Research

The evolution of primate general and cultural intelligence

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There are consistent individual differences in human intelligence, attributable to a single 'general intelligence' factor, *g*. The evolutionary basis of *g* and its links to social learning and culture remain controversial. Conflicting hypotheses regard primate cognition as divided into specialized, independently evolving modules versus a single general process. To assess how processes underlying culture relate to one another and other cognitive capacities, we compiled ecologically relevant cognitive measures from multiple domains, namely reported incidences of behavioural innovation, social learning, tool use, extractive foraging and tactical deception, in 62 primate species. All exhibited strong positive associations in principal component and factor analyses, after statistically controlling for multiple potential confounds. This highly correlated composite of cognitive traits suggests social, technical and ecological abilities have coevolved in primates, indicative of an across-species general intelligence that includes elements of cultural intelligence. Our composite species-level measure of general intelligence, 'primate g_S', covaried with both brain volume and captive learning performance measures. Our findings question the independence of cognitive traits and do not support 'massive modularity' in primate cognition, nor an exclusively social model of primate intelligence. High general intelligence has independently evolved at least four times, with convergent evolution in capuchins, baboons, macaques and great apes.

Keywords: social learning; behavioural innovation; tool use; cognitive evolution;
brain evolution; culture

1. INTRODUCTION

Intelligence has been described as 'a very general mental ability that ... involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience' [1]. It has been suggested that social learning and culture are a cause as well as a consequence of enhanced human and primate intelligence [2–7].

In humans, performance on diverse tests of cognitive ability typically show positive correlations, with substantial variation accounted for by a single factor, termed general intelligence or '*g*'. *g* is composed of subfactors that represent more specific abilities, such as 'verbal comprehension' or 'working memory' [1,8–10]. Considerable controversy surrounds the meaning of *g*, particularly whether it can be linked to underlying factors, such as brain size, neural plasticity or processing speed [9–11]. Unfortunately, IQ-test-based approaches are not appropriate for other animals, and understanding of the evolutionary origins

of human intelligence and of the relationship between intelligence and culture remains limited.

In primates, numerous hypotheses address the evolution of intelligence, typically based on correlates of increased brain volume, assumed to covary with cognitive capacity (e.g. [12–16]). 'Ecological intelligence' hypotheses suggest that foraging challenges (e.g. 'extractive foraging' or 'cognitive mapping') drove cognitive evolution, while 'social intelligence' hypotheses postulate a connection between the complex social lives of primates and their large brains and advanced cognition [12–14]. Several researchers have envisaged a key role for social learning, one aspect of social intelligence, in driving the evolution of intelligence [3–7]. Wilson [4] suggested that through social learning, individuals expose themselves to novel environmental conditions and experiences, thereby increasing the rate of genetic change, and also driving brain expansion. Boyd & Richerson [5] view human cognition as having evolved to be specifically adapted to the acquisition of cultural knowledge, a view now termed the 'cultural intelligence' hypothesis and supported by comparative analysis [2]. Similar claims are made by several authors [3,6,7]. For example, a related cultural intelligence hypothesis argues that evolved changes in the reliance on social learning favoured the evolution of

Table 1. Principal components analysis (PCA) on five primate cognitive measures extracts a single dominant component. PCA used a roots > 1 extraction criterion. $n = 62$, d.f. $= 14$, g_{S1} variance contribution $= 0.65$, Bartlett's $\chi^2 = 145.4$, $p < 0.0001$. See electronic supplementary material, figure S1, for scree plot, and main text for details of measures.

	component 1 (g_{S1})
extractive foraging	**0.84**
innovation	**0.75**
social learning	**0.82**
tactical deception	**0.74**
tool use	**0.88**

Table 2. PCA (orthogonal solution) across primate species of eight cognitive and socio-ecological measures. PCA used a roots > 1 extraction criterion. $n = 44$, d.f. $= 35$, g_{S2} variance contribution $= 0.47$, component 2 variance contribution $= 0.16$, Bartlett's $\chi^2 = 152.4$, $p < 0.0001$. See electronic supplementary material, figure S1, for scree plot, and main text for details of measures.

	component 1 (g_{S2})	component 2
diet breadth	0.32	**0.71**
extractive foraging	**0.88**	0.11
innovation	**0.78**	−0.002
percentage fruit	0.13	**0.69**
social group size	−0.046	**0.69**
social learning	**0.80**	0.29
tactical deception	**0.68**	0.35
tool use	**0.88**	0.045

enhancements in other cognitive capacities such as individual learning [3,7]. We use the term cultural intelligence to refer to the cognitive capacities underlying culture. Social intelligence hypotheses have attracted recent support but the debate is not settled, and several authors have pointed out that the domains are difficult to separate [6,17–21]. This issue, together with controversies over whether social cognition and social learning are adaptive specializations [22,23] and overmodularity in primate cognition [24,25], would be clarified by knowledge about the extent to which measures of social and ecological performance covary [20]. While factors ranging from social group size to diet [12,16,20,26] correlate positively with primate brain volumes, the patterns of association between these factors [20], their relationship to a concept of primate intelligence and the consanguinity of non-human primate and human intelligence remain contentious and poorly understood.

Experimental studies of primates are a productive vehicle for exploring the psychological abilities of small numbers of species, and have been effective at delineating commonalities and differences in ape and human cognition [2,27]. Primate genera differ in their performance in laboratory tests of cognition, with great apes typically outperforming other primates [27,28]. Similarly, within two primate species, individual performance covaried across 11 laboratory tasks in cotton-top tamarins *Saguinus oedipus* and five laboratory tasks in common chimpanzees *Pan troglodytes*

[29,30]. These and related data from other mammals and birds [31–33] can be viewed as consistent with the hypothesis that a single general factor may underlie laboratory performance. This in turn raises the possibility that general intelligence may explain interspecific variation in the capacity to modify behaviour (i.e. behavioural flexibility; [34]) outside of the laboratory, including variation in social learning, innovation and tool use. However, comparative estimates of learning and cognition using experimental data are challenging, and laboratory tests have been criticized as being unfair to particular species, of questionable ecological validity and for failing to provide data on large numbers of species or on a broad range of cognitive capabilities [6,17,35].

An alternative approach, taken here, is to collate and analyse data from the published literature on the incidence of traits associated with behavioural flexibility in animal populations, on the assumption that the rate of incidence reflects the cognitive abilities of that species [34,36–38]. Such an approach, which is feasible in groups such as primates and birds where there is a tradition of reporting such behaviour, circumvents the aforementioned problems with experimental studies and provides useful, quantitative, continuous measures of performance for large numbers of species across broad domains. While such data are subject to reporting and other biases, these can be addressed statistically. These behavioural flexibility measures thus provide a valuable complement to experimental data.

Here, the tendencies to (i) discover novel solutions to environmental or social problems (henceforth 'innovation' [6]), (ii) learn skills and acquire information from others ('social learning'), (iii) use tools, (iv) extract concealed or embedded food (extractive foraging [12,39]), and (v) engage in tactical deception [40] were used as five ecologically relevant measures of behavioural flexibility. These are broad domains, each probably encompassing a range of underlying neurocognitive processes [41]. Further analyses incorporated (vi) diet breadth, (vii) percentage of fruit in the diet, and (viii) measures of social group size, thought to reflect the cognitive demands of exploiting/locating foods and tracking social relationships [12,20]. We compiled measures of (i)–(iv) and (vi), while the remaining measures came from published compilations (§2).

We had two objectives. First, we investigated the relations between numerous measures of behavioural flexibility in primates, using statistical methods that control for potential confounds and simultaneously incorporating continuous variables relevant to social, cultural, ecological and technical intelligence. Plausibly, underlying general processes linking different aspects of cognitive performance would lead to cross-species associations in cognitive measures. If, on the other hand, primate intelligence is organized into domain-specific modules that reflect species-specific ecological and social demands, cognitive measures need not covary across species.

Second, we examined the pattern of phylogenetic variation to determine whether enhanced cognitive abilities have evolved independently on multiple occasions and, if so, in which lineages. If cognitive

Table 3. Correlation of cognitive and socio-ecological measures across primate species. Figures are correlation coefficients. EF, rate of extractive foraging; I, rate of innovation; SL, rate of social learning; TD, rate of tactical deception; TU, rate of tool use; DB, dietary breadth; %F, percentage of fruit in diet (typically measured as a percentage of foraging time); GS, social group size. EF, I, SL, TD and TU are corrected for research effort differences. Figures in bold are statistically significant correlations ($p < 0.025$). See the main text and the electronic supplementary material for details of measures.

	EF	I	SL	TD	TU	DB	%F	GS
EF	1	**0.60*****	**0.68*****	**0.54*****	**0.74*****	**0.42*****	0.13	0.06
I		1	**0.55*****	**0.51*****	**0.56*****	0.18	0.08	0.12
SL			1	**0.54*****	**0.69*****	**0.44*****	**0.32*****	0.12
TD				1	**0.58*****	**0.36*****	0.21	**0.30****
TU					1	**0.28****	0.24	−0.05
DB						1	**0.40*****	**0.25***
%F							1	0.14
GS								1

*$p < 0.025$.
**$p < 0.01$.
***$p < 0.001$.

performance reflects evolutionarily conserved abilities homologous with human intelligence, then the high-scoring species might be those most closely related to humans. Conversely, if performance is dominated by past convergent selection favouring high intelligence, the data will not necessarily fit an 'apes outperform monkeys, who outperform prosimians' model. Our previous work has examined pairwise correlations between three measures of behavioural flexibility [6], and extensive past research has examined the relation between socio-ecological variables, cognitive measures and brain volume (see above). Here we examine, for the first time in a single set of analyses, multiple and ecologically relevant measures of behavioural flexibility from several behavioural domains together with socio-ecological variables, brain measures and laboratory-learning data.

2. MATERIAL AND METHODS
The electronic supplementary material provides additional information on data, methods and analysis, and details supplemental analyses and validation of measures.

(a) *Data collection*
Over 4000 articles published over a 75 year period, mainly drawn from four leading primate behaviour journals, were examined for examples of innovation, social learning, tool use and extractive foraging in all living primates, using keywords (e.g. 'novel' or 'traditional') to classify behaviour patterns (e.g. as innovation or social learning). Inter-observer reliabilities are high [6]. The observation frequencies for each of these four measures of behavioural flexibility were calculated as the total number of reported examples of each class. The innovation, social learning and tool-use compilations expanded on previously compiled datasets [6], while the extractive foraging compilation was new. Examples of innovation, social learning and tool use came from varied behavioural contexts, including foraging behaviour, locomotion, anti-predator behaviour and social displays. Social learning included learning from both family members and other individuals. We removed cases that simultaneously qualified as more

than one of our measures of behavioural flexibility (e.g. innovative tool use), with the exception of reports of social learning and another measure, which we maintain are independent, since the innovator/original tool user/ extractive forager is not the social learner. Tactical deception data were compiled from a published source [40]. This resulted in 62 species (electronic supplementary material) with non-zero scores in at least one of the five behavioural flexibility measures. Dietary breadth data were compiled by allocating foodstuffs to 13 categories (invertebrate prey, vertebrate prey, fruit, etc.) with species thus scored between 1 and 13. Extractive foraging and dietary breadth data were successfully validated against existing categorizations (electronic supplementary material). Data are archived online in the Dryad repository (http://datadryad.org). Group size, tactical deception and dietary data were compiled from published sources (electronic supplementary material). Where appropriate, these measures were (i) corrected for research effort by taking the perpendicular offset residuals from a linear regression of number of published articles on each species in the *Zoological Record* on observation frequency, and (ii) repeated after first partialing out the potential confounding effect of body mass, brain volume or research effort. We discuss and assess the reliability of the measures employed in the electronic supplementary material.

The most appropriate measure of brain size is controversial with no single preferred measure [17,42], so we considered four measures: (i) neocortex ratio (neocortex/rest of brain), (ii) executive brain ratio (neocortex + striatum/brainstem), (iii) neocortex size, and (iv) residuals of neocortex on rest of brain (excluding cerebellum). Brain component volumes were taken from multiple sources, providing data for 56 species (electronic supplementary material).

(b) *Analysis*
We used principal components and factor analysis (PCA/FA) to examine interrelations between variables. We conducted PCA and FA with and without diet and group-size measures because, depending on perspective, these measures can be viewed as measures of behavioural flexibility, correlates of cognitive

performance or sources of selection for intelligence. The inclusion of diet and group-size measures with our five measures of behavioural flexibility allowed us to examine the pattern of covariation of the eight measures, and to investigate whether the behavioural flexibility measures clustered together more strongly with each other than with the socio-ecological variables. Where we addressed evolutionary questions, we corrected for phylogeny using independent contrasts [43], implemented with the computer program Comparative Analysis by Independent Contrasts [44]. Other potential confounding variables considered included brain volume, body size, group size, research effort and correlated error in research effort, and data were also reanalysed without the great apes, and at the genus level (see §3 and electronic supplementary material). Since data were not available for all species for all variables, analyses differ in sample size depending on data availability. All statistical tests were two-tailed with $\alpha = 0.05$.

3. RESULTS

(a) *Across-species analyses*

A PCA of cognitive measures alone, including research-effort-corrected measures of innovation, social learning, tool use, extractive foraging and tactical deception, in all 62 primate species for which full data were available, revealed a single dominant component, henceforth referred to as primate g_{S1}, which explained over 65 per cent of the variance in cognitive measures (table 1). The 'S' subscript denotes that primate g is an across-species construct. Loadings for all measures were positive and ranged from 0.74 for tactical deception to 0.88 for tool use. A second eight-variable PCA that also incorporated the three socio-ecological variables (diet breadth, percentage fruit in diet and group size) generated a major component (henceforth g_{S2}) that explained 47 per cent of the variance (eigenvalue = 3.77, significantly higher than all other components), on which the five original measures and, to a lesser extent, diet breadth loaded significantly (table 2), and which covaried strongly with g_{S1} ($r = 0.95$, $p < 0.0001$). The eight-variable PCA also extracted a second component, on which diet breadth, percentage fruit in diet and group size loaded (table 2). The results of the eight-variable PCA thus support the interpretation of the primary component as a general cognitive measure. All 10 pairwise correlations between the five cognitive measures were strongly significant ($p < 0.001$; table 3). There was no significant correlation between diet breadth and innovation rate, suggesting that innovation rate is not simply an index of diet breadth (see also [41]). FAs gave equivalent results to the PCAs (electronic supplementary material, table S1).

We took several approaches to address potential confounding variables. The observed associations were not caused by data points that qualified simultaneously for more than one measure, since these were removed. Nor are the associations an artefact of the covariance of each individual measure with brain volume, body mass or correlated error variance in research effort: analyses using residuals of each cognitive measure from
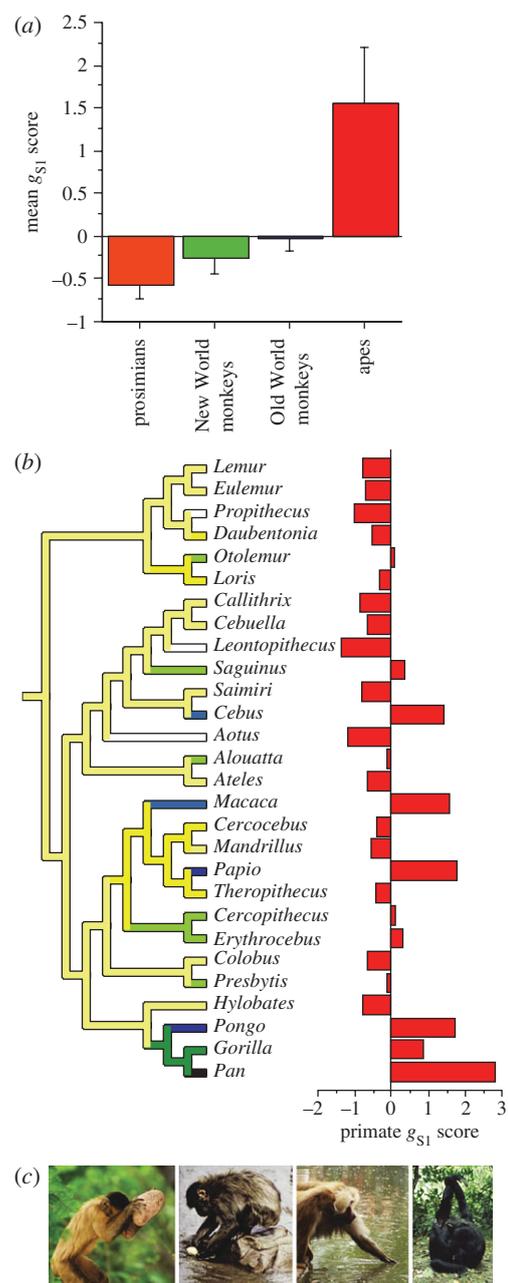

Figure 1. Phylogenetic distribution of general intelligence. (a) Mean and standard error primate g_{S1} scores for apes, Old World monkeys, New World monkeys and prosimians. Apes ($\bar{x} \pm$ s.e. $= 1.55 \pm 0.65$) score more highly than other primate taxa, but no significant mean differences were found between Cercopithecoidea ($\bar{x} \pm$ s.e. $= -0.02 \pm 0.15$), Ceboidea ($\bar{x} \pm$ s.e. $= -0.26 \pm 0.18$) and Prosimii ($\bar{x} \pm$ s.e. $= -0.48 \pm 0.17$) (ANOVA $F_{3,56} = 8.17$, $p < 0.0001$; Fisher's PLSD, critical differences: ape versus prosimians = 0.93, versus New World = 0.81, versus Old World = 0.77, $p \leq 0.0001$). (b) Primate intelligence scores, as measured by primate g_{S1}, showing phylogenetic relatedness based on a composite tree [45]. Multiple convergent evolutionary events favoured high intelligence across primate lineages with independent responses to selection in Hominoidea, *Macaca*, *Cebus* and *Papio*. (c) Photographs illustrating examples of behavioural flexibility in the four high g_S lineages, covering foraging, technical and social domains (from left to right: *Cebus* nut-cracking (Copyright © L. Candisani/Minden Pictures), *Macaca* food washing, *Papio* fishing (Copyright © iStockphoto.com/R. Bursch), *Pan* handclasp grooming (a putative cultural tradition) (Copyright © M. Nakamura).
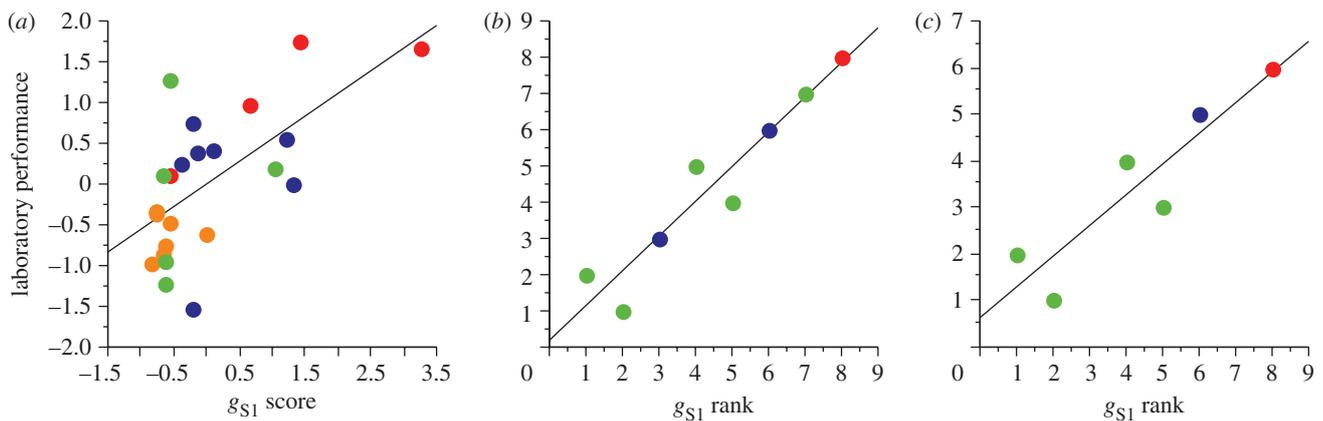
Figure 2. Primate g_{S1} covaries with performance of primate species in laboratory tests of comparative intelligence. g_{S1} score correlates strongly with three measures of performance, (a) Deaner *et al.*'s [28] measure compiled across multiple hetero-geneous cognitive tasks ($n = 18$, $r^2 = 0.36$, $p = 0.009$; similar results are obtained using independent contrast analysis: $n = 17$, $r^2 = 0.23$, $p = 0.047$), (b) the combined performance across all learning tasks in the Riddell & Corl [50] dataset ('combined Riddell rank'; $\rho = 0.95$, $p = 0.012$), and (c) 'learning sets', the single task (from [50]) that provides the largest dataset ($\rho = 0.89$, $p = 0.048$). Deaner *et al.* [28] examined the sources contained within the Riddell & Corl [50] dataset, and thus these datasets are not fully independent. However, we include both since they represent different criteria and methodologies for data compilation. Regression lines are included for illustration. Red, apes; blue, Old World monkeys; green, New World monkeys; orange, prosimians.

multiple regressions that included (i) relative brain volume, (ii) body mass, or (iii) with no correction for research effort, or (iv) with five independent measures of research effort, gave equivalent results (electronic supplementary material). To account for the possibility that observers may be more willing to ascribe behavioural flexibility to the great apes than to other primates, we repeated the analysis with great apes removed, finding equivalent results (electronic supplementary material).

(b) Extant genera variation

To address the concern that there may be error in individual species data, particularly in the case of species that have not been well studied, we repeated the PCA using the same procedures at the genera level. Once again, we found a single dominant component ($\chi^2 = 116.28$, $p < 0.0001$, variance contribution = 75%). The same pattern was observed when the analysis also incorporated Deaner *et al.*'s [28] genus-level composite index of performance in laboratory tests of cognition ($\chi^2 = 131.12$, $p < 0.0001$, variance contribution = 73%). Deaner *et al.*'s reduced model measure (inversed so that high scores represent high performance) loads heavily on g (loading = 0.73). This supports the argument that laboratory performance is reliant on general intelligence and demonstrates the covariation of six cognitive measures across extant primate genera.

(c) Phylogenetic analysis

If the relationship between different measures of primate cognitive ability reflects an evolutionary history of coevolution, then the primate g_S component should remain when phylogeny is taken into account using independent contrasts for each measure. Repeated in this manner [44], the five-variable PCA revealed a single component on which all cognitive measures loaded, although innovation and tactical deception loaded less strongly than in the across-species analyses ($n = 57$, d.f. = 14, $\chi^2 = 70.20$, $p < 0.0001$, variance

contribution = 0.53; extractive foraging, social learning and tool-use loadings = 0.76–0.84, innovation and tactical deception loadings = 0.66 and 0.55, respectively). The eight-variable PCA using independent contrasts revealed a degree of subdivision in the variance, with two components ($\chi^2 = 93.25$, $p < 0.0001$), suggesting that some cognitive measures have coevolved more tightly than others. Social learning, tool use and extractive foraging all loaded heavily on the dominant component (loadings 0.79–0.84), which accounted for 38 per cent of the extracted variance, while innovation and tactical deception loaded somewhat more weakly, but still substantially, on this dominant component (loading = 0.59 and 0.51, respectively), as did diet breadth (loading = 0.56). Tactical deception also loaded on a second component together with group size, with percentage fruit loading negatively (variance contribution = 0.18; loading = 0.52, 0.73, −0.73 for tactical deception, group size, per cent fruit in diet, respectively). While it might be tempting to interpret this subdivision as indicative of correlated 'socio-technical' and 'Machiavellian' components of general intelligence, the loading of tactical deception on the dominant component of the eight-variable PCA, together with the absence of two components in the five-variable independent contrast PCA, or the aforementioned extant species five-variable and eight-variable PCAs, or the FAs, leaves us guarded against over-interpreting this finding.

(d) The evolution of primate g

PCA can be used to calculate factor scores for each component it extracts, providing a composite score for the variables loading on a component. We calculated g_{S1} factor scores to provide a composite g_S measure for each species, which can be interpreted as a measure of comparative general intelligence. On average, the Hominoidea (excluding humans) out-scored other taxa, but no significant mean differences

Table 4. The relationship between primate general intelligence, g_S and brain volume. Regressions of four popular brain-size measures on g_{S1} scores, each conducted on both species values and independent contrasts. Figures in bold are statistically significant ($p < 0.05$). We find that g_{S1} is a significant predictor of brain size measured as neocortex ratio, executive brain ratio and neocortex size, but not residuals of neocortex on rest of brain. The latter uses a less than satisfactory reference variable, containing components that may coevolve with neocortex [16,49], and is consistently more conservative than other measures [6,12]. The relationships with measures 1–3 show a similar pattern but are weakened when the effect of body mass is statistically removed (electronic supplementary material, table S2).

brain measure	analysis	r^2	F	p
1. neocortex ratio	across-species	0.35	14.88	**0.0006**
	independent contrasts	0.27	10.13	**0.003**
2. executive brain ratio	across-species	0.55	22.37	**0.0002**
	independent contrasts	0.25	5.86	**0.026**
3. ln (neocortex volume)	across-species	0.55	13.91	**0.0009**
	independent contrasts	0.19	6.39	**0.018**
4. residuals of neocortex on rest of brain	across-species	0.01	0.18	0.67
	independent contrasts	0.03	0.75	0.39

in g_{S1} scores were found between Cercopithecoidea, Ceboidea and Prosimii (figure 1a).

To investigate the distribution of species' g_{S1} factor scores, we mapped them onto a primate phylogeny using MacClade v. 4.08. There was considerable overlap between primate superfamilies, and substantial variation within primate subfamilies (e.g. Cercopithecinae), which may represent measurement error, variation in evolutionarily labile cognitive abilities (i.e. independent evolutionary events) or phenotypic plasticity. To reduce measurement error, we pooled data for each genus (figure 1b). The analysis revealed multiple convergent evolutionary events favouring high general intelligence across primate lineages, with four independent responses to selection in *Cebus*, *Papio*, *Macaca* and Hominoidea (figure 1b). This interpretation involves fewer evolutionary events, and is thus more parsimonious, than all alternative scenarios, such as that high general intelligence evolved once in the common ancestors of apes and Old World monkeys and was then repeatedly lost. Some variance among genera is probably attributable to measurement error and error variance is expected to be highest in the least-studied taxa. Nonetheless, we note a correspondence between those primates with high g_{S1} scores and those renowned for complex cognition and rich behaviour (e.g. *Pan*, *Pongo*, *Cebus*, *Macaca* [3,13,27,46–48], figure 1c). Moreover, to address the concern that the data for little-studied species may be unreliable, we repeated the phylogenetic reconstruction with the less well-studied species removed, finding similar results (electronic supplementary material).

(e) Covariation with brain volume and laboratory performance

Table 4 and electronic supplementary material, table S2 illustrate the strong associations of g_{S1} with several measures of brain volume, while g_{S1} is also an effective predictor of the performance of primate species and genera in laboratory tests of cognition (figure 2). These observations lend credence to the view that primate g_{S1} is a genuine measure of comparative intelligence. Moreover, PCA combining genus-level measures of cognitive performance in the laboratory with the aforementioned measures of behavioural

flexibility again reveals a single dominant component (§2b). The positive correlations of g_{S1} with brain size and laboratory performance, together with the steps taken to account for differences in research effort, and the finding that the results hold when the great apes are removed from the analyses (electronic supplementary material), undermine any suggestion that g_S is merely an artefact of reporting biases that flatter species deemed intelligent or that are easy to observe, or of over-reporting of intelligent behaviour in a small number of species. The finding that prosimians do not score significantly lower than New and Old World monkeys undermines the suggestion that g_S is an artefact of underreporting of prosimian behavioural flexibility. The weak loadings of group-size measures on g_{S1} rule out the potential artefact of more reports of behavioural flexibility in species with large groups.

(f) Covariation of group size with g_S and laboratory performance

If social complexity is the prominent factor driving the evolution of intelligence in non-human primates [12–14,20,49,51–54], then we would expect indicators of social complexity to be good predictors of g_S and of performance in laboratory tests of cognition. We explored the relationship between social group size and both g_{S1} and Deaner *et al.*'s [28] index of performance in laboratory tasks of cognition (reduced model), but found no significant relationships (g_{S1}: $n = 58$, $r^2 = 0.04$, $p = 0.12$; laboratory performance: $n = 16$, $r^2 = 0.002$, $p = 0.85$). This contrasts with the strong positive relationship between primate g and Deaner *et al.*'s measure (figure 2a), and implies that general intelligence, rather than exclusively social intelligence, best explains the performance of primates in laboratory tests of cognition.

4. DISCUSSION

Our analyses suggest that ecologically relevant cognitive abilities, from multiple domains, have coevolved in primates, revealing an across-species general intelligence, with general rather than purely social intelligence probably driving brain evolution. Seemingly, key cultural capabilities, notably social learning, tool use and

behavioural innovation, form part of a highly correlated composite of cognitive traits. Thus, elements of cultural intelligence appear to be part of general intelligence. Our composite general intelligence measure correlates with brain volume measures and laboratory learning performance; nonetheless, general intelligence is not the result of a confounding effect of brain volume. High levels of general intelligence evolved independently at least four times, with independent responses to selection favouring high g_S in capuchin, baboon, macaque and ape lineages.

Several hypotheses have been proposed concerning the factors favouring the evolution of the large primate brain and, since these have been presented as alternative explanations, concern has been expressed that seemingly conflicting findings have not been reconciled [38,55,56]. By suggesting that selection may have favoured general intelligence, rather than a single specialized domain, our analysis helps to alleviate such disquiet. Significantly, the analysis extends the finding that primate taxa consistently differ in performance across multiple domains from the laboratory [28] to ecologically valid natural contexts. Our analyses also extend comparative findings that link innovativeness (assessed on the basis of published reports or experimental tests) with asocial-learning performance, tool use and reduced neophobia (in birds and primates) and with social learning (in primates; reviewed in [37,57,58]). We note that primate g_S contains social (social learning, tactical deception), technical (tool use, innovation) and ecological (extractive foraging, diet breadth) intelligence components, supporting a battery of hypotheses regarding the factors driving brain evolution [6,7,12–17,20,26], but not the hypotheses that social or ecological intelligence is the sole cause of brain evolution. Indeed, social and ecological intelligence may be intrinsically linked in group-living animals [19,21]. If social pressures are the major driving force behind primate cognitive evolution, our results suggest they have resulted in abilities extending beyond the social domain. Similarly, if a 'cultural drive' process has operated across primates, as envisaged by multiple authors [3,4,6,7], it seemingly has also favoured non-cultural capabilities.

(a) Sociality

Moreover, while our analysis (electronic supplementary material, table S3) confirms the widely observed relationship between group size and brain size [12,20], we find that group size does not covary with primate g_S, nor predict genera's performance in laboratory tests of cognition (laboratory data drawn from Deaner *et al.* [28]). Similarly, previous work has found weak or no correlations between primate group size and reported frequencies of social learning [23] and tactical deception [54], although our sample supported a correlation between tactical deception rate and group size. To the extent that group size measures social complexity, the group size findings are inconsistent with the view that social complexity selects for an intelligence applied to multiple domains. This raises the possibility that social

complexity may not have been as important a driver of primate general intelligence as is widely believed. However, group size is 'at best a crude proxy' of social complexity [20, p. 649] and more sophisticated measures of social structure and complexity would be valuable. For example, it is plausible that rates of social learning may be predicted by factors such as tolerant gregariousness and the number of available individuals to learn from, rather than group size *per se* [7]. Moreover, our findings, since they concern non-human primates, do not conflict with the hypothesis that social factors differentially favoured intelligence in humans [2,5]. Thus, our analyses do not preclude the possibility that adaptations to a cultural niche have been favoured in the lineage leading to humans [2,5]. Indeed, high general intelligence, by allowing animals to construct a niche where behavioural flexibility provides advantages, may predispose subsequent evolution of specializations in particular abilities.

(b) Experimental tests

Recently, the need for experimental verification of comparative results has been stressed [38,55,56]. Our analysis makes testable predictions, for example, that congeners' g-scores will be paralleled in experimental tests of cognition, and that high-g species should exhibit strong performance on all aspects of cognition. For instance, we predict that genera, such as *Cebus* and *Gorilla*, in which tool use is not widely observed, will be found to be capable of using tools in appropriate circumstances—as recently observed in wild individuals (e.g. [46,59]). Ideally, experimental investigations of general intelligence should extend beyond the laboratory, since captive conditions may influence cognitive development and performance [7,60,61]. Species differences in general intelligence are likely to extend beyond primates. For example, rooks *Corvus frugilegus*, members of the large-brained and behaviourally flexible corvid parvorder [37], use tools in captivity but apparently not in the wild [62,63], a finding consistent with the idea that such tool use can result from a generalized cognitive ability.

(c) Comparisons with human intelligence

The strong correlation between distinct measures of primate cognitive performance is strikingly evocative of the correlations in performance on different IQ tests observed in humans. A possible explanation for this correspondence is that the g factor reported in humans reflects underlying general processes that evolved in common ancestors and are thus shared in our extant primate relatives. However, caution is warranted in interpreting this finding since here the observed associations occur across rather than within species [57]; in this respect, further within-species analyses would be valuable [30]. It is hard unequivocally to establish the nature of the correspondence between primate and human g measures given the very different measures and levels of analysis used, and the structure and level of human intelligence may be greatly reliant on language or another uniquely human capability. That said, primate g_S is

highly consistent with current definitions of human intelligence that emphasize novel problem-solving abilities [1,9]. For instance, high performers on our measure are species frequently reported to devise novel solutions, solve social and ecological problems, learn quickly and from experience, construct and manipulate tools and to learn from and deceive others [7,27]: qualities attributed to intelligent humans. Moreover, primate g_S covaries with performance in laboratory tests.

(d) Brain volume and cognition
Links between brain volume and cognitive capacity are controversial, both within humans and across animal species [1,11,38,55,64,65]. Here, we show that primate g_S correlates with absolute forebrain volume measures and two of the three deployed relative measures, a result mirrored by analyses of laboratory-learning performance [42,66]. Similarly, within humans, g shows a modest correlation with total brain and grey matter volumes [9,11,67,68]. Our data, combined with the multiple studies linking various cognitive measures and brain volume across species [55], and recent findings demonstrating survival pay-offs to brain enlargement [37,69,70], suggests the 'volumetric stance' is warranted: brain component volumes are related to functionally relevant cognitive capacities.

In common with many human scientists and neuroscientists [1,9,11,65], we note that the mechanisms behind the brain volume–cognition relationship are unknown and require study. It is important to establish if, how and why characteristics such as brain cell composition, connectivity, numerosity and diversity are linked to brain volume, why these characteristics vary across brain regions, how this variation is linked to cognitive function and whether common links between structure and function are found across taxa [65]. Adequate tests of cognitive function will be essential for this exercise. Note that comparisons across large taxonomic divides with very different brain architectures [64] will be problematic. For example, the scaling rules of brain enlargement may differ, even between mammalian orders [65], something that comparative studies analysing relationships within multiple orders should account for [70]. Common findings in different taxa strengthen confidence in the observed relationships. For example, similar relationships between innovation rate, tool-use rate, individual learning measures and relative forebrain volume are found in both birds and primates [37].

A variety of neural and cognitive mechanisms will underlie a particular act like innovation or social learning, and purportedly complex cognitive processes may in fact have simple underlying mechanisms [41,64]. Accordingly, we envisage that such behaviour is unlikely to be the sole province of large-brained taxa [34,64,71]. However, our frequency data suggest that brain enlargement may facilitate more varied forms of behavioural flexibility, rather than simply the presence or absence of a broad category of behaviour such as social learning, extractive foraging or innovation. While our data do not allow us to examine the complexity of the processes underlying behavioural flexibility, it is possible that brain enlargement affords motor, processing or perceptual (especially visual) improvements that facilitate behavioural flexibility and are shared across cognitive domains, contributing to the correlated performance we observe. We suggest that brain enlargement facilitates improvements in the sophistication or efficiency of behavioural flexibility and the variety of problems to which it is applied, and that it may be necessary for some, but by no means all, advanced cognitive processes.

(e) Underlying mechanisms
The coevolution of cognitive performance documented in this study suggests that conserved general processes, as opposed to specialized modules [24,25], may be an important part of primate cognitive evolution, although we cannot exclude coevolution of distinct modules, modularity outside of the domains that we measure, or the evolution of modularity in the human lineage. For example, our data do not address whether spatial cognition varies independently from other cognitive measures [30,33,72]. While correlations between cognitive abilities cannot be used to demonstrate or disprove modularity [73], we can show the abilities we measure evolve together, and our data thus do not support the 'massively modular' view that cognitive abilities evolve independently [25]. Massive modularity is an extreme form of the modularity thesis, and more moderate views allow for coevolution of semi-independent modules. The general process view is arguably more parsimonious than even moderate modularity. We suspect the truth will lie somewhere in between, with shared general processes, themselves a product of evolution, sitting alongside adaptive specializations of aspects of cognition and perception. However, our results suggest that the view that components of intelligence and behavioural flexibility can evolve independently without constraint is untenable.

Our data are consistent with the increasingly accepted view that common processes are involved in both social and individual learning [74–76]. If much social learning is the result of general processes, then behaviour patterns acquired by social learning are expected to span multiple domains, a prediction supported by data from individual species such as the chimpanzee and the guppy *Poecilia reticulata* [71,77]. Where social learning is an adaptive specialization, on the other hand, it might be expected to be restricted to a particular domain, such as learning about certain predators or foods.

Regarding the mechanisms underlying g_S, the observed correlations with brain volume suggest that differences in brain structure underlie g_S, but g_S could additionally plausibly be a product of positive feedback from niche construction [11,78,79]. For example, individuals from species with a slight g_S advantage may be able to inhabit more challenging environments, thus exposing themselves to circumstances favouring the expression of behavioural flexibility and to selection for further increases in flexibility.

Our analysis provides empirical confirmation of the assumption that primate species differ in their general

intelligence, and that it covaries with brain encephalization and social-learning abilities. Our data are consistent with findings that great apes' social-learning abilities are superior to other primates [7,77] and broadly consistent with van Schaik and Burkart's meta-analysis of taxonomic differences in primate cognition [7], although our data provide no evidence for a difference between prosimians and monkeys. However, only eight prosimian species are represented in our database, limiting the statistical power of comparisons with prosimians. Humans are located within the superfamily with the highest *g* scores, but the analysis conflicts with a *Scala naturae* conception, suggesting instead that convergent selection may have repeatedly favoured intelligence in distant primate lineages.

(f) *Implications for the evolution of cultural transmission*

The discussion above suggests numerous reasons to urge caution when discussing the evolution of social learning and the capacities underlying culture. Reconstruction of evolutionary patterns of social learning will require investigation of numerous and widespread taxa, and data on deficiencies in both social-learning mechanisms (such as imitation) and social-learning strategies (such as the capability for pay-off-based copying) will be important alongside positive data. The social-learning data we analyse compile the results of a considerable body of published work describing primate behaviour, but still represent an early step in reconstructing the evolution of social learning and other underlying cultural capabilities. In particular, much of our data comes from observational reports of social learning, carrying the problem that neither social learning nor the underlying social-learning process is experimentally established [61]. Statistical methods for detecting social learning in natural populations will enhance the reliability of observational reports [80,81].

Since neither social learning nor culture is a unitary trait [77], but instead involve multiple processes, evolutionary reconstruction of social learning might usefully focus on particular mechanisms or capabilities (e.g. conformist social learning). In this respect, information on the developmental and neurocognitive mechanisms underlying social and individual learning is valuable, such as the compatibility of social and individual information-gathering processes, and understanding of the circumstances under which social learning is utilized [82].

If social-learning processes coevolve with, or even form part of, general cognitive processes, identifying a single factor as specifically favouring the evolution of social learning may prove challenging and perhaps even misguided. Positive feedback processes, such as social learning or cultural evolution, favouring further increases in cognitive flexibility, in turn facilitating enhanced social learning, will compound the problem of identification of a 'key' causal factor [3,7,83]. Social-learning efficacy may also change as a by-product of selection on another process, a consideration potentially important for theoretical models of the evolution of social learning. For example, selection favouring

increased social tolerance or grouping may facilitate social learning [7,84]. In principle, recently developed statistical methods may be able to select between alternative causal models [85], which would help establish to what extent the enhanced capacity for social learning was a key driver of primate intelligence or a by-product of some other driver. For the moment, we are unable to distinguish between these alternatives. However, we can, at least, confirm the existence of a positive relationship between the key capabilities underlying culture (e.g. enhanced social learning, behavioural innovation, tool use) and general intelligence across the primate order.

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