Animal Behaviour 90 (2014) 281–286

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 19 November 2013
Initial acceptance 19 December 2013
Final acceptance 16 January 2014
Available online 12 March 2014
MS. number: 13-00964

Keywords:
behavioural flexibility
brain development
cognition
learning
play

Play behaviour is common across mammals, but it is particularly frequent in primates. Several explanations for the occurrence of play have been proposed, both adaptive and nonadaptive. 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 data set of the frequency of social and nonsocial play across primates, I tested two predictions of this hypothesis: (1) that the frequency of play is associated with the amount of postnatal brain growth; and (2) that the frequency of play is associated with measures of behavioural flexibility. I found support for both predictions, and, notably, the results suggest that social and nonsocial play may contribute to different aspects of behavioural flexibility.

Play behaviour is often qualitatively easy to recognize but difficult to define, a characteristic that has rendered a trait frequently observed in most mammals (Burghardt, 2005; Fagen, 1981) 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 that 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 particular focus as it is prominent in 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, 1981; 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 that play facilitates motor training and the development of the musculoskeletal system by modulating plasticity in local neural connectivity (Byers & Walker, 1995). Others instead emphasize training for behavioural flexibility as a buffer against unexpected events (Špinka, Newberry, & Bekoff, 2001).

However, not all evolutionary explanations are adaptive. Spencer (1872) first argued that play is merely a product of surplus energy. In a similar vein, Pagel and Harvey (1993) raised the possibility that 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 to serve a developmental purpose. Contrary to nonadaptive hypotheses, field studies have demonstrated a link between frequency of juvenile play and survival (Cameron, Linklater, Stafford, & Minot, 2008; Fagen & Fagen, 2004) suggesting that 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 not provided evidence to support the behavioural development hypothesis (Sharpe, 2005a, 2005b, 2005c; Sharpe & Cherry, 2003).

In the 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 have suggested that play is more prevalent in mammals with larger

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http://dx.doi.org/10.1016/j.anbehav.2014.02.004

brains (Byers, 1999; Fagen, 1981), large brain size itself being a predictor for some measures of behavioural flexibility (Deaner, Isler, Burkart, & van Schaik, 2007; Reader & Laland, 2002; Sol, 2009; Sol, Bacher, Reader, & Lefebvre, 2008). However, comparative analysis reveals at best an inconsistent relationship between the frequency of play and brain size (Iwaniuk, Nelson, & Pellis, 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 (Diamond & Bond, 2003; Pellis & Iwaniuk, 2000). Evidence in favour of this hypothesis comes from an association between brain growth and a qualitative measure of adult play across primates (Pellis & Iwaniuk, 2000). However, whether this measure accurately reflects the developmental consequences of juvenile play is unclear.

Although 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 nonadaptive explanations. For example, although play behaviour could contribute to distributed neural systems mediating cognitive abilities (Barton, 2012), the allometric patterns driven by coevolution 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 nonsocial 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 using an exploratory comparative analysis of social and nonsocial play in primates, combined with data on pre- and postnatal brain development and a range of measures of behavioural flexibility.

METHODS

Data on the mean time budget, expressed as a percentage, for social and nonsocial play were taken from Graham (2011). Social and nonsocial play were measured independently. These data were collected through a literature search and include studies of social play only where the play behaviour was explicitly described as 'social play', defining nonsocial play as play that was not associated with a partner or dyad. Social play data were available for 14 species, whereas only 11 species had data on nonsocial play. Comparisons involving social play were therefore run using all available data and only species for which data were available for both variables. As discussed by Graham (2011), these data are the best available but have a number of limitations. Many of the data are from captive animals, which vary to some extent from wild populations, and do not control for variation in the age of observed individuals.

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. The relationships between play and prenatal/postnatal brain growth, lactation period (age at weaning) and juvenile period (age at sexual maturity) were explored with and without controlling for body size.

To test for associations with behavioural flexibility I examined two data sets: (1) Reader, Hager, and Laland's (2011) 'reduced' data set of the frequency of extractive foraging, innovation, social transmission and tool use (the 'reduced' data set removes cases that simultaneously qualified as more than one behavioural category to produce more independent measures); and (2) Byrne and Corp's (2004) data on the frequency of tactical deception, 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 S1). These behaviours can be categorized into two groups: those mainly associated with physical tasks (extractive foraging, tool use and innovation) and those involving social behaviour (tactical deception, social transmission and group size, taken from PanTHERIA; Jones et al., 2009).

All variables were log-transformed with the exception of the proportion of time spent in social or nonsocial play. As generally recommended for proportional/percentage data these variables were arcsine-transformed (Sokal & Rohlf, 1995). The key results were also repeated using log-transformed play measures and the same results were obtained suggesting the choice of transformation does not affect the results (Supplementary Table S2).

It is widely acknowledged that interspecific data are not independent, owing 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 while correcting for this nonindependence, I used a phylogenetic generalized least squares (PGLS) analysis implemented in BayesTraits (Pagel, 1999; available from http://www.evolution.rdg.ac.uk) across the 100 most supported phylogenies obtained from the 10kTrees project (Arnold, Matthews, & Nunn, 2010). The analyses address multiple hypotheses and the overlap between data sets is incomplete. As such, sample size varies between some tests and in some cases the low sample size may limit the power of the analysis. In addition some tests are not independent and were performed to confirm patterns not explained by allometry or to reject alternative hypotheses, inflating the number of tests. For this reason I present raw P values, uncorrected for multiple testing. Results near to the significance threshold should therefore be viewed as preliminary, and should ideally be confirmed with independent data sets. Although in some cases a one-tailed test could be justified, the average result of a more conservative two-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 (Fig. 1) 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 no significant association with prenatal brain growth before ($t_6 = 2.243$, $R^2 = 0.45$, $P = 0.066$) or after ($t_4 = 0.103$, $R^2 = 0.135$, $P = 0.923$) controlling for prenatal body growth. Rates of nonsocial 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 nonsocial play and prenatal brain growth ($t_6 = 0.782$, $P = 0.464$).

Neither social ($t_5 = 0.666$, $P = 0.530$) nor nonsocial ($t_5 = 0.039$, $P = 0.970$) play is associated with longer juvenile periods. Both,