



Doing what your neighbour does: neighbour proximity, familiarity and postural alignment increase behavioural mimicry

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Nonconscious behavioural mimicry, acting similarly to one's social partner, is thought to be a core component of group cohesion and coordination. However, the mechanisms contributing to this phenomenon are poorly understood. Understanding why behaviour is mimicked in some contexts but not in others is an important step in developing hypotheses about how and why some behaviours spread between social partners. Here we examine mimicry of routine vigilance during grazing episodes in a population of free-ranging bighorn sheep, *Ovis canadensis*, rams. Results indicate that vigilance bouts are more likely to be mimicked when neighbouring rams are in closer proximity, more familiar with one another and posturally aligned. Additionally, older rams are more likely than young rams to mimic the vigilance bouts of others, and mimicry occurs more often when the initiating ram is lower ranking than the mimicking ram. We interpret these findings within the framework of biases in attentiveness to particular individuals as a possible mechanism leading to the occurrence of behavioural mimicry.

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Social, group-living animals often synchronize their behaviours with others because behaving similarly is, in essence, the glue that holds groups together (Dunbar & Shultz, 2010; Duranton & Gaunet, 2016; Gautrais, Michelena, Sibbald, Bon, & Deneubourg, 2007; Lakin, Jefferis, Cheng, & Chartrand, 2003; Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2002). If individuals acted independently of one another, a social group would cease to exist. Instead, it turns out that behaviours are surprisingly contagious between individuals of a social group (Chartrand & Bargh, 1999; Chartrand & van Baaren, 2009; Christakis & Fowler, 2009; Ginelli et al., 2015; Hatfield, Cacioppo, & Rapson, 1994). Nonconscious behavioural mimicry, also dubbed 'the chameleon effect', occurs when an individual's behaviour changes to become more similar to that of a social partner, and this change is unintentional and often unnoticed by the actor (Chartrand & Bargh, 1999). Although possible higher-level cognitive processes have been suggested to contrast behavioural mimicry from behavioural contagion (Yoon & Tennie, 2010), in this paper we use the terms in a similar manner, with only the linguistic distinction that it is behaviours that are contagious and individuals that mimic.

In contrast with imitation, contagious behaviours typically consist of reflexive behaviours that do not need to be learned (Miller, Gallup, Vogel, Vicario, & Clark, 2012; Zentall, 2003). For example, observing a yawn elicits a yawning response in several different species (e.g. birds: Gallup, Swartwood, Militello, & Sackett, 2015; Miller et al., 2012; dogs: Joly-Mascheroni, Senju, & Shepherd, 2008; Romero, Konno, & Hasegawa, 2013; primates: Demuru & Palagi, 2012; Palagi, Leone, Mancini, & Ferrari, 2009). In birds, preening behaviour is contagious (Palestis & Burger, 1998); in marmosets, gnawing and sent marking are contagious (Massen, Šlipogor, & Gallup, 2016); in humans, laughter contagion can be near impossible to prevent (Christakis & Fowler, 2009; Provine, 1992, 1996), and in many different species, individuals eat more, or resume eating, when alongside other individuals that are eating (e.g. domestic dogs, *Canis familiaris*: Ross & Ross, 1949a, 1949b; domestic chickens, *Gallus gallus domesticus*: Hughes, 1971; humans: Herman, 2015).

Behavioural mimicry is one mechanism for synchronizing the activities of individuals in a group, and this synchronization can ultimately promote group cohesion and coordination. For example, in birds, stretching and yawning often precede a change in activity from resting to flight, and these behaviours appear to be contagious to other group members (Miller et al., 2012). This contagion provides a means of preparing the group for flight and synchronizing the group's change in activity.

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While contagion is likely a fundamental behaviour for group-living animals, it may not manifest equally across all individuals. Why does contagion occur with some individuals, in some contexts, and not in others? While biases in the spread of contagious behaviours have been studied extensively in humans (reviewed in: van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009; Duffy & Chartrand, 2015), significantly less is known about these biases in nonhuman animals. Biases in the spread of contagious behaviours in nonhuman animals have primarily been investigated using yawn contagion, where mixed results have stirred debate. Research on canine and primate species suggests that yawn contagion is more likely to occur between individuals that are more familiar or emotionally close (Campbell & de Waal, 2011; Demuru & Palagi, 2012; Palagi et al., 2009; Palagi, Norscia, & Demuru, 2014; Romero, Ito, Saito, & Hasegawa, 2014; Romero et al., 2013). In contrast, Massen, Vermunt, and Sterck (2012) found that yawn contagion was not affected by relationship quality in chimpanzees, and no familiarity bias has been found for contagious yawning in young dogs (Madsen & Persson, 2013). In humans there is mixed support for an affiliation bias in yawn contagion (Massen, Church, & Gallup, 2015; Norscia & Palagi, 2011). Interestingly, while yawn contagion in budgerigars was not found to have a familiarity bias, the authors state that their unpublished data indicates a familiarity bias for stretching contagion in this species (Gallup et al., 2015), suggesting that familiarity biases may not affect all behaviours equally.

A possible sex bias in yawn contagion has also been investigated but does not appear consistent across species or studies. For example, in wolves, *Canis lupus*, a shorter latency to contagion was found for females (Romero et al., 2014), whereas chimpanzees, *Pan troglodytes*, showed the highest response rate for males observing male yawns (Massen et al., 2012). In contrast, a review of studies on human yawn contagion concluded there is no sex bias (Gallup & Massen, 2016), and several animal studies have also found no sex bias (Buttner & Strasser, 2014; Campbell, Carter, Proctor, Eisenberg, & de Waal, 2009; Campbell & de Waal, 2011; Joly-Mascheroni et al., 2008; Madsen, Persson, Sayehli, Lenninger, & Sonesson, 2013; Romero et al., 2013). Outside of yawn contagion, it appears that little is known about biases in the spread of contagious behaviours in nonhuman animals. Understanding the conditions necessary for behaviour contagion to occur can help to guide investigations into the mechanisms underlying these contagious behaviours and allow us to understand how this phenomenon might manifest across a diversity of group-living species.

Here we examine vigilance behaviour in bighorn sheep, *Ovis canadensis*, to determine whether individuals are more likely to mimic group members that are more socially relevant to them. Vigilance behaviour is defined as an individual sheep raising its head from grazing to scan its surroundings, often looking in several directions before returning to grazing. In group-living species, individual bouts of vigilance do not appear to be independent of one another; but rather, they cluster together in 'waves of collective vigilance' (Pays et al., 2007). This synchronization of vigilance behaviour has been noted in a range of different species (e.g. ungulates: Pays, Sirot, & Fritz, 2012; birds: Fernandez, Capurro, & Rebores, 2003; marsupials: Pays, Dubot, Jarman, Loisel, & Goldizen, 2009; Pays, Goulard et al., 2009), and Pays, Goulard et al. (2009) suggested that allelomimetic effects may be responsible for the synchrony. However, it is not yet clear whether the strength of these mimicry effects may differ between dyads. If so, the occurrence of this vigilance synchronization may partially depend on individuals in the group maintaining particular spatial arrangements.

In this study, we compare the frequency of vigilance mimicry across interacting dyads with different social and spatial features.

Because increased attentiveness to particular individuals increases behavioural mimicry (van Baaren, 2009), we predicted that the frequency of behavioural contagion would be higher from individuals of higher social relevance, as they should elicit greater levels of attention. Studies of visual monitoring in group-living animals typically correlate attention with the degree of competition or threat posed by an individual (e.g. Cameron & du Toit, 2005; Keverne, Leonard, Scruton, & Young, 1978; Lane, 2008; Li et al., 2012; McNelis & Boatright-Horowitz, 1998; Pannozzo, Phillips, Haas, & Mintz, 2007). These findings demonstrate that visual monitoring is not distributed equally across group members, but rather, it is biased towards higher-ranking animals. Interestingly, visual monitoring also appears to be biased towards affiliated partners such as kin, mates or other socially bonded individuals (Lane, 2008; reviewed in Dunbar & Shultz, 2010). Functionally, visual monitoring and other forms of social attention (e.g. auditory) are necessary for the coordination of behaviour so that these individuals are able to remain in a group together (Dunbar & Shultz, 2010). Thus, individuals of high social relevance may stem from both competitive and affiliative relationships. In both cases, a bias in attention towards these individuals is predicted to lead to an increase in the probability of behavioural mimicry.

Here we investigate several social features of the interacting dyad that are anticipated to influence the likelihood of mimicry. Based on the evidence that social monitoring is biased according to the perceived level of threat/competition from an individual, we predicted that the vigilance behaviour from rams of higher rank, older age and closer proximity would be more contagious. In addition to social monitoring for threats, increases in attentiveness may also occur for the purpose of maintaining cohesion with affiliative partners, as outlined above. We therefore expected that increased social attention must underlie behaviours expressing synchrony and maintenance of proximity. Here, we use association indices to denote dyads that spent proportionally more time together, and we use postural alignment as an indicator of behavioural synchrony and real or perceived in-group membership. Alignment between two individuals in a group is suggested to occur as a result of competing forces of attraction and repulsion towards neighbouring individuals (Katz, Tunström, Ioannou, Huepe, & Couzin, 2011). Consequently, maintaining alignment with a neighbour is likely to depend on maintaining an optimal distance from them, resulting in interindividual synchrony of movement. Furthermore, perception of in-group membership may stem from aligning (and/or moving) in the same direction as a neighbouring individual. A type of 'blurring' between self and other has been described in response to military drill in humans (McNeill, 1997), during which members spend long periods of time standing or moving while synchronously aligned. Furthermore, pedestrians waiting to cross a road mimic the road-crossing behaviour of other pedestrians they are waiting alongside (Faria, Krause, & Krause, 2010), and drivers of motor vehicles tend to match the speed of other vehicles travelling alongside them (Connolly & Åberg, 1993). Pedestrians have also been shown to gaze-follow from those oriented in the same direction as them (Gallup, Chong, & Couzin, 2012; Gallup, Hale et al., 2012), even when familiarity (e.g. real group membership) is accounted for (Gallup, Chong et al., 2012). This gaze following does not occur when pedestrians are approaching one another (i.e. moving in opposite directions) (Gallup, Chong et al., 2012). Interestingly, it has been suggested that humans avoid looking at others as a means of avoiding social interaction with them (Gallup, Hale et al., 2012; Laidlaw, Foulsham, Kuhn, & Kingstone, 2011), and this avoidance can result in failure to mimic the behaviour of individuals that are within their line of sight (Gallup, Hale et al., 2012). Consequently, we predicted that neighbouring rams that are posturally aligned (and hence

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