Title:

The relationship between play, brain growth and behvioural flexibility in primates

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Abstract:

Play behaviour is common across mammals, but is particularly frequent in primates. Several explanations for the occurrence of play have been proposed, both adaptive and non-adaptive. One popular explanation is that play supports the development of complex cognition and behavioural flexibility. This hypothesis is supported by a relationship between the relative size of several brain regions, including the neocortex and cerebellum, and the frequency of social play. However, a direct link with either behavioural flexibility or brain maturation has yet to be shown. Using a comparative dataset of the frequency of social and non-social play across primates I test two predictions of this hypothesis: i) the frequency of play is associated with the amount of postnatal brain growth, and ii) the frequency of play is associated with measures of behavioural flexibility. I find support for both predictions and, notably, the results suggest social and non-social play may contribute to different aspects of behavioural flexibility.

Key words: Play, behavioural flexibility, learning, brain development, cognition

Introduction:

Play behaviour is often qualitatively easy to recognise but difficult to define, a characteristic that has rendered a trait frequently observed in most mammals (Fagen, 1981; Burghardt, 2005) difficult to study and explain (Graham & Burghardt, 2010). Renewed interest in the evolutionary significance and developmental origins of play has led to greater clarification of the sort of behaviour that can be classified as play (Burghardt, 2005, 2010; Graham & Burghardt, 2010). Play has been defined as behaviours which are incompletely functional, spontaneous, atypical, repeatable and initiated in the absence of stress (Burghardt, 2010). Within this general classification three main subcategories can be identified; solitary play, object play and social play (Graham & Burghardt, 2010). Social play, play involving mutual interactions between multiple individuals, has attracted the particular focus as it is prominent in the juveniles of socially complex taxa, such as primates, and is thought to contribute to the development of social cognition (Lewis, 2000).

All forms of play begin early in infancy and peak during the early juvenile period (Bekoff & Byers, 1985; Fagen, 1981; Fairbanks, 2000), a developmental trajectory that has greatly influenced attempts to explain the adaptive value of play. Groos (1898) first suggested that play may act as preparation for behaviours important in adulthood. Derivations around this theme have some circumstantial support, for example the correlation between the timing of play and synaptogenesis in the cerebellum may suggest play facilitates motor training and the development of the musculo-skeletal system by modulating plasticity in local neural connectivity (Byers & Walker, 1995). Others instead emphasise training for behavioural flexibility as a buffer against unexpected events (Špinka *et al.,* 2001).

However, not all evolutionary explanations are adaptive. Spencer (1872) argued that play is merely a product of surplus energy. In a similar vein, Pagel & Harvey (1993) suggested play may simply be a means of passing time in species with delayed sexual maturity and could be a neutral trait with respect to fitness that, in some cases, has secondarily been selected upon to serve a developmental purpose. Contrary to non-adaptive hypotheses, field studies have demonstrated a link between frequency of juvenile play and survival (Fagen & Fagen, 2004; Cameron *et al*., 2008) suggesting play may contribute to evolutionary fitness and therefore be open to the action of selection. However, attempts to test direct links between play in juveniles and adult behaviour have, however, not provided evidence to support the behavioural development hypothesis (Sharpe & Cherry, 2003; Sharpe, 2005a-c).

In absence of a direct link between play and adult behaviour focus has shifted to indirect measures of behavioural flexibility, in particular brain size and structure. A number of authors suggested play is more prevelant in mammals with larger brains (Byers, 1999; Fagen, 1981), large brain size itself being a predictor for some measures of behavioural flexibility (Reader & Laland, 2002; Sol *et al*., 2008; Deaner *et al*., 2007; Sol, 2009). However, comparative analysis reveals at best an inconsistent relationship between the frequency of play and brain size (Iwaniuk *et al*., 2001). A more intriguing relationship is found when the sizes of individual brain components are considered. In primates, the frequency of social play has been linked to the relative size of the neocortex (Lewis, 2000), cerebellum (Lewis & Barton, 2004), amygdala, hypothalamus (Lewis & Barton, 2006) and striatum (Graham, 2011). These structures are implicated in the expression of both social behaviour and the ability to predict and perform sequential actions, behaviours necessary in the production of play (Graham & Burghardt, 2010). Finally, if juvenile play is selected for as a means of learning, or fine tuning, adult behaviour it is predicted that the frequency of play should be associated with variation in postnatal brain growth (Pellis & Iwaniuk, 2000; Diamond & Bond, 2003). Preliminary evidence in favour of this hypothesis was found across primates (Pellis & Iwaniuk, 2000) but in this study a qualitative measure of adult play was used in the analysis, and whether this measure accurately reflects the developmental consequences of juvenile play is unclear.

Whilst these studies suggest a link between the evolutionary elaboration of play behaviour and the size of relevant neural regions, the continued lack of comparative evidence directly linking play and behavioural flexibility leaves the door open for non-adaptive explanations. For example, although play behaviour could contribute to distributed neural systems mediating cognitive abilities (Barton, 2012) the allometric patterns driven by co-evolution between brain components (Barton & Harvey, 2000) could potentially explain some of the observed relationships. It is also not yet possible to reject Pagel and Harvey’s (1993) neutral hypothesis as the expression of play behaviour could conceivably be linked to the elongation of life history traits associated with brain development (Barton & Capellini, 2011). In addition, no study has found a relationship between non-social play and neural phenotypes raising questions over the relevance of this type of play, and the potential for different aspects of play to be associated with different adult traits.

Here I attempt to bridge this gap by using comparative analyses of social and non-social play in anthropoid primates, together with data on pre- and post-natal brain development and a range of measures of behavioural flexibility. The results provide evidence for an association between postnatal brain growth and the frequency of play, but do not support the contention that social play has more relevance for adult cognition than non-social play. Instead, non-social play is found to be associated with measures of behavioural flexibility predominantly involving physical tasks, whilst social play is associated with rates of tactical deception, but not social transmission.

Methods:

Data on the mean time budget, expressed as a percentage, for social and non-social play were taken from Graham (2011). Social and nonsocial play are measured independently. These data were collected through a literature search and include studies of social play only where the play behavior was explicitly described as 'social play', defining nonsocial play as play that was not associated with a partner or dyad. Social play data are available for 14 species, whereas only 11 species have data on non-social play. Comparisons involving social play were therefore run using all available data and only species where data are available for both variables.

Data on brain growth and life history traits were taken from Barton and Capellini (2011), prenatal growth is defined by the size of the trait at birth (neonatal brain size) and postnatal growth is defined as the adult trait minus the neonatal trait. Associations were sought between play and prenatal/postnatal brain growth, lactation period (age at weaning) and juvenile period (age at sexual maturity), with and without controlling for body size.

To test for associations with behavioural flexibility I examined two datasets: i) Reader *et al.*'s (2011) 'reduced' dataset of the frequency extractive foraging, innovation, social transmission and tool use (the 'reduced' dataset removes cases that simultaneously qualified as more than one behavioural category to produce more independent measures); and ii) Byrne and Corp's (2004) data on the frequency of tactical deception which was derived from the 1990 database of tactical deception in primates (Byrne & Whiten, 1990). Both Reader *et al.* and Byrne *et al.*'s raw data are influenced by research effort; therefore, in both cases a measure of research effort was included as a separate variable in the regression analyses (see Supplementary Table 1). These behaviours can be categorized into two groups; those mainly associated with physical tasks (extractive foraging, tool use and innovation) and those involving social behavior (tactical deception, social transmission and group size, taken from PANTHERIA (Jones *et al*., 2008)).

All variables were log-transformed with the exception of the proportion of time spent in social or non-social play. As generally recommended for propotional/percentage data these variables were arcsine-transformed (Sokal & Rohfl, 1995). The overlap between the datasets are incomplete, as such sample size varies between some tests and in some cases the low sample size may limit the power of the analysis. For this reason I also present raw p-values, uncorrected for multiple testing, results near to the significance threshold should therefore be viewed as preliminary. The key results were repeated using log-transformed play measures and the same results were obtained suggesting the choice of transformation does not affect the results (Supplementary Table 2).

It is widely acknowledged that interspecific data are not independent due to the taxa's shared evolutionary history (Felsenstein, 1985). To test for evolutionary associations between the frequency of play and life history or behavioural traits whilst correcting for this non-independence I used a Phylogenetic Generalised Least Square (PGLS) analysis implemented in Bayes Traits (Pagel, 1999; available from http://www.evolution.rdg.ac.uk) across the 100 most supported phylogenies obtained from the 10Ktrees project (Arnold *et al*., 2010). The average result of a 2-tailed test across the 100 trees is presented below.

Results:

Play, brain growth and life history

Rates of social play are significantly associated with postnatal brain growth both before ($t_6 = 3.457$, $R^2 = 0.666$, $p = 0.014$) and after ($t_4 = 3.3463$, $R^2 = 0.798$ $p = 0.026$) controlling for postnatal body growth. There is a no significant association with prenatal brain growth before ($t_6 = 2.243$, $R^2 = 0.45$, $p = 0.066$) or after controlling for prenatal body growth ($t_4 = 0.103$, $R^2 = 0.135$, $p = 0.923$). Rates of non-social play also show a significant association with postnatal brain growth after controlling for body mass ($t_4 = 3.344$, $R^2 = 0.719$, $p = 0.029$) but not before ($t_6 = 2.004$, $R^2 = 0.401$ p =

0.092). There is no association between non-social play and prenatal brain growth (t_6 = 0.782, p = 0.464).

Neither social (t_5 = 0.666, p = 0.530) nor non-social play (t_5 = 0.039, p = 0.970) are associated with longer juvenile periods. Both, however are associated with longer periods of lactation before (social play: t_5 = 4.034, R^2 = 0.765, p = 0.007; non-social play: t_5 = 3.129, R^2 = 0.662, p = 0.020) and after (social play: t_3 = 0.2.841, R^2 = 0.784, p = 0.047; non-social play: t_3 = 3.850, R^2 = 0.792, p = 0.018) controlling for postnatal body growth, a proxy for variation in maturity at birth.

Play and behavioural felxibility

Associations with Reader *et al.*'s measures of behavioural flexibility involving physical tasks were examined using the 11 species for which data on both non-social and social play exist. For non-social play there is a strongly significant association with tool use (t_9 = 4.354, R^2 = 0.704, p = 0.003), and weaker associations with innovation rate (t_9 = 3.092, R^2 = 0.546, p = 0.018), and rates of extractive foraging (t_9 = 2.871, R^2 = 0.510, p = 0.024). For social play there is a narrowly non-significant association with tool use (t_9 = 2.299, R^2 = 0.408, p = 0.055) and the relationships with other traits are non-significant (extractive foraging: t_9 = 1.699, p = 0.113; innovation: t_9 = 1.901, p = 0.099). When the additional three species are added for social play the strength of the association with tool use slightly increases (t_{12} = 2.482, R^2 = 0.365, p = 0.032) but the other traits remain non-significant (extractive foraging p = 0.069; innovation p = 0.081).

Turning to social behaviour, rates of social play are found to be associated with a higher frequency of tactical deception (t_6 = 2.747 R^2 = 0.555, p = 0.033) whereas non-social play is narrowly non-significantly associated (t_4 = 2.720, p = 0.053). This difference is not due to sample size as when the test was repeated with the reduced dataset social play is still significantly associated with tactical deception (t_4 = 4.498, p = 0.011). However, there is no association between social play and social transmission (t_9 = 1.884, p = 0.102), whereas non-social play shows narrowly significant association (t_9 = 2.451, R^2 = 0.431, p = 0.044). After controlling for body size non-social play shows a narrowly non-significant relationship with group size, often used as a proxy of social complexity, (t_9 = 2.326, p = 0.053), but there is no association between social play and group size (t_9 = 1.471, p = 0.184).

Discussion:

Primates are amongst the most playful taxa (Burghardt, 2005). Combined with their diversity of social ecology (Kappeler & van Schaik, 2002), behavioural flexibility (Reader & Laland, 2002) and cognitive ability (Deaner *et al.*, 2006; Reader *et al.*, 2011) they provide a powerful group within which to test hypotheses regarding the adaptive benefits of play. The complexity of social relationships has long been argued to be a major driver of the expansion of the primate brain (Brothers, 1990; Dunbar, 1998; Dunbar & Shultz, 2007), and it has been strongly suspected that play contributes to the development of skills necessary for navigating social relationships as adults (Groos, 1898; Fagen, 1981; Bekoff, 2001). Previous studies have provided indirect link between social play and behavioural complexity by studying the relationship between play and the size of relevant brain regions (Lewis, 2000; Lewis & Barton, 2004, 2006; Graham, 2011). The results presented here add two key components to the evidence supporting an adaptive explanation linking play, brain development and adult behaviour.

The first is a robust association between higher rates of play and greater amounts of postnatal brain growth. Both the frequency of social and non-social play are associated with postnatal brain growth after correcting for postnatal body growth, confirming the results of Pellis and Iwanuik (2000). This is a key prediction of the hypothesis that play is involved in fine tuning adult behaviours or motor control by facilitating an exaggerated interaction between an individual and their environment during periods of brain maturation, in particular synaptogenesis and myelination (Byers & Walker, 1995; Pellis & Iwanuik, 2000; Lewis & Barton, 2006). A variant of this hypothesis is that the juvenile period is extended in species where play-mediated learning is particularly important for the development of adult behaviour (Groos, 1898; Pellis & Iwanuik, 2000). It has previously been argued that primates have an extended juvenile period that evolved in response to the need to acquire the necessary behavioural skills to navigate their complex social relationships (Joffe, 1997). The analyses presented here suggest that the frequency of play is associated with longer periods of lactation, but not longer periods of juvenile period (the time between weaning and sexual maturity). This relationship is independent of variation in neonatal maturity but could reflect investment in postnatal brain growth (Barton & Capellini, 2011) rather than investment in time to permit learning. It is possible that the key variable affecting the development of the relevant behaviours is the degree of plasticity in brain maturation associated with play, rather than the duration of the period of play.

The relationship between play and postnatal brain growth could be due to motor or social training (Byers & Walker, 1995; Fagen, 1981; Bekoff, 2001) or more general training for unexpected events (Špinka *et al.,* 2001). The second key contribution of this study is begin to delineate between these possibilities by contrasting the relationship between play and different measures of adult behaviour. Associations were found with measures of behavioural flexibility roughly divisable into two groups comprising of social and non-social behaviours. Here, it is notable that non-social and social play show different strength of associations with different behaviours.

Non-social play shows a consistent relationship with non-social behaviours in adults including innovation rate, rates of extractive foraging and tool use, but generally show much weaker associations with social traits. These datasets were filtered to remove overlapping datapoints (Reader *et al*., 2011) so the consistency of the relationships is not explained by behaviours categorised under multiple groups. A major component of non-social play is object play, and it is notable the strongest association found was with tool use. Graham and Burghardt (2010) have suggested that object play may be a developmental precursor to complex, flexible tool use, citing potential examples in Japanese macaques (Nahallage & Huffman, 2007) and dolphins (Parra, 2007). Indeed, it is notable that other tool using clades, such as corvids show a high rate of object play (Heinrich & Smolker, 1998; Diamond & Bond, 2003). The results presented here lend support to this contention. A key question is whether the association is merely due to the fine tuning of motor behaviour or the development of an understanding of the physical connectedness between objects (Viasalberghi & Trinca, 1989; Tomasello & Call, 1997; Visalberghi & Tomasello, 1998). Evidence supporting causal understanding in tool using primates varies between species (Viasalberghi & Limongelli, 1994; Limongelli *et al*., 1995) and the extent to which play is associated with learning causality rather than mediating trial and error, or motor skills is an open question. One intriguing aspect of the present study however, is the significant association between non-social play and innovation rate. This provides some support for Špinka *et al*.'s (2001) hypothesis that play may train for the unexpected, both kinematic and cognitive, and may also suggest non-social play confers some understanding beyond that which is directly experienced.

In contrast, social play shows no strong association with any of the non-social behaviours. Social play is often discussed as a learning mechanism to indirectly improve the social cohesion within a group by developing cooperative, non-aggressive behaviour (Fagen, 1981; Bekoff, 2001; Graham and Burghardt, 2010). However, the only significant association found is with a measure of a more subversive aspect of Machiavellian intelligence, tactical deception. Neither social transmission nor social group size, a commonly used measure of social complexity (e.g. Dunbar, 1998), are associated with rates of social play. Data on tactical deception is considered controversial by some (see commentary associated with Whiten & Byrne, 1988) but has provided interesting insights into brain and cognitive evolution (e.g. Byrne & Corp, 2004; Reader *et al.*, 2011). Tactical deception is considered to be a learnt ability (Byrne & Whiten, 1991; Byrne, 1997) that is cognitively sophisticated, requiring some ability to understand the perspective of others as well as interpreting social cues and dominance hierarchies (Mitchell & Thompson, 1986; Whiten & Byrne, 1988; Cheney & Seyfarth, 1990), abilities similar to those often cited as being developed during social play (Lewis, 2000). The results presented here may suggest that social play makes a more direct contribution to an individual's fitness through the development of an ability to manipulate social peers rather than to simply foster non-aggressive, altruistic relationships (Lee, 1984; Bekoff, 2001). An alternative explanation may be that social play contributes to a range of core behaviours that can be deployed in different social situations; both in reciprocity and deception, but measures such as social transmission do not reflect these former behaviours and directly as frequency of tactical deception reflect the latter. Indeed understanding the physical nature of the action (imitation) is perhaps more important than understanding the intention of the individual observed performing the action (emulation) in social transmission (Byrne, 2003; Horner & Whiten. 2005).

It is, however, highly likely that the underlying pattern that different categories of juvenile play contribute to the development of different adult behaviours is robust. This is further reflected in the difference in results obtained when seeking evolutionary associations between rates of play and the size of different brain structures (Lewis, 2000; Lewis & Barton, 2004, 2006; Graham, 2011) which may reflect an underlying disparity in the neural networks influenced by play behavior contrary to a proposed unity in the neural basis of play (Špinka *et al*., 2001) and cognition (Deaner *et al*., 2006). Indeed, despite their strong coevolutionary relationship the relative size of the cerebellum and neocortex in adult primates are associated with different behavioural tasks (tool use and social group size respectively) suggesting a distributed neural basis to behavioural specialization (Barton, 2012). Further, more nuanced data on subcategories of play in a wider range of species will be necessary to further dissect these relationships. The results of this study, however, provide comparative evidence directly linking play with variation in a number of cognitively demanding behaviours. Together with a robust association with brain maturation, and previous results demonstrating links between brain structure and frequency of play structures (Lewis, 2000; Lewis & Barton, 2004, 2006; Graham, 2011), these results place play in a clear adaptive framework on which future studies will be able to build.

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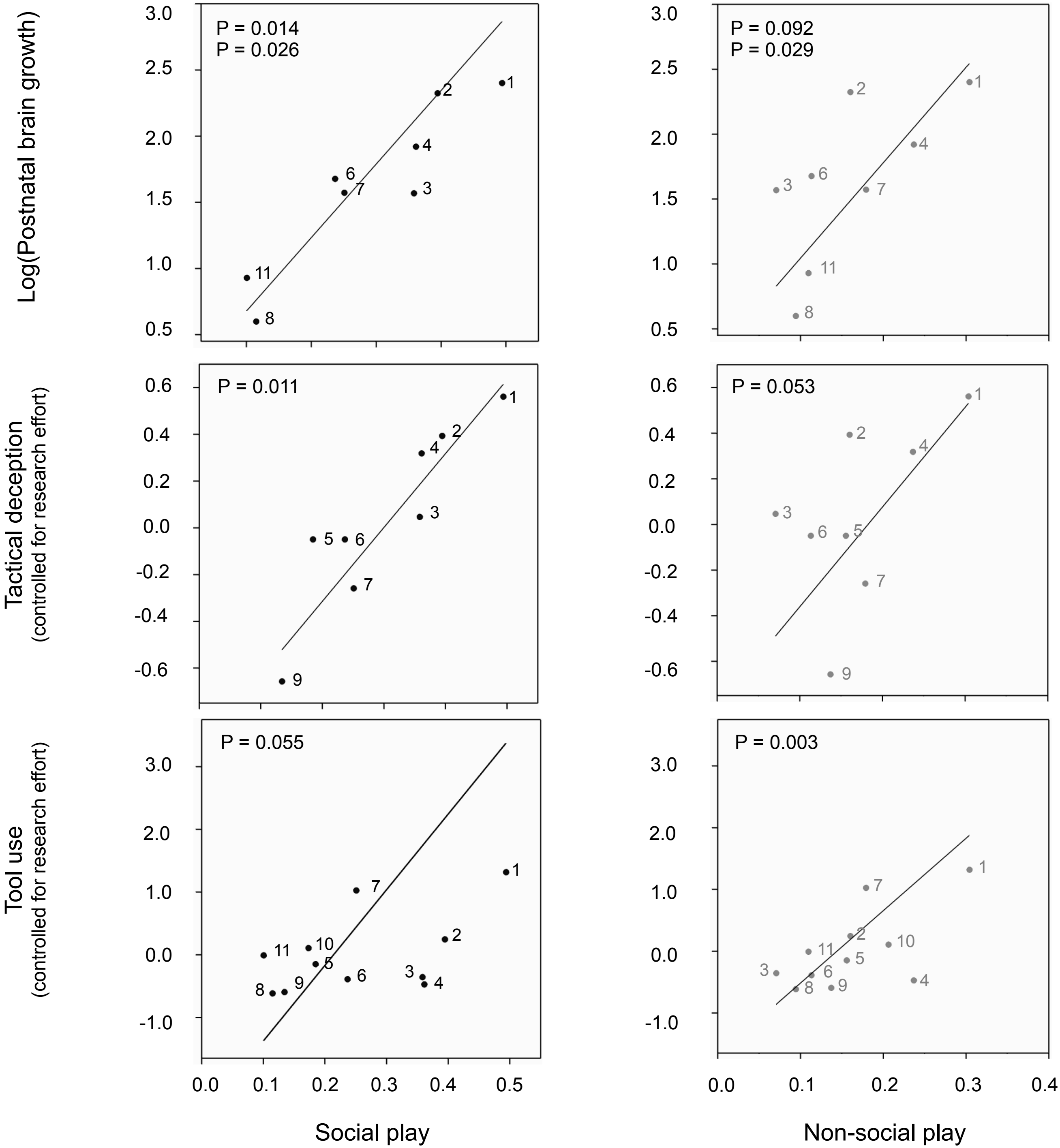
Figure 1: Relationships between social and non-social play and key variables. Plots for tactical deception and tool use were generated by regressing each dataset against research effort and plotting the residuals, along with the PGLS regression equation obtained using these residuals. This is for illustration purposes only, the results in the main text are derived from multiple regressions where research effort was included as an independent variable in the PGLS regression. P-values for these corresponding tests are displayed for each variable, for postnatal brain growth P-values are given with (bottom) and without (top) correcting for body mass. Data labels: 1) *Pan troglodytes*, 2) *Gorilla gorilla*, 3) *Hylobates lar*, 4) *Papio spp.*, 5) *Piliocolobus badius*, 6) *Macaca mulatta*, 7) *Cebus albifrons*, 8) *Callithrix jacchus*, 9) *Saguinus oedipus*, 10) *Pithecia pithecia*, 11) *Nycticebus coucang*.



Log(Postnatal brain growth)
P = 0.014
P = 0.026
P = 0.092
P = 0.029
Tactical deception
(controlled for research effort)
P = 0.011
P = 0.053
Tool use
(controlled for research effort)
P = 0.055
P = 0.003
Social play
Non-social play