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Macaques attend to scratching in others

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Self-directed behaviours in primates as a response to increasing psychological or physiological stress are a well-studied phenomenon. There is some evidence that these behaviours can be contagious when observed by conspecifics, but the adaptive function of this process is unclear. The ability to perceive stress in others and respond to it could be an important part of sustaining cohesiveness in social primates, but spontaneously acquiring stress-related behaviours (and potentially emotional states) from all group mates via contagion could be maladaptive. To investigate this, a group of captive Barbary macaques, *Macaca sylvanus*, were presented with videos of conspecifics engaging in self-directed behaviour (scratching) and neutral behaviour. Behavioural responses as a result of exposure to the stimuli were compared (1) between familiar and unfamiliar individuals, and (2) within familiar individuals to consider the modulating effects of social relationships. Our results did not show contagious scratching in this species. However, there were differences in how individuals attended to the scratching stimuli. Subjects were more attentive to scratching videos than to neutral videos and familiar than unfamiliar individuals. Within the familiar individuals, subjects were more attentive to those to whom they were weakly bonded. We suggest that increased attention to scratching behaviours may be adaptive in order to monitor and avoid stressed group mates, whose subsequent behaviour may be unpredictable and aggressive. Monitoring group mates who are not allies may also be adaptive as they may pose the biggest risk. These findings will help increase our understanding of subtle cues that can be communicative in primates, and also the evolutionary steps towards understanding others.

In a wide range of animal taxa, humans included, individuals produce self-directed behaviours that often appear irrelevant to current activities (Tinbergen, 1952). Although a social function of these behaviours is yet to recognized, these behaviours, which, for example, include scratching, face touching, self-grooming and yawning in primates (Mohiyeddini, Bauer, & Semple, 2013; Pavani, Maestripieri, Schino, Turillazzi, & Schucci, 1991; Schino, Troisi, Perretta, & Monaco, 1991; Troisi, 1999), have been shown to reliably indicate the presence of both psychological and physiological stress (Maestripieri, Schino, Aureli, & Troisi, 1992; Troisi, 2002). Mice, *Mus musculus*, presented with a novel environment increase chewing behaviours irrelevant to that of feeding or escape in response to stress (Hennessy & Foy, 1987). Many bird species increase rates of preening in stressful situations, for example when disturbed while resting (Delius, 1988). High rates of scratching follow intense intragroup aggression in macaques, particularly in the victims (Aureli, van Schaik, & van Hoof, 1989) and chimpanzees, *Pan troglodytes*, scratch more frequently when the difficulty of cognitive tasks increases (Leavens, Aureli, Hopkins, & Hyatt, 2001) or when frustration is induced through an unsolvable task (Waller, Misch, Whitehouse, & Herrmann, 2014). Thus, in some contexts, there is a demonstrable relationship between stress and self-directed behaviour in animals.

Unhelpfully, the term stress is used variably throughout the literature, to describe situations from mild stimulation to extreme adverse conditions (Koolhaas et al., 2011). Here, we define stress as a biological response elicited to cope with disruptions to an animal's homeostasis (Moberg, 1999), and a natural and common response to challenges animals face in their environment. We separate stress from distress, which can be observed after prolonged periods of extreme stress, and leading to often unnatural, exaggerated and stereotyped behaviours (e.g. feather plucking in parrots and trichotillomania in humans, van Zeeland et al., 2009). The behaviours associated with stress, however, are usually variants of normal functional behaviours (e.g. self-grooming, which also serves a hygienic function (Maestripieri et al., 1992).

Our current understanding of the adaptive value of these behaviours is that they function to reduce the physiological stress

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response, playing an important role in how animals cope with stress (Koolhaas et al., 1999). For example, increasing chewing and gnawing behaviours attenuates physiological stress responses of rodents, including a reduced activation of stress-associated neural systems (Berridge, Mitton, Clark, & Roth, 1999) and endocrinological responses (Hennessy & Foy, 1987). In bushbabies, *Otolemur garnettii*, individuals that perform increased scent marking in response to stress exhibit a lower cortisol response, and therefore appear to cope with stress more effectively (Watson, Ward, Davis, & Stavisky, 1999), and in human males, those who engage in increased self-directed behaviours during stressful events report lower experienced stress afterwards (Mohiyeddini et al., 2013). The evidence for self-directed behaviours as a coping mechanism is convincing; what we do not know, however, is whether or not these behaviours are socially relevant.

When scientists focus on behaviours that are associated with underlying emotional states there is a tendency to focus on the feelings of the actor and subsequently ignore the potential responses these behaviours may elicit in the receiver (Waller & Micheletta, 2013). Historically, this has been particularly true for the study of facial expression (Darwin, 1872; Fridlund, 1994), and may also be the case for the study of self-directed behaviour. To understand the evolution of stress behaviours, it is imperative to fully explore their functional value and not only their causal value (Tinbergen, 1952). One proposal is that these behaviours could also have a social function by providing information to a social audience about internal states (Bradshaw, 1993). If so, self-directed behaviours may not just function as a coping mechanism, but could be an important aspect of the social repertoire of some gregarious animals. Specifically within the primates, a communicative function of stress behaviours has been proposed (Bradshaw, 1993; Maestripieri et al., 1992; Nakayama, 2004; Waller et al., 2014), but empirical evidence remains elusive.

Although a social function of self-directed behaviours remains undocumented in any species, we do know that these behaviours can, in some cases, be contagious when observed by others. A contagious response has been reported following the observation of both yawning (dogs, *Canis familiaris*, Joly-Mascheroni, Senju, & Shepherd, 2008; budgerigars, *Melopsittacus undulatus*, Gallup, Swartwood, Militello, & Sackett, 2015; chimpanzees, Anderson, Myowa–Yamakoshi, & Matsuzawa, 2004; gelada baboons, *Theropithecus gelada*, Palagi, Leone, Mancini, & Ferrari, 2009) and scratching (rhesus macaque, *Macaca mulatta*, Nakayama, 2004; Japanese macaque, *Macaca fuscata*, Feneran et al., 2013). In a handful of these examples, the contagious response has been sensitive enough to be triggered experimentally through the presentation of videos (Feneran et al., 2013; Paukner & Anderson, 2006) and, particularly for the primates, have been discussed mostly alongside the subject's (and species') capacity for empathic behaviours (Lehmann, 1979). However, spontaneous acquisition of stress behaviours (and therefore potentially the acquisition of stress itself) may lack adaptive value. Cognitive function and decision making are significantly impaired in stressed individuals (McEwen & Sapolsky, 1995) and prolonged stress has many recognized negative effects on health (Sapolsky, 1996). If cognitive function and decision making are impaired in the individuals surrounding a stressed animal, this may not produce an optimal social environment that allows for the mitigation of stress or may not allow for a response to stressed group mates in a way that would be the most advantageous. Responding to the stress of others spontaneously through emotional contagion, therefore, has the potential to be a maladaptive strategy. Instead, a more adaptive strategy could be to monitor these behaviours in others and respond to them in a facultative way that is functional (such as a positive or negative social interaction) and provides an advantage for one or all individuals.

If responses to stress behaviours go beyond contagious affect and, instead, elicit functional responses in others, we could expect both the production of a signal and the response to it to be influenced by the sender–receiver relationship (Guilford & Dawkins, 1991; Micheletta et al., 2012). Signals often occur more frequently if the audience contains key social partners (Slocombe et al., 2010), and the response to signals can become stronger as social relationships become more important (Micheletta & Waller, 2012). By addressing how social relationships affect the production and response to communicative behaviours, we can, as a first step, begin to understand their function. A stronger response by friends or kin could suggest a function to facilitate cooperative efforts (Micheletta et al., 2012; Slocombe et al., 2010), whereas a stronger response by competitors could suggest that a signal functions to facilitate competition (Muroyama & Thierry, 1998). In the context of stress, by attending and responding to the stress behaviours of friends and kin, individuals could capitalize on important opportunities to manage social relationships and maintain a cohesive social group (Clay & de Waal, 2013). Conversely, monitoring the potential stress in competitors could provide opportunities to maximize competitive efforts by being able to taking advantage of another's weakness (Byrne & Whiten, 1989).

Assessing when and how animals respond to the negative emotions of conspecifics could significantly contribute to our understanding of sociality, and has the potential to inform us regarding the evolutionary steps that may have led to the ability to understand others. In the following experiment, we aimed to assess whether behaviours directly related to stress are socially functional, and whether or not these lead to responses in observers. As a species characterized as highly gregarious and cooperative (Thierry, Singh, & Kaumanns, 2004) the Barbary macaque, *Macaca sylvanus*, provides an excellent model for the study of social behaviour in animals. We predicted that the macaques would respond to the stress behaviours of others, particularly those with whom they had close social bonds, and in a way that may provide further opportunities for cooperation.

METHODS

Subjects and Housing

This study was conducted between February and December 2015. We tested six, unrelated adult Barbary macaques (two males, four females) currently living in a social group at the Monkey Haven, Isle of Wight, U.K. Subjects had free access to a naturalistic, grassy outdoor area (20 × 12 m and 4 m high), filled with trees, logs, ropes, swings and a waterfall. New novel enrichment devices were provided to the animals weekly. Animals also had free access to a smaller outdoor area (5 × 5 m and 4 m high), and a heated indoor area (5 × 3 m and 3 m high). Subjects could be separated into each of the areas as needed; however, the smaller outdoor area was used for all experiments. Prior to this study, all subjects had been exposed to cognitive testing and were habituated to the presence of the experimenter. Macaques were fed daily with assorted fruits and vegetables, nuts, cereals, seeds and commercial monkey pellets. Water was available ad libitum. Our experiments never impacted on the normal dietary and husbandry routines of the animals.

Stimuli and Apparatus

For each animal, we prepared 20 experimental videos: 10 scratching videos and 10 neutral videos. Half featured a familiar individual (another Monkey Haven group mate) and half featured an unfamiliar individual (a Barbary macaque from an unknown