Quantifying social complexity

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Social complexity has been invoked as a driving force shaping communicative and cognitive abilities, and brain evolution more generally. Despite progress in the conceptual understanding of societal structures, there is still a dearth of quantitative measures to capture social complexity. Here we offer a method to quantify social complexity in terms of the diversity of differentiated relationships. We illustrate our approach using data collected from Barbary macaques, *Macaca sylvanus*, at 'La Forêt des Singes' in Rocamadour, France, as well as simulated data sets for a proof-of-concept. Based on affiliative and agonistic behavioural categories, we calculated four indices that characterize social relationships (diversity of behavioural patterns, dyadic composite sociality index, relative interaction frequency and tenor). Using cluster analyses, we identified four different relationship types: rarely interacting agonistic dyads, rarely interacting affiliative dyads, moderately frequently interacting ambivalent dyads and frequently interacting affiliative dyads. We then calculated for each individual a derived diversity score that integrates information about the number and diversity of relationships each subject maintained. At the individual level, one may be interested to identify predictors of this individual diversity score, such as age, rank or sex. At the group level, variation in the relative shares of affiliative and agonistic interactions affects the distribution of individual diversity scores more than the interaction frequency, while the omission of ambivalent relationships (i.e. a discontinuous variation in the share of affiliative or agonistic relationships) leads to greater variation in diversity scores. The number of realized relationships had only a moderate effect. Overall, this method appears to be suited to capture social complexity in terms of the diversity of relationships at the individual and group level. We suggest that this approach is applicable across different species and facilitates quantitative tests of putative drivers in brain evolution.

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Ever since Jolly (1966) and Humphrey (1976) proposed that group living played a crucial role in driving brain evolution, researchers have aimed to operationalize different aspects of social life to test predictions from this 'social brain hypothesis' (Dunbar, 1998; Dunbar & Shultz, 2007a). In particular, it has been proposed that social complexity is the key driver in the evolution of primate brains and cognition (Bergman & Beehner, 2015; Platt, Seyfarth, & Cheney, 2016; Seyfarth & Cheney, 2015; but see DeCasien, Williams, & Higham, 2017).

In some of the earlier studies (Dunbar, 1998; Humphrey, 1976; Jolly, 1966), group size was used as a proxy for social complexity, although it was conceded that this is only a crude measure for social complexity (Dunbar, 1998). Byrne and Whiten (1988) noted that primate social complexity is characterized by behaviours involving cooperation, manipulation and deception, and Freeberg, Dunbar, and Ord (2012) pointed out that in complex social systems, individuals frequently interact in many different contexts with many different individuals, and often repeatedly with the same individuals over time see also (Seyfarth & Cheney, 2015). Bergman and Beehner (2015), finally, proposed that social complexity could best be understood in terms of the number of differentiated relationships individuals maintain.

While all of these concepts cover important aspects of social complexity, there is no agreement how to quantify the notion of social complexity at the individual and the group level, despite the existence of numerous indices that describe specific aspects of a social relationship between two individuals (Blumstein & Armitage, 1997; Cords & Aureli, 1993; Fraser, Schino, & Aureli, 2008; Silk, Alberts, & Altmann, 2003). For example, Sapolsky,

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Alberts, and Altmann (1997) created a social connectedness index, based on eight behaviours including affiliative and agonistic categories. Subsequent studies by Silk and colleagues (Silk, Alberts, & Altmann, 2006; Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012; Silk, Altmann, & Alberts, 2006; Silk et al., 2003, 2010) quantified social bonds in terms of their (1) strength by the composite sociality index (CSI; including grooming and proximity data as a measure for social integration), (2) quality by a grooming equality index (indicating the difference in grooming given and received) and (3) stability by investigating the consistency of relationships to three top partners based on the CSI and the subsequent calculation of a partner stability index (PSI). Using a different approach, Fraser et al. (2008) used nine different behaviours (affiliative, but also submissive and aggressive behaviour) to derive three principal components termed value, compatibility and security of a given relationship (but see Silk, Cheney, & Seyfarth, 2013). All these indices are used to describe a given relationship between two individuals, but they have not been integrated in a way that would allow researchers to capture social complexity in a quantitative and comparative fashion.

The aim of this paper is to introduce a method to describe social complexity in a quantitative way. At the individual level, social complexity has been defined as the number of differentiated (in the sense of different types of) relationships individuals maintain (Bergman & Beehner, 2015); at the group level, this notion of social complexity would affect the distribution (average and skew) of individual levels of social complexity. This conception requires the quantification of the different types of relationships that exist within a group, the assessment of individual social complexity and ultimately the assessment of the distribution of different types of relationships across individuals at the group level. We are borrowing from concepts describing ecological diversity to derive measures of diversity at the social level. The aim is to derive variables that can be used to facilitate comparisons between groups (or species).

To illustrate our approach, we first used behavioural data recorded from Barbary macaques, *Macaca sylvanus*, living in the enclosure 'La Forêt des Singes'. Second, as a proof-of-concept, we created different simulated data sets in which we varied the type and frequency of interaction, as well as group size, to explore how this variation affects our suggested measure of social complexity at the group level. To arrive at this measure, we first derived a set of indices that describe the diversity of different behavioural patterns that make up a relationship, as well as the frequency and tenor of the relationship, as proposed by Silk et al. (2013). We then used cluster analysis to identify different types of relationships. Finally, we calculated the diversity of relationship types individuals maintain (individual relationship diversity index or 'IRDI'). This is largely in line with Bergman and Beehner's conception of social complexity. We suggest that the distribution of the IRDI at the group level provides a measure of complexity that can be applied in broader comparative studies, such as testing core predictions from the 'social brain hypothesis'.

METHODS

We used behavioural data collected from Barbary macaques at the monkey park 'La Fôret des Singes' in Rocamadour, France, during two periods, i.e. the birth season (April to June 2009, hereafter 'season 1') and mating season (September to October 2009, hereafter 'season 2'). In total, there were 100 days and 598.5 h of observation of 19 female focal animals differing in age, rank and matrilineal descent. These females encompassed the majority of all adult ($N = 24$) females in the group. In total, the group consisted of 56 subjects, including 23 males aged 5 years and older, and nine

juveniles and infants, in addition to the 24 females aged 5 years and older mentioned above. Observations followed the focal animal sampling rule with continuous recording of defined behaviours for 30 min (Martin & Bateson, 2007). Behavioural data were recorded using a portable minicomputer (Tungsten E2, PalmOne, Inc. 2005, Milpitas, CA, U.S.A.) running custom forms created with the Pendragon software (Version 5.0, Pendragon Software Corporation, Buffalo Grove, IL, U.S.A.). The data were originally collected for different purposes, but deemed suitable for this study.

Determining Interaction Patterns

For simplicity, we reduced the behavioural contexts in which interactions were recorded to three aggressive categories (threats, chases, attacks; ethogram in Hesler & Fischer, 2007) and two affiliative categories, i.e. body contacts and grooming interactions. We did not consider ambiguous behaviours such as a bared teeth display that is shown in submissive and affiliative interactions (Hesler & Fischer, 2007). Further, we excluded submission, as it is often a response to aggressive behaviour, yielding redundant information. We further excluded behaviours of triadic interactions, i.e. infant handling, or other behaviours, which involved a third animal, to keep the analysis simple. In summary, we determined counts of threat (abbreviated as t in the following equations), chase (c), attack (a), body contact (bc) and grooming (g) interactions for 416 dyads (out of a possible total number of 1275) in spring and 421 dyads in autumn.

Choice of Indices

First, we calculated the behavioural diversity index (BDI) to describe the diversity of different behavioural interactions (see Silk et al., 2013; equation 1).

$$\frac{1}{\left(p_t^2 + p_c^2 + p_a^2 + p_{bc}^2 + p_g^2 \right)} \tag{1}$$

We derived this score from the Simpson diversity index, which is frequently used in ecology to operationalize ecosystem diversity based on species number and evenness of species distribution (Begon, Townsend, & Harper, 2006; Simpson, 1949). Here we treated the different behaviour categories as 'species'. The BDI, therefore, takes into account the number of different behaviours and the evenness of their distribution; both of these factors contribute to the diversity of a relationship. Since only proportions are included, the index describes the diversity only and not absolute or relative frequency of specific behaviours (Magurran, 2003).

Second, we employed the dyadic composite sociality index (DCSI) as a measure for the strength of affiliative relationships (Silk et al., 2003, 2013; Silk, Alberts, et al., 2006), which focuses on the frequency dimension of affiliative relationships (equation 2).

$$\frac{\left(R_{bc}/\overline{R}_{bc} + R_g/\overline{R}_g \right)}{2} \tag{2}$$

We calculated the index by dividing the rates R (i.e. the number of interactions per hour of observation time) of body contacts (bc) and grooming (g) from one dyad by the mean rates of all dyads, and by dividing this term by N, the number of behaviours involved. Therefore, it shows the divergence of dyad X from the mean of all dyads. Also, using rates ensures correction for different observation times of individual focal animals.

Third, we determined the interaction frequency index (IFI; equation 3), which is a modification of the DCSI.