Electronic Supplementary Material: Reader, Hager & Laland

Supplemental Data: Figures

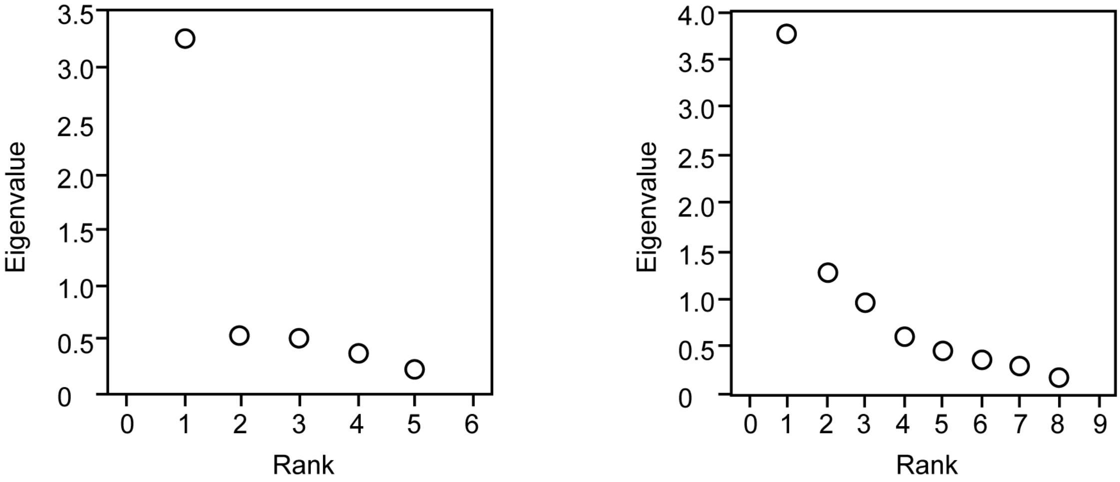

Figure S1. Scree plots for principal components analyses. The plots illustrate the dominance of the first component. Left panel: 5-variable analysis. Right panel: 8-variable analysis.

Supplemental Data: Tables

Table S1. Principal component and factor analyses. Non-rotated and oblique rotated solutions gave broadly similar results to the PCA presented in the main text, as did factor analyses.

(a) 5-variable analyses. All analyses extract one component/factor.

	PCA	FA
Extractive foraging	.84	.65
Innovation	.75	.47
Social learning	.82	.60
Tactical deception	.74	.48
Tool use	.88	.75
VARIANCE	**65%**	**58%**

(b) 8-variable analyses. All analyses extract two components/factors

	PCA (non-rotated)		PCA (oblique)		FA (non-rotated)	
Factor	1	2	1	2	1	2
Diet breadth	.57	.53	.21	.69	.53	.48
Extractive foraging	.85	-.24	.88	.00	.84	-.20
Innovation	.72	-.31	.81	-.10	.68	-.26
Percent fruit	.39	.58	.02	.70	.30	.45
Population group size	.23	.65	-.16	.72	.19	.32
Social learning	.85	-.05	.78	.20	.83	.01
Tactical deception	.76	.06	.64	.28	.70	.09
Tool use	.83	-.30	.90	-.07	.81	-.23
VARIANCE	**47%**	**16%**	**47%**	**16%**	**43%**	**9%**
INTERCORRELATION			**.28**			

Table S2. Regressions of brain size on g_1 with the effect of body mass removed. The effect of body mass was statistically controlled for through multiple regression, for both across-species and independent contrast analyses. The relationships with brain measures 1-3 are weaker than when body mass is not included, with some non-significant (see Table 4 main body), reflecting the well-known finding that ratio and absolute brain measures are to some degree confounded with body size [1]. Deaner *et al.* [2] have argued that absolute brain measures correlate more strongly with cognitive performance in primates than do relative brain measures. The observation that the relationship between primate *g* and brain size measures remain significant, or near significant, for the independent contrast data suggests that the relationship is not solely a confound of body mass.

Brain measure	*Analysis*	*N*	*t*	*P*
1. Neocortex ratio	Across-species	29	1.71	0.10
	Independent contrasts	28	2.79	**0.01**
2. Executive brain ratio	Across-species	20	2.63	**0.02**
	Independent contrasts	19	1.94	**0.07**
3. Ln (neocortex volume)	Across-species	29	1.32	0.20
	Independent contrasts	28	2.08	**0.05**
4. Residuals of neocortex on rest of brain	Across-species	29	0.37	0.72
	Independent contrasts	28	1.13	0.27

Table S3. Group size remains a significant predictor of brain size for two brain measures. Since there are statistically significant positive relationships between population group size and both tactical deception and diet breadth (Table 3, main text), we conducted multiple regressions to investigate whether group size remained a predictor of brain size when deception and diet breadth were included as independent variables. Group size remained a significant predictor of brain size for two brain measures.

Brain measure	*Analysis*	*N*	*t*	*P*
1. Neocortex ratio	Across-species	30	3.75	**0.0009**
	Independent contrasts	29	2.89	**0.008**
2. Executive brain ratio	Across-species	20	1.19	0.25
	Independent contrasts	19	0.33	0.74
3. Ln (neocortex size)	Across-species	30	2.00	**0.06**
	Independent contrasts	29	0.20	0.84
4. Residuals of neocortex on rest of brain	Across-species	30	3.36	**0.002**
	Independent contrasts	29	2.32	**0.03**

Supplemental Experimental Procedures and Results

1. Data collection

(*a*) *Innovation, social learning, tool use, extractive foraging*. We surveyed articles in four journals (*Primates*, *American Journal of Primatology*, *Folia Primatologica* and the *International Journal of Primatology*), as well as other relevant literature, collating examples of behaviour in each category. These publications were chosen because they are the leading primate behaviour journals, and collectively publish the bulk of primate behavioural research. Following previous work [3-5], we used keywords (e.g. 'novel', 'extract', or 'traditional') to classify behaviour patterns (e.g. as 'innovation', 'extractive foraging' or 'social learning'), so that the judgment of whether a behaviour pattern qualified in a category was made by the expert author of the article. This approach aims to avoid subjective bias on our part imposed during data collation. The surveyed articles were published between 1925-2000, with considerable change in taxonomic nomenclature during this period. Where species have had more than one name, or have experienced changes or ambiguities in nomenclature, we searched and categorized using relevant alternative names, and favoured grouping over splitting species (Table E2). Species names were subsequently checked against the leading contemporary taxonomy [6]. Further details on data collection methods, and examples of behaviour classified as innovations are described elsewhere [3,7-9].

Extractive foraging is defined as feeding on foods that must first be extracted from matrices in which they are embedded or encased, including nutmeat, shellfish, snails, eggs, brains, bone marrow, roots, tubers, and ant and termite mounds [10]. Extractive foraging data were validated against an existing categorization [10] used in previous work on cognitive evolution [11]. There were significantly more reports of extractive foraging in genera that Gibson [10] categorized as extractive foragers (*Ateles, Callimico, Callithrix, Cebuella [Gibson specifies only 'marmosets'], Cebus, Daubentonia, Gorilla, Lagothrix, Macaca, Miopithecus, Papio, Pan, Pongo, Saimiri*), compared with Gibson's non-extractive foragers (Mann-Whitney test: U = 131.5, $n_1 = 14$, $n_2 = 44$, $p = 0.001$), a result that holds when prosimians and tarsiers are excluded from the analysis (Mann-Whitney: U = 73.0, $n_1 = 13$, $n_2 = 22$, $p = 0.02$) or when based on reports per unit of research effort (all primates: Mann-Whitney: U = 141.0, $n_1 = 14$, $n_2 = 44$, $p = 0.002$; simians: Mann-Whitney: U = 79.0, $n_1 = 13$, $n_2 = 22$, $p = 0.03$). Thus although concern has been expressed that quantitative measures of extractive foraging are difficult to assemble [12], independently compiled classification schemes corroborate our extractive foraging measure. Moreover, experimental studies of extractive foraging in callitrichid monkeys show that published reports of extractive foraging predict performance in response to novel extractive foraging tasks under experimental conditions [13], supporting the use of literature reports to estimate species differences in extractive foraging.

The frequencies of social learning, innovation, tool use, extractive foraging, and tactical deception were corrected for research effort by taking the perpendicular offset residuals from a linear regression of research effort (see below) on observation frequency (both log transformed), forced through the origin. Linear regression is suitable because a clear direction of causality is established [14], with orthogonal offsets appropriate because there is measurement error in both dependent and independent variable. While we correct for research effort we cannot rule out the possibility of systematic reporting biases distorting our findings. However, below we describe measures that we adopted (e.g. repeating the analyses with great apes removed) which found no evidence that such biases were operating. Reader & MacDonald [8,9] further discuss the methodology of accounting for differences in research effort.

(*b*) *Tactical deception*. Deception data were taken from Byrne & Whiten [15], who compiled instances of tactical deception by surveying primatologists using a standardized request. While this survey has drawn criticism (see peer commentary to [16], it has been defended [16], and has the advantage of being largely independent of other datasets. We counted observations of tactical deception categorized by Byrne & Whiten [15] as level 1 ('evidence for tactical deception outweighs competing explanations') and above, with repeated observations of tactical deception in the same category and by the same observer considered as a single datum. To account for the fact that some instances of tactical deception may qualify for other measures of behavioural flexibility (e.g. innovative deception; [17], we noted acts simultaneously classified as deception and another measure during our data collection and removed these from the database. Similarly, we removed from our database examples of 'social tool use' [18], which we did not consider as tool use, despite some arguments to the contrary [18].

(*c*) *Diet breadth*. Diet breadth data were compiled by allocating prey to 13 categories (1. Invertebrate prey, 2. Vertebrate prey, 3. Fruit, fungus, and honey, 4. Seeds, nuts, 5. Exudates, 6. Flowers, 7. Nectar/Pollen, 8. Roots, tubers, bulbs, truffles, 9. Leaves, shoots, stems, herbs, buds, 10. Wood, bamboo, 11. Bark, 12. Pith, and 13. Lichen), with each species given a score between 1-13 to specify diet breadth. Dietary items consumed were taken from a single source [19], with subspecies' diets pooled. Initial categorization was based on the consensus of categories utilized in previous studies [20-25], with additional categories to account for additional foodstuffs. These categories were then collapsed to the 13 final categories based on consideration of foraging strategy, covariance between diet types, nutritional content, and the contribution of a particular foodstuff to the diet. For example, all 11 fungus-eating species eat fruit, and because fungi are likely to be spatially and temporally distributed in a similar manner to fruit, these two categories were combined. This new dietary breadth measure is validated by strong correlations with previously published dietary breadth estimates (versus Jernvall & Wright [21], whose data were also compiled from Rowe [19]: $r^2 = 0.58$, $F_{1,209} = 287.04$, $p < 0.0001$; versus Eeley & Foley [20], $r^2 = 0.46$, $F_{1,41} = 34.36$, $p < 0.0001$).

(*d*) *Percent fruit (and seeds) in diet*. Percentage fruit in diet data were compiled from Smuts *et al*. [26], and percentage fruit and seeds from Kaplan & Robson [27]. The former measure has the advantage that the rapid change in state (e.g. ripening) and spatial distribution of fruits, but not seeds, lends itself well to notions of ecological intelligence [28]. However, this first dataset includes only 52 species. The Kaplan & Robson [27] measure compensates for the inclusion of seeds by providing data for substantially more species (104). Accordingly here our analyses utilize the latter measure [27]. Values for species common to the Kaplan & Robson [27] and Smuts *et al*. [26] datasets differ by less than 5% [27].

(*e*) *Grooming clique size, population group size and foraging group size*. Data on grooming clique size, so-called population group size (social group size), and foraging group size were obtained from published sources [29-31]. Kudo & Dunbar [29] argue that grooming clique size is the best population-size measure of the cognitive demands of tracking social relationships, but this measure is available for only 29 species, reducing the power and generality of analyses. Conversely, foraging group size is probably not a good measure of such cognitive demands [32]. Accordingly, our analyses here of group size use population group size, for which there are data for 169 species. All three group size measures co-vary strongly.

(*f*) *Research effort*. The intensity of behavioural research on each species was assessed by surveying the number of published articles per species in the *Zoological Record,* between years 1993-2001. This source was suitable since it includes primate behavioural research but not biomedical studies. We also collated data for species not in the behavioural flexibility databases, to allow genus-level estimates of research effort to be made. Five additional measures of research effort were computed by searching the number of published articles on each species in five leading behaviour journals (*Primates*, *International Journal of Primatology*, *American Journal of Primatology*, *Folia Primatologica*, *Animal Behaviour*) by searching www.scopus.com, 1960-2005, for a given primate species, using all common alternative Latin names, in articles, abstracts or keywords of all document types.

(*g*) *Body mass*. Body mass data were taken from Smith & Cheverud [33], supplemented by data from additional sources [34-36] that met the criteria of being based on measurements of > 2 individuals of each sex, or > 8 unsexed individuals.

(*h*) *Brain component volumes*. Volumes of relevant brain regions were taken from Stephan *et al*. [37], supplemented by additional data from both serial sections of brains and magnetic resonance imaging [8,38-43]. The compatibility of utilizing these separate sources was validated by comparing measures on the 8 species for which both slices and scan methods had been employed, which exhibited no significant differences (paired t-test, $t = 0.53$, $df = 7$, $p = 0.61$), a finding consistent with other studies comparing alternative methods for measuring primate brains [39]. In total, brain volumes for 56 primate species were used (Table E2).

(*i*) *Cognitive performance in the laboratory*. Deaner et al. [44] compiled a continuous index of global variable means for the relative performance of 24 primate genera in laboratory tests of cognition. The tests are a heterogeneous complex of tasks, including detour problems, patterned string problems, tool use, invisible displacement tasks, object discrimination learning sets, reversal learning, oddity learning, delayed response tasks, and sorting tasks. We examined to what extent Deaner et al's index (reduced model) can be predicted by our primate *g* measure, using linear regression. Genus-level analyses were based on the genera named in the composite phylogeny used for phylogenetic analysis [45] (see below). However, a slightly modified classification scheme was used for analyses including the Deaner et al. index, to match their listed genera: *Cebuella* was grouped with *Callithrix*; *Mirza* with *Microcebus*; *Petterus* was renamed *Eulemur*; and *Euoticus*, *Galago*, *Galagoides* and *Otolemur* were grouped together under *Galago*. Two further measures of primate learning performance in the laboratory were also employed, based on Riddell & Corl [46]. These authors compiled published performance data in six different learning tasks. The largest single data set ('learning sets') includes data on six species of primate (excluding humans), and by comparing performance across the various tasks it was possible to rank nine primate species ('combined Riddell rank'; [8]. In ascending rank the species are *Callithrix jacchus* and *Saimiri sciureus* (ranked equally), *Papio hamadryas*, *Galago senegalensis*, *Cebus albifrons*, *Ateles geoffroyi*, *Macaca mulatta*, *Cebus capucinus*, and *Pan troglodytes*. Spearman rank correlation was employed to examine the relationship between ranked primate *g* and laboratory performance.

(*j*) *Summary*. Table E1 summarizes the number of records and number of species covered by each variable. Studies covered 251 species of primates, but because of overlapping datasets reported analyses range from 8 to 62 species. Table E2 lists the names and alternative Latin names of (*i*) those species used in analyses, (*ii*) those species for which brain data were available, and (*iii*) those species with non-zero scores in at least one of the five behavioural flexibility measures.

Table E1. Details of the number of records and number of species covered by each variable.

Measure	***Number of records***	***Number of species***
Innovation	588	62
Social learning	469	62
Tool use	656	62
Extractive foraging	430	62
Tactical deception	95	62
Diet breadth	N/A	236
% fruit and seeds [27]	N/A	104
Population group size [30]	N/A	169
Laboratory performance [46]	N/A	8
Neocortex ratio	N/A	56
Executive brain ratio	N/A	56
Ln (neocortex volume)	N/A	56
Residuals of neocortex on rest of brain	N/A	56

Table E2. List of species names and alternative names used to group the same species and in surveys of research effort, those species for which brain data were available, and those species with non-zero scores in at least one of the five behavioural flexibility measures (Y= data available). The initial list of species names came from the sources employed in our analyses [8,9,19,37,45,47], and were subsequently checked against the leading contemporary taxonomy [6]. Thus the table does not contain all current primates or all alternative names, and includes misspellings present in published literature.

Species	**Alternative names**	**Brain data available**	**Behavioural data available**
Allenopithecus nigroviridis			
Allocebus trichotis			
Alouatta belzebul			
Alouatta caraya			
Alouatta coibensis	*A. palliata coibensis*		
Alouatta fusca	*Alouatta guariba*		Y
Alouatta palliata		Y	Y
Alouatta pigra	*A. palliata pigra*		
Alouatta sara	*A. seniculus sara*		
Alouatta seniculus		Y	Y
Aotus azarai	*Aotus azarae*		
Aotus brumbacki			
Aotus hershkovitzi			
Aotus infulatus			
Aotus lemurinus			
Aotus miconax			
Aotus nancymaae			
Aotus nigriceps			
Aotus trivirgatus		Y	
Aotus vociferans			Y
Arctocebus calabarensis			
Ateles belzebuth			
Ateles fusciceps			
Ateles geoffroyi		Y	Y
Ateles paniscus			
Avahi laniger	*Avahi laniger laniger*	Y	
Avahi occidentalis	*Avahi laniger occidentalis*	Y	
Brachyteles arachnoides			
Cacajao calvus			
Cacajao melanocephalus			
Cacajao rubicundus	*Cacajao calvus rubicundus*		
Callicebus brunneus			
Callicebus calligatus	*Callicebus caligatus*		
Callicebus cinerascens			
Callicebus cupreus			
Callicebus donacophilus			
Callicebus dubius			
Callicebus hoffmannsi			
Callicebus modestus			
Callicebus moloch		Y	
Callicebus oenanthe			
Callicebus olallae			
Callicebus personatus			
Callicebus torquatus			
Callimico goeldii		Y	
Callithrix argentata			
Callithrix humeralifer			
Callithrix jacchus		Y	Y

Callithrix pygmaea	*Cebuella pygmaea*	Y	Y
Cebus albifrons		Y	Y
Cebus apella		Y	Y
Cebus capucinus			Y
Cebus olivaceus			Y
Cercocebus aterrimus	*Lophocebus aterrimus*		
Cercocebus galeritus			Y
Cercocebus torquatus		Y	Y
Cercopithecus ascanius		Y	Y
Cercopithecus campbelli			
Cercopithecus cephus			
Cercopithecus denti	*Cercopithecus wolfi denti*		
Cercopithecus diana	*Cercopithecus roloway*		Y
Cercopithecus dryas			
Cercopithecus erythrogaster			
Cercopithecus erythrotis			
Cercopithecus hamlyni			
Cercopithecus lhoesti			
Cercopithecus mitis		Y	Y
Cercopithecus mona			Y
Cercopithecus neglectus			
Cercopithecus nictitans		Y	
Cercopithecus petaurista			
Cercopithecus pogonias			
Cercopithecus preussi			
Cercopithecus salongo			
Cercopithecus solatus			
Cercopithecus wolfi			
Cheirogaleus major		Y	
Cheirogaleus medius		Y	
Chiropotes albinasus			
Chiropotes satanas			
Chlorocebus aethiops	*Cercopithecus aethiops*		Y
Colobus angolensis			
Colobus guereza			
Colobus polykomos			
Colobus satanas			
Daubentonia madagascariensis		Y	Y
Erythrocebus patas		Y	Y
Eulemur coronatus	*Petterus coronatus*		
Eulemur fulvus	*Petterus fulvus, Lemur fulvus*	Y	Y
Eulemur macaco	*Petterus macaco*		Y
Eulemur mongoz	*Petterus mongoz*	Y	
Eulemur rubriventer	*Petterus rubriventer*		
Euoticus elegantulus			
Euoticus inustus	*Galago matschiei*		
Galago alleni			
Galago granti	*Galago senegalensis granti*		
Galago moholi			
Galago senegalensis			
Galagoides demidoff	*Galago demidovii*		
Galagoides zanzibaricus			
Gorilla gorilla		Y	Y
Hapalemur aureus			
Hapalemur griseus			
Hapalemur simus			
Hylobates agilis	*H. lar agilis*		
Hylobates concolor	*Nomascus concolor*		Y
Hylobates gabriellae	*Nomascus gabriellae*		Y
Hylobates hoolock	*Bunopithecus hoolock*		

Hylobates klossii	*Hylobates klossi*		
Hylobates lar		Y	
Hylobates leucogenys	*Nomascus leucogenys*		
Hylobates moloch			
Hylobates muelleri	*H. agilis muelleri*		
Hylobates pileatus			Y
Hylobates syndactylus	*Symphalangus syndactylus*		
Indri indri			
Lagothrix flavicauda			
Lagothrix lagotricha	*Lagothrix lagothricha*		
Lemur catta		Y	Y
Leontopithecus chrysomelas			Y
Leontopithecus chrysopygus			
Leontopithecus rosalia			
Lepilemur dorsalis			
Lepilemur edwardsi			
Lepilemur leucopus			
Lepilemur microdon			
Lepilemur mustelinus			
Lepilemur ruficaudatus		Y	
Lepilemur septentrionalis			
Lophocebus albigena	*Cercocebus albigena*	Y	Y
Loris tardigradus		Y	Y
Macaca arctoides	*Macaca speciosa*		Y
Macaca assamensis			
Macaca cyclopis			
Macaca fascicularis	*Macaca irus, Macaca cynomolgus*		Y
Macaca fuscata			Y
Macaca maura	*Macaca maurus*		
Macaca mulatta		Y	Y
Macaca nemestrina			Y
Macaca nigra			
Macaca ochreata			
Macaca radiata			Y
Macaca silenus			Y
Macaca sinica			
Macaca sylvanus			Y
Macaca thibetana			Y
Macaca tonkeana	*Macaca tonkeanna*		Y
Mandrillus leucophaeus	*Papio leucophaeus*		
Mandrillus sphinx	*Papio sphinx*	Y	Y
Microcebus coquereli	*Mirza coquereli*		
Microcebus murinus		Y	
Microcebus rufus			
Miopithecus talapoin	*Cercopithecus talapoin*	Y	
Nasalis concolor	*Simias concolor*		
Nasalis larvatus		Y	
Nycticebus coucang		Y	
Nycticebus pygmaeus			
Otolemur crassicaudatus	*Galago crassicaudatus*	Y	Y
Otolemur garnettii			Y
Pan paniscus		Y	Y
Pan troglodytes		Y	Y
Papio anubis	*Papio hamadryas anubis*	Y	Y
Papio cynocephalus	*Papio hamadryas cynocephalus*	Y	Y
Papio hamadryas	*Papio hamadryas hamadryas*	Y	Y
Papio papio	*Papio hamadryas papio*		Y
Papio ursinus	*Papio hamadryas ursinus*		Y
Perodicticus potto		Y	
Phaner furcifer			

Pithecia aequatorialis			
Pithecia albicans			
Pithecia irrorata			
Pithecia monachus	*Pithecia monacha*	Y	
Pithecia pithecia			
Pongo pygmaeus		Y	Y
Presbytis comata	*Presbytis aygula*		
Presbytis frontata			
Presbytis geei	*Trachypitheus geei; Semnopithecus geei*		
Presbytis melalophos			
Presbytis potenziani			
Presbytis rubicunda			
Presbytis vetulus	*Trachypitheus vetulus; Kasi vetulus; Presbytis senex*		
Procolobus badius	*Colobus badius*	Y	Y
Procolobus kirkii	*Colobus kirkii*		Y
Procolobus verus			
Propithecus diadema			
Propithecus tattersalli			
Propithecus verreauxi		Y	Y
Pygathrix avunculus	*Rhinopithecus avunculus*		
Pygathrix brelichi	*Rhinopithecus brelichi*		
Pygathrix nemaeus		Y	
Pygathrix roxellana	*Rhinopithecus roxellana*		
Saguinus bicolor			
Saguinus fuscicollis			Y
Saguinus imperator			
Saguinus inustus			
Saguinus labiatus			Y
Saguinus leucopus			
Saguinus midas		Y	
Saguinus mystax			Y
Saguinus nigricollis			
Saguinus oedipus		Y	
Saguinus tripartitus			
Saimiri boliviensis			
Saimiri oerstedii			Y
Saimiri sciureus			Y
Saimiri ustus			
Saimiri vanzolinii			
Semnopithecus entellus	*Presbytis entellus*	Y	Y
Tarsius bancanus			
Tarsius dianae			
Tarsius pumilis			
Tarsius spectrum			
Tarsius syrichta		Y	
Theropithecus gelada			Y
Trachypithecus auratus	*Presbytis aurata, P. auratus; Trachypitheus aurata; T. auratus; Semnopithecus auratus; S. aurata*		
Trachypithecus cristatus	*Presbytis cristata*		
Trachypithecus francoisi	*Presbytis francoisi; Semnopithecus francoisi*		
Trachypithecus johnii	*Presbytis johnii; Semnopithecus johnii; Kasi johnii*		Y
Trachypithecus obscurus	*Presbytis obscura*		
Trachypithecus phayrei	*Presbytis phayrei*		
Trachypithecus pileatus	*Presbytis pileatus*		
Varecia variegata		Y	

2. Brain volume measures

Any study of primate brain evolution should note that only a small proportion of primate brains have been measured, correlational analyses are employed, and conclusions must be necessarily tentative. While information on neuronal and nonneuronal cell composition would be extremely valuable for these comparative analyses, it is currently not available for a sufficient number of primate species to conduct robust analyses [48-50]. The most appropriate measure of brain size is controversial [1,50-52], so we consider four popular brain volume measures:

(a) *neocortex ratio* (neocortex over rest of brain), chosen because it is the most commonly used measure [11,53];

(b) *executive brain ratio* (neocortex and striatum over brainstem), supported by the observation that the neocortex and striatum are functionally and phylogenetically linked [54]. The widely used approach of using brainstem volume (sum of mesencephalon and medulla oblongata) as a reference variable makes the assumption that such areas are evolutionarily conservative [51,54]. This is preferable to using body mass as a reference variable, since body mass, unlike brainstem volume, is a rather inaccurate measure of body size [51];

(c) *neocortex size*, argued to be reflective of raw information processing power [55];

(d) *residuals of neocortex on rest of brain* (excluding cerebellum), used by [8]. This measure avoids the risk of confounding enlarged neocortex volumes with diminished cerebellum volumes, which may be important if the cerebellum plays a greater role in cognition than previously thought, as suggested by Barton [56]. Rest of brain was used as the reference variable here since brainstem data were not available for specimens measured by MRI.

Residual measures (such as measure d) require a reference group to be defined (here, all primates with available data), and species values will change with changes in the reference group. Ratio and absolute brain component measures (measures a-c) carry the advantage that they do not change with the reference group, but the disadvantage that they correlate with body mass [1].

3. Phylogenetic analyses

Where we address evolutionary questions we correct for phylogeny using independent contrasts implemented with the CAIC computer program [57]. CAIC makes fewer type I errors than across-species analyses even when the branch lengths and phylogeny are uncertain or inaccurate [57]. All brain and body sizes, apart from the executive brain ratio, were natural-log transformed before taking contrasts since CAIC assumes that different lineages are equally likely to make the same proportional change in size. Across-species analyses were also conducted using these natural-log transformed values. Independent contrasts were regressed through the origin using least-squares regression [57]. The primate phylogeny was a composite tree [45], with a prior version of this tree used for sensitivity analyses [47]. For the purposes of this analysis an assumption of equal distances between phylogenetic nodes was made. We report the results of both independent contrasts and species-level analyses because questions have been raised over whether independent contrast analyses are always more valid than analyses treating species as independent data points (e.g. [58].

In order to investigate the distribution of primate *g* across the primate phylogeny, we pooled data across species into genera and conducted a genus-level PCA, generating primate *g* scores for each genus. These scores were then *ln* transformed and converted to *z* scores before using MacClade 4.08 [59] to reconstruct the evolution of primate g_{S1}. A linear parsimony algorithm was applied with minimum values at each branch displayed on figure 1b. We used the Purvis [45,47] phylogeny, despite the fact that a newer phylogeny including 30 additional species had recently become available [60]. That is because the Purvis phylogeny adopts nomenclature closer to that of the authors of the original articles that are the sources of our data, easing unambiguous allocation of a report of behavioural plasticity and phylogenetic analysis. Reconstructing the evolution of primate *g* using the new phylogeny gives identical results to those presented.

The reconstruction process was repeated at the species level, generating qualitatively similar results (i.e. evidence for convergent evolution favouring high intelligence in Hominoidea, Macaca, Cebus, and Papio). In the species-level analysis we addressed the concern that the data for little-studied species may be unreliable, by repeating this procedure removing species with a research effort of less than 10, <20 and <40 studies in the database. Again, the qualitative picture did not change, with evidence for independent evolutionary events favouring high intelligence in Hominoidea, Macaca, Cebus, and possibly Papio. We are less confident of Papio, where the high score reflects a relatively small number of reports of our measures of behavioural flexibility in comparatively little studied species (*Papio papio, Papio ursinus*). The analyses also hint at selection for intelligence in other lineages (e.g. *Saguinus*, *Erythrocebus*), but these trends require further data for confirmation.

4. Confounding variables and reliability

Inter-observer reliabilities in data categorization are high (0.83-0.95) [3]. We conducted analyses to statistically control for common ancestry, brain size, body mass, research effort, or correlated error in research effort, and at the genus level (see main text or below). The prominence of a single general intelligence component in a PCA (or factor in an FA) holds in all cases. Confidence in the methods is enhanced by the observation that other studies using similar procedures have investigated but not found evidence for various forms of bias. For instance, Lefebvre *et al.* [4,5,61] collected avian foraging innovation data from published literature, and demonstrated that their findings were not affected by population size, journal source, editorial policy, research effort, or observer bias (ornithological interest measured as the frequency of photographs in birding publications and by questionnaire). Furthermore, Lefebvre's innovation measure also correlates with laboratory measures of learning performance [62]. In primates, previous work examining pairwise correlations between innovation, social learning, and tool use found that the results were unaffected by the removal of reports from captivity or where human intervention was implicated [3].

While we cannot exclude the possibility that some of our measures, particularly social learning and tactical deception (where underlying processes are difficult to assess without experimentation, see e.g. [63], may be prone to reporting biases beyond those associated with research effort [3,64]. Such reporting biases could result from assumptions about the cognitive abilities of primates closely related to humans, or from differences in cognitive performance in the laboratory priming researchers to look for and report behavioural flexibility in high-performing species. We endeavoured to establish whether such biases may account for our major findings. For instance, if primatologists were prone to expect more intelligent behaviour amongst great apes than other primates, and if such expectations led to inadvertent reporting biases, our findings should be substantially weakened by repeating the analyses with the great apes removed. Such an analysis would also control for the possibility that the observed patterns of variation are solely reliant on the great apes. In fact, removing the great apes does not affect our findings (see below).

Combined, these observations, and the positive associations of primate *g* with brain size and laboratory performance (see main text), suggest that our methods generate a robust operational measure of behavioural flexibility, or intelligence. Although the tactical deception database [15] has received criticism (see peer commentary on Whiten & Byrne [16]), it forms only a small part of our data and its exclusion does not change our basic findings. More generally, questions over the validity of any single measure do not negate the message that multiple cognitive measures covary (Table 3).

5. Principal components and factor analyses

We conducted principal components analyses, utilizing 5-8 measures of cognitive performance, employing a roots-greater-than-1 extraction criterion, all of which revealed a single dominant component that we call 'primate g_S'. Where more than one component was extracted (8-variable analysis), axes were rotated to maximize the variance accounted for, but retained an orthogonal (independent) component design so that the axes can be regarded as powerful descriptive dimensions. We also conducted factor analyses to investigate whether our findings were robust to the analysis technique.

(a) Extant species variation

The reported observation of a single dominant component in a PCA (and a single dominant factor in FA) of measures of cognitive ability is not an artefact of the covariance of each individual measure with brain volume, body mass or error variance in research effort, nor does it result from our removal of cases that qualify for more than one variable. Equivalent results were found for PCA using residuals of each cognitive measure from multiple regressions that include (1) relative brain volume ($\chi^2 = 82.97$, $p < 0.0001$, variance contribution = 84%), (2) body mass ($\chi^2 = 135.40$, $p < 0.0001$, variance contribution = 59%), (3) employing five independent measures of research effort ($\chi^2 = 107.32$, $p < 0.0001$, variance contribution = 81%), (4) without accounting for research effort ($\chi^2 = 189.00$, $p < 0.0001$, variance contribution = 72%), (5) without removal of cases that simultaneously qualified for more than one measure of behavioural flexibility (N = 69, $\chi^2 = 273.68$, $p < 0.0001$, variance contribution = 74%), and (6) with the great apes removed ($\chi^2 = 42.04$, $p < 0.0001$, variance contribution = 45%).

(b) Independent contrast variation

Independent contrasts were forced through the origin by duplicating each data row and taking the reciprocal of the duplicated data [65]. (See [66] for an alternative procedure). Since this procedure inflates χ^2 values [67], we report significance values from analyses not forced through the origin, which produced similar results.

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