

Research

Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals

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Understanding human cognitive evolution, and that of the other primates, means taking sociality very seriously. For humans, this requires the recognition of the sociocultural and historical means by which human minds and selves are constructed, and how this gives rise to the reflexivity and ability to respond to novelty that characterize our species. For other, non-linguistic, primates we can answer some interesting questions by viewing social life as a feedback process, drawing on cybernetics and systems approaches and using social network neo-theory to test these ideas. Specifically, we show how social networks can be formalized as multi-dimensional objects, and use entropy measures to assess how networks respond to perturbation. We use simulations and natural ‘knock-outs’ in a free-ranging baboon troop to demonstrate that changes in interactions after social perturbations lead to a more certain social network, in which the outcomes of interactions are easier for members to predict. This new formalization of social networks provides a framework within which to predict network dynamics and evolution, helps us highlight how human and non-human social networks differ and has implications for theories of cognitive evolution.

Keywords: network; sociality; primates; psychology; systems; ecological psychology

1. INTRODUCTION

Any attempt to solve the problem of human cognitive evolution really comes down to asking: ‘What makes us different from other animals?’ More particularly, why is it that only we have institutions such as marriage, money and monarchy? Why is that only we send rockets to the moon, or transplant hearts, lungs, and even faces, from one person to another? More prosaically, why did hundreds of thousands of people file past Kate Middleton’s wedding dress at Buckingham Palace during the summer of 2011? And why is it that only we seem able to recognize both the significance and the absurdity of such behaviour in a reflexive, meta-aware, ironic fashion? As these activities capture how human persons engage with, relate to and behave in the world, answers to these questions fall within the purview of scientific psychology. But, sadly, we do not seem to have made all that much progress on why we alone can do this, and we have no better idea about how we got to be this way. For example, despite all its fanfare, the rise of Evolutionary Psychology [1–3], with its promise of ‘revolutionizing’ the discipline

through the incorporation of evolutionary biology, has really only shown us that we fight, fear, forage and fornicate much as other species do and, perhaps, rely on similar underlying psychophysiological mechanisms when we do so. Understanding the kinds of psychological creatures we are now, and how we came to be this way, remains an enduring puzzle.

One reason for this may be because our recent attempts to ‘naturalize’ human psychology via the application of evolutionary theory have neglected the sociocultural and historical processes by which human selves and minds are created and sustained. This matters because there is a good argument to be made that these processes help give rise to the psychological reflexivity and ability to respond to novel circumstances that appear to be uniquely human. We should therefore treat the sociocultural environment as part and parcel of the ‘natural’ environment—which of course it is—and not separate them. The inclusion of sociocultural and historical processes into our consideration of cognitive evolution is made more productive, we would argue, if we adopt a theoretical framework that recognizes the ‘mutuality’ of organism and environment: the idea that they are interdependent, forming mutually reinforcing feedback loops, so that each can only be fully understood in terms of the other.

One way forward, then, is to take a step back, and return to those thinkers who emphasized the mutuality of organism and environment in just this way; people

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such as John Dewey, George Herbert Mead, Jakob von Uexküll, Lev Vygotsky and James Gibson [4–11]. Their ideas have always sustained a presence within psychology, while simultaneously being regarded as either implausible or esoteric. Here, we advocate specifically for these views, as we believe these ideas deserve greater prominence, not least because they provide a useful alternative to standard approaches within cognitive and comparative psychology (for a review see Barrett [12]).

(a) *A relational, ecological view of cognition*

A relational view of psychology begins with the understanding that cognition is ‘embodied’. We need to recognize that, first and foremost, brains evolved as behaviour-control systems designed to help animals move around in, and engage actively with, the world, not to allow them to think about it in an abstract, logical, disembodied manner [13–17]. As Brooks [13] points out, the vast majority of evolutionary history has been spent refining the perception and action mechanisms that permit an organism to survive and reproduce in a dynamic environment. So-called ‘higher’ cognitive faculties such as language, problem-solving, reason and expert knowledge all appear relatively late in the day, evolutionarily speaking. This, in turn, implies that all these ‘higher’ faculties—those that we consider to be the most complex from a human perspective—must actually be quite simple to implement once the essential perceptual and motor processes that enable an organism to act in the world are available [13] (see also [14–16]). What is more, these perceptual and motor processes must, as a direct consequence, underpin the evolution and elaboration of the ‘higher’ functions, so that they are not free of bodily influence in the manner we tend to assume. Recent work identifying the mosaic evolution of neocortical–cerebellar networks, and the explosive evolution of the cerebellum itself [15], further point to dynamic action in the world as a key driver of brain evolution. The same can be said of the so-called mirror and canonical neurons [18], which force us to recognize that we are dealing, not with separate sensory and motor systems, but with a single, integrated process of sensorimotor coordination, as Dewey [4] suggested in his classic paper on the reflex arc.

More specifically, an embodied approach draws heavily on Gibson’s [9] idea that organisms regulate their behaviour with respect to the ‘affordances’ of the environment: the opportunities and possibilities for action that particular objects and resources offer an animal [9]. For a human, a fork offers the possibility of feeding, but not for a fish, a dog or a crow, all of whom lack hands. This clearly highlights the affinity between an embodied, ecological perspective and von Uexküll’s [7] concept of the ‘Umwelt’: the environment as perceived and experienced by the organism (see Barrett [12] for a more thorough review). By detecting and exploiting the affordances of the environment, animals can regulate their behaviour in appropriate ways. The marriage of ecological psychology with more recent notions of embodiment [12,19] provides us with an alternative perspective on the evolution of

cognition, one in which the active perception of the environment is central and where sensorimotor processes operate in an ongoing loop of continual adjustment and feedback, rather than in a linear stimulus–response fashion.

This last point reveals another strong affinity between an embodied, ecological approach and a cybernetic, or systems, approach to behaviour, most notably Powers’ [20] perceptual control theory (PCT) (see also Cziko [21]). Similar to Gibson’s ecological psychology, this is a theory that dispenses with stimulus–response psychology, seeing psychological processes, instead, as homeostatic feedback mechanisms. Under this view, an organism varies its behaviour, so that its perception of the world remains constant. The task for us, accordingly, is to identify the control variable in question, and demonstrate that animals act to ensure this remains stable in the face of perturbation [20,21] (see also [12,22]).

At first glance, it might be difficult to see how a strongly cybernetic, ecological view of behaviour and psychology ties to those aspects of human life that appear to be unique: our reflexivity and our ability, not only to respond to, but invent, novelty. As Noble [23] and Costall [24] have suggested, however, Gibson’s work leads naturally to Mead’s [6] work in social psychology. As Mead [6] saw it, the objects that humans encounter are ‘collapsed acts’: we view them teleologically, as being ‘for’ something. Not only does this make clear that both naturally formed and human-manufactured artefacts fall under this description, but it also leads directly to Mead’s theory of mind and self because these are ‘social objects’ that are similarly brought into being, and maintained, by our actions, specifically those revolving around the use of public language. Mead’s [6] ideas regarding the nature of human psychological life can thus be seen as ‘ecological’ in this important, relational sense (see also [10,11,24–26]).

(b) *An ecological approach to human cognition: George Herbert Mead’s theory of mind*

In Mead’s theory [6], the communicative process by which a human mind comes into being has two phases. The first phase, which Mead [6] calls the ‘conversation of gestures’, characterizes the communicative interactions of non-human animals. Mead’s argument was that non-humans undoubtedly communicate with each other, but that they have no sense they are doing so. One animal produces some action or gesture that is responded to by the other, which then elicits a further response from the first in a very ‘conversational’ way. Neither animal, however, needs to understand that its own gestures are causing the other animal to act. They ‘know how’ to communicate but they do not ‘know that’ they are doing so. Animals that engage each other in this way cannot respond to their own gestures from the standpoint of others; in this sense, their communication is ‘unconscious’ (or perhaps ‘non-conscious’). The second phase that emerges—both evolutionarily and developmentally—is the ‘conversation of significant gestures’: a form of conscious communication, via language (significant symbols),

that arises out of the process of unconscious communication. Once communication via significant symbols is possible, it gives rise to the capacity to respond actively to our own gestures from the standpoint of others. For example, Mead [6] suggests that, when we ask someone to fetch us a chair, the vocal gesture we make ‘calls out’ in us the same response that it calls out in the person to whom it was directed. For Mead [6], it is this capacity to turn our vocal gestures back on ourselves—this reflexivity—that characterizes the emergence of thought, and our ability to communicate intentionally and not just ‘unconsciously’.

Accordingly, then [6] (see also [10,11]) mind is something we do, rather than some distinct capacity we possess. Mind is, in other words, a form of social participation: a process, not a thing. It is important to note, however, that Mead [6] was not denying a central role for the evolved nature of the human brain, nor was he suggesting that all human cognition was produced by cultural processes alone. Instead, the process is one of mutual enhancement and integration: the nature of the human brain is instrumental in the process of creating minds—thus we should not expect to find that, with appropriate social and cultural scaffolding, chimpanzees would be capable of developing fully human minds—but minds cannot be reduced to brain function alone (and, by the same token, this implies that unique chimpanzee minds have arisen via similar evolutionary, historical processes). The sociocultural foundations of human cognition are thus laid clear by this framework: mind is an active process by which we set out to make sense of our particular social environment and is itself changed as a result of that interaction through feedback processes designed to control our perceptions of ourselves and of others [6] (see also [27]). This adds a further interesting twist to a cybernetic, PCT view of behaviour as applied to humans, a point to which we will return later.

Another great advantage of this perspective is that it permits an investigation of the ‘social intelligence’ of other species in a manner that recognizes evolutionary continuity, yet does not impose human psychological constructs such as ‘concepts’ and ‘representations’ on other species as a matter of course. More specifically, the idea that the demands of social life have shaped the size and structure of the brain, and how primates think about the world, is now well established in both cognitive and comparative psychology [28]. Studies of non-human primates, however, have often approached this issue in heavily anthropocentric, and often explicitly anthropomorphic, terms: ‘bonds’ and ‘relationships’ have been construed, not just as human constructs used to make sense of structured patterns of behaviour between individuals, but as possessing clear psychological reality for the animals themselves, despite an absence of unequivocal evidence to show that the animals possess the reflexive, propositional or conceptual knowledge needed (see Barrett *et al.* [29] for review).

Given Mead’s views, an equally plausible hypothesis is that non-human primate social life involves a lot of ‘know-how’ aimed at controlling an individual’s perception of social space but very much less in terms of ‘knowing that’ [30]. In addition, the ecological

systems approach we advocate reverses the usual question of asking what precursors to human cognition do non-human species possess [12] but, instead, asks how social life functions on its own terms.

(c) *Social networks embody social ‘know-how’*

In this respect, our previous and ongoing work with baboons has proved valuable for reconfiguring how we think about group dynamics from a systems perspective, where social structure is viewed as an ongoing process of dynamic homeostatic adjustment and not as the static product of behavioural interaction. This approach builds on Flack *et al.*’s [30] previous ‘knock-out’ experiments, in which the effects of removing key individuals from a group were examined in relation to network structure. Their suggestion was that behavioural interactions within groups act to structure the kinds of ‘social niches’ it is possible to create and maintain, while these in turn influence subsequent behavioural strategies and tactics in an ongoing mutually reinforcing cycle. Social network structure thus reflects the dynamic feedback processes of social interaction: again, as Mead [6] and Powers [20] have argued.

We begin from the premise that, as the number of individuals with whom a given individual interacts, and the number of contexts in which they can do so, increases, the number of possible outcomes given a particular social situation also increases, and the certainty of interaction outcomes necessarily decreases. Individuals can control this local complexity by acting in ways that constrain the range of possible outcomes; that is, they can act in ways that structure social niche space more strongly [29–32]. A reliably structured pattern of engagement between pairs of individuals not only reduces the set of possible interactions for that pair, but also indirectly constrains the rest of the interaction network because it affects both the behaviour of their neighbours and that of their neighbours’ neighbours. As an obvious example, dominance hierarchies result from individuals constraining their agonistic interactions with others, which results in highly predictable interaction outcomes that minimize injury rate and reduce the uncertainty of interactions between dyads [33]. The same is true for cooperative behaviour [34].

(d) *Social interaction, uncertainty reduction and information theory*

The idea that uncertainty reduction drives social interaction is not new and has emerged independently in several disciplines. It has come to be seen as central to individual fitness [35–37], although it still lacks a formal analytical framework [37–40]. We suggest that progress can be made in this direction using social network neo-theory [41], because consistency in dyadic patterns of behaviour, along with any changes in consistency, can be captured, in abstract terms, by the topological features characteristic of interaction networks [35,42]. We refer to this as network ‘neo-theory’ to distinguish it from earlier incarnations that were more strongly sociological and human-oriented [43]. We therefore envisage an interaction network as an information transfer medium within a particular context, where information can also be gained from the

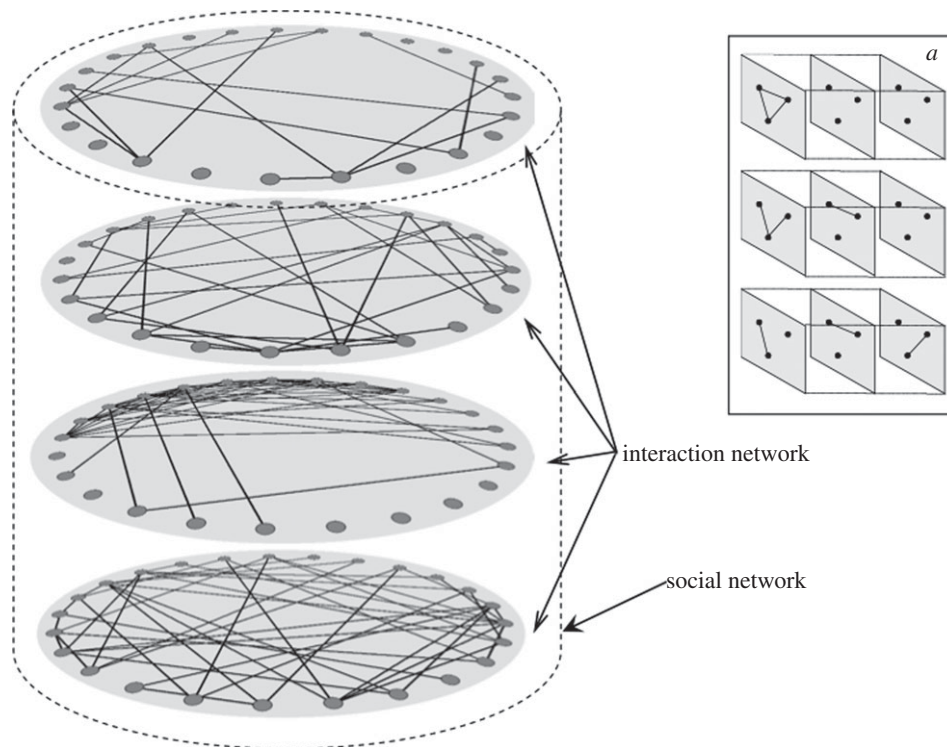


Figure 1. A social network is composed of b interaction networks between n individuals (here $n = 25$). Links between individuals are defined as interactions in b different behavioural contexts (dimensions). The clustering coefficient of an individual is calculated by estimating the number of triangular interactions (all members of a triad are connected), given all the possible triads in which that individual is involved. When individuals can interact in several behavioural dimensions, triangular interactions and triads can form in a number of different ways (inset a : where $b = 3$). We can see that, in these three cases, if we simply assumed the social network to be the union of the three interaction networks, then the clustering coefficient of all three vertices would be unity, when, in fact, all three examples present very different clustering configurations that have different structural information. Conceptualizing the network as a multi-dimensional object eliminates this problem.

reduction in interaction uncertainty. The advantage of considering this latter structural source of information is that it can be readily estimated as Shannon entropy [44]. As is well known, Shannon extended the thermodynamic concept of entropy to communication [44] and, since then, it has been applied in many fields as a measure of uncertainty [45]. The entropy of an interaction network is a measure that integrates behavioural consistency (and hence uncertainty reduction) across all individuals in the network, in a probabilistic fashion, because the links (known formally as edges) in the network represent the probability that two individuals will interact [46]. This formalization does not assume any 'active' information transfer between individuals (e.g. intentional symbolic communication) because it relies only on 'structural information' (i.e. the patterns of behaviour used to generate the links between individuals) and is therefore broadly applicable [47]. The concept of entropy has also been proposed as a valuable tool to understand network evolution [48].

In addition to capturing uncertainty reduction, we have also developed a means by which social networks can be analysed as multi-dimensional objects. That is, rather than viewing a social network as a single two-dimensional matrix, we can conceive of it as a layered series of interlinked matrices, the 'depth' of which corresponds to the number of different matrices that make up the layers. This is important because group members interact with one another in several social or behavioural contexts, referred to as 'dimensions' hereafter (e.g.

grooming, aggression, proximity maintenance, play, sexual behaviour, food sharing, allomothering) and, classically, we integrate information (in a sense, we 'flatten' or 'compress' it) across these behavioural dimensions to define the social network to which individuals belong [30,49,50] (figure 1). Interactions in one dimension, however, are not independent of those in others [30]. For example, two members of a monkey group can groom each other only to the extent that they can maintain spatial proximity. Therefore, reducing the uncertainty of interaction outcomes in a given context can be achieved not only by controlling interactions in that particular context, but also through indirect influences of interactions in other contexts. One individual can reduce the likelihood of grooming or fighting with another by avoiding proximity to that individual. This kind of information is lost, however, when we approximate social networks as 'flat' unidimensional objects.

In studies of human social networks, this potential information loss is compensated for by the ability of individuals to ascribe a set of identities to others in the network. In this way, individuals become objects that can be referenced through multiple categories that range from the geographical (e.g. nationality, city of residence) to the social (e.g. profession, group memberships, family ties) [49,50]. Such role ascription is an obvious problem when considering non-linguistic animals because, while roles may be ascribed to them by human observers, they cannot do so for themselves.

This, in turn, makes comparison between human and non-human networks difficult. If, however, we reconfigure the set of identities used to categorize individuals so that each is viewed, not as a property of individuals (the ‘nodes’ in the network), but as a property of the *relationships* (links) that exist *between* individuals, then we can produce a measure that is comparable across both humans and other non-linguistic species. Characterizing identities in this way makes sense because non-linguistic animals can acquire information and categorize conspecifics only to the extent that they interact with them, and/or can assess their interactions with others [31]. In other words, we can think of a social network, not as a single matrix linking individuals that possess a distinct set of identities, but as a set of individuals that interact in a number of behavioural contexts. In the latter situation, multi-dimensional ‘information’ is stored by the interactions themselves, i.e. as a set of interaction networks defined by their behavioural context.

Once we are able to characterize the multi-dimensional nature of a social network, we can then identify and study within-social-network constraints (i.e. those that occur *between* the different behavioural dimensions) that describe the social network’s global efficiency in uncertainty reduction, as well as identify the standard within-interaction-network constraints (i.e. those that occur within a single behavioural dimension) [51]. This is useful because different behavioural dimensions are likely to be differentially constrained [52] and their intersection may produce an aggregate reduction of uncertainty that cannot be derived solely from the reduction in each of the component networks. That is, there may be synergistic effects between behavioural dimensions that cannot be captured by a simple comparison of correlated changes among the interaction networks that represent these dimensions. Using our approach, it becomes possible to think of a social network, not simply as the sum of its component interaction networks, but as a multi-dimensional object with emergent properties of its own.

We therefore propose that social networks be considered as multi-dimensional objects composed of n individuals that can interact in b behavioural dimensions and that they do so in ways that serve to reduce uncertainty (i.e. produce a decrease in entropy). A mathematical representation of a social network in this case is not a matrix of $n \times n$ individuals but a third-order tensor of $n \times n$ individuals $\times b$ behavioural dimensions. Considering a social network as a higher-order tensor offers new avenues for the formalization of social structure and dynamics, allowing us to extend Flack *et al.*’s [30] earlier consideration of the relationship between networks and social organization. It becomes possible to estimate interaction uncertainties by measuring the global social network’s entropy, and thereby provides a means by which to test our central premise that uncertainty reduction drives overall social network dynamics.

Significantly, this means that, if we view the global social network as a system that carries benefits for the individuals that comprise the network, then we can expect selection to act on social behaviour in ways that maintain and/or restore the topology of the

network in the face of perturbation [45,53,54]. This is because perturbations to the social network will increase uncertainty: the potential outcomes of interactions in various behavioural contexts will be more difficult to predict because the social network structure has moved away from its stable state. Thus, as argued by PCT [20], we should expect individuals to be capable of varying their behaviour in order to maintain and control a particular goal state, and these changes in behaviour should therefore feed through to stabilize network structure, and so reduce uncertainty in the network as a whole [30]. One way of checking that our multi-dimensional approach is viable is to demonstrate that these tensors display small-world properties because studies in a wide range of disciplines have found this to be a key feature of social networks [41,49,50]. As we are able to show that this is the case (see electronic supplementary material), we feel justified in proceeding to more specific tests.

From our formalization, we predict, therefore, that perturbations to the network will be followed by a corresponding reconfiguration of interaction networks, which restructures the topology of the social network as a whole, thereby minimizing entropy. Accordingly, because of the degrees of freedom associated with increasing uncertainty, we expect the least constrained interaction network (the most uncertain) to change the most. We take advantage of natural removals (i.e. the death of particular females) from a chacma baboon (*Papio hamadryas ursinus*) social network to test these ideas.

2. METHODS

We collected agonistic, nearest-neighbour and grooming data between March 1997 and October 2006 from our main study troop of baboons in the De Hoop Nature Reserve, South Africa [55]. Data for these analyses come from all adult females ($n \sim 12$), who were individually recognizable and habituated. Data were collected using electronic data loggers, while following the animals on foot from dawn to dusk on each sampling day [55]. We used these data to construct a multi-dimensional social network for these females, composed of separate agonistic, spatial and grooming interaction networks.

(a) *Changes in interaction network topology*

To test our prediction, we took advantage of unique natural ‘knock-outs’ [30] to investigate the effects of a disturbance to the agonistic interaction network, caused by the death of females holding a particular rank, on the spatial and grooming interactions of other females. Disruptions to the dominance hierarchy will affect agonistic interactions because this structure reduces overall aggression in the troop [34,52]. We compared the nearest neighbour and grooming networks before and after the death of the dominant female in the troop (‘high’ treatment). We then compared these with patterns observed after the disappearance of a low-ranking female (‘low’ treatment), and to data from a comparable period during which no females died, and the network remained stable (‘control’). This study design, based on the before-after-control-impact (BACI) approach used in ecology

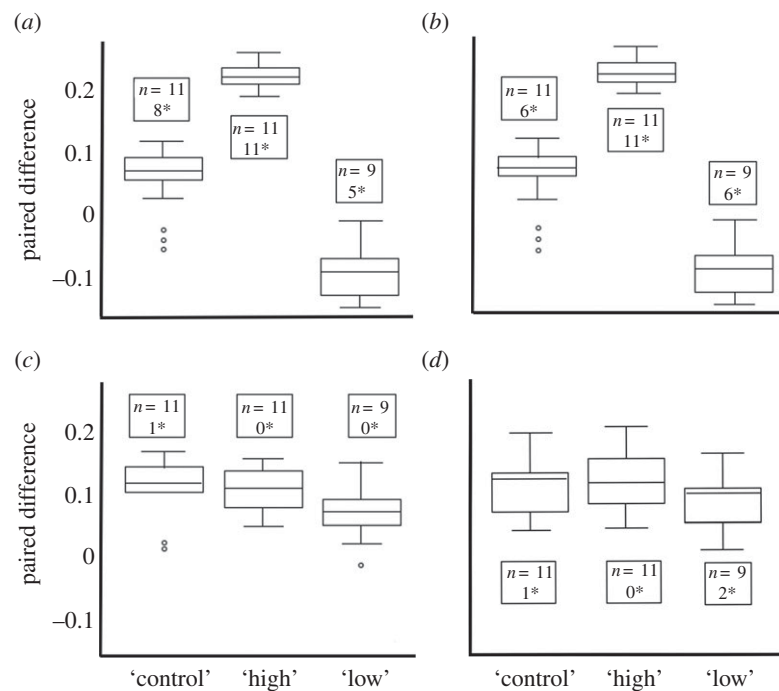


Figure 2. Paired differences in (a,c) in- and (b,d) out-clustering coefficients for the nearest neighbour (a,b) and grooming (c,d) directed weighted social networks. Captions associated with each boxplot provide the number of paired comparisons calculated (n) and the number of individuals that had a significant change in clustering coefficient after the treatment (asterisk).

[56], allowed us to account for inherent variability in network features owing to both food availability cycles [57] and perturbation owing to changes in troop composition [55]. Social networks were therefore compared across the following three treatments:

control (no individuals died):

before: from September 2003 to February 2004

after: from March 2004 to August 2004

dominant female disappearance ('high'):

before: from September 2000 to February 2001

after: from March 2001 to August 2001

low-ranking female disappearance ('low'):

before: from November 1997 to April 1998

after: from May 1998 to October 1998

We also compared the observed variation in network features with a simulated removal condition, in which individuals were simply artificially removed from the control network and the network measures then re-calculated.

For each of these six periods, we derived three directed and weighted interaction networks from the agonistic, spatial and grooming data, respectively. The network nodes represented individual females and the edges represented the rate at which female i was observed as (i) the nearest neighbour; (ii) the aggressor; (iii) the groomer of female j , given the number of times i was observed. The indices were calculated with a sampling period of one day to address problems of pseudoreplication [58]. The resulting association index matrices AI_{ij} were not symmetrical and therefore AI_{ij} is not the same as AI_{ji} , i.e. the interaction indices are directional, in addition to being

weighted. For each interaction network, we then calculated the females' clustering coefficients [59], accounting for weight and directionality in the data (for details, see electronic supplementary material).

(b) Uncertainty and constraints on the global social network

Given that we are interested in the capacity of the global social network to reduce uncertainty for its members, we estimated the Shannon entropy of this object [44] from the joint entropy of the interaction networks (see electronic supplementary material). We first inferred the constraint of each behavioural dimension by estimating the entropy for each interaction network under each condition. We could then test whether the least constrained dimension (*post hoc* inference) was the one that changed most in the wake of female disappearance.

3. RESULTS

(a) Changes in interaction network topology

After the dominant female disappeared and the agonistic network changed ('high' treatment), all females became significantly more 'cliquish' in their spatial associations (figure 2a,b): a given female's nearest neighbours were also very likely to be recorded as the nearest neighbours of each other (i.e. if A's nearest neighbours were B and C, then B was also likely to be the nearest neighbour of C and vice versa). Significant differences in clustering were also observed in the 'low' treatment. Interestingly, however, the 'high' knock-out condition was the only treatment in which *all* individuals changed their behaviour significantly: the paired differences here were significantly greater than those observed in the other two treatments

Table 1. In- and out-clustering coefficient mean paired differences (in-cc and out-cc, and associated s.e.) in spatial proximity (figure 2*a,b*) for the three treatments ('control', 'high', 'low') and associated test that the samples come from the same distribution based on two-sample permutation tests for small sample sizes (observed *t*-statistic based on *n* samples generated for the permutation distribution (t_n) and associated *p*-values).

	control	high	low
in-cc	0.06 (0.014)	0.23 (0.005)	−0.07 (0.012)
'control'	—	—	—
'high'	$t_{705432} = 11.4, p < 0.0001$	—	—
'low'	$t_{167960} = 7.0, p = 0.0003$	$t_{167960} = 25.0, p < 0.0001$	—
out-cc	0.07 (0.010)	0.22 (0.006)	−0.10 (0.012)
'control'	—	—	—
'high'	$t_{705432} = 12.5, p < 0.0001$	—	—
'low'	$t_{167960} = 11.0, p < 0.0001$	$t_{167960} = 26.1, p < 0.0001$	—

(table 1 and figure 2*a,b*). Changes in the agonistic interaction network did not affect the grooming behaviour of female baboons under either the 'high' or 'low' treatment (figure 2*c,d*).

Thus, the loss of the dominant female, and the resulting instability in the dominance hierarchy (i.e. agonistic interaction network), was compensated for by a homeostatic adjustment in the spatial association network. This suggests that dominance serves to regulate the interactions of all group members, even in the absence of specific 'policing' behaviours. This is reinforced by the fact that the loss of low ranking female from the network, while significant, did not produce the same behavioural adjustments across all females.

(b) *Uncertainty and constraints on the global social network*

The earlier-mentioned results from the 'knock-out' events show that, as with [30], perturbations to the agonistic interaction network lead to compensatory adjustments in the spatial interaction network. Given this, we could test whether there was also a reduction in the joint entropy of the global social network (the multi-dimensional tensor), because the increased conservatism of female spatial association should reduce the uncertainty of their behavioural interactions across all inter-related dimensions. That is, the shifts seen in the interaction networks allow us to test whether our multi-dimensional tensor approach withstands scrutiny, providing a 'proof of concept'. As figure 3*a* shows, perturbations to the agonistic interaction network did indeed result in compensatory shifts in the global social network for both 'high' and 'low' treatments. That is, there was a drop in joint entropy, such that all interactions showed lower uncertainty (more conservatism) than had been the case prior to the females' death. In all cases, the drop in joint entropy was greater than that derived from a simple simulated perturbation (random removal of individuals from the 'before' social networks). We therefore consider this to be a formalization of the effects observed in Flack *et al.* [30] because a more certain social network corresponds to one in which behavioural interactions are more conservative. This is consistent with our hypothesis that network dynamics can be profitably investigated at the global social network scale, and allow us to study network dynamics

in a non-reductionist fashion. We were also able to use our entropy measure to show that the spatial interaction network was the least constrained in all conditions (figure 3*b*). This observation, in conjunction with the observed changes in the spatial interaction networks after the natural removals (figure 2*a,b*), supports our prediction that the least constrained behavioural dimension should be the one that changes most in order to restore network stability.

4. DISCUSSION

Our results show that when the interaction network in one behavioural dimension is perturbed, the baboons in our study population made compensatory adjustments in another behavioural dimension, restoring network stability by reducing the uncertainty of interactions. Thus, variation in the joint entropy of the social network provides a way to track the effects of social perturbations and offer support for our proposition that social structure dynamics can be understood under the premise of uncertainty reduction. Our findings also indicate that, even without specific mechanisms for conflict management, such as the 'policing' studied by Flack *et al.* [30] in captive macaques, dominance stabilizes the social network, promotes network robustness and increases its information content. Our study design allowed us to confirm that it was this specific aspect of social structure, and not ecological variability or the constraints of captivity that generated the observed network differences. Evidence for such effects in the wild indicates that they may have wide generality and significance for studies of sociality across a broad array of species.

Both our formalization of the social network as an *n*-dimensional tensor, and our use of Shannon entropy provide meaningful, and biologically relevant, ways to describe network dynamics, which can be applied across both human and non-human species. The demonstration that the identities, or 'roles', assigned to individuals in a network can be reconfigured as properties of the behavioural interactions that exist between individuals in the network also has significant implications for the study of non-human societies more generally. It counters the long-standing reluctance [60] to consider group-level features, such as 'roles', in the social analysis of species other than humans, where such roles can be ascribed only to the animals 'from the outside' in the same way we

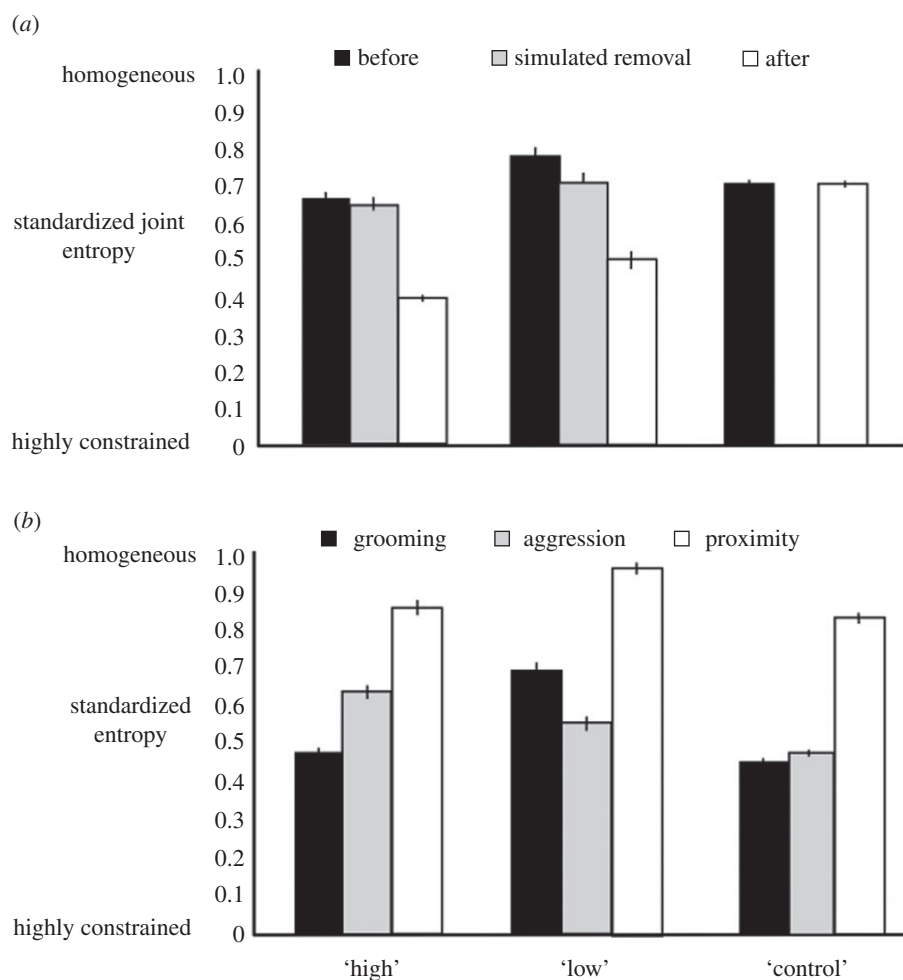


Figure 3. (a) Changes in the standardized joint entropy of the social network under the different treatments and (b) the entropy of each interaction network for each treatment 'before' conditions. These values range from zero (highly constrained interactions) to unity (homogeneous interactions). Error bars are jack-knifed standard errors.

ascribe identities to individual humans in social networks, and are not features about which the animals themselves can be assumed to have knowledge. In our formulation, 'roles' are emergent properties of the intersecting behavioural dimensions that make up the global social network. The role of the dominant female in structuring the network, for example, emerges from the manner in which her behavioural interactions influence the social niche space of other individuals and the manner in which they engage with each other, but there is nothing in this formulation that requires dominant animals to recognize or adopt this role in any formal sense. This allows us to take advantage of the kind of systems perspective used so productively by authors such as Crook [61,62] to understand mammalian, and specifically primate social systems, without requiring the ascription of roles in a manner that cannot be supported in the absence of language.

Lastly, our conception of social networks as multi-dimensional objects allows us to derive hypotheses about the evolution of social network complexity. Under an uncertainty minimization process, the network will reach a minimum entropy, H_{\min} , given b , the number of behavioural dimensions and n , the number of individuals. Trivially, H_{\min} would be zero: individuals would be most certain of interaction

outcomes if they did not interact at all. If individuals need to engage with others, however, as they must in social and gregarious species, then H_{\min} will depend on b and n . If we assume that population size (the number of vertices in the network) remains quasi-constant, e.g. when the population is at carrying capacity, then the only way for individuals further to reduce their uncertainty is to increase b . They would, in other words, need to develop new behavioural dimensions in which to interact with others as a means of improving the predictability of their interactions and reducing uncertainty. We therefore propose that our paradigm provides a mechanistic process by which the coevolution of behavioural complexity (b) and social complexity (H_{\min}) can be investigated.

Although we may now seem very far from the issues discussed in §1, our ideas concerning the evolution of behavioural complexity lead us back to the consideration of why humans differ from other primates, in terms of our ability to recognize our own roles, and those of others, and how such knowledge feeds back and influences the manner in which we fulfil them. Johnson [63], for example, investigating human social dynamics, noted that there are interesting scalar effects to be observed as human group size increases (see also White [64]). Once group size (in any context, from hunter-gatherer groups to

artificially convened groups in laboratory settings) exceeds around six individuals, there needs to be some form of (at least semi-) formal leadership or hierarchical structure in place if the group is to continue functioning productively. That is, in human groups, even when the number of individuals involved is small, the emergence of ascribed roles to self and others seems to be a universal means of dealing with the stresses imposed by the differing goals and perspectives of the group's members. Once hierarchical structures are in place, group productivity again increases. This has clear links to our ideas concerning the multi-dimensional nature of social networks, and the use of entropy measures to characterize behavioural certainty and network stability. That is, when network stability is threatened in human networks, overt role ascription and hierarchical structure are, apparently, used to increase the certainty of interactions within the group (reduce entropy), and so restore stability. Why humans require formal role ascription to achieve this, when non-human animals do not, is an interesting question, but it suggests that the human ability (and, presumably, the requirement) to engage in explicit rule-following, as opposed to rule-satisfying, behaviour may be crucial [65]. As such, it also suggests that, as Mead [6] argued, the use of language is key to understanding this distinction [6,65], and that it is, potentially, the richness of contexts in which we interact that forces this symbolic referencing of roles.

This brings us to the other point of linkage with the beginning of the paper, namely Mead's theory of self-formation, and how this hinges on the idea of roles. For Mead [6], selves emerge only in relation to others, and he used what he referred to as 'the game' to get this point across. In order to play the game (of social life), one has to appreciate and understand not only one's own role, but also the roles of all the other 'players', and language is the means by which one's actions are named, pointed out and interpreted by others, and vice versa ('symbolic interactionism'). (See also Goffman's [66] classic work on the presentation of the self in everyday life, which draws on Mead's ideas.)

These ideas are easily translated into the terms we have been using here; that is, the idea of individual humans as nodes in social networks, in which their position can only be understood in relation to others, and where the set of identities they hold (their roles) influences their behavioural interactions with others, and so network structure. This again suggests, as argued earlier, that what is crucially different about humans is the manner in which they recognize and understand their role in the network, follow explicit rules of conduct, and how this process is brought about socially, i.e. the manner in which it is mediated by language [6,65]. This is not to say, of course, that human networks do not also contain information in the form of the relationships (behavioural interactions) that occur between nodes: know-how is as important a part of human life as knowing that. Rather, the idea is that human networks contain both these sources of information, whereas non-human networks contain only one, and that the need for this 'second level' of understanding—of seeing ourselves

'objectively'—is itself an emergent property of increasing social complexity [67]. In other words, the use of language (i.e. symbolic communication) to mediate social interactions, with explicit rules of conduct as an important element of social life, emerges as a means to reduce uncertainty created by the increased 'richness' of interaction contexts. Exploring this distinction in comparative perspective is, we feel, a productive means of pursuing questions regarding both social and cognitive evolution in their own right, as opposed to a more anthropocentrically oriented approach. Moreover, when we consider this in the broader context of the embodied-ecological framework, which emphasizes the manner in which human psychology is constructed developmentally via social interactions with others [6,10,11,68,69], our position has clear implications for the strongly adaptationist school of human evolutionary psychology.

In particular, it calls into question the idea that since the rise of agriculture, cultural changes have occurred at a pace that is too fast to allow human brains (and hence behaviour) to adapt. As Pinker [3, p. 42] has noted: 'Our brains... are not wired to cope with anonymous crowds, schooling, written language, governments, police, courts, armies, modern medicine, formal social institutions, high technology and other newcomers to human experience.' But this seems odd, given that we are the ones who invented all these things, and have put them to exceptionally good use. If we were able to devise, invent, improve and modify all of these things, why cannot we cope with them? By contrast, the embodied-ecological-systems framework, with its emphasis on the cultural, social and historical construction of humans, and the reflexive manner in which these feedback on each other in the creation of human persons, selves and minds [6,10,11,25,26], suggests that human minds are more than able to keep pace with cultural change because they are, in large part, created by and through such cultural processes [11].

Our minds are constantly being transformed over the course of our individual development, and also over historical time, by the inclusion of psychological tools, such as language, and material culture into our daily lives. Viewed as a process, it becomes clear that our minds have not just been shaped by evolution, but also have been formed by those sociocultural processes that occur during development, processes that have, and will, vary in both time and space. As we take on the social practices that give rise to new psychological tools, so we take on the entire history of our culture as well. Human cognitive evolution is, then, an ongoing and contingent process. We are different psychological creatures to the peoples of 100, 10 000 and 100 000 years ago, and the people of 1000 years hence (assuming humans are still around) will be very different psychological creatures to us. As Dewey [25,26] noted and as Hacking [69] has pointed out more recently (see also Hacking [70]), this potentially raises a deep paradox for the human/social sciences, and psychology in particular. The reflexive nature of human selves, and their creation and maintenance via sociocultural processes, means that identity is not fixed and self-contained, but is an ongoing process of construction [4,25,26,68–72]. Arguing that a large part of what it means to be a 'person' are the categories used to describe them,

Hacking [69] shows how we are able to construct new 'human kinds' (e.g. the 'alcoholic', 'autistic child' and 'the homosexual', represent some of the 'kinds' Hacking identifies) and demonstrates that these have interesting 'looping effects'; people so labelled by these constructions change and reconstruct their selves as a consequence, and their lived experience then feeds back on itself to determine how such kinds are realized, recognized, studied and also exploited and enhanced.

Psychology, with its desire to understand human kind and 'kinds', may well be instrumental in generating the kinds of humans that it studies, thereby raising some interesting and possibly painful questions about the nature of psychology as a science, and what it means for our understanding of human cognitive evolution [4,25,26,72]. On the positive side, it means that, even if we cannot come to fully understand the past evolution of human cognition, the possibility remains that we can study its ongoing and future evolution, through an understanding of the entanglement of cultural practices and historical events with our biological heritage.

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