

Innovation and social learning: individual variation and brain evolution *

SIMON M. READER **

Department of Biology, McGill University and Faculty of Biology, Utrecht University

Abstract—This paper reviews behavioural, neurological and cognitive correlates of innovation at the individual, population and species level, focusing on birds and primates. Innovation, new or modified learned behaviour not previously found in the population, is the first stage in many instances of cultural transmission and may play an important role in the lives of animals with generalist or opportunistic lifestyles. Within-species, innovation is associated with low neophobia, high neophilia, and with high social learning propensities. Indices of innovative propensities can be calculated for taxonomic groups by counting the frequency of reports of innovation in published literature. These innovation rate data provide a useful comparative measure for studies of behavioural flexibility and cognition. Innovation rate is positively correlated with the relative size of association areas in the brain, namely the hyperstriatum ventrale and neostriatum in birds, and the neocortex and striatum in primates. Innovation rate is also positively correlated with the reported variety of tool use, as well as interspecific differences in learning. Current evidence thus suggests similar patterns of cognitive evolution in primates and birds.

Keywords: birds; brain evolution; individual differences; innovation; learning; primates.

INTRODUCTION

When an animal performs an act that appears to be a significant departure from its usual repertoire, what is it in the animal's external and internal environment that prompts this novel behaviour pattern? Imagine, if you will, an animal incorporating a new food source in its diet, such as a British titmouse opening milk bottles and drinking the cream inside (Fisher and Hinde, 1949; Hinde and Fisher, 1951). What

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**Current address, and address for correspondence: Simon Reader, Utrecht University, Behavioural Biology, Padualaan 14, P.O. Box 80086, 3508 TB Utrecht, The Netherlands; e-mail: s.m.reader@bio.uu.nl

kinds of processes are involved in the expression of this novel behaviour pattern, this ‘innovation’? Are tits pre-adapted to innovate, or are all birds equally likely to discover novel solutions to existing problems (or apply familiar solutions to novel problems)? If taxonomic differences in innovation do exist, what underlies these differences: for example, are innovative taxa characterised by enhanced brain size or elaborate brain structures? Does innovation have other cognitive correlates? Are the correlates of innovation common to many taxonomic groups, or is there little regularity across taxa?

Innovation, operationally defined as ‘a new or modified learned behaviour not previously found in the population’ (Reader and Laland, *in press*), provides a useful tool to quantify taxonomic differences in cognition and behavioural flexibility (Lefebvre, 2000). Lefebvre and co-workers (1997) pioneered the use of innovation rate, the reported frequency of behavioural innovation collated from published articles, to quantify differences in foraging behaviour between avian parvorders. Innovation rate has been shown to correlate with: neural measures such as the size of the neostriatum-hyperstriatum ventrale (Neo-HV) complex, cognitive measures such as tool use frequencies, enhanced rates of evolutionary divergence, and ecologically important factors such as the success of birds introduced to novel environments (Wyles et al., 1983; Timmermans et al., 2000; Lefebvre et al., 2002; Sol et al., 2002; Nicolakakis et al., 2003). At the population level, the identity of innovators will have important consequences for determining the spread of innovations through animal groups. Thus the question ‘who innovates?’ is important from the point of view of ecology, evolution, and cultural transmission.

In this review, I examine neurological, cognitive and behavioural correlates of behavioural innovation. I direct the question ‘who innovates?’ at three levels: relationships between individuals, relationships between populations, and relationships between species and other higher taxonomic levels. There may be similarities between relationships at these three levels, but this need not always be the case, and researchers should not assume that empirical or theoretical findings at one level necessarily hold true at other levels. For example, imagine that a particular species, perhaps a large-brained one, demonstrates a high propensity to be innovative and to learn from others (‘social learning’, Heyes and Galef, 1996), but that particular individuals specialise in either locating new food sources (‘producing’) or exploiting the finds of others (‘scrounging’; Giraldeau and Caraco, 2000). If individuals’ roles are consistent, a negative correlation between innovation and social learning propensities, an apparent trade-off, may be observed at the individual level. However, the species’ innovative and social learning propensities may be high relative to other species, and inter-specific comparisons may demonstrate a positive correlation between innovation and social learning rates at this level of analysis. Below, I concentrate my review on birds, where much of the relevant work has been done, but contrast the avian findings with other taxa, particularly primates, which have also received substantial attention from students of innovation.

PROCESSES UNDERLYING INNOVATION

A number of candidate processes may accompany the adoption of an innovation, such as exploration, neophobia, and asocial and social learning (Reader and Laland, in press). Turning back to the tit example, imagine that milk bottles have just been introduced into a new locality. What must happen for this bird to discover and utilise the new food source?

Novelty responses are likely to determine local birds' first contacts with the novel food source. Animals can respond to novelty positively (neophilia), or negatively (neophobia; Archer and Birke, 1983; Greenberg, in press). For example, the tit may preferentially explore novel objects, or avoid such objects in preference for the familiar. The relationships between neophobia and neophilia may be complex rather than forming a simple continuum (Greenberg and Mettke-Hofman, 2001; Greenberg, in press). For instance, ravens are frequently highly attentive to novelty (neophilia) while simultaneously being very fearful of novel objects (Heinrich, 1995, 1999; Greenberg, in press).

For exposition, novelty responses can be grouped into four categories: responses to novel foods, areas, inanimate objects and animate objects. For example, the tit may have to explore a novel area (doorsteps), investigate a novel object (milk bottles), and try a novel food (cream). Animate objects may include conspecifics (which may take a number of roles, e.g., mates, territory holders, information sources), predators, prey, and parasites. The divisions between contexts are of course rather arbitrary: foods may be animate or inanimate objects, and a novel area may be characterised by novel objects. Responses in one context may correlate with responses in all other contexts. Alternatively, responses in one context (e.g., responses to inanimate objects) may not correlate with responses in another context (e.g., responses to foodstuffs), a phenomenon described as context-specificity. The pumpkinseed sunfish provides an example of context-specific behaviour, where individual fishes' responses to a potentially threatening stimulus (a red-tipped stick) and a novel food were not correlated, though their responses within each context were (Coleman and Wilson, 1998). Attraction to novelty is likely to speed innovation, whereas avoidance of novelty is likely to slow innovation.

Learning will also play a critical role in innovation, and indeed forms part of some definitions of innovation (Reader and Laland, in press). Innovation and learning can be considered as separate processes, learning following a rewarding innovation, but the animal may learn about the affordances and characteristics of the object before receiving any reward. In the cream-drinking tit these might include learning how best to grip the bottle, or the fact that there is a foil cap that can be removed or pierced. If the innovative act is rewarding, it is likely to be repeated with increased efficacy, perhaps due to improved recognition of white, glass objects as food sources, or more efficient opening of the bottles.

Learning may also speed the spread of innovations. Naïve birds that come across previously-opened bottles, and form an association between the bottle and the food inside, or birds that observe other birds opening and drinking from bottles, and so

are attracted to the novel objects, may learn to utilise the new food source as a consequence of the behaviour of others (an example of social learning).

The propensity to innovate might be expected to correlate positively with performance in asocial learning tasks. However, there is controversy over the relationship between asocial and social learning. A number of authors have argued that there may be a trade-off between social learning and individual (or asocial) learning, perhaps as a consequence of different psychological mechanisms or neural substrates being involved (Boyd and Richerson, 1985; Rogers, 1988). Others have argued that non-imitative social learning and individual learning share the same underlying psychological mechanisms, and that social learning is simply socially-biased individual learning (Heyes, 1994; Fragaçzy and Visalberghi, 2000). These and other researchers would predict that asocial and social learning propensities correlate positively with one another. The resolution of this controversy will have implications for relationships between innovativeness and social learning performance, to the extent that innovativeness correlates with asocial learning performance.

For an innovation to occur and to persist a range of processes are involved, including but not limited to, spatial exploration, neophobia (fear of novelty), object exploration, asocial and social learning, plus other processes not considered above, such as play, creativity, and the ability to inhibit existing responses (Kummer and Goodall, 1985; Kothbauer-Hellman, 1990; Hauser, in press; Reader and Laland, in press).

EMPIRICAL FINDINGS

What do the hypothesised relationships outlined above look like, at the individual, population and species level? As I detail the empirical data below, it will become apparent that few studies explicitly address innovation but many examine related variables. Thus much work remains to be done, particularly on the processes underlying innovation, and I hope this review will point to directions for further work and research priorities.

Individual differences

Novelty responses and learning. Responses to novel objects are a well-established correlate of avian innovation, as measured by the time taken to solve novel foraging tasks. In feral pigeons *Columba livia*, zenaïda doves *Zenaidura aurita*, cut-throat finches *Amadina fasciata*, and zebra finches *Taeniopygia guttata*, those birds that are least reluctant to approach novel objects (a measure of inanimate object neophobia, henceforth ‘object neophobia’) are the quickest to solve novel tasks (Whittle, 1996; Seferta et al., 2001; Bouchard, 2002). Wild-caught Carib grackles *Quiscalus lugubris* are neophilic, in that they approach novel objects more rapidly than control objects (Reader and Lefebvre, unpubl. data). The most neophilic grackles are also the fastest to solve novel foraging tasks (Reader

and Lefebvre, unpubl. data). Webster and Lefebvre (2001) presented a novel foraging task to 15 wild-caught individuals of each of five Barbadian species (three Passeriformes: Carib grackles, Lesser-Antillean bullfinches *Loxigilla noctis*, and shiny cowbirds *Molothrus bonariensis*, and two Columbiformes: zenaida doves and common ground doves *Columbina passerina*). Although the number of solutions was small, Webster and Lefebvre used the number of attempts on the foraging task as a probable correlate of innovation. Individual variation in attempts on the novel task was predicted by latency to approach it, which was in turn predicted by latency to feed near novel objects, supporting the results above. In Carib grackles, individual behaviour was consistent within the various contexts of novelty response tested (sampling novel foods, entering novel spaces and approaching novel objects). However, novelty responses were context-specific, that is, behaviour was not consistent across contexts, and object neophilia was the most closely associated with innovation (Reader and Lefebvre, unpubl. data).

In feral pigeons (Bouchard, 2002), and cut-throat and zebra finches (Whittle, 1996; data reanalysed in Seferta et al., 2001), animals that performed well in innovation tasks were also superior in social learning tasks. In grackles, an attempt was made to separate the innovative performance from asocial learning of the innovation by examining performance subsequent to the first solution of a novel task, the first occasion the bird receives a food reward. Grackles show evidence of learning the tasks, and those birds that initially solved one task rapidly also outperformed other birds in the learning phase of other tasks, perhaps suggesting that innovative and asocial learning performance are correlated (Reader and Lefebvre, unpubl. data).

Individual characteristics such as age, sex, competitive ability and social or dominance rank are determinants of the likelihood of innovation in species as diverse as birds, primates and fish (Bunnell et al., 1980; Bunnell and Perkins, 1980; Hauser, 1988; Langen, 1996; Laland and Reader, 1999a, b; Reader and Laland, 2000, 2001; di Bitetti and Janson, 2001). The proverb ‘necessity is the mother of invention’ often rings true, with many animals apparently forced to switch to novel strategies when established behaviour patterns are unsuccessful (Reader and Laland, in press). While subordinates may tend to be the first to discover or sample novel resources, they may not profit from their discoveries. A number of avian studies have demonstrated that innovator subordinates are usurped by dominants (Katzir, 1982, 1983; Stahl et al., 2001), and in primate groups, low-ranking monkeys may not express a learned behaviour in order to avoid the attention of dominants (Drea and Wallen, 1999).

Temperament is also likely to influence the probability of innovation. In guppies *Poecilia reticulata*, individuals’ latencies to swim novel mazes to locate a food reward was found to be consistent across tasks, after measures were taken to exclude hunger level, sex, and age as possible explanations for this result (Laland and Reader, 1999a). Laland and Reader concluded that some ‘personality’ variable, such as boldness, might be responsible for these individual differences. In great tits *Parus major*, consistent individual differences were found in exploratory styles, with birds

that approached a novel object more quickly also quicker to visit all artificial trees in a novel environment, compared with birds that approached a novel object more slowly (Verbeek et al., 1994). These differences were found to correlate with other behavioural measures, such as aggressiveness, dominance rank, risk-taking in fighting behaviour, and social learning from conspecifics (Verbeek et al., 1999; Marchetti and Drent, 2000). Responses to novelty were heritable (Dingemanse et al., 2002; Drent et al., 2003), and to the extent that novelty responses predict innovation, this suggests innovative propensities may also be heritable. In greylag geese *Anser anser* faecal corticosterone concentrations were higher in individuals that completed a novel foraging task than their respective controls (Pfeffer et al., 2002), an important first step in uncovering the hormonal correlates of innovation.

Neural correlates. Selection experiments and examination of natural variation in brain size in non-human animals have examined the relationships between individual variation in brain size and the general problem-solving abilities that are likely to be correlates of innovation. However, at the individual level there is little compelling evidence for positive correlations between brain size and problem-solving performance (Miller and Tallarico, 1974; Johnston, 1982).

Population differences

Few studies have examined population differences in innovation or novelty responses. This is surprising, because such experiments should in theory be relatively simple to perform while having the advantage that they avoid some of the problems associated with cross-species comparisons (Macphail, 1982). For example, populations could be presented with novel tasks or novel objects, and their responses measured. There is some evidence for population differences in asocial learning tasks in Barbadian zenaida doves. Group-foraging doves from a site with dense, ephemeral food patches learned a shaping task more quickly than territorial doves from a site 9 km away (Carlier and Lefebvre, 1996). These results suggest that the scramble competition associated with group-foraging favours asocial learning (Carlier and Lefebvre, 1996). Moreover, given the close proximity of the two sites, genetic isolation seems unlikely, perhaps suggesting that the population differences in learning are themselves learned.

Species, genera and order differences

Quantifying innovation. Lefebvre and colleagues have collated large numbers of published observations of innovation, with the data set currently standing at 2213 cases (see above). Reader and Laland (2002) compiled similar innovation rate data for primates. Innovation rate data has a number of advantages: it is quantitative, direct, ecologically relevant and available for hundreds of species (Lefebvre et al., 1997). The collection of such data is vulnerable to various potential biases, such as differences in research effort or the effect of common ancestry (Harvey and Pagel,

1991), but these can be taken into account and controlled for (Lefebvre et al., 1997, 1998, 2001; Lefebvre, 2000; Nicolakakis and Lefebvre, 2000; Reader and Laland, 2002; Reader, in press; Reader and MacDonald, in press).

Novelty responses and learning. Innovation rate correlates with performance in laboratory and field asocial learning tests. Examination of the associative learning data of Gossette (1968) and Sasvàri (1985) revealed positive correlations between innovation frequency and learning performance (see Timmermans et al., 2000; Webster and Lefebvre, 2001). Further, the same relationship was found in primates when the captive learning data of Riddell and Corl (1977) was examined in conjunction with the primate innovation data set (see Reader and MacDonald, in press). The aforementioned study by Webster and Lefebvre (2001) of five avian species revealed a positive across-species relationship between innovation frequency and learning test performance in both the field and captivity. Neophobia also correlated with inter-specific differences in innovation in the Webster and Lefebvre study, and in a Day et al. (2003) study of callitrichid monkeys. There are few other examinations of interspecific relationships between novelty responses and innovation, though several authors have addressed species differences in neophobia and neophilia (e.g., Glickman and Sroges, 1966; Greenberg and Mettke-Hofman, 2001; Mettke-Hofmann et al., 2002).

Innovation rate correlates positively with another purported cognitive measure, the reported frequency of tool use in both birds and primates (Lefebvre et al., 2002; Reader and Laland, 2002). However, in birds, innovation rate correlates negatively with food storing propensities. In both North American corvids and European parids, but not in European corvids, the most innovative species tend to be the ones that store the least (Lefebvre and Bolhuis, in press). These trends suggest that there might be some trade-off between food storing and innovation, but that innovation, tool use and learning correlate together (Lefebvre and Bolhuis, in press).

Primate innovation rate also correlates with the reported frequency of social learning (Reader and Laland, 2002). The relationship between the reported frequency of social learning and innovation rate in birds is less clear (Bouchard, 2002; Lefebvre and Bouchard, in press). This last discrepancy might reflect the difficulties in estimating species' reliance on social learning from observational reports. Experimental results generally indicate a correlation between social learning and asocial learning (Lefebvre and Giraldeau, 1996; Lefebvre et al., 1996; Reader and Lefebvre, 2001).

Neural correlates. Innovation rate, corrected for research effort, correlates with relative brain size in both birds and primates (Lefebvre et al., 1997; Reader and Laland, 2002). Brain regions involved in higher order and multimodal integration (neocortex and striatum in primates, the Neo-HV complex in birds) are enlarged in taxa with high innovation rates, compared to groups where few innovations are reported (Timmermans et al., 2000; Reader and Laland, 2002). Further, relative neocortex size correlates with the incidence of tactical deception in primates

(Byrne, 1993; Reader, 2000). The incidence of deception was collated by sending questionnaires to experienced field primatologists (Byrne, 1993) or by collating examples described as deception from the published literature (Reader, 2000). Tactical deception is likely to reflect innovative propensities (Byrne, in press).

DISCUSSION

Where correlates of innovation have been examined in both birds and primates, similar relationships are generally found. Roper (1986) hypothesised that innovators should be 'both exploratory and intelligent' (p. 582). The brief review presented above supports this idea. Innovative individuals and species are characterised by being attracted to novel objects, and superior in asocial and social learning tasks, in comparison with those who are less innovative. Additionally, innovative taxa are characterised (neurologically) by possessing large brains relative to their body size and (behaviourally) by tending to be more proficient in contexts such as tool use. It is clear that individuals, populations and species differ in their propensities to discover novel solutions to environmental and social problems. Moreover, while research at one level can inform that at other levels, researchers should be cautious to distinguish findings according to the level of study.

We have seen that novelty responses are not simply characterised on a single continuum and may be context-specific. Depending on the innovative act, only particular novelty response contexts may be relevant. Thus innovation may also be context-specific. For example, the fact that a bird is innovative in feeding contexts may provide no information about its exploratory responses in a novel locality. However, there is evidence that some potential correlates of innovation, such as spatial exploration and object exploration, do form part of a correlated set of traits, or a behavioural syndrome (Drent et al., 2003). The pervasive influence of novelty responses on innovation has been somewhat neglected (Greenberg, in press). Across-individual level studies of innovation should include novelty responses as confounding variables, and comparative studies of innovation and other cognitive capacities would also benefit from this approach: novelty responses may be key intervening variables and of interest in themselves. Fortunately, relevant comparative studies are beginning to be made. For example, Mettke-Hofmann et al. (2002) measured novelty responses across a taxonomic group (parrots). Such analyses allow the evolutionary lability of novelty responses to be addressed, and their links with innovation rate or other cognitive measures determined.

Across-taxa, cognitive measures such as tool use and associative learning, as well as neural measures such as the relative size of the brain and its main integrative areas (mammalian neocortex and the avian Neo-HV complex) are associated with innovation rate in both primates and birds (Lefebvre et al., in press). The parallel results suggest a pattern of convergent evolution in the two groups whose ancestors diverged more than 280 million years ago, particularly in the expansion of structures involved in multimodal integration capacities (Rehkämper and Zilles, 1991; Emery

and Clayton, in press). Though the brains of birds and primates are very different, allometric, developmental, architectonic, immunocytochemical and tracing results indicate that the Neo-HV complex is the avian counterpart to the mammalian neocortex (Rehkämper et al., 1991; Rehkämper and Zilles, 1991; Waldmann and Gunturkun, 1993; Emery and Clayton, in press). The fact that several cognitive measures covary across taxa suggests that they have evolved together, perhaps suggesting they are all part of a general problem-solving ability; only food-storing in birds appears to provide an exception (Reader and Laland, 2002; Seyfarth and Cheney, 2002; Lefebvre and Bolhuis, in press).

Innovation may play an important role in the lives of many animals, particularly those animals that live generalist or opportunist lifestyles, or animals forced to adapt to new circumstances, such as individuals of species threatened by human-caused changes in the environment. Innovation rate also provides a useful tool to examine taxonomic and population differences in cognition. That said, the heuristic and explanatory power of innovation rate analyses would be much improved by a focus on the development, mechanisms and function of innovation. The costs, constraints, benefits, psychological mechanisms, and neurobiological processes that underlie innovation are ripe for study.

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