Competing Interests**

437 We have no competing interests.

438

441

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# Figure and table captions

Table 1. PGLS analyses of the relationship between innovation rates as the outcome variable and brain size as a factor, controlling for an estimate of research effort on each species (number of publications in a survey of the Zoological Record). For each innovation rate measure we ran a model assessing the effect of relative brain size, by including body mass as a cofactor (top of each pair of rows), and absolute brain size, by not including body mass as a cofactor (lower of each pair of rows; body mass results are thus marked not applicable [NA] for these rows). All models were strongly significant (p<0.001). Significant relationships between innovation rate and body mass or brain size are in bold.

Figure 1. Number of reports of innovation, tool use and extractive foraging in our survey of non-human primates. Of the 584 reports of innovation (shaded), 264 or 45% were classified as 'technical innovation' (i.e. innovative tool use) and 320 or 55% were classified as 'non-technical innovation'. In a second set of analyses, we used a broader definition of technical innovation that included novel tool use and novel extractive foraging behaviour patterns. With this broader definition, 351 or 60% were classified as 'technical innovation' and 223 or 40% were classified as 'non-technical innovation'.

Figure 2. Best-supported graphs using phylogenetic exploratory path analyses including either (a) technical innovation rate, (b) non-technical innovation rate, or (c) technical innovation rate including extractive foraging [EF], together with social learning rate, brain size, body size, a life history composite measure, social group size and diet breadth. Edges, i.e. lines, between pairs of variables indicate significant correlations between these variables while taking their correlation with the other variables into account. P-values are indicated for those edges. Analyses of total innovation rate (i.e. technical and non-technical innovations combined) gives very a similar picture to Fig 2b. Dotted boxes indicate tightly covarying suites of variables

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# Tables

| | | Brain measure | Model | | Research Effort | | Body mass | | Brain size | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | λ | r | β | p | β | p | β | p |
| All (167 species) | Innovation | Relative | 0.58 | 0.55 | 0.33 | <0.0001 | -0.10 | 0.61 | 0.37 | 0.19 |
| | | Absolute | 0.58 | 0.56 | 0.33 | <0.0001 | NA | NA | 0.23 | **0.016** |
| | Technical innovation | Relative | 0.81 | 0.37 | 0.12 | 0.0002 | -0.09 | 0.60 | 0.36 | 0.12 |
| | | Absolute | 0.81 | 0.38 | 0.12 | 0.0002 | NA | NA | 0.25 | **0.005** |
| | Non-technical innovation | Relative | 0 | 0.58 | 0.30 | <0.0001 | -0.01 | 0.91 | 0.07 | 0.64 |
| | | Absolute | 0 | 0.58 | 0.30 | <0.0001 | NA | NA | 0.06 | 0.16 |
| | Technical innovation with extractive foraging | Relative | 0.71 | 0.52 | 0.24 | <0.0001 | 0.00 | 1.00 | 0.28 | 0.27 |
| | | Absolute | 0.71 | 0.52 | 0.24 | <0.0001 | NA | NA | 0.28 | **0.003** |
| | Non-technical innovation without extractive foraging | Relative | 0 | 0.50 | 0.22 | <0.0001 | -0.04 | 0.74 | 0.11 | 0.46 |
| | | Absolute | 0 | 0.51 | 0.22 | <0.0001 | NA | NA | 0.06 | 0.11 |
| Innovators (48 species) | Innovation | Relative | 0 | 0.79 | 0.58 | <0.0001 | -0.48 | 0.11 | 0.98 | **0.015** |
| | | Absolute | 0 | 0.78 | 0.56 | <0.0001 | NA | NA | 0.37 | **0.0002** |
| | Technical innovation | Relative | 0.31 | 0.73 | 0.54 | <0.0001 | -0.82 | **0.027** | 1.52 | **0.027** |
| | | Absolute | 0.33 | 0.70 | 0.49 | <0.0001 | NA | NA | 0.49 | **0.001** |
| | Non-technical innovation | Relative | 0 | 0.64 | 0.41 | 0.0001 | -0.17 | 0.59 | 0.45 | 0.26 |
| | | Absolute | 0 | 0.65 | 0.40 | 0.0001 | NA | NA | 0.24 | **0.012** |
| | Technical innovation with extractive foraging | Relative | 0.32 | 0.77 | 0.59 | <0.0001 | -0.60 | 0.08 | 1.28 | **0.006** |
| | | Absolute | 0.26 | 0.76 | 0.56 | <0.0001 | NA | NA | 0.51 | **0.0002** |
| | Non-technical innovation without extractive foraging | Relative | 0 | 0.53 | 0.34 | 0.004 | -0.35 | 0.32 | 0.69 | 0.14 |
| | | Absolute | 0 | 0.53 | 0.33 | 0.005 | NA | NA | 0.24 | **0.027** |
| | Foraging innovation | Relative | 0 | 0.72 | 0.29 | <0.0001 | -0.48 | 0.14 | 0.88 | **0.040** |
| | | Absolute | 0 | 0.69 | 0.29 | <0.0001 | NA | NA | 0.28 | **0.006** |
| | Technical foraging innovation with extractive foraging | Relative | 0.15 | 0.73 | 0.52 | <0.0001 | -0.68 | **0.041** | 1.23 | **0.006** |
| | | Absolute | 0 | 0.71 | 0.48 | <0.0001 | NA | NA | 0.31 | **0.003** |
| | Non-technical foraging innovation without extractive foraging | Relative | 0 | 0.45 | 0.27 | 0.004 | -0.13 | 0.63 | 0.27 | 0.46 |
| | | Absolute | 0 | 0.46 | 0.27 | 0.004 | NA | NA | 0.10 | 0.23 |

## Figures

Figures are provided in two PDF files (NavarreteFigure1.pdf, NavarreteFigure2.pdf).

## Supplementary material

The dataset to be uploaded to Dryad is included here for reference (NavarreteESM.xls). The electronic supplementary material (PDF file) details additional analyses (NavarreteESM2.pdf).

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