



Object movement re-enactment in free-ranging Kune Kune piglets



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ARTICLE INFO

Article history:

Received 20 January 2017

Initial acceptance 13 March 2017

Final acceptance 28 June 2017

MS. number: 17-00068R

Keywords:

affordance learning

bidirectional control procedure

pigs

social learning

two-action test

vertical transmission

Learning by observing others is especially beneficial for young and naïve individuals. The relationship to the social partner is thus important. While peers are often used as demonstrators to test for social learning abilities in a species, thereby studying horizontal transmission of information, this study focused on the vertical transmission of information, i.e. learning across generations, in a highly social species. Half-a-year-old piglets of the Kune Kune breed, *Sus scrofa domestica* (in contrast to the usual subjects in studies on pigs raised and kept in seminatural conditions), were first exposed to their mother or aunt pushing one of two differently coloured bars to either the left or right side to open a sliding door, and were then tested after 1 min, 1 h and 1-day retention intervals. Results indicated that subjects recalled the movement of the door, rather than using local or stimulus enhancement. A second test series revealed that the pigs used the demonstrated opening technique and even remembered it after a delay of 24 h. Nonexposed piglets did not show a side bias during their first encounters with the apparatus; however, habit formation was at play during later test sessions and was possibly the reason for long-term memory of the self-acquired techniques. Altogether, this study revealed that piglets learned how to solve a manipulative foraging problem from both their mother and their aunt, probably by acquiring some information through observation and then memorizing it for up to a day.

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Animals living in social groups have plenty of opportunities to learn from the behaviour of group mates. A century of social learning research has revealed many examples of observational learning, in a variety of different species and contexts (Galef & Laland, 2005; Heyes & Galef, 1996; Heyes, 1994, 2009; Hoppitt & Laland, 2008; Huber, 2011; Thorndike, 1898; Thorpe, 1957; Zentall & Galef, 1988; Zentall, 2006). Examples of social influences on the adaptive modification of behaviour range from food selection (Galef, 1996) and predator avoidance (Mineka, Davidson, Cook, & Keir, 1984) to learning of songs (Catchpole & Slater, 2008; Marler & Slabbekoorn, 2004), routes (Helfman & Schultz, 1984) and motor skills (Terkel, 1996). The functional value of social learning is seen in the possibility of providing another way of adapting behaviour to changing environments, filling the gap between species-typical, genetically predisposed behaviour and asocial (individual) learning (Boyd & Richerson, 1988; Galef & Laland, 2005; Laland, 2004; Zentall, 2006). While individual learning, as an adaptive modification of behaviour, benefits individuals by

allowing them to fine-tune behaviour to the rapidly changing properties of the local circumstances, social learning has the additional advantage of limiting the errors on the way to the correct solution (Nicol, 2006). Directly adopting solutions previously found and proven advantageous by others can be a quick and safe shortcut.

In addition to research on the functions and values of social learning, studied both in the laboratory and in the wild, experimental psychologists have investigated the cognitive mechanisms underlying social transmission of information. Several experimental paradigms have been used to test the various hypotheses about these mechanisms. The bidirectional control procedure, developed by Heyes and Dawson (1990), is used by many researchers as an unconfounded test for imitation (Akins & Zentall, 1996; Heyes, Dawson, & Nokes, 1992; Kis, Huber, & Wilkinson, 2015; Klein & Zentall, 2003; Miller, Rayburn-Reeves, & Zentall, 2009; Wood, Kendal, & Flynn, 2013). As a simpler variant of the two-action test (Dawson & Foss, 1965; Whiten & Ham, 1992), two groups of observer animals are exposed to two demonstrators (one for each group) performing the same action on an object in two different directions (left, right). The original two-action test, in comparison, either involves two different actions, such as pulling and pushing (Bugnyar & Huber, 1997), or the same action with two

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different body parts, such as hand and mouth (Voelkl & Huber, 2000). Imitation occurs when subjects perform the demonstrated action more often than the alternative action (Heyes & Dawson, 1990). Despite its simplicity, the bidirectional control procedure has advantages over the two-action test, in that it allows for the comparison of similarly difficult behaviours but still rules out several nonimitative mechanisms. It controls for social influences, such as social facilitation (Zajonc, 1965) and contagious behaviour (Thorpe, 1957) because both observer groups watch a demonstration. Furthermore, it is easy to change the conditions in such a way that the species' ability in different forms of social learning can be distinguished. In principle, observers can learn either about the actions of the demonstrator or about some static (e.g. shape) or dynamic features (e.g. movements) of the manipulated object. If the two demonstrators move the object in different directions by manipulating it from different sides, observers can match the demonstrated action simply by attending to that side and then executing the only possible action; this is called local enhancement (Thorpe, 1957). The same holds if the manipulated part is distinctive, such as specifically coloured; this is called stimulus enhancement (Spence, 1937). If the two demonstrations are not different in these respects, the observer could learn either about the object affordances, i.e. the operating characteristics of the object, or about the form of a caused object movement. The first is called affordance learning (Byrne & Russon, 1998; Tomasello, Kruger, & Ratner, 1993) and the second object movement re-enactment (Custance, Whiten, & Fredman, 1999). It is, of course, difficult to distinguish 'copying what the object does' from 'copying what the model does with the object', with the latter being analogous to 'copying what body parts do' (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Finally, the observer could focus on the demonstrator's behaviour and learn about some aspects of the movements, also called movement imitation (Heyes, 1994; Huber, 1998). The latter distinction is difficult to make and would require further controls, such as the ghost control (the object is moved automatically; Heyes, Jaldow, Nokes, & Dawson, 1994) or detailed motion analyses (Voelkl & Huber, 2007).

Some have argued that 'true' imitation can only be assumed if observers are able to produce the copy of the behaviour in the absence of the demonstrator and after a considerable time has elapsed since the last presentation, meaning the observer is able to copy the behaviour from memory ('deferred imitation'; Piaget, 1952). The observer's response therefore cannot derive from response facilitation, in which one response from the individual's repertoire may be enhanced or primed by seeing it done, thereby increasing the probability that the response will occur (Byrne, 1994; Zentall, 2006). Instead, matching the demonstration is the result of an enduring representation of the demonstrator's behaviour (Huber et al., 2009). So far, long-term imitation has been demonstrated only in chimpanzees, *Pan troglodytes* (Tomasello, Savage-Rumbaugh, & Kruger, 1993) and dogs, *Canis lupus familiaris* (Fugazza, Pogány, & Miklósi, 2015), which were able to copy the behaviour after 48 or 24 h, respectively.

A group of species with high practical relevance are farm animals, because advanced knowledge about their social learning abilities is likely to have implications for animal husbandry and welfare (Nicol, 1995). Domestic pigs, *Sus scrofa domesticus*, and domestic chickens, *Gallus gallus domesticus*, have been among the first species to be investigated experimentally in this respect (Nicol & Pope, 1994a, 1994b). In recent years, further studies on pigs (Figuerola, Solà-Oriol, Manteca, & Pérez, 2013; Oostindjer et al., 2011) and chickens (Salva, Daisley, Regolin, & Vallortigara, 2009), and also goats, *Capra hircus* (Baciadonna, McElligott, & Briefer, 2013; Nawroth, Baciadonna, & McElligott, 2016), cows, *Bos taurus* (Costa, Costa, Weary, Filho, & von Keyserlingk, 2015) and horses,

Equus caballus (Krueger, Farmer, & Heinze, 2013; Rørvang, Ahrendt, & Christensen, 2015), have shed more light on social learning in farm animals. Like many farm animals, the pig is a social species, also in its domesticated form (Stolba & Wood-Gush, 1989). It is able to eavesdrop on informed conspecifics to find food and can also use 'tactical behaviour' to counteract exploitation (Held et al., 2010; Held, Mendl, Devereux, & Byrne, 2000, 2002). Nevertheless, following social cues is cognitively less demanding than learning about the behaviour of conspecifics. In early studies of observational learning in commercially farmed pigs, researchers found only modest information transfer from a pretrained demonstrator to litter mates (Nicol & Pope, 1994a). In the first experiment, pigs showed enhanced preference for a novel food over a known one after observing a sibling eating the novel food, but did so also in the asocial condition when only pre-exposed to the sight and smell of the novel food. A local enhancement effect was found in a second experiment, but only in one-third of observers. Observers searched for food at the same location where they had seen a demonstrator feeding before. Finally, in a third experiment, pigs observed a trained sibling demonstrator pressing one of two panels for a food reward. They outperformed control pigs that observed untrained siblings by pressing significantly more at a panel of the same colour/position as that used by their demonstrator. However, probably due to insufficient force of most of the presses to trigger the reward delivery mechanism, this effect was only found in the number of nonrewarded observers, and not in the number of rewarded panel presses.

An important factor for social learning is the role of the demonstrator. Learning from siblings (horizontal information transfer) may be less relevant and efficient than learning from the mother (vertical information transfer), as suggested by Nicol and Pope (1994a). Piglets direct most attention towards her (Oostindjer, Kemp, van den Brand, & Bolhuis, 2014). Indeed, strong evidence of social facilitation was found when piglets could observe or participate with the sow while she was eating a flavoured food; in comparison to nonobserver control and no-cue piglets, they were quicker and more interested in eating the food eaten by the sow (Oostindjer et al., 2011). In a second experiment, piglets preferred to eat from a feeder that was previously used by the sow, but only if there was food with the flavour assigned to the sow; if the flavour of the food changed between demonstration and test phase, the feeder was not preferred by piglets. This indicated effects of both local and stimulus enhancement.

In addition to intraspecific social learning, pigs have shown the potential of heterospecific social learning. For example, Held, Mendl, Devereux, and Byrne (2001) provided nonsystematic evidence that pigs could be trained to use the movements of a human demonstrator as a guide to the location of a food reward.

Still, the studies of social learning in pigs conducted so far have not revealed strong social learning effects beyond social facilitation and enhancement. It is therefore not clear whether pigs are indeed unable to learn about the behaviour of the model (imitation) or the manipulated objects (emulation) or whether the limited observation effects are the consequence of the artificial raising and housing system, as it could lead to the pigs not reaching their full potential during development. To decide between these alternatives, we tested free-ranging piglets that had been raised by their mother and aunts, and that together formed a natural matriline system (sounder).

In the current study, we aimed to extend knowledge about intraspecific social learning in pigs by employing the standard test for movement imitation, the two-action test (Dawson & Foss, 1965). Here we administered a variant, the bidirectional control procedure (Heyes & Dawson, 1990; Kis et al., 2015; Miller et al., 2009) in combination with a two-object task (Campbell, Heyes, &

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