

# Social Learning in Humans and Nonhuman Animals: Theoretical and Empirical Dissections

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The past decade has seen a resurgent, concerted interest in social learning research comparing human and nonhuman animals. Such research has involved not only examination of the basic mechanisms and processes of social learning but also determinations of which species and age classes engage in these various sorts of social learning. It has considered the costs and benefits of social learning and the circumstances that favor reliance on social rather than asocial learning. As a result of such investigations, the study of social learning has become one of the most important and intensely researched fields of comparative psychology. This renaissance, fostered by multidisciplinary collaborations, has resulted in significant methodological and conceptual innovations.

In this special issue, we present a synthesis of work that consolidates what is currently known and provides a platform for future research. Consequently, we include both new empirical studies and novel theoretical proposals describing work with both human children and adults and a range of nonhuman animals. In this introduction, we describe the background of this special issue and provide a context for each of the eight articles it contains. We hope such introduction will not only help the reader synthesize the interdisciplinary views that characterize this broad field, but also stimulate development of new methods, concepts, and data.

The survival of any animal, human or nonhuman, depends on its acquiring a range of skills, among others how to extract food from defended sources, how or where to hide to avoid predators (or be successful as one), and how to increase access to mates. Some of these skills might be genetically canalized and some might be acquired through individual, trial-and-error learning. However, successful development of many such skills would not occur in the absence of interaction with knowledgeable others. Consequently, the study of social learning has become a major focus of research in those sciences interested in the behavior of both humans and

nonhumans, and the effort devoted to such research has increased greatly in recent years.

Figure 1 provides a measure of that increase, presenting the number of peer-reviewed papers published since 1982 and listed in PsycINFO that include *social learning* or *imitation* as keywords. For comparison, we have also provided similar data for publications listing as a keyword *theory of mind* (another active area of contemporary research in social cognition). Of note here are the distinct trajectories taken by *theory of mind* compared with *social learning* and *imitation*. Whereas since 1981 papers with *theory of mind* as a keyword have increased in frequency almost linearly, those listing *social learning*, *imitation*, or both dip toward the end of 2001 and then climb rapidly (it is worth noting that of the 166 papers that include both *social learning* and *imitation* as keywords, 103—or 62%—were published since 2001).

There are many possible reasons for this climb since 2001 in the number of papers with *social learning* and *imitation* as keywords. One is the attention drawn in the social psychology literature to the role that copying plays in smoothing interactions and increasing liking between social partners (e.g., Chartrand & Bargh, 1999, with current citations exceeding 600). Another is investigation of the neural underpinnings of imitative behavior, including the possible implication of mirror neurons (e.g., Iacoboni et al., 1999, with current citations exceeding 950) and the linking of these to deficits associated with autism (Williams, Whiten, Suddendorf, & Perrett, 2001, with current citations exceeding 250). Yet another plausible explanation lies in the growing body of evidence that humans are not the only animals for whom cultural transmission plays a significant role in the development of behavioral repertoires (Whiten et al., 1999, with current citations exceeding 650). A rising tide of scientific studies of such cultural phenomena in both human and nonhuman species has focused attention on the evolution of culture, its development and transmission from generation to generation by processes of social learning.

The link between the macro perspective on culture (an inherently population-level phenomenon) and the micro perspective focused on underlying social learning mechanisms was explicit in the pairing of a 2010 Royal Society Discussion Meeting—Culture Evolves (<http://www.cultureevolves.org>)—with a satellite meeting—Social Learning in Humans and Nonhuman Animals: Theo-

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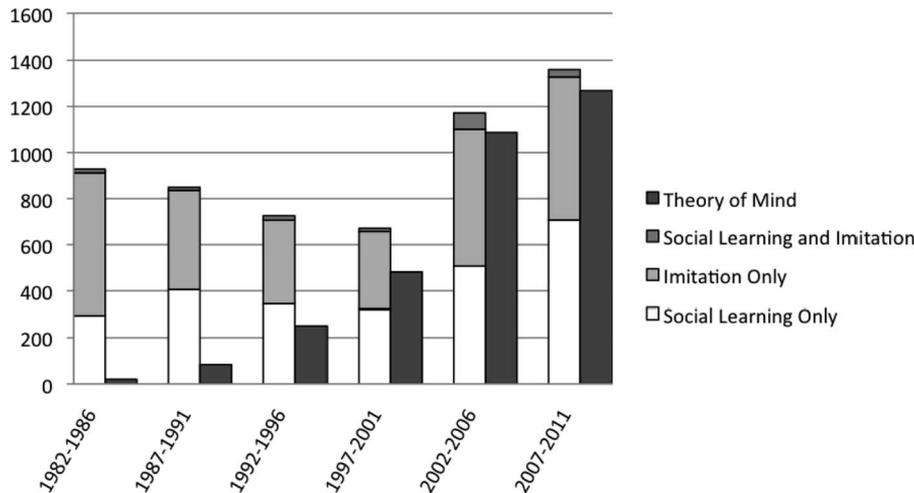


Figure 1. Number of peer-reviewed publications listed in PsycINFO since 1982 that have only *social learning*, only *imitation*, both *social learning* and *imitation*, and *theory of mind* as keywords.

retical and Empirical Dissections—held at the Kavli Royal Society International Centre at Chichley Hall that followed immediately after. The satellite meeting brought together an international community of scientists active in developing taxonomies, theories, and conceptual schemes for the dissection of different kinds of social learning, and empirical studies aimed at implementing such dissections. The presentations provided frameworks for synthesizing the interdisciplinary views that characterize the broad field of social learning while stimulating the development of new methods, concepts, and data. It is from these presentations that the articles included in this special issue have emerged. Papers presented at the Culture Evolves Discussion Meeting have already been published in a special issue of *Philosophical Transactions of the Royal Society B* (Volume 366, whole issue 1567, pp. 935–1187; see Whiten, Hinde, Laland, & Stringer, 2011).

Commensurate with the increasing focus on issues relating to social learning evident in Figure 1 has been an effort by contemporary authors to identify and define the multiple mechanisms that underpin such learning. Consider the oft-cited example of Imo, the then-1.5-year-old female Japanese macaque who discovered that a sand-covered sweet potato could be washed by taking it into a nearby stream, thereby making it palatable. The practice subsequently spread throughout Imo's troop along clearly defined social networks. At one time, this was suggested to be “probably the single most impressive case of imitation on record” (Premack, 1984, p. 17). The same behavior if reported today would be assigned to one of numerous alternative categories of social learning, including various forms of imitation (action, motor, contextual, procedural, automatic, vocal, cognitive, and program level), as well as goal and result emulation, affordance learning, object movement reenactment, observational conditioning, or contagion (Byrne, 2002; Byrne & Russon, 1998; Call & Carpenter, 2002; Galef, 1988; Heyes, 1994, 2011; Hoppitt & Laland, 2008; Subiaul, 2007, 2010; Want & Harris, 2002; Whiten & Ham, 1992; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Zentall, 2001, 2006, 2011). As a result, for many, the ascription of imitation to the impressive case of sweet potato washing is no longer justified (Galef, 2004; Kendal, Kendal, & Laland, 2007). At the heart of a

number of the articles we present are the application and development of these taxonomies of social learning and the associated dissection of empirical cases.

Here, Zentall's (2012) concise yet comprehensive review of the main branches of this social learning literature emphasizes that any attempt to understand social learning will be incomplete unless it both ranges across the animal kingdom (e.g., the data on avian imitation is compelling, rendering as suspect any claims that the capacity for imitation belongs to humans only) and strives to distinguish a host of alternative mechanisms of social learning that might underlie specific cases. Zentall's review draws attention to the fact that despite the increased attention focused on social learning research in the past few decades, we remain a long way from understanding the underlying cognitive and neural processes that enable animals to match their behavior to that of a demonstrator.

Burkart, Kupferberg, Glasauer, and van Schaik (2012) present empirical work suggesting that even when engaged in basic forms of social learning such as local enhancement, marmoset monkeys (*Callithrix jacchus*) use the perceived intentions of a model to guide their behavior. Adapting Woodward's (1998) highly influential habituation–dishabituation paradigm, Burkart and colleagues presented monkeys with an agent who repeatedly approached and interacted with one of two objects. The marmosets perceived the agent's behavior as goal-directed whether the agent was a conspecific or a robot, but not if it was a black box. Social facilitation and enhancement learning were strongest when the agent was a conspecific and weakest when the agent was a black box. It has been suggested that social learning guided by intention understanding is necessary for cumulative culture in humans, but the existence of sensitivity to intention in marmosets indicates that such sensitivity is not sufficient for cumulative culture to emerge.

Delineating processes of social learning is a prominent feature of the articles by Zentall and by Burkart and colleagues, an endeavor with a long pedigree in the comparative and nonhuman animal literature. In contrast, as Want and Harris (2002) lament, research with humans has tended to lag in assimilating the taxonomies outlined previously as standard practice. Even now, many

papers continue to be published that use *imitation* as a blanket term for any form of copying. Here, Huang's (2012) contribution represents a clear exception to this rule. Huang presents three novel experiments identifying the conditions under which infants engage in emulation learning. In these experiments, infants are presented with varying degrees of information about the outcomes (or end states) associated with a series of novel objects. Huang's study shows that emulation (learning from the results of others' actions) is relatively efficient when (a) the target items involve outcomes that are self-contained and are produced with a single-step action but not when the items comprise two separate parts that can be combined into a novel end configuration; (b) that seeing the items in both the starting and end states facilitates emulation more than seeing the items in their end states alone, as does seeing an adult model in static postures consistent with the target actions; and (c) that infants' encoding of bodily cues from static body postures may be susceptible to the concurrence of the spatiotemporal causal relations of objects. Huang's article makes an important contribution in showing how young children can produce specific object-directed outcomes in the absence of a full demonstration.

Given that very young children appear capable of identifying how to bring about object-related outcomes by observing aspects of their beginning and end states, one could expect children to be increasingly unconstrained by the specifics of what is modeled before them. Yet, the results of an increasing number of recent studies suggest that children may replicate even those actions of a model that have no apparent purpose and even after the causal irrelevance of those actions has been made explicit (e.g., Kenward, Karlsson, & Persson, 2011; Lyons, Damrosch, Lin, Macris, & Keil, 2011; Nielsen & Blank, 2011; Nielsen & Tomaselli, 2010). This phenomenon, known as *overimitation*, features in varying degrees in many of the articles included in this special issue, and it is a core focus of the contribution of McGuigan (2012). McGuigan shows that, unlike young children (Flynn, 2008; Flynn & Whiten, 2008; McGuigan & Graham, 2010), adults will overimitate to the extent of transmitting irrelevant actions down *diffusion chains* of several individuals, simulating cultural transmission. More important, however, McGuigan demonstrates that such overimitation is influenced by the transparency of the actions; the more obvious the irrelevance of the actions, the less likely they are to be passed on. For McGuigan, overimitation springs from a conformity bias, a human propensity for acquiring culture that becomes increasingly strong with age (Whiten, in press).

Caldwell, Schillinger, Evans, and Hopper (2012), building on previous research with adults, show that full demonstration by a live model is not necessary for overimitation or the transmission of information with high fidelity. In their study, participants were shown either a photograph or live model of two different spaghetti towers (model towers built of uncooked spaghetti with modeling clay junctions). Participants were then instructed not to copy the demonstrated model but to build the tallest tower possible. But copying is exactly what they did; rather than attempt to build the tallest tower, participants simply replicated the demonstrated model. Thus, despite not seeing a full demonstration (i.e., observing a model build a tower) and relying only on a model of a completed tower (i.e., end state), participants reproduced models with high fidelity. For Caldwell and colleagues, these results cast doubt on the hypothesis that imitation is necessary for the high-fidelity transmission of information.

These results lead us back to the link between imitation and culture that runs through this special issue. The contribution by Nielsen (2012) is explicitly focused on this link. He notes (as do others in our special issue) how the high-fidelity copying characteristic of overimitation facilitates rapid transmission of information while simultaneously enabling nonfunctional traditions to be similarly passed on. However, he raises questions regarding the capacity of overimitation to support innovation and speculates that something else may be needed to drive the vast technological advances characteristic of the *Homo* lineage. The answer, he suggests, may be found in the pretend play children engage in—a possibility that presupposes the existence of childhood in the first place, which Nielsen argues may be a relatively recently evolved trait of our species. What Nielsen does not dispute is that the evolution of overimitation as a copying strategy is likely to have been pivotal in the evolution of human cumulative culture. But why might it have emerged in the first place? The answer might lie in a species-specific increase in the use of copying to satisfy social motivations.

Directly copying others can be a particularly powerful form of learning that permits the rapid acquisition of new skills. However, humans also copy for socially oriented reasons: We will imitate to communicate, to be like others, to be liked by others, and to show others that we are alike (Dijksterhuis, 2005; Nadel, Guérini, Pez , & Rivet, 1999). Here, Over and Carpenter (2012) argue that these social factors have been largely ignored in many accounts of imitation. Their article fully articulates how social motivations function to drive imitation across varying circumstances and experimental arrangements, and using this approach, they explain apparent paradoxes in the literature (notably that children will both overimitate and selectively imitate). For Over and Carpenter, children's choices about what to copy are influenced by three primary factors: (a) the relationship between personally acquired and socially acquired information, (b) their identification with the model and the social group in general, and (c) the social pressures they experience to imitate in particular ways. For Over and Carpenter, failing to acknowledge the strong pull in humans to do as others do will result in an incomplete picture of imitation that, they conclude, is a profoundly social process.

This highly social view of imitation provides an interesting complement to the argument provided by Heyes (2012), who raises questions as to whether there is anything inherently social about social learning and asks whether the constituent mechanisms of social learning are distinct in any way from those supporting asocial learning. Heyes's answer is that there are no fundamental differences; rather, both social and asocial learning depend on a common set of associative learning processes that operate in similar ways across animal species. What, then, of arguments that humans are uniquely imitative (e.g., Meltzoff, 1988)? How does this fit with the view outlined by Over and Carpenter? For Heyes, the answer is relatively straightforward. What makes human learning different is that the effects of social living have affected the input mechanisms for learning but not the actual learning mechanisms per se. In humans, doing as others do is so strong because from early in infancy such copying behavior is highly rewarded. The nature of the input sets us apart from other animals, not the cognitive processes we use in acquiring behavior.

This special issue includes a wide range of perspectives on social learning incorporating new empirical work on human chil-

dren (Huang), human adults (McGuigan; Caldwell et al.), and monkeys (Burkart et al.) together with contrasting and complementary theoretical views and reviews that outline what is unique and shared among phylogenetically distant species (Heyes; Over & Carpenter; Nielsen; Zentall). This reflects the unprecedented interest in social learning that has emerged in the past decade, and the questions raised by the contributors to this issue will help ensure that this interest continues to grow. We have greatly deepened our understanding of social learning, but as Zentall reminds us, we still have a lot to learn.

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## References

- Burkart, J., Kupferberg, A., Glasauer, S., & van Schaik, C. (2012). Even simple forms of social learning rely on intention attribution in marmoset monkeys (*Callithrix jacchus*). *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- Byrne, R. W. (2002). Imitation of novel complex actions: What does the evidence from animals mean? *Advances in the Study of Behavior*, 31, 77-105. doi:10.1016/S0065-3454(02)80006-7
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioural and Brain Sciences*, 21, 667-684. doi:10.1017/S0140525X98001745
- Caldwell, C. A., Schillinger, K., Evans, C. L., & Hopper, L. M. (2012). End state copying by humans (*Homo sapiens*): Implications for a comparative perspective on cumulative culture. *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- Call, J., & Carpenter, M. (2002). Three sources of information in social learning. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 211-228). Cambridge, MA: MIT Press.
- Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology*, 76, 893-910. doi:10.1037/0022-3514.76.6.893
- Dijksterhuis, A. (2005). Why we are social animals: The high road to imitation as social glue. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science* (Vol. 2: *Imitation, human development, and culture*, pp. 207-220). Cambridge, MA: MIT Press.
- Flynn, E. (2008). Investigating children as cultural magnets: Do young children transmit redundant information along diffusion chains? *Philosophical Transactions of the Royal Society of London B*, 363, 3541-3551. doi:10.1098/rstb.2008.0136
- Flynn, E., & Whiten, A. (2008). Cultural transmission of tool use in young children: A diffusion chain study. *Social Development*, 17, 699-718. doi:10.1111/j.1467-9507.2007.00453.x
- Galef, B. G. (1988). Imitation in animals: History, definition and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3-28). Hillsdale, NJ: Erlbaum.
- Galef, B. G. (2004). Approaches to the study of traditional behaviors of free-living animals. *Learning & Behavior*, 32, 53-61. doi:10.3758/BF03196006
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, 69, 207-231. doi:10.1111/j.1469-185X.1994.tb01506.x
- Heyes, C. (2011). Automatic imitation [Review]. *Psychological Bulletin*, 137, 463-483. doi:10.1037/a0022288
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- Hoppitt, W., & Laland, K. N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior*, 38, 105-165. doi:10.1016/S0065-3454(08)00003-X
- Huang, C. (2012). Outcome-based observational learning in human infants. *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Giacomo, R. (1999, December 24). Cortical mechanisms of human imitation. *Science*, 286, 2526-2528. doi:10.1126/science.286.5449.2526
- Kendal, J. R., Kendal, R. L., & Laland, K. N. (2007). Quantifying and modelling social learning processes in monkey populations. *International Journal of Psychology & Psychological Therapy*, 7, 123-138.
- Kenward, B., Karlsson, M., & Persson, J. (2011). Over-imitation is better explained by norm learning than by distorted causal learning. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1239-1246. doi:10.1098/rspb.2010.1399
- Lyons, D. E., Damrosch, D. H., Lin, J. K., Macris, D. M., & Keil, F. C. (2011). The scope and limits of overimitation in the transmission of artefact culture. *Philosophical Transactions of the Royal Society B*, 366, 1158-1167. doi:10.1098/rstb.2010.0335
- McGuigan, N. (2012). The role of transmission biases in the cultural diffusion of irrelevant actions. *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- McGuigan, N., & Graham, M. (2010). Cultural transmission of irrelevant tool actions in diffusion chains of 3- and 5-year-old children. *European Journal of Developmental Psychology*, 7, 561-577. doi:10.1080/17405620902858125
- Meltzoff, A. N. (1988). The human infant as "homo imitans." In T. R. Zentall & B. G. J. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 319-341). Hillsdale, NJ: Erlbaum.
- Nadel, J., Guérini, C., Pezé, A., & Rivet, C. (1999). The evolving nature of imitation as a format for communication. In J. Nadel & G. Butterworth (Eds.), *Imitation in infancy* (pp. 209-234). Cambridge, England: Cambridge University Press.
- Nielsen, M. (2012). Imitation, pretend play and childhood: Essential elements in the evolution of human culture? *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- Nielsen, M., & Blank, C. (2011). Imitation in young children: When who gets copied is more important than what gets copied. *Developmental Psychology*, 47, 1050-1053. doi:10.1037/a0023866
- Nielsen, M., & Tomaselli, K. (2010). Over-imitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychological Science*, 21, 729-736. doi:10.1177/0956797610368808
- Over, H., & Carpenter, M. (2012). Putting the social into social learning: Explaining both selectivity and fidelity in children's copying behavior. *Journal of Comparative Psychology*, ●●●, ●●●-●●●.
- Premack, D. (1984). Pedagogy and aesthetics as sources of culture. In M. S. Gazzaniga (Ed.), *Handbook of cognitive neuroscience* (pp. 15-35). New York, NY: Plenum Press.
- Subiaul, F. (2007). The imitation faculty in monkeys: Evaluating its features, distribution and evolution. *Journal of Anthropological Sciences*, 85, 35-62.
- Subiaul, F. (2010). Dissecting the imitation faculty: The multiple imitation mechanisms (MIM) hypothesis. *Behavioural Processes*, 83, 222-234. doi:10.1016/j.beproc.2009.12.002
- Want, S. C., & Harris, P. L. (2002). How do children ape? Applying concepts from the study of non-human primates to the developmental study of "imitation" in human children. *Developmental Science*, 5, 1-14. doi:10.1111/1467-7687.00194
- Whiten, A. (in press). Social cognition: Making us smart, or sometimes making us dumb? Overimitation, conformity, non-conformity and the transmission of culture in ape and child. In M. Banaji & S. Gelman (Eds.), *The development of social cognition*. Oxford, England: Oxford University Press.
- Whiten, A., Goodall, J., McGew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999, June 17). Cultures in chimpanzees. *Nature*, 399, 682-685. doi:10.1038/21415
- Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, G. Beer, & M. Milinski (Eds.), *Advances in the*

- study of behaviour* (Vol. 21, pp. 239–283). New York, NY: Academic Press.
- Whiten, A., Hinde, R. A., Laland, K. N., & Stringer, C. B. (2011). Culture evolves. *Philosophical Transactions of the Royal Society B*, *366*, 938–948. doi:10.1098/rstb.2010.0372
- Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Learning & Behavior*, *32*, 36–52. doi:10.3758/BF03196005
- Williams, J. H. G., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience and Biobehavioral Reviews*, *25*, 287–295. doi:10.1016/S0149-7634(01)00014-8
- Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, *69*, 1–34. doi:10.1016/S0010-0277(98)00058-4
- Zentall, T. R. (2001). Imitation in animals: Evidence, function and mechanisms. *Cybernetics and Systems*, *32*, 53–96. doi:10.1080/019697201300001812
- Zentall, T. R. (2006). Imitation: Definitions, evidence, and mechanisms. *Animal Cognition*, *9*, 335–353. doi:10.1007/s10071-006-0039-2
- Zentall, T. R. (2011). Social learning mechanisms: Implications for a cognitive theory of imitation. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems*, *12*, 233–261. doi:10.1075/is.12.2.03zen
- Zentall, T. R. (2012). Perspectives on observational learning in animals. *Journal of Comparative Psychology*, ●●●, ●●●–●●●.

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