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The importance of witnessed agency in chimpanzee social learning of tool use ☆

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ABSTRACT

Social learning refers to individuals learning from others, including information gained through indirect social influences, such as the results of others' actions and changes in the physical environment. One method to determine the relative influence of these varieties of information is the 'ghost display', in which no model is involved, but subjects can watch the results that a model would produce. Previous research has shown mixed success by chimpanzees (*Pan troglodytes*) learning from ghost displays, with some studies suggesting learning only in relatively simple tasks. To explore whether the failure of chimpanzees to learn from a ghost display may be due to neophobia when tested singly or a requirement for more detailed information for complex tasks, we presented ghost displays of a tool-use task to chimpanzees in their home social groups. Previous tests have revealed that chimpanzees are unable to easily solve this tool-use task asocially, or learn from ghost displays when tested singly, but can learn after observing conspecifics in a group setting. In the present study, despite being tested in a group situation, chimpanzees still showed no success in solving the task via trial-and-error learning, in a baseline condition, nor in learning the task from the ghost display. Simply being in the presence of their group mates and being shown the affordances of the task was not sufficient to encourage learning. Following this, in an escalating series of tests, we examined the chimpanzees' ability to learn from a demonstration by models with agency: (1) a human; (2) video footage of a chimpanzee; (3) a live chimpanzee model. In the first two of these 'social' conditions, subjects showed limited success. By the end of the final open diffusion phase, which was run to determine whether this new behavior would be transmitted among the group after seeing a successful chimpanzee use the task, 83% of chimpanzees were now successful. This confirmed a marked overall effect of observing animate conspecific modeling, in contrast to the ghost condition.

This article is part of a Special Issue entitled: insert SI title.

1. Introduction

To ask "how 'social' is social learning?" may seem paradoxical. By its very definition, social learning refers to individuals learning from others, necessitating some kind of social context. Indeed, for both humans (Over and Carpenter, 2012) and chimpanzees (Hopper et al., 2011) individuals may copy others for purely social reasons. However, much of what is referred to as 'social learning' is more specifically 'observational learning'; learning from the direct observation of others. In contrast, the more global term of social learning can also refer to information gained through indirect social influences, including the results of others' actions that cause changes in the physical environment. As Zentall (2011, 2012) notes, there are numerous examples of social learning that are likely mediated by such 'non-social' social learning mechanisms.

Consider chimpanzees (*Pan troglodytes*) in the wild cracking nuts with tools, a behavior that a variety of evidence suggests is transmitted socially (Inoue-Nakamura and Matsuzawa, 1997; Biro et al., 2003; Marshall-Pescini and Whiten, 2008; Luncz and Boesch, 2014). The performance of this behavior by a skilled individual could facilitate the learning of a naïve chimpanzee in two main ways. In one, direct observation of the proficient chimpanzee would allow imitative learning of the required actions (Whiten and Ham, 1992; Whiten et al., 2004). Alternatively, encountering the raw materials and/or by-products of the activity, such as an

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assemblage of hammers, anvils and cracked nuts, might facilitate learning of hammering through, for example, efforts to produce unshelled nuts or learning about the crucial properties of the materials (Byrne, 1998). Such 'non-observational' social learning (i.e. not dependent on observing the actions of another), has been described as a form of 'emulation' (Tomasello, 1999); reaching the same goal through independent means (Wood, 1989).

Beyond a simple dichotomy of imitation versus emulation, a number of social learning mechanisms have been identified (Whiten et al., 2004; Zentall, 2012; Moore, 2013), and it has been proposed that the social learning mechanism that individuals use may be mediated by the complexity of the task (Acerbi et al., 2010; Hopper et al., 2010). Much previous research has been concerned with distinguishing different social learning mechanisms used by a number of species, and their respective requirement for models with agency, including humans (Huang and Charman, 2005; Flynn and Whiten, 2013), apes (Call et al., 2005; Tennie et al., 2006), monkeys (Bugnyar and Huber, 1997; Subiaul et al., 2004; Hopper et al., 2013), dogs (Miller et al., 2009; Lakatos et al., 2014), rats (Heyes et al., 1994; Zohar and Terkel, 1991), birds (Akins et al., 2002; Auersperg et al., 2014), and reptiles (Kis et al., in press). To distinguish emulative from imitative learning, two key controls that have been used are 'end-state' and 'ghost display' conditions (reviewed in Hopper, 2010), often in conjunction with 'two-action' or 'bi-directional' tasks (Akins and Zentall, 1996; Zentall, 1996; Klein and Zentall, 2003). In an end-state condition naïve observers are shown the completed form of a task, and sometimes the initial state too, but no information is provided about the methods used to reach that end-state. In contrast, in a ghost display, championed by Zentall and colleagues, the observer sees only the required movements (or mechanical affordances) of objects, occurring without a live model. If learning arises from either of these two kinds of display, it is inferred that the observer was able to learn the task through emulation.

To date, studies with a number of species have indicated that subjects learn more quickly, and copy more accurately, after seeing a live (conspecific) model demonstrate the required actions, than they do when simply learning about the affordances of a task, for example via a ghost display (Hopper, 2010 provides a review). Indeed, Zentall (2012) noted that "the effect of demonstrator reinforcement may be to act as a catalyst to bring out imitative learning in an observer" (p. 121) and an early study by Zentall and Levine (1972) clearly demonstrated this effect. In that study, rats were presented with a lever that could be pressed in order to obtain a liquid reward. Naïve rats were tested in one of four conditions: (1) a rat in an adjacent cage pressing its lever and drinking the liquid, (2) a rat in the adjacent cage drinking the liquid when its lever moved automatically (it was yoked to the demonstrator's actions in condition 1; a ghost display), (3) a rat in the adjacent cage that neither pressed the bar nor drank liquid but simply provided social support, or (4) an empty cage. The rats learnt most quickly after seeing the full demonstration (condition 1) compared to the rats' responses in the other three conditions. Furthermore, there was no difference between the responses of the rats that saw the ghost display or the empty cage, although rats in both these conditions were significantly more successful than those that were provided with a live companion who did not provide any demonstration (condition 3; the authors concluded that the responses of the rats in this condition were inhibited due to social facilitation, *sensu* Zajonc, 1965).

Considering Zentall and Levine's (1972) study, although the rats that saw the ghost display ultimately learnt how to press the lever to obtain the liquid reward, it took them longer than those that saw a live model demonstrate the required actions, despite the only difference across conditions being the model's failure to interact with the lever (see also Zentall and Hogan, 1976). It could be argued that certain tasks, such as tool-use tasks, are simply too complex to be learnt via emulative means, and individuals require a social demonstration that provides more information (Hopper et al., 2010; Whiten et al., 2009). However, in addition to considering the quantitative difference between the information provided in a ghost display compared to that given by a live model (e.g., number of cues provided), it has also been suggested that live models provide a qualitative advantage because a live model has agency and is goal-directed (Cannon and Woodward, 2012; Kano and Call, 2014).

It has been proposed that the success of children at learning from ghost displays, which can exceed that of chimpanzees (e.g., Hopper et al., 2010; Caldwell et al., 2012), is due to children's ability to attribute agency to any sequence of actions that appear as if the actions are goal-oriented; the 'Agency Attribution Hypothesis' (Subiaul et al., 2007). Children readily attribute agency to inanimate objects that act in a purposeful way (Subiaul et al., 2011) or that interact with animate beings (Gerson and Woodward, 2012), and even young infants can identify actions that are driven by agency (Saxe et al., 2007). However, despite this, attribution of agency does not always increase children's ability to replicate the actions seen (Subiaul et al., 2011) and there is perhaps a potential interplay between task complexity and the need for a model with agency for imitation to occur.

Our previous research has shown that chimpanzees are capable of learning how to operate tool-use tasks from observing live conspecific models (Whiten et al., 2005), but that a ghost display is often not sufficient to allow learning (Hopper et al., 2007), despite aiding learning of simpler tasks (e.g., bidirectional tasks, Hopper et al., 2008). To further assess chimpanzees' requirement for a live model in order to learn tool use, we presented chimpanzees with either nonsocial displays – providing information purely about the mechanical properties of a task – or demonstrations of a task solution given by a live agent. Additionally, and extending upon our previous research, which has tested chimpanzees' ability to learn from conspecifics (Whiten et al., 2005; Hopper et al., 2007), we wished to address whether chimpanzees might also learn tool-use from watching a human model (Hayes and Hayes, 1952; Nagell et al., 1993; Horner and Whiten, 2005) or from a video of a chimpanzee (Price et al., 2009; Hopper et al., 2012), both of which represent forms of models with agency.

It is well established that for social primate species, the presence of group mates can encourage exploration leading to increased success in operating (simple) novel tasks (Harlow and Yudin, 1933; Dindo et al., 2009). Consistent with this, chimpanzees appear better able to learn in tests of emulation when given social support (i.e. when conspecifics are present: Hopper et al., 2008; Tennie et al., 2010a) than when tested alone (Hopper et al., 2007, although the differing responses of chimpanzees in these studies could also relate to the differing complexity of the tasks involved). Indeed, Zentall (2006) noted that "an isolated animal in a novel environment may be fearful, and fear in an enclosed environment may reduce exploratory behavior. If the presence of a conspecific reduces fear and increases exploratory behavior, it may lead to a higher probability (by chance) that the target behavior will be performed . . .Thus, experiments concerned with imitation must include a control for the possibility that the presence of another animal might result in an increase (or decrease) in motivation that could lead to facilitate performance of the target behavior" (p. 338). Therefore, to test the importance of social support, we presented chimpanzees in a social group setting with ghost displays of a complex tool-use task that chimpanzees (1) rarely solve asocially (Whiten et al., 2005), and (2) fail to learn from ghost displays when tested singly (Hopper et al., 2007).

In this study, four social groups of chimpanzees were presented with a series of conditions escalating in their predicted power to elicit social learning, to 'titrate' the amount of information