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Psychological limits on animal innovation

Sarah F. Brosnan [a,b,*], Lydia M. Hopper [c]

[a] Department of Psychology, Neuroscience Institute, Georgia State University, Atlanta, GA, U.S.A.
[b] Department of Philosophy, Georgia State University, Atlanta, GA, U.S.A.
[c] Lester E. Fisher Center for the Study & Conservation of Apes, Lincoln Park Zoo, Chicago, IL, U.S.A.

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Innovation is a way by which animals adopt a new behaviour or apply a current behaviour to a novel situation. Although exploring a new behaviour is itself risky for the animal, a growing body of research indicates that it is fairly widespread across animal species. While there have been explorations of when innovation is most likely and which individuals are most likely to innovate, less has been explored about the psychological mechanisms underlying innovation. Here we consider some psychological limits on innovation. We focus on five factors that my limit the invention of novel behaviours (neophobia, conservatism, conformity, functional fixedness and the endowment effect). The feature common to each of these is that individuals tend to stick with existing behaviours, or the existing uses of those behaviours, rather than exploring novel options. This in turn limits animals' willingness to try less common behaviours unless they are forced through circumstances to explore alternate strategies. Despite the similar functional outcomes, it is critical to understand the underlying mechanisms present in different situations in order to make strong predictions about when innovation is, or is not, expected to emerge. We then consider how transmission biases and social learning mechanisms influence and limit the spread of inventions among individuals. Of course, these 'limits' are beneficial in other circumstances, and throughout this review we consider the trade-offs for these psychological mechanisms.

Like many excellent scientists, Bill Hamilton was smart, creative, and loved what he did (Dawkins, 2000; Segerstråle, 2013). Additionally, he was noted for his willingness to think innovatively about problems in evolutionary biology, a risky proposition that led to 'glorious' results (Queller, 2001). As a result, while most scientists advance their field in incremental ways, Hamilton's innovations literally changed the foundations of evolutionary biology. If, however, the rewards to innovation are so great, why is it not more common in humans or other species?

While on the surface innovation seems to be an advantage, as it offers the opportunity for individuals to be more productive, exploit novel resources, or adapt to changing environments, there are also limits to the benefits (Reader & Laland, 2003). After all, the current solution has allowed individuals to survive up to this point, and any change may be less beneficial rather than more. While some change and flexibility can be good, especially if an animal can build upon its already-learned skills (Seed & Boogert, 2013), too much, or too rapid, change can lead to negative consequences (Berends, Goldring, Stein, & Cravens, 2010). For instance, there are drawbacks to changing faster than one's environment, or making changes in response to what may be fleeting ecological circumstances. Moreover, there may simply be high costs to innovating; a new solution may be equally (or more) likely to be detrimental than beneficial. For instance, a subordinate who lacks good access to food may eat something poisonous while trying out a novel food source. All of these possibilities suggest that a certain level of hesitancy to adopting novel behaviours is warranted.

Research thus far indicates that individuals primarily innovate if their existing behaviour pattern no longer provides a benefit or when an individual has no other option. Therefore, the most likely innovators are those for whom the benefits of increased resources are the highest. For example, Laland and Reader (1999a) found that among guppies, *Poecilia reticulata*, innovation was seen in smaller individuals more than larger ones, and in females (for whom fecundity is limited by body size and condition, such that increased resources are directly tied to increased reproductive output), but not males (for whom there is no such link). But innovation may not occur even in situations in which it would be a substantial benefit. Why, then, would individuals fail to innovate

* Correspondence: S. F. Brosnan, Department of Psychology, Georgia State University, P.O. Box 5010, Atlanta, GA 30302, U.S.A.
E-mail address: sbrosnan@gsu.edu (S. F. Brosnan).

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in a circumstance like this, where the potential benefits outweigh the potential risks? One barrier to innovation may be a number of evolved behavioural propensities, or psychological mechanisms, that influence behaviour in consistent ways. It is these psychological mechanisms that we consider below.

Here, we follow a global definition of innovation, including processes from the moment of discovery through establishment (Reader & Laland, 2003). We include in our considerations both the discovery of a novel behaviour to solve a problem and the application of an existing behaviour to a novel situation (van Horik, Clayton, & Emery, 2012; Ramsey, Bastian, & van Schaik, 2007). Within this definition, we follow a framework from anthropology that identifies three key phases to innovation: invention, transmission and preservation (Erwin, 2004; Mesoudi & O'Brien, 2008a, 2008b; Rose & Felton, 1955). The first of these, invention, is the creation of a novel behaviour or technology. The second phase is transmission, in which the invention spreads to other individuals though social means (Hoppitt & Laland, 2013). The third phase is preservation, in which a sufficiently large number of individuals adopt the invention that the behavioural variation is maintained in the social group (note that as a result of chance and competing pressures, even beneficial inventions often do not become widespread; Kummer & Goodall, 1985; Nishida, Matsusaka, & McGrew, 2009; Reader & Laland, 2003). Because our focus is on the psychological mechanisms that limit invention and transmission, we also focus on larger-brained, group-living species, including nonhuman primates (hereafter, primates), birds and fish.

In this review, we consider five psychological mechanisms that may inhibit both invention and transmission: (1) neophobia (a hesitancy to approach a novel object, locale or food item; Greenberg, 2003), (2) conservatism (the disinclination to explore/adopt new possibilities or opportunities; Hrubesch, Preuschoft, & van Schaik, 2009), (3) conformity (the tendency to do what your peers do; Boyd & Richerson, 1985), (4) functional fixedness (the disinclination to use familiar objects in novel ways; Hanus, Mendes, Tennie, & Call, 2011) and (5) the endowment effect (the bias towards preferring an existing option over a new one; Jones & Brosnan, 2008; also see Appendix, Table A1). The feature common to each of these mechanisms is that individuals tend to stick with familiar behaviours, and the existing uses of those behaviours, rather than exploring novel options. We additionally consider how certain transmission biases (Laland, 2004) and social learning mechanisms (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009) may inhibit, rather than encourage, the transmission and preservation of novel behaviours among animals. Although we have chosen to focus on how these limit innovation, this is within a framework of considering the trade-offs that exist for any of these behaviours. Thus, throughout we also consider the benefits that these psychological mechanisms may provide.

PSYCHOLOGICAL MECHANISMS THAT MAY LIMIT INNOVATION

Neophobia

Recent research has begun to demonstrate interindividual differences but intraindividual consistency in animals' innovative ability (Laland & Reader, 1999b; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Thornton & Samson, 2012), indicating a link between innovation and personality (Hopper et al., in press; Massen, Antonides, Arnold, Bionda, & Koski, 2014). One classic example of this link is that bold individuals (i.e. those who are less neophobic) may be more likely to innovate than others because they are more likely to explore novel objects or explore in novel situations, something that may covary with rank (Boogert, Reader, & Laland, 2006; Greenberg, 2003). One prominent manifestation of intraspecies differences in neophobia occurs during foraging; animals that are highly neophobic are less likely to innovate and exploit new food resources. Food neophobia is common in omnivores, which must be appropriately hesitant in trying novel foods (to avoid negative consequences from poisonous or otherwise unpalatable foods). Although a certain level of caution may protect animals, it also reduces their ability to exploit novel food sources and so animals must be flexible in their responses. For example, although rhesus macaques, *Macaca mulatta*, show food neophobia (Johnson, 2000), they are less neophobic towards more desirable foods with a high sugar content (Johnson, 2007). One way that socially living animals can circumvent individual neophobia, which may increase their chances of survival, is through social influences, such as acquiring information about novel foods from conspecifics (Chiarati, Canestrari, Vera, & Baglione, 2012; Galef, 2001; Gustafsson, Krief, & Saint Jalme, 2011).

Not only does neophobia influence an animal's likelihood to explore new foods, but individual differences in boldness may also interact with the speed at which individuals can learn new skills (Tebbich, Stankewitz, & Teschke, 2012). Indeed, in a recent study with cavies, *Cavia aperea*, bolder, more active and more aggressive animals were faster learners on a novel task, but less aggressive animals paid more attention to stimuli changes and were therefore better at the reversal learning task (Guenther, Brust, Dersen, & Trillmich, 2014). If there is a negative correlation between neophobia and learning speed, it seems likely that neophobia interacts with innovation in two ways. First, less neophobic individuals may be more likely to invent, as they are less inhibited in their exploration of a novel object. On the other hand, these less neophobic individuals may also be less likely to benefit from the transmission of an invention (see below for more discussion of transmission), as they are less likely to change an existing behavioural pattern.

Conservatism

Conservatism is the disinclination to explore or adopt novel solutions to problems when a productive one is already known (Hrubesch et al., 2009). Conservatism protects individuals against the costs of a failed exploration, but also reduces the likelihood of both invention and the transmission of inventions. Conservative individuals may fail to explore alternate approaches to a problem as long as the solution that they already know is providing some benefit. For instance, in foraging tasks, it may be that individuals do not innovate until they are unable to acquire food through known mechanisms, for example, because the food is not available (e.g. a seasonal fruit) or because the food is being monopolized by another individual (Boesch, 2013). This explanation has been posited to explain why lower-ranking individuals are likely to innovate (Katzir, 1983; Reader & Laland, 2001; Sigg, 1980); they are driven beyond their inherent conservatism because their currently known solution is not providing any, or enough, benefit (Hopper, Schapiro, Lambeth, & Brosnan, 2011). In two recent experiments, captive chimpanzees were presented with novel problem-solving tasks that could be solved in more than one manner to obtain food rewards (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). In both studies, after subjects learned one solution, they failed to explore alternative solutions, and were thus classed as 'conservative' (see also Dean, Kendal, Schapiro, Thierry, & Laland, 2012).

More recent studies, however, have shown flexible, nonconservative learning by apes (Hopper et al., in press; Lehner, Burkart, & van Schaik, 2011; Manrique, Völter, & Call, 2013; Tonooka, Tomonaga, & Matsuzawa, 1997). For instance, Manrique et al. (2013) presented chimpanzees, *Pan troglodytes*,

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