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ARTICLES

Response facilitation in the domestic fowl

WILL HOPPITT*, LAURA BLACKBURN† & KEVIN N. LALAND‡
*Sub-Department of Animal Behaviour, University of Cambridge
†Department of Zoology, University of Cambridge
‡Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews

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Response facilitation is an alternative learning process that could account for some imitative phenomena. It occurs when the presence of a conspecific performing an act temporarily increases the probability that an observing animal will perform the same act. This process could have important implications for social-learning research, because it provides a plausible means by which social learning could occur in animals, yet it superficially resembles imitation and consequently affects the interpretation of current popular ‘two-action’ tests of imitation. However, there is little good evidence on response facilitation effects, because cases of behavioural synchrony can usually be explained by other factors, so some researchers remain sceptical as to the importance of the process. We conducted an experimental study of social-learning processes in domestic fowl to evaluate whether response facilitation is a plausible explanatory term. Strong behavioural synchrony was observed in hens in preening, sitting and dustbathing behaviour. In the case of preening, we found strong evidence that this synchrony was unlikely to be accounted for by alternative social-learning processes or by external factors influencing birds in the same way. We conclude that there is compelling evidence for response facilitation in the domestic fowl.

Keywords: behavioural synchrony; contagion; domestic fowl; *Gallus gallus domesticus*; imitation; preening; response facilitation; social facilitation; social learning

The topic of social learning in animals has attracted much interest among ethologists and psychologists (Heyes & Galef 1996; Galef & Giraldeau 2001; Shettleworth 2001; Galef & Heyes 2004). Social learning is often broadly defined as learning that is influenced by observation of, or interaction with, a conspecific or its products (Box 1984; Heyes 1994). Although social learning does not necessarily result in concordance between the observer’s and the demonstrator’s behaviour, it is social learning that results in matching behaviour that has attracted most attention. Such learning can potentially result in the social transmission of acquired information through a population (Galef 1976), resulting in increased homogeneity of behaviour that extends beyond the period of interaction (Galef 1988). Examples include the spread of foraging skills or vocalizations through populations of birds and mammals (Lefebvre & Palameta 1988; Heyes & Galef 1996; Fragaszy & Perry 2003). The possibility that these processes could help to maintain simple animal ‘cultures’ in natural populations has been a topic of major interest, with researchers looking for cases of culture in a wide range of taxonomic groups (e.g. Fleagle 2003; Siegel 2004).

An area of debate in the field of social learning is the extent to which social learning observed in nonhuman animals is homologous to the processes underlying culture in humans. For instance, it has often been argued that imitation and teaching are important in maintaining human but not animal culture (Galef 1992, 2004; Tomasello 1994), although this is contentious (Laland & Hoppitt 2003; Whiten et al. 2004). Although social learning of matching behaviour has been demonstrated numerous times in nonhuman animals, this could occur by many routes besides imitation (or teaching). Consequently, central to the resolution of debates over animal ‘cultures’ is an understanding of those social-learning processes that can

Correspondence and present address: W. Hoppitt, Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, Bute Medical Building, Queen’s Terrace, St Andrews, Fife KY16 9TS, U.K. (email: whoppitt@yahoo.com). L. Blackburn is at the Department of Zoology, University of Cambridge, New Museums Site, Cambridge, CB2 3EJ, U.K.

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generate findings in animals that resemble those resulting from imitation, but that none the less are the result of a different, perhaps simpler, psychological mechanism.

Over the last century, much effort in social-learning research has gone into devising experimental procedures that can isolate imitation from other social-learning processes (Galef 1988), although this research programme is hindered by differences in opinion on how imitation should be defined and demonstrated empirically (e.g. Galef 1988; Tomasello 1990; Heyes 1994, 1996; Byrne & Tomasello 1995; Byrne & Russon 1998; Byrne 2002). Widely regarded as the most successful method for testing for an imitative ability is the 'two-action method' (Dawson & Foss 1965). The experimental subjects must solve a task in one of two ways (e.g. by pushing a bolt or turning a handle to open a box containing food). Half of the subjects observe a demonstrator using one solution, and the other half observe the alternative method. Subjects are then tested to see which method they use, and if each group tends to use the method that they observed more frequently than the other group, then this is taken as evidence of imitation. The best examples of the two-action test have been carefully designed so that each alternative action involves interaction with exactly the same part of the experimental apparatus, to rule out local enhancement as an explanation for differences between groups. Each action should also ideally result in exactly the same movement of the experimental apparatus, to rule out the possibility that the observer is recreating the movements of the experimental apparatus (Custance et al. 1999), rather than the action itself (Akins & Zentall 1996; Zentall et al. 1996). A good example of the two-action method is Zentall et al.'s (1996) study showing that pigeons, *Columba livia*, learned to press a lever for food in the same way that they had observed being demonstrated earlier, either by pushing the lever with their beak or stepping on it with their foot.

The two-action test has been used to test a number of other species for imitative ability, with positive results found in budgerigars, *Melopsittacus undulatus* (Dawson & Foss 1965; Galef et al. 1986), quail, *Coturnix japonica* (Akins & Zentall 1996), starlings, *Sturnus vulgaris* (Campbell et al. 1999; Fawcett et al. 2002), marmosets, *Callithrix jacchus* (Bugnyar & Huber 1997), capuchin monkeys, *Cebus apella* (Custance et al. 1999) and chimpanzees, *Pan troglodytes* (Whiten & Custance 1996). Many view these results as the most convincing cases of animal imitation (Whiten et al. 2004), but others are not convinced. Byrne (2002) defined two types of imitation, production imitation, where the observer learns a new pattern of behaviour, and contextual imitation, where the observer learns to use an existing action in a novel context. The two-action test does not inherently test for production imitation, because it does not show that the alternative actions are novel, although individual cases may be made. However, it potentially provides evidence consistent with contextual imitation.

Byrne (1994, 1999, 2002), however, provided an alternative explanation for the data generated by two-action tasks, i.e. response facilitation, defined as when 'the presence of a conspecific performing an act (often resulting in reward) increases the probability of an animal which sees it doing the same' (Byrne 1994, page 237). So in Zentall et al.'s (1996) study, the pigeons that observed a demonstrator pecking may not have learned by imitation to peck at the lever, but instead may have been transiently more likely to peck at any object that they encountered as a result of having recently seen another pigeon pecking. To be sure of a case of contextual imitation, it must be shown that the observers have learned to use the target action in that context. One way to eliminate response facilitation as an explanation could be to introduce a significant delay between demonstration and exposure to the task, to let the possible effects of response facilitation wear off. However, it is difficult to know how long a response facilitation effect could last, and consequently how long the delay must be. Another option is to show that learning by observation of the demonstrator is context dependent. So, for example, one could show that pigeon observers learned to peck or step on the lever in response to a light being lit up, after seeing a demonstrator responding in such a way.

Another term with a similar meaning to response facilitation is contagion, which refers to 'matching behaviour limited to those unlearned responses that are typical of a species' (Zentall 1996, page 224). Possible cases of contagion include synchronized predator evasion in flocks and herds of animals (Armstrong 1951) and synchronous courtship behaviour (Nuechterlein & Storer 1982; Zentall 1996). Here we use the more general term 'response facilitation', because such an effect could potentially be a result of experience and need not necessarily be unlearned (Hoppitt 2005). Contagion could be seen as a special case of response facilitation that requires no experience of other individuals' behaviour.

Aside from providing another explanation that must be ruled out in tests of animal imitation, response facilitation seems to be an interesting possibility in its own right (Byrne 1994). Through synchronizing individuals' behaviour, response facilitation might effectively 'teach' animals when and where to perform certain actions. For example, an individual of a frugivorous species might learn that the fruit of a particular tree is good to eat, if the animal is predisposed to eat in the tree with other individuals who are eating the fruit. Response facilitation could result in social learning functionally equivalent to contextual imitation, by a similar process to Suboski's (1990) releaser-induced recognition learning.

Perhaps one reason that the response facilitation explanation has received little attention by imitation researchers is that it is primarily a theoretical construct, and there is little evidence of it. Although numerous cases of behavioural synchrony in many species might be regarded as cases of response facilitation, there are almost always alternative explanations. For example, animals moving around together will encounter the same environments and locations together and may therefore engage in synchronous behaviour. In addition, groups of animals will experience many external factors simultaneously and respond to them in the same way. For example, Armstrong (1951) noted that, although individuals of many species of birds start singing at approximately the same time each morning, this could be explained by a threshold light intensity triggering dawn song. We are aware of no strong empirical evidence that behavioural synchrony is a result of response facilitation and not alternative processes.