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How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals

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Abstract: The human species is more reliant on cultural adaptation than any other species, but it is unclear how observational learning can give rise to the faithful transmission of cultural adaptations. One possibility is that teaching facilitates accurate social transmission by narrowing the range of inferences that learners make. However, there is wide disagreement about how to define teaching, and how to interpret the empirical evidence for teaching across cultures and species. In this article I argue that disputes about the nature and prevalence of teaching across human societies and nonhuman animals are based on a number of deep-rooted theoretical differences between fields, as well as on important differences in how teaching is defined. To reconcile these disparate bodies of research, I review the three major approaches to the study of teaching – mentalistic, culture-based, and functionalist – and outline the research questions about teaching that each addresses. I then argue for a new, integrated framework that differentiates between teaching types according to the specific adaptive problems that each type solves, and apply this framework to restructure current empirical evidence on teaching in humans and nonhuman animals. This integrative framework generates novel insights, with broad implications for the study of the evolution of teaching, including the roles of cognitive constraints and cooperative dilemmas in how and when teaching evolves. Finally, I propose an explanation for why some types of teaching are uniquely human, and discuss new directions for research motivated by this framework.

Keywords: Cooperation; cultural transmission; evolution; teaching; pedagogy; theory of mind

1. The adaptive value of teaching

The human species is more reliant on cultural adaptation than is any other species (Boyd & Richerson 1985; Boyd et al. 2011; Dean et al. 2012, Hill et al. 2009; Whiten & Erdal 2012). Much of the knowledge and behavior that allows humans to adapt to a uniquely broad range of ecologies is accumulated over multiple generations, leading to adaptations more complex than any one individual could produce in a lifetime (Boyd & Richerson 1996; Tennie et al. 2009). For example, Oceania was only settled through the combination of sophisticated navigational knowledge and complex double-hulled canoes (see Kirch 2002), and the Arctic could not have been settled without new technologies for clothing and shelter, as well as food-gathering techniques (Boyd et al. 2011).

In culture as in biology, the accumulation of adaptive changes across many generations occurs only when transmission is sufficiently faithful. A variety of mechanisms work to make genetic replication incredibly accurate, but it is less clear what makes cultural transmission faithful, or how much fidelity is necessary (see Dawkins 1982; Henrich & Boyd 2002; Henrich et al. 2008). The problem is that – unlike genes – cultural variants do not physically replicate. Instead, they replicate through the inferential process of social learning, by which social learners use – among other inputs – others' behavior to make and support inferences about the world. This often entails acquiring the same behaviors or mental representations held by others. In such cases the range of inferences that can be made based on a single behavior may be quite broad, and making an accurate inference can depend on

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background knowledge (see Boyer 1998; Sperber & Wilson 1995). One possible way that faithful transmission may be maintained under such circumstances is that variation in learner inferences is decreased by *attractors*, that is, innate or learned psychological dispositions that restrict the range of inferences made by learners (Boyer 1998; Sperber 2000). One problem with attractors as a solution to this inferential frame problem is that attractors can only change over historical time, at the pace of the factors of the environment, physical world, or psychology in which they are rooted. Culture can change faster than biology (Perreault 2012), such that genetically evolved cognitive attractors may not be able to keep pace with culturally evolving mental representations. This may also apply to attractors shaped by environmental change. As a result, attractors may help to explain faithful transmission for domains of social learning in which content varies only superficially over time and space. However, attractors are difficult to reconcile as a mechanism for explaining the diversity of complex, locally adaptive beliefs and technologies used by humans. For example, our information-rich psychology might include attractors that influence the human creation and use of sharp tools to cut materials. Still, it is a long way from "things that cut" to the sophisticated production process required to produce a Damascus steel blade, a product which modern techniques and present-day scientists have yet to recreate (see Reibold et al. 2006).

In addition to an inherited information-rich psychology, humans may also rely on help from knowledgeable models to narrow the range of a learner's inferences, making social learning accurate beyond the proper domains of existing attractors. Overt teaching can function this way, and psychologists studying social learning have pointed out that models can provide subtle cues that greatly enhance the accuracy of social learning. For example, models may use gaze to establish joint attention (Tomasello et al. 2005), or use ostensive cues to mark some knowledge as generalizable (Csibra & Gergely 2009; 2011).

In most forms of social learning, the mental capacities and strategies for copying others evolve in the learners. Such learner-driven mechanisms can be adaptive, provided they are mixed with asocial learning strategies that produce new, locally adaptive information (Boyd & Richerson 1985; 1995; Galef 1995; Giraldeau et al. 2002; Rogers 1988). In contrast, teaching also requires the evolution of mental capacities and strategies for when to teach on the part of models who perform teaching behaviors. As a result, teaching may only be adaptive in a subset of the situations in which social learning more generally evolves.

Mathematical modeling suggests that teaching – defined as behavior evolved to facilitate learning in others – is adaptive when information is difficult for learners to acquire independently or through observation, but not when it is so rare that relatives are unlikely to possess it (Castro & Toro, 2014; Fogarty et al. 2011). Assuming that these conditions are met by cumulative cultural knowledge in humans and not by other forms of culture, this could explain why humans teach more than other animals. There is some experimental evidence suggesting that humans do facilitate cumulative cultural learning through teaching (Dean et al. 2012; cf. Caldwell & Millen 2009), and psychologists often characterize teaching as ubiquitous across human societies and as unique to humans (see Csibra & Gergely 2009; 2011; Kruger & Tomasello 1996; Premack & Premack 2004; Strauss et al. 2002). However, cultural anthropologists studying childhood and learning in diverse societies claim that teaching is unique to Western cultures and absent elsewhere (Gaskins & Paradise 2010; Lancy & Grove 2010; Paradise & Rogoff 2009; see also review by Hewlett et al. 2011). At the same time, biologists have documented teaching in nonhuman (and some non-cultural) animals including ants, meerkats, pied babblers, and several additional species (see reviews: Caro & Hauser 1992; Hoppitt et al. 2008; Thornton & Raihani 2008). Precisely what qualifies as "teaching" is still hotly debated (see Csibra 2007; reply by Thornton 2007; see also Byrne & Rapaport 2011; reply by Thornton & McAuliffe 2012).

I argue here that discrepancies in empirical claims across disciplines follow from deep-rooted theoretical differences among them, due to disciplinary differences in focal research questions. To better address the evolutionary origins and adaptive design of teaching behavior, I propose a framework that synthesizes existing comparative and anthropological research on teaching behavior. In a review of the three major approaches to the definition and study of teaching – mentalistic, culture-based, and functionalist – I outline the research questions that drive the discipline-specific approaches, and address the ways in which each approach might benefit from this synthesis (Section 2.4). I then propose a framework based in the functionalist approach that structures the study of teaching according to the adaptive problems each type solves (Section 3), and demonstrate its utility by restructuring existing comparative and anthropological data on teaching (Section 4) and by building on this preliminary empirical review to generate novel research questions unique to the integrative approach (Sections 5, 6, and 7). Specifically, I discuss the implications for the study of the psychology of teaching, and clarify how problems of cooperation may constrain the evolution of teaching differently for the roles of learner and teacher. Finally, I synthesize these insights to illuminate why humans are such prolific and intensive teachers, relative to other animals.

2. What is teaching, in theory?

2.1. Mentalistic definitions of teaching

Mentalistic approaches define teaching as *behavior with the intent to facilitate learning in another* (Pearson 1989, p. 63). This approach seeks to explain the design of mental mechanisms that make teaching possible, often in order to explain individual-level and species-level variation in teaching abilities. For example, Tomasello et al. (1993) argue that the establishment of joint attention and holding representations about the mind of the other are necessary prerequisites to teaching. It follows that teachers need theory of mind (ToM) to identify the need for teaching, to figure out what it is that they ought to teach, and to tailor the difficulty of the task to match the skill level of the pupil (Kruger & Tomasello 1996). Elsewhere, researchers from this school of thought apply the same line of reasoning to social learning capacities, including imitation (for review, see Caldwell & Whiten 2002). In this view, the absence of theory of mind in nonhuman animals explains why only

humans engage in "powerful forms of cultural learning" such as teaching and imitation (Tomasello 1999).

Similarly, the mentalistic approach uses variation in theory of mind capacities to explain variation in human teaching capacities, at the individual level. For example, Ziv and Frye (2004) argue that teaching is only possible when teachers and pupils both consciously recognize (a) intentionality and (b) knowledge differences between individuals. They cite a range of studies showing that children who have better success on theory of mind (ToM) tests also teach more or use more effective methods for teaching (Davis-Unger & Carlson 2008; Strauss et al. 2002; Ziv & Frye 2004), and perform better as pupils (Wellman & Lagattuta 2004). Olson and Bruner (1996) argue that without theory of mind there can be no ascription of ignorance, and therefore there will be no attempt to teach. According to Strauss et al. (2002), "in order to teach, one needs to know when knowledge, beliefs, skills, etc. are missing, incomplete, or distorted, as well as how people learn" (p. 1476). This goes beyond simply having the intent to teach, to having the intent to teach based upon a range of mental representations of others' mental states. This approach builds on Vygotsky's (1978) concept of the "zone of proximal development," the narrow range of learning just outside a child's developing abilities, within which a child can learn, building on his or her present competencies through scaffolding by knowledgeable others (Guberman & Greenfield 1991; for review, see Pelissier 1991). In this view, only a teacher who identifies this proximal zone of development (through ToM) can understand that teaching is needed, and can then intend to teach.

2.2. Culture-based definitions of teaching

Culture-based definitions of teaching focus on *teaching* as it happens in formal classrooms in Western societies, in contrast to informal social learning in more "traditional" societies. This approach is most commonly used in sociocultural anthropology and cross-cultural psychology. The research goals include describing cross-cultural variation in the prevalence of teaching, with some work focused on direct comparison of formal schooling versus everyday learning in childhood (e.g., Maynard 2004; Paradise & Rogoff 2009). These definitions underlie nearly all of the cross-cultural data on teaching, which are crucial to our understanding of human variation in teaching behavior.

Researchers taking this approach contrast teaching with other forms of social and individual learning outside of the Western cultural context (e.g., Lancy 2010). Rather than using an explicit definition, researchers in this approach identify teaching from a shifting set of ostensive features, including: (1) the teacher intends to teach, (2) knowledge transmission is unidirectional (teacher to pupil), (3) pupils are passive recipients of knowledge who do not collaborate interactively with the teacher, (4) knowledge is communicated explicitly, often by verbal instruction, and (5) the activity is marked in some way and recognized as "teaching" by its participants. These criteria are not applied as a strict checklist, but as a set of characteristics arrived at inductively via contrasts between *teaching* as the ethnographer understands it, and other types of social learning. Note that in this approach, "social learning" is used in the colloquial sense to refer to learning that happens in a social context or interaction; therefore, it is not limited to the functionalist learning mechanisms that have evolved to facilitate the transfer of social information.

Types of social learning that are not considered "teaching" are described as natural, simple, informal, observational, practical learning, or guided instruction (Paradise & Rogoff 2009), in contrast with "formal" learning via teaching. In informal social learning, (a) learning takes place within an activity, the focus is on completing a task rather than on learning or teaching; (b) learners are often expected to observe rather than participate; and (c) the responsibility for attending, learning, and ending a learning period lies with the learner rather than the model (Gaskins & Paradise 2010). In other words, learning is common through *intent participation*, defined as "listening-in" and "keen observation" (Rogoff et al. 2003), or through *legitimate peripheral participation*, in which learning a given activity is also inextricably linked to the learner's building a sense of shared identity with other practitioners (Lave & Wenger 1991). Learners must, therefore, identify with their models prior to learning about an activity.

In contrast, teaching is a "marked" event, such that a behavior is only teaching when participants label the activity as "teaching" *instead of* something like "line-fishing" or "weaving." In this framework, "teaching" that is embedded in another activity is informal learning, rather than formal learning or teaching. It is so fully integrated into the learner's everyday experiences that they appear to learn through "a kind of osmosis" (Gaskins & Paradise 2010, p. 87). This type of learning is thought to allow for automatic, collaborative, highly effective learning through experience, "with little dependence on coercion and explicit teaching" (Paradise & Rogoff 2009, p. 124). This fashion of learning works, researchers argue, because informal learners are always interested, such that learning happens without any need for teaching, and learning happens without fail (Paradise & Rogoff 2009; Spindler & Spindler 1989).

From this perspective, teaching is not a generally useful mechanism to make difficult learning easier. Instead, it is a means of forcing passive or uninterested pupils to learn. A number of researchers suggest this is unique to Western societies. Mead (1970, p. 12), for example, argues that in the shift toward Western ways of learning, "the emphasis has shifted from learning to teaching, from the doing to the one who causes it to be done, from the spontaneity to coercion, from freedom to power," and that the shift toward teaching means "the shift from the need for an individual to learn something which everyone agrees he would wish to know, to the will of some individual to teach something that it is not agreed that anyone has any desire to know" (p. 3). Rogoff et al. (2003) contrast informal learning with the "factory-efficiency" model of teaching, where information transfer is unilateral and divorced from culturally valued activities. Rather than being collaborative social partners, in this factory-efficiency model, "[t]eachers were cast as technical workers who were supposed to insert information into the children, who were seen as receptacles of knowledge or skill" (p. 181).

Lancy and Grove (2010) equate teaching with explicit or abstract verbal instruction, which they claim is rare in non-Western societies. They discuss "the near total absence of children being taught (in the explanatory, didactic sense) by adults" (p. 145), and explain in an endnote that only three examples of this kind of teaching exist in the

ethnographic literature on non-Western societies. Lancy and Grove also present several examples of guided learning that they do not consider "teaching," but which would be considered teaching by the *mentalistic* definition mentioned above. For example, teaching is absent in canoe-building among the Warao, where "there is not much verbal instruction… but the father does correct the hand of his son and does teach him how to overcome the pain in his wrist from working with the adze" (Wilbert 1976; quoted in Lancy & Grove 2010, p. 161). Weaving apprenticeships in which "actual instruction begins in earnest when the master sits beside the boy at the loom and begins to demonstrate some simple patterns, which the novice copies" are not classed as "teaching," because prior to instruction, pupils offset the cost of teaching through menial labor, and again there is little explicit verbal explanation (Lancy & Grove 2010, p. 160).

2.3. Functionalist definitions of teaching

Functionalist definitions of teaching are grounded in the observable behavioral causes and outcomes of teaching behavior, instead of the teacher's motivational state or on local context. This approach aims to explain the evolutionary roots and adaptive design of teaching behavior, in part by demonstrating that "teaching" is not a uniquely human behavior. Functionalist approaches have similarly been applied to social learning more broadly, opening up the spectrum of social learning mechanisms beyond pure imitation, to include a range of mechanisms by which nonhuman (and human) animals may gather information through social transmission (for reviews, see Heyes & Galef 1996; Fragaszy & Perry 2003). The functionalist approach to teaching differs from the mentalistic one in that there is less focus given to mental mechanisms – a practical innovation for studying nonverbal species (see Caro & Hauser 1992). To this end, functionalist definitions build on a basic theoretical definition of teaching as *behavior evolved to facilitate learning in others*. To enable the empirically rigorous study of teaching in nonhuman animals, Caro and Hauser (1992) established three operational criteria for identifying behavior that functions as teaching: (1) behavior is contingent on the presence of a naïve learner, (2) it provides no immediate benefit (or even generates a cost) for the teacher, and (3) it can be shown to facilitate learning in others.

Subsequent functionalist approaches to teaching have sought to update Caro and Hauser's (1992) operational criteria, but not their conceptual definition. Hoppitt et al. (2008) argue that the cost criterion does not reliably distinguish between behavior that evolved for teaching versus alternative functions, so it may lead to false positives. For example, food provisioning may result in offspring learning about parental food preferences, but probably evolved because it increases offspring survival rates (Hoppitt et al. 2008). However, if food provisioning leads to learning by offspring at an immediate cost to parents, the Caro and Hauser (1992) definition would categorize this as teaching. Without rejecting the usefulness of the Caro and Hauser operational definition, Hoppitt et al. (2008) offer a revision of the broader theoretical definition of teaching that separates the *process* of learning from the *behavior* of teaching, such that teaching can be viewed as an accessory to other well-established social learning processes, and teaching does not have a single behavioral profile. For example, learning may happen through teaching by *tolerance* of close observation – where the adaptation of tolerance is on the part of the teacher – as compared with close observation, where the adaptation is on the part of the learner, who persists in observing. In this way, teaching can evolve alongside existing social learning processes, increasing learning accuracy through small modifications of a model-turned-teacher's behavior. The typology laid out by Hoppitt and colleagues distinguishes among teaching via local enhancement, observational conditioning, imitation, opportunity provisioning, and coaching. Teaching behavior is conceptually distinguishable from other social learning behavior because *non-teaching* is *inadvertent*, such that the adaptation for teaching is not on the part of the demonstrator.

Thornton and Raihani (2008) point out that the Caro and Hauser (1992) operational definition can also lead to false negatives in the study of teaching in nonhuman animals (see also Thornton & McAuliffe 2012; cf. Byrne & Rapaport 2011). Thornton and Raihani suggest that teaching be defined instead by "key characteristics" (p. 1825): "(1) it is a form of cooperative behavior with response-dependent fitness payoffs; (2) its function is to facilitate learning in others; and (3) it involves the coordinated interaction of a donor and a receiver of information." The key characteristics do not stipulate behavioral guidelines for identifying these key characteristics in the field, but do predict that teaching will be observed where its utility in increasing the pupil's learning efficiency is the highest (e.g., it most improves on other learning mechanisms). A major function of these key characteristics is to distinguish teaching from other forms of social learning, communication, and social interactions such as "punishment," which do not evolve because of the learning benefits they create for the learner.

Thornton and Riahani (2008) and Hoppitt et al (2008) do not include human-specific forms of teaching within their frameworks. However, the novel functionalist definition of Csibra and Gergely (2009; 2011) focuses on teaching as a uniquely human trait. Although like the mentalistic approaches, this definition describes a number of mental characteristics of teaching, it differs from mentalistic approaches (e.g., Kruger & Tomasello 1996), in that its primary research question is on the functional or adaptive role that teaching serves, and on how teaching evolved (in humans). Csibra and Gergely (2009; 2011) argue that the adaptive value of teaching is the driving causal force in the evolution of those mental capacities, rather than the capacities acting as constraints on the evolution of teaching. Since they argue that the adaptive function of teaching is to facilitate transfer of abstract, generalizable knowledge, their definition of teaching is narrower than other functionalist definitions. In Csibra and Gergely's approach to teaching, which they term *natural pedagogy*, the adaptation that makes knowledge transmission possible is a motivational system. This system evolves to facilitate the sharing of generalizable knowledge with others, and its adaptive function is to speed up the rate at which naïve (human) learners gain "reliable, new, and relevant information" about the world (Gergely et al. 2007, p. 140).

According to Csibra and Gergely (2006) this function does not necessarily require theory of mind capacities or a conscious intentionality to achieve, but rather any evolved psychology that would function to facilitate

learning in others, for this particular informational domain. Thus, the teaching adaptation includes communicative capacities: behavioral markers, or *ostensive cues*, that highlight and mark the act of teaching for teacher and pupil. By this definition, teaching behavior requires: "(1) explicit manifestation of generalizable knowledge by an individual (the 'teacher'), and (2) interpretation of this manifestation in terms of knowledge content by another individual ('the learner')" (Csibra & Gergely 2006, p. 5). It does not require that teachers or pupils are consciously aware of these processes, unlike the mentalistic or culture-based definitions. By this definition, the teaching adaptation is both a special learning mechanism (because it requires an adaptation by both parties) and a special type of communication (because it evolved specifically to convey generalizable, abstract content such as "tigers are always dangerous," as opposed to fleeting, concrete content about the current state of the world, such as "there is a tiger behind you"). Thus, it characterizes teaching as an adaptation to facilitate learning in others, for a particular type of content (generalizable knowledge) and kind of learning (knowledge transfer) in a single species (humans).

2.4. On the benefits of integrating existing approaches

The mentalistic, culture-based, and functionalist approaches are each tailor-made research programs designed to address questions about specific aspects of teaching. Mentalistic approaches investigate the psychological prerequisites for teaching, and use these factors to explain individual- and species-level variation in teaching capacities. Culture-based definitions focus on the features of Western-style classroom teaching, and highlight qualitative cross-cultural differences in the means by which children learn. Finally, functionalist definitions of teaching focus on the evolutionary costs and benefits of teaching behavior to better understand the evolutionary origins and functional design features of teaching behavior. The problem with the current division of labor is that each approach could make better use of the findings in the other two fields to address their own primary research questions. Recent attempts at dialogue across these approaches have, unfortunately, been stymied by definitional debates about what constitutes teaching (see, e.g., Csibra 2007; Thornton et al. 2007). The systematic framework I propose subsequently aims to integrate core research questions from each approach, and synthesize extant data on teaching behaviors, as identified by these approaches.

Mentalistic definitions would benefit from integration with the functionalist and culture-based approach in several ways. First, integrating mentalistic questions about the psychological prerequisites for teaching with functionalist studies of teaching-like behavior in nonhuman animals would reshape mentalistic endeavors to ask why *intentional* and *theory-of-mind* based teaching might have evolved in humans alone. Some nonhuman animals regularly facilitate learning in conspecifics without human-like theory of mind capacities, so the answer cannot be that only humans can facilitate others' learning. Mentally representing the intent-to-teach has no adaptive value by itself; only the *teaching behavior* has adaptive value. It follows that as long as pupils act as if they expect to receive relevant information, and learn it effectively, an interaction can fulfill the adaptive function of teaching. What, then, is unique about intentional teaching? Mentalistic approaches integrated with a functionalist framework could make better use of cross-species comparative data by relating psychological capacities more closely to behavioral adaptations, and to the social learning problems these behaviors address. One possibility is that theory of mind helps to address only a subset of adaptive problems in which one individual facilitates learning in another, and that there are alternative psychological mechanisms that might also suffice (see sect. 5 for possibilities). This can generate new and interesting questions for the mentalistic approach to teaching. For example, are there socio-ecological conditions that are specific to human evolution, under which conscious intent-to-teach might provide adaptive benefits? Under what conditions is our species' apparently unique teaching psychology better-adapted than the simpler alternatives?

Integrating the mentalistic approach with the culture-based approach's emphasis on documenting cross-cultural variation in learning capacities could provide a broader range of human behaviors against which to test hypotheses about the psychology of intentional teaching. When humans facilitate others' learning, do they always use theory of mind, or are there other mental mechanisms that promote functionally equivalent behavior? Descriptively, what sorts of social learning problems does intentional teaching solve for humans, and how does this vary cross-culturally? Explaining the full range of variation in human teaching behavior may shed light on teaching's role in making cumulative cultural adaptation possible.

Culture-based approaches would benefit from integration with the mentalistic and functionalist approaches. While useful in generating rich descriptions of cross-cultural differences in how children learn, culture-based approaches could benefit from the integrative study of teaching in order to better explain how such cross-cultural variation emerges, why it persists, and why this type of variation is characteristic across human populations but atypical in nonhuman animals. By establishing a baseline of what is universal behavior across human societies, researchers could more precisely focus on aspects of teaching behavior that may be culture-specific, in contrast. Both the mentalistic and functionalist approaches assume that teaching behavior is driven by a species-typical psychology of teaching. Researchers adopting the culture-based approach, especially those conducting long-term ethnographic fieldwork, are in the unique position to evaluate the validity of these claims; however, this requires a common framework across the major approaches. This framework would provide a yardstick by which to compare cross-cultural variation quantitatively, strengthening the original research aims of the culture-based approach to the study of teaching.

Functionalist definitions of teaching are focused primarily on the evolutionary origins and adaptive consequences of teaching. Functionalist approaches are to some degree already the basis for productive comparative work. For example, one typology links kinds of teaching behavior to the forms of learner-driven social learning behavior from which teaching may be derived (Hoppitt et al. 2008), and the earliest functionalist definition was an explicit attempt to enable cross-species comparisons on the basis of behavior rather than a teacher's mental state (Caro & Hauser 1992). Similar efforts have proven fruitful in the social learning literature more broadly (e.g., see Whiten [2011]

on chimpanzee learning). However, the functionalist approach could benefit from integration with the culture-based and mentalistic approaches in several ways. Despite acknowledging exceptional levels of teaching in humans, existing functionalist frameworks do not explain the apparently unique qualities of human teaching within the same framework they use to study teaching in other species. This is akin to studying kin selection according to a framework that does not explain the behavior of eusocial insects. One exception is Csibra and Gergely's (2009; 2011) explanation of the evolution of teaching as an adaptation; however, their approach defines teaching as a uniquely and universally human adaptation, while not explaining behaviors that function to facilitate learning in others for nonhuman animals.

If humans are abnormally prolific and sophisticated teachers in comparison to other animals, it is all the more important that any framework for understanding the evolution of teaching should be tested against the human case. This is not to say that functionalists should abandon their study species of choice, only that the frameworks used would benefit by integrating research on human teaching. The best data available on the range of human variation in teaching behavior come from ethnographers in the culture-based approach, and this evidence suggests that Western-style teaching is cross-culturally rare. Even by the broader functionalist definition, there is a lack of systematic empirical work documenting that teaching happens across all human societies. Only a few papers have recently begun to address the question at all, and none include direct cross-cultural comparisons, in part because there has so far been no comprehensive framework by which to collect comparative data (Hewlett et al. 2011; Kline et al. 2013). Despite this, functionalist researchers state that "[t]eaching is ubiquitous in human societies" (Thornton & McAuliffe 2006, p. 227), and that "[i]ndeed, all human children must be taught" (Thornton & McAuliffe 2012, p. e8). This disconnect is, again, most likely due to a difference in definitions: surely, humans in all societies facilitate learning in other humans – but only an integrative framework can allow us to evaluate human uniqueness in theoretically interesting ways, and with quantitative data.

Without a common framework across which human and nonhuman behavioral data can be compared, functionalist frameworks will continue to only hint at the explanation for uniquely human teaching behavior, and as a result may only be providing part of the evolutionary explanation for why teaching evolves in any species. It may be that functionalist researchers prefer to eschew ethnographic data because of its qualitative, often subjective nature. However, the range of variation in human teaching behavior documented by ethnographic descriptions can inform the development and evaluation of integrative functionalist frameworks (see sect. 4.2) and the richness of anthropological descriptions of human behavior can shape operational criteria, for example, in the development of an ethogram of human teaching behavior for cross-cultural application (Kline 2013). A synthesis along these lines might also help to make sense of the theoretical and empirical rift between traditional functionalist approaches as applied to nonhuman animals, and Csibra and Gergely's (2006; 2009; 2011) functionalist approach to natural pedagogy as a human-specific adaptation for teaching. The typology proposed below (see sect. 3) will suggest that these two approaches are discussing two different teaching types, evolved to solve two different adaptive problems in the domain of social learning.

The functionalist approach would also benefit from further integration with the mentalistic approach, and such a synthesis need not detract from the ease with which functionalists can study teaching behavior in nonhuman animals, as it has in the past (see Caro & Hauser 1992). Integrating questions from the mentalistic approach with functionalist methodologies may generate and address novel research questions. For example, functionalist frameworks excel at outlining adaptive problems and the behavioral adaptations that might solve them. Mentalistic approaches work to enumerate the psychological mechanisms that produce behavioral consequences. Translating empirical research between approaches via a cohesive framework would, therefore, shed light on the socioecological circumstances under which a given psychology might be selected for. These psychological adaptations need not be established as criteria for identifying teaching, but rather could be used to generate novel hypotheses about the evolution of teaching psychology and the psychological underpinnings of cumulative cultural evolution. Investigating such hypotheses can shed light on the role of psychological constraints on the evolution of teaching and other social learning capacities, across species. Given the potentially important function of teaching as a means of faithful cultural transmission, this question is relevant to broader problems in the comparative study of the evolution of culture, and cumulative cultural adaptation.

3. A taxonomy of teaching adaptations

The taxonomy that I propose is based on a functionalist approach, but endeavors to provide a framework that unites functionalist, mentalistic, and culture-based inquiries into the study of teaching behavior in human and nonhuman animals. As a conceptual definition, the framework defines teaching as *behavior that evolved to facilitate learning in others*. This framework focuses on a number of distinct teaching types, many of which have been proposed elsewhere (e.g., Caro & Hauser 1992; Hoppitt et al. 2008), but differs from previous functionalist frameworks in that the teaching types as defined here are directly tied to specific adaptive problems that are inherent in social learning. In contrast, Hoppitt et al. (2008) base their categories on documented forms of social learning from which teaching may be derived; Caro and Hauser (1992) originally proposed a simpler taxonomy based on descriptions of teacher behavior (*coaching* vs. *opportunity teaching*).

The taxonomy I propose aims to cover the full range of possible adaptive problems that teaching could evolve to address, and incorporates all known teaching mechanisms in humans and other animals into a cohesive theoretical framework. By focusing on the specific adaptive function of particular teaching types, the framework is a tool tailored for integrating research on the contexts in which teaching is likely to have evolved, and for creating an ethogram of what each teaching type may look like "in the wild." In addition, the framework can be used to integrate existing data from the mentalistic, functionalist, and culture-based approaches for comparative analysis across species (sect. 4.3) and across

human populations (sect. 4.2). Distinguishing between multiple adaptive problems and the teaching mechanisms that address them can generate novel research questions with respect to the psychological adaptations required for each teaching mechanism (sect. 5); the costs, benefits, and cooperative dilemmas each type poses from the perspective of the pupil (sect. 6.2) and the teacher (sect. 6.1); the relative prevalence of the variety of teaching mechanisms cross culturally (see further on in this section); and for questions about teaching and human uniqueness (sect. 7).

The illustrative examples that follow below are based on long-term fieldwork in Fiji, and should not be regarded as defining the teaching types. (For ethnographic background that includes an evaluation of the importance of teaching versus other learning mechanisms, see Kline et al. [2013].) As more than one teaching type can solve a given learning problem, the taxonomy is meant to be modifiable and expandable, should additional teaching types be observed in the laboratory or field. Social learning problems may overlap in real life, so that more than one teaching type might occur on a given occasion.

For all the teaching types discussed below, it will be important in practice to distinguish between actors' baseline behaviors versus their behavior during an episode of teaching. Likewise, it will be important to distinguish between teaching and other forms of social learning. Since other forms of social learning do not require any modification of the model's behavior, demonstrating such differences will be sufficient to rule out alternative forms of social learning. Ruling out direct benefits to the teacher may be sufficient to distinguish teaching from other forms of social influence. However, precisely how these behavioral changes are quantified will vary by activity and by species (and in humans, perhaps by culture), so the possibilities are not laid out in detail. To facilitate comparative work, it may be necessary to use an ethogram of behavioral features of teaching tailored for a species or population (e.g., see ethogram for human teaching by Kline [2013]).

In some cases, demonstrating differences from baseline behavior may not be enough to rule out alternate explanations. Functionalists have typically followed Caro and Hauser (1992) to distinguish teaching from alternate explanations by demonstrating that the benefits to the teacher are indirect and derived through improved pupil learning. Documenting that there are direct benefits to the teacher would suggest that an alternative explanation is possible, though it would not necessarily rule out teaching, since behaviors can evolve due to more than one type of benefit. This heuristic can be used as an operational definition of teaching, but it is only one of many possible criteria that can be used as evidence of adaptive design. For additional possibilities, see Kline (2013), Hoppitt et al. (2008), and Thornton and Raihani (2008).

3.1. Teaching types

Teaching potentially solves a number of different adaptive problems that arise in social learning, and that cannot be addressed by learner behavior alone. In order to learn, pupils must (a) attend to, and (b) have access to, relevant information, defined as novel information which is useful and/or in some way connected to the pupil's prior knowledge (Sperber & Wilson 1995). This includes information that is accessed through experience, observation, or direct communication. When attention or relevant information (or both) would otherwise be lacking, teaching may make learning possible, more efficient, or more accurate. Teaching can therefore be thought of as a set of adaptive behaviors, perhaps derived from existing social learning behaviors (see Hoppitt et al. 2008).

3.1.1. Teaching by social tolerance. *Adaptive problem*: A pupil attends to relevant stimuli, but does not have the knowledge or skill to undertake some task because it requires observing a conspecific's behavior. This means that purely asocial learning mechanisms would not be sufficient, and that social learning by any means is only possible with modification of the model's behavior. The learning problem could be solved through *teaching by social tolerance* – defined as teaching in which the teacher does not stop the pupil's close and intrusive observation. For example, in Fiji, women who are cooking often tolerate close observation by children, even to the degree of pausing their own work, as children stick their hands into bowls or grab and manipulate mixing tools that are crucial to the women's food preparation tasks. This kind of teaching by social tolerance can be distinguished from the social tolerance that evolved for other functions, in that the degree of tolerance toward pupils is greater than species-typical tolerance toward other conspecifics. It is worth noting here that many species are highly tolerant of young conspecifics, in general (presumably because they impose little threat or cost to adults). Where this is the case, evidence for teaching by social tolerance might include heightened social tolerance in situations, or during activities, when the potential gains in learning for the young are especially high. For example, in a quantitative observational study in Fiji – a hierarchical society where corporal punishment of children is permissible – I found that 100% of children's physical intrusions into others' activities were tolerated (Kline 2013).

3.1.2. Teaching by opportunity provisioning. *Adaptive problem*: A pupil attends to relevant stimuli, but lacks the opportunity to undertake some task because it is too difficult or dangerous to explore independently. When this is true, *teaching by opportunity provisioning* may solve the learning problem. Teaching by opportunity provisioning occurs when a teacher creates opportunities for the pupil to practice – opportunities for asocial learning – that would otherwise not exist (cf. Caro & Hauser 1992; Hoppitt et al. 2008). For example, adults in Fiji sometimes make day-to-day tasks easier so that children can participate, as when one 4-year-old boy who apparently knew (in theory) how to fetch water from a well using a bucket and rope could only do so with the help of his uncle's physical strength. (The task was far slower and much more water was spilled than if the uncle had completed the task alone). Other instances of teaching by opportunity provisioning may or may not include a scaffolding component, in which the teacher scales up the difficulty of the learning opportunities with the maturity or skill of the pupil.

3.1.3. Teaching by stimulus or local enhancement. *Adaptive problem*: A learner may not attend to a relevant stimulus, though it is accessible. This category may include cases where the pupil is afraid of, or otherwise repelled by, a

learning-relevant stimulus. Since asocial and social learning both depend upon the attention of pupil, learning is unlikely to happen in this context without intervention by a teacher. Once attention is stimulated by a teacher, other learning mechanisms might suffice for producing adaptive behavior on the part of the pupil. Therefore, *teaching by stimulus or local enhancement* might evolve to facilitate initial bouts of individual learning. Teaching by stimulus or local enhancement is defined as a teaching type in which the teacher stimulates the pupil's interest in a stimulus or location, potentially leading to a discovery or skill development following the pupil's individual learning. This may occur with varying levels of effort by the teacher and resistance by the pupil. As in many other societies (Bryant & Barrett 2007), Fijian adults often make use of both pointing and *motherese* (infant-directed speech) to manipulate a child's attention toward relevant stimuli. The target of attention can include anything from a relative walking across the village, to a breaching dolphin, or even an otherwise unremarkable object such as a palm leaf or a hinged house door.

3.1.4. Teaching by evaluative feedback. *Adaptive problem*: Pupils may not attend to existing feedback or possible consequences regarding their behavior, although they have access to that information. That is, the pupil either over- or under-uses a behavior, and does not have cognitive access to information about the resulting outcome. As in the previous category, learning by other mechanisms is unlikely without intervention by a teacher. Teaching by evaluative feedback can solve this adaptive problem, when a teacher provides positive or negative reinforcement conditioned on the pupil's behavior, and in a format to which the learner is receptive. This may be particularly common for opaque social rules or costly outcomes. For example, Fijian adults and even older children teach young children that touching another person's head is *tabu* ("taboo," or forbidden), by scolding children whenever they happen to do so. There are many opportunities for children to make this "mistake," because a toddling child is often at head-height with adults who are sitting cross-legged on the floor, as is typical in Fiji. Elsewhere, teaching by evaluative feedback is called coaching, training, or encouragement/ discouragement (e.g., Caro & Hauser 1992). This teaching type may include the extremes – removing a behavior from the pupil's repertoire altogether, or making it omnipresent – as well as reinforcement that depends on the particulars of the situation.

3.1.5. Direct active teaching. *Adaptive problem*: A pupil lacks both attention and access to a relevant stimulus or information. As a result, the pupil cannot gain this information through individual learning mechanisms, and has no way to solve the "frame problem" by observing others' behavior. This may arise either in an evolutionarily novel situation, when no alternative social or asocial learning mechanisms exist to interpret the fitness-relevant components of that situation, or when a pupil simply lacks background knowledge. Hence, the frame problem may shift with pupils' changing knowledge levels. The frame problem may be solved by *direct active teaching*. This is similar to what Gergely and Csibra (2009; 2011) define as teaching, but is not necessarily limited to humans, and does not require ostensive cues (at least by definition). *Direct active teaching* is characterized by (1) manifestation of *relevant* information by the teacher to the pupil and (2) interpretation of this manifestation in terms of knowledge content by the pupil. It differs from other teaching adaptations in that it requires some shared background knowledge as well as a means of direct communication, so that the teacher can identify and communicate the relevant information to the pupil. In Fiji, for example, direct active teaching might include a father's verbal explanation to his 8-year-old daughter, complete with pointing and illustrative hand movements, of how to extract a turtle intestine from the rest of the carcass. It could also include a non-verbal demonstration, punctuated with exaggerated movements, by an expert weaver to a novice weaver. Alternatively, it might include an exclusively verbal description of where turtles lay their eggs, what butterflies eat, and where dolphins sleep, as when one mother replied to her 4-year-old son's questions about wild animals.

Note that while direct active teaching may include all "teaching" as categorized by the culture-based definitions, it is a much broader definition. Direct active teaching does not use the same criteria for identifying teaching as the culture-based definitions. In practical applications it would subsume the culture-based definition, but dispenses with the requirements of teacher intentionality, unidirectional transmission, pupil passivity, and labeling of the activity as "teaching" by the teacher and pupil. The culture-based definition and this definition of direct active teaching share in common the requirement for "direct" or "explicit" communication of information. However, they differ slightly even here, in that direct communication is not exclusively verbal under the definition of direct active teaching.

3.2. How this framework integrates across existing approaches

Much of the present debate over the form and distribution of teaching behaviors results from different schools of researchers focusing on *different teaching adaptations* as if these represent the entire category of "teaching." The more fine-grained approach outlined here has the potential to restructure these debates by integrating the full range of documented variation in teaching adaptations across human and nonhuman animals. Frameworks with similar goals have proven fruitful for asocial and social learning mechanisms other than teaching (e.g., Heyes 1994), especially concerning the evolutionary origins of imitation and its purported uniqueness in humans (for reviews, see Caldwell & Whiten 2002; Tennie et al. 2009; Tomasello et al. 1993), leading to a more sophisticated understanding of why humans alone have cumulative culture (e.g., Enquist & Ghirlanda 2007; Tennie et al. 2009). Because this framework covers all of the informational contexts in which teaching might evolve, it provides a comprehensive structure by which to categorize known (and future) teaching behaviors – a necessity for future comparative and anthropological studies of teaching.

This framework categorizes teaching types according to theoretically significant learning problems, rather than by behavioral profile, or based on known mechanisms of social learning. The latter is important, because the adaptive problems solved by teaching may not be a one-to-one match to those solved by already-catalogued social or asocial learning mechanisms. These learning problems

are not content-specific, but instead describe informational contexts in which teaching could facilitate learning. While some mechanisms may have non-teaching analogues (e.g., Hoppitt et al. 2008), this approach allows for straightforward comparative empirical applications, since learning problems can be analyzed in terms of these contexts rather than according to domains of content to be learned. This approach does not prevent researchers motivated by the research questions of mentalistic or culture-based approaches from continuing to focus such questions. Instead, it clarifies the interpretation of their research as it is relevant to the other approaches, and facilitates comparative and anthropological work. Subsequently, I demonstrate the utility of this framework by using it to reinterpret the existing data on the prevalence of teaching in humans and other animals, and to re-examine what evolutionary theory can tell us about why humans are such prolific and intensive teachers.

4. Reconsidering the prevalence of teaching

4.1. Broad claims and limited evidence

The prevalence of teaching in humans and other animals is a contentious issue. Some researchers make sweeping statements about the omnipresence of teaching cross-culturally, contrasting animal societies with "human societies, where teaching is common" (Thornton & Raihani 2010, p. 297) or claiming that "it is (almost) incontrovertible that teaching is ubiquitous in human beings, which means that, with few exceptions, every person in every society has taught and has been taught by others" (Strauss et al. 2002, p. 1476). In contrast, others claim teaching is uniquely Western (Gaskins & Paradise 2010; Lancy & Grove 2010; Paradise & Rogoff 2009; for review, see Hewlett et al. 2011). In reality, the story may be more complicated. For example, my own field work in Fiji suggests that not only is teaching common there, contrary to previous claims (Hocart 1929; Lancy & Grove 2010; Ritchie & Ritchie 1979), but also, that the prevalence of teaching varies adaptively across domains and life stage (see Kline et al. 2013). This suggests that a study including only some age groups or domains might seem to document an absence of teaching, especially if teaching is defined as Western-style formal verbal instruction, as it has been in the mentalistic approach.

Based on mentalistic or culture-based definitions of teaching, it seems obvious that animals lacking in the ability to consciously represent others' mental states cannot teach. On the other hand, animal behaviorists identify a number of species that display what they call teaching, based on observable behavior. Unlike much of the anthropological field research on teaching in non-Western human populations, these studies typically adhere to strict criteria enumerated in operational definitions (e.g., Caro & Hauser 1992), which may cause false negatives in the study of teaching (Thornton & Raihani 2010). Even so, Csibra (2007, p. 96) critiques established examples of teaching in nonhuman animals on the grounds that they "do not seem to be particularly good examples of the activity that, as humans, we would call 'teaching'" and suggests further that these behaviors might instead be labeled "scaffolding," or "charitable information donation." The problem with these and other claims about teaching-in-general is that each is based on a definition of teaching that is aimed at a focused research question within particular disciplines, and disagreements often result when researchers have not settled on the same approach. The present taxonomy illuminates the distribution of different teaching behaviors across species and societies, and thereby facilitates comparative studies of the psychological adaptations they may entail, their evolutionary function and origin, and their cross-cultural prevalence. In the following two sections, I use qualitative and descriptive observations of teaching behavior in humans and nonhuman animals to illustrate how the framework might be applied. The examples given below are best viewed as candidate instances of teaching behavior, rather than as clear evidence of teaching behavior, in both humans and animals.

4.2. Teaching in humans

Here, I provide examples for each type of teaching distinguished in the present framework. This is not a comprehensive review of teaching in humans, but rather a collection of illustrative examples drawn from throughout the ethnographic literature on teaching in humans. In many cases, these same ethnographic examples have been used as examples of "non-teaching" under *culture-based* definitions. Ethnographers often describe these behaviors in terms of teachers' mental states, including teachers' expected outcomes. These mental states are sometimes included in the descriptions below. However, in this framework, mental states do not function to distinguish between teaching types, so these details should be regarded only as contextual information, not as diagnostic features of teaching behavior.

4.2.1. Teaching by social tolerance. In humans, it is common for children to learn by observation and participation (Lancy & Grove 2010; Lave & Wenger 1991; Paradise & Rogoff 2009; Rogoff et al. 2003). Where knowledgeable actors tolerate interference or some other cost in order to permit learners to observe or participate, learning-by-observation can be classified as a low-effort form of teaching. This form of learning is common in Fijian villages where children's poking and prodding laundry to be washed, or fish to be cleaned, is not stopped by the adult even though it slows down the adults' work (personal observation). During early stages of a human apprenticeship, targeted tolerance of observation may be the predominant method of teaching (see Coy 1989). Hogbin (1970, p. 143) explains that in Wogeo, New Guinea: "Children are also encouraged to work side by side with their parents even when their efforts are likely to be a hindrance," and children's interference is tolerated during canoe making, with the expectation that they will learn and be able to contribute in the future.

4.2.2. Teaching by opportunity provisioning. In humans, it is common for adults to assign "chores" to children in many different cultural contexts (Lancy 2008). These chores are often assigned according to the child's physical capabilities (Bird & Bliege-Bird 2002; Bliege-Bird & Bird 2002; Kline et al. 2013), and are sometimes explained solely in terms of their role in the economy of the household, which is one possible explanation for their existence (Lancy 2008). However, chores can also function to

provide learning opportunities for a large variety of tasks that adult humans must learn to perform, so may sometimes constitute teaching by opportunity provisioning, especially where they are fused with play (see Bock [2002] for a life history treatment that analyzes these alternative explanations as tradeoffs). Minimally, opportunity provisioning may simply involve providing access to a stimulus that is otherwise unavailable to children. In a description of music lessons in Bali, McPhee (1969) explains that a music teacher simply plays music for his students without modification, and expects that the students will learn as a result of their unique access to his playing. This is opportunity provisioning (rather than teaching by enhancement or social tolerance) because the music is produced only for the students, creating an otherwise nonexistent opportunity for observation. Some storytelling can provide opportunities for naïve individuals to learn from second-hand experience; for example, inexperienced hunters may learn a great deal from the details of stories (MacDonald 2007). When these stories are preferentially provided to naïve learners, they can be considered teaching. In a study of Inuit childhood, Briggs (1998) reports that adults may create dramatic situations or social dilemmas to challenge children, causing them to learn important lessons about social conduct and emotional regulation through these adult-manufactured experiences. Quizzing or question-and-answer sessions may also provide an opportunity for learning to make high-risk decisions without actual danger. Among the Fort Norman Slave, fathers may verbally quiz their sons about travel paths according to hypothetical ice conditions – if boys answer incorrectly, they are "mildly chastised and urged to reconsider" (Basso 1972, p. 40).

4.2.3. Teaching by stimulus or local enhancement. Human adults point, vocalize, gaze at, or touch objects in the presence of infants, sometimes using stereotyped speech (see Brand et al. 2002) and/or gesture (see Fernald & Mazzie 1991). These behaviors often persist until the infant engages with the stimulus. There is some evidence that the degree to which different modalities are used to manipulate children's attention varies cross-culturally (Akhtar & Gernsbacher 2008) and that the overall frequency of stimulus enhancement also differs across populations, along with socio-cultural models of proper childcare (Lancy 2007). Nevertheless, prosodic features of infant-directed speech may be a human universal (Bryant & Barrett 2007). Among the Warao of South America, canoe makers may require boys to be present when they plan to build boats, with the assumption that they will learn through exposure without any instruction (Wilbert 1976). This differs from opportunity provisioning in that the canoe-makers must make the boats whether or not the boys observe them. In Native North American societies, it is common for adults to expect children to learn by seeing (Cazden & John 1971), and adults may specifically direct their attention by pointing or otherwise focusing children's attention, and sometimes naming stimuli (Lee 1967).

4.2.4. Teaching by evaluative feedback. Human adults often encourage or discourage a broad range of behaviors in children (Gaskins & Paradise 2010; Lancy & Grove 2010; Paradise & Rogoff 2009; Rogoff et al. 2003). Adults might slap a child's hand as the child tries to touch a fire, poisonous animal, or other dangerous object. In cultures where "early" walking is undesirable, adults may also physically punish a child who attempts to walk (e.g., among the Beng; Gottlieb 2004). In Nepal, adults give explicit verbal feedback, or may shame children who are considered old enough to know better, in a variety of domains (Levy 1996). Shaming through verbal teasing is common across cultures (see Lancy 2010, p. 87; Lancy & Grove 2010, p. 157; Rogoff et al. 2003). In Javanese society, adults tell stories about children who failed to learn and grew up to be useless to society, to motivate children to learn their chores (Geertz 1961).

Direct active teaching may be common in humans in a range of behavioral domains including food selection and preparation, hygiene, mating behaviors, religious ritual, abstract concepts (like mathematics), and word learning. Further, many populations of humans have formal or semi-formal institutions to promote direct active instruction, including Western-style schools, bush-schools, apprenticeships, or tutor–pupil privileged relationships. Among the Wogeo of New Guinea, orphans are considered to be disadvantaged because they must learn despite a lack of the "deliberate instruction" that most children can expect from their parents (Hogbin 1970, p. 143). Yurok-Karok adults provide "special instruction" for children who seem interested in weaving (Pettitt 1946, p. 46). Pettitt suggests that this is because learning by observation alone would not be sufficient. Social norms and kinship terms of address are often explicitly taught through verbal instruction and labeling of relatives (see Lancy & Grove 2010, p. 150). In New Guinea, Wogeo men verbally critique children's hand-made toy boats, offering theories and solutions for the boats' poor performance, which children then implement and retest (Hogbin 1970).

Direct active teaching is not always verbal. Among the Warao of South America, a father might physically reposition his son's wrist as the son learns to make a canoe, in order to prevent wrist pain (Wilbert 1976). Similarly, a Wogeo man in New Guinea might reposition his son's hands on a digging stick, while also explaining that it prevents back pain (Hogbin 1970). Instruction may also consist of demonstration without extensive verbal explanation, as when Dioula master weavers sit side by side with their apprentices in order to show them simple patterns, after years of more menial and basic tasks (Tanon 1994). Demonstration can also be combined with hands-on practice, as when a Tlingit mother shows her daughter how to weave, then takes turns with her daughter, weaving alternate rows on the same basket (Laguna 1965). This method is also common in Fiji, where one woman reported that this is how she learned to weave from her mother, and how she taught her adopted daughters. Her own mother agreed this is how she taught all of her daughters, and said that *her* mother taught her the same way – covering a total of four generations (personal observation). As Navajo girls learn to weave, they may also be shown rather than told (Reichard 1934), and any verbal or nonverbal feedback is likely to be immediately relevant rather than abstract.

4.3. Teaching in other animals

As with the review of teaching in humans, the review of teaching in nonhuman animals is not meant to be

exhaustive; therefore, some possible examples of teaching may not be included here. In addition, it should be noted that the examples offered below include quantitative studies, some of which adhere to Caro and Hauser's (1992) criteria for documenting teaching, as well as qualitative observations and anecdotal evidence. I include the latter in order to be consistent across discussions of humans and nonhuman animals, and because anecdotal cases presented here may inspire excellent future quantitative studies.

Teaching by social tolerance can also be described as tolerance of information scrounging. High-tolerance behavior such as this has been documented in several nonhuman primate species, though it has not always been characterized as having evolved to facilitate learning in others. In vervets, yellow baboons, mantled howlers, and capuchins (see Rapaport & Ruiz-Miranda 2002), adults are highly tolerant of close observation and even intrusive touching by immatures. Unlike food scrounging among adults, social tolerance of interference by immatures cannot be explained by the potential cost of an ensuing fight (Blurton-Jones 1967), because of the relative weakness and small size of immatures as compared to the adults they are observing – such that the costs of exclusion would predict the opposite pattern (exclude immatures, tolerate more formidable adults) from that predicted by teaching by social tolerance.

Teaching by opportunity provisioning has also been observed in the wild, especially among predators. Wild meerkats hunt and disable prey (Ewer 1969), then present it to meerkat pups. Careful quantitative work shows that adult meerkats disable the prey to different degrees depending on the developmental stage of the pups, as gauged by the pups' food calls. The pups then finish processing the prey and so develop the skills to manage the prey without being exposed to the risk of injury, for instance from scorpion stings (Thornton & McAuliffe 2006). Domestic cat mothers also capture and recapture prey, allowing their offspring to interact with it (observations by Ewer 1969; followed by experimental work by Caro 1980). This has also been observed in river otters (Liers 1951), cheetahs (Kruuk & Turner 1967), and tigers (Schaller 1967). Observational studies suggest that Orcas that are beached along with their offspring sometimes flip live prey toward their offspring, and may do the same in the ocean (Lopez & Lopez 1985).

Teaching by stimulus or local enhancement has been described in animal skill-acquisition, and especially foraging, across species. In river otters, some mothers have been seen to drag their offspring into the water repeatedly until they learn to swim (Liers 1951), and a similar behavior has been observed in the California sea lion (see Caro & Hauser 1992). Quantitative observational data show that long-tailed macaque mothers in one population intensify and exaggerate tool use (in this case, using human hair as dental floss) in the presence of their infants (Masataka et al. 2009). Golden lion tamarin adults have occasionally been observed to locate hidden prey and then emit a food-transfer call (typically used for transferring already-obtained food items), leaving the young to extract the prey on their own before eating it (Rapaport & Ruiz-Miranda 2002). Experimental work shows that domestic hens increase pecking intensity towards palatable food, when their chicks appear to be eating unpalatable food (Nicol & Pope 1996). Experiments also show that tandem-running ants that have located a food source will lead naïve ants to that food source and are responsive to feedback from the naïve ants (Franks & Richardson 2006; Richardson et al. 2007). Quantitative observational data show that Atlantic spotted dolphins chase prey longer and make more referential body-orienting movements in the direction of prey when calves are present (Bender et al. 2009). Observational work suggests that Orcas accompany and may lead offspring toward hunting grounds, and charge alongside their offspring in beaching attempts. The adult does not actually beach in these cases, but the offspring do (Lopez & Lopez 1985). In some of these foraging examples, it would most likely be more efficient for adults to kill the prey and provision offspring directly – which suggests that these behaviors may function to facilitate learning in offspring.

Teaching by evaluative feedback has been observed across a number of nonhuman animal taxa. Female river otters have been seen to nip at the noses of their young if they run ahead, rather than following behind (Liers 1951). In chimpanzees, mothers or older siblings may take unfamiliar food away from an infant or juvenile, restricting its diet, and captive macaques may prevent offspring from exploring novel stimuli, or stimuli known to be dangerous (see Caro & Hauser 1992). However, it is not clear how widespread these food-limiting behaviors are among nonhuman primates (Fairbanks 1975; see also Hikami et al. 1990). Primate mothers of many species encourage their offspring to walk by setting them down and then looking/calling for them to join (e.g., chimps, gorillas, rhesus macaques, free-living yellow baboons, spider monkeys: see Caro & Hauser 1992; see also Maestripieri 1995; 1996). Experimental work shows that adult pied babblers emit a purr-call while provisioning nestlings, such that nestlings learn to associate the call with food (Raihani & Ridley 2008); further work shows that the purr-call encourages fledglings to approach adults in both food-related and non-food-related circumstances (Raihani & Ridley 2007). An alternative explanation for such examples is that giving feedback evolved to alter behavior in real time – for instance, to lower the costs of parental care by eliciting independent locomotion – rather than to facilitate learning. For this teaching type, it may often be necessary to distinguish between direct and indirect benefits to the potential teacher, in order to distinguish between teaching and other explanations for behavior. For example, while feedback from female cowbirds shapes male cowbird song development and content, there is no evidence that female fitness is dependent upon males modifying their song (Smith et al. 2000). As a result, this kind of feedback resulting in behavioral modification is more likely to have evolved via intersexual selection than through selection on teaching behavior.

4.3.1. Direct active teaching. There are no observed examples of direct active teaching in nonhuman animals, with the exception of Boesch's (1991) anecdotal account of two potential instances of "demonstration" of nut-cracking techniques by chimpanzee mothers. While much of the evidence given above is similarly anecdotal, the lack of similar observations of direct active teaching in chimpanzees or in any other nonhuman species suggests that these observations should be cautiously interpreted.

5. Psychologies of teaching

The present taxonomy of learning problems paired with specific adaptations for teaching generates novel hypotheses about the landscape of possible teaching psychologies. Specifically, this framework suggests that a suite of psychological mechanisms could underlie each of the different teaching types, and that for at least some teaching behaviors, more than one evolved psychological mechanism is possible. In addition, it suggests that pupil and teacher psychologies should be considered separate adaptations that may have coevolved under selection pressures for particular teaching types. For some teaching types, pupil psychologies will match those of social learners, as argued by Hoppitt et al (2008), while teacher psychologies will be adapted for each teaching type.

An overarching problem for teachers and pupils alike is to limit teaching to information that is useful for the pupil's learning process. In other forms of social learning, this is a problem for the pupil, but, by definition, not for the model, who simply serves as a stimulus. There are three categories of information to consider in this context (and in communication more broadly): prior information which the recipient already knows, novel information which has no utility, and novel information which is useful and/or in some way connected to the pupil's prior knowledge (Sperber & Wilson 1995). The latter type is useful in the learning process, and considered *relevant* information (Sperber & Wilson 1995), because it is novel and can be interpreted by the recipient, who may use it to generate new inferences. By definition, only relevant information will promote pupil learning.

5.1. Pupil psychology

For teaching to have any adaptive consequences, the pupil's psychology must be sensitive to relevant information in the context of teaching. For teaching by social tolerance and by opportunity provisioning, pupils are already motivated to learn about relevant stimuli, and sensitive to relevant information (in both cases, the learning problem is access rather than interest). For these teaching types, teacher behaviors evolved to take advantage of pre-existing behaviors or motivations in pupils, and pupil behaviors and motivations would need little to no modification for teaching to be effective, at a minimum.

In teaching by local enhancement and by evaluative feedback, pupils must be sensitive to teacher cues and feedback that indicate relevant information. This is not a teaching-specific psychological adaptation in pupils, because the same kinds of cues are germane to other forms of social behavior. For example, social learners may already attend to others' demonstrated interest and to positive or negative social reinforcement. In all of these teaching types, the adaptation is on the part of the teacher, who displays these behaviors preferentially toward naïve learners, thereby facilitating learning.

In contrast, *direct active teaching* is characterized by manifestation of relevant information by the teacher to the pupil, as well as the pupil's interpretation of that information as generalizable. Because direct active teaching is a solution to the frame problem, it is expected to evolve only when pupils have very limited or very costly alternative individual or social learning mechanisms available. As a result, in direct active teaching, the pupil's only indication that information is relevant comes from the teacher.

There are a number of hypothetical pupil psychologies that would make this possible. First, in mentalistic approaches to teaching, pupils must theorize about the teacher's motivations and recognize that a teacher *intends* to teach. In this model of the pupil's psychology, a pupil who recognizes teaching may be receptive, or may reject a teacher's influence (see sect. 6.2 on skeptical pupils). This model also predicts that direct active teaching will be limited to species with theory of mind capacities, since a pupil's receptiveness to direct active teaching depends upon recognizing the teacher's intent.

Alternatively, teachers and pupils may have evolved a system of communication to reliably indicate the exchange of relevant, generalizable information. This suggests that direct active teaching is a result of teacher behavior creating new selective pressures on pupils. Such a process of coevolution may have created a novel teaching type in humans, derived from ancestral ones shared with nonhuman animals. Csibra and Gergely (2006) argue that such a special communication system is a defining feature of (human) teaching: When teachers mark their behavior using ostensive cues (e.g., eye gaze, use of pupil's name, soliciting joint attention, etc.), pupils act as if they expect to receive relevant information that *should be learned*. This does not necessarily require that teachers or pupils consciously theorize about the contents of the other's mind. It only requires that ostensive cues reliably result in learning receptivity on the part of the pupil. This is not a novel style of reasoning that applies only to teaching. For example, animals may respond to behavioral solicitations of play or grooming, without theorizing about the mind of the conspecific making the request. This suggests that direct active teaching need not be restricted to species with theory of mind capabilities, at least not from the perspective of the evolved psychology of the pupil.

5.2. Teacher psychology

For most teaching types, teachers can build upon existing pupil behaviors and motivations to shape pupil learning. However, teachers must still have psychological adaptations that make teaching more likely in situations in which it will be adaptive. This means that teachers must be selective in their efforts, teaching only those pupils from whose learning the teacher will also benefit (see sect. 6). All else equal, teachers must provide teaching when it is beneficial for the pupil – and that means providing information when it is *relevant*.

Again, theory of mind is one solution to the problem of relevance. For all teaching types, teachers could use theory of mind to assess what pupils know or do not know, and could subsequently provide information that is useful given the pupil's mental state. Theory of mind capacities may be necessary when the teacher's explicit proximate goal is to produce conceptual change in a pupil – shaping the pupil's understanding to match a predetermined concept as known by the teacher (e.g., Carey 2000). In other cases, the need for theory of mind capacities is less clear. For example, theorizing about the pupil's mind may only be necessary when there is expected to be great heterogeneity in pupils' knowledge states, and

when their knowledge status is not tied to any cues that would be reliably present (over an evolutionary time span).

In cases when pupils' learning needs are reliably tied to cues of age or maturity, teachers do not need to assess a particular pupil's mental state in order to provide relevant information. Instead, teachers may simply provide information that is typically relevant to pupils at a particular life stage or in a given situation. For instance, human adults in many societies interact with pre-verbal infants through modified infant-directed language (see review by Snow 1995) and gesture (Iverson et al. 1999). The proximate mechanism for this is not necessarily that adults theorize about the contents of infants' minds and strategically expose them to intensified emotional expression and to age-relevant vocabulary. Instead, it may be that the adult's own emotional reaction to young children, or their desire to see babies react, directly motivates behaviors such as *motherese* or "baby talk," and other infant-directed behaviors. At the ultimate or evolutionary level, the motivational system matters very little, so long as children are exposed to relevant stimuli. The same sort of mechanism is evidently at work in meerkats. Adult meerkats provide pups with dangerous prey (scorpions), and depend primarily on vocal cues of immaturity to determine how much to disable the prey before provisioning (Thornton & McAuliffe 2006).

Alternatively, teachers may provide relevant knowledge based on pupil-specific cues that depend on a metacognitive understanding of a behavior or task. Meta-representation for the purposes of teaching means that the teacher holds representations of her own knowledge, which is itself in the form of representations (Sperber 2000). In common parlance, this is "knowing about" or having conscious knowledge of a task. Csibra and Gergely (2006) argue that teachers must meta-represent their own knowledge, analyze it, and selectively provide information to pupils that is relevant to the task at hand and adjusted to the learner's performance. As long as teachers meta-represent their own knowledge, they could use cues from pupil behavior or from the context to deduce which bits of their knowledge are relevant, without employing theory of mind (Csibra & Gergely 2009; 2011). When relevance is based on behavioral (as opposed to mental) assessment, the teacher does not distinguish between what the pupil *knows* and what the pupil *does*, and only provides feedback on aspects of the behavioral performance of a task.

There is some evidence for a role for metacognition in teaching. Conscious access to one's own knowledge may play a minor role in language-learning (Karmiloff-Smith 1985) and a more important role in what appears to be metacognition *of* metacognitive instruction – instruction on learning how to think about one's own metacognition in order to learn more effectively (Adams et al. 1998; Gourgey 1998). There is also evidence that metacognitive awareness of teaching may make children more sensitive and sophisticated teachers (Davis-Unger & Carlson 2008).

Intuitively, it may seem far easier to theorize about another's mind than to evaluate that person's task performance through metacognition and behavior-matching. However, it is important to realize that while theory of mind may be an "easy" task for humans, it is not necessarily the case for other animals. Both theory of mind and metacognition are hypothetically feasible solutions for the problem of providing relevant information from the perspective of the teacher. Alternatively, teaching behaviors that are produced reliably in response to a cue (of pupil age or maturity, for example) may not require either theory of mind or metacognition. This suggests that predictions about the role and prevalence of teaching across species that are based only on species differences in theory of mind or metacognition may not be robust. It may require more than considering cognitive constraints to explain why some teaching types are more common than others, some species are more avid teachers than others, or why direct active teaching seems to be so rare. Another factor to consider is the cooperative nature of teaching.

6. Teaching as cooperation

Teaching is a cooperative behavior, as it benefits both the pupil and teacher through the pupil's improved social learning outcomes. This distinguishes teaching from other forms of social influence or reinforcement, which are better explained by direct benefits to the actor, or an actor's self-interested preferences. As a result, teachers may only evolve when assortment between pupils and teachers is possible – by kinship, reciprocity, or spatial assortment, for example. Formal models suggest that teaching (in general) should be exceedingly rare, and limited only to information that pupils cannot learn by other social or individual learning mechanisms, and to information that can be learned from relatives (Castro & Toro 2014; Fogarty et al. 2011). This section goes beyond those analyses to examine the costs and benefits of specific teaching types, and to consider two cooperative problems that may act as barriers to the evolution of teaching. First, from the perspective of the teacher, why facilitate another's learning? Second, from the learner's perspective, why believe what another teaches you? Thus far, research on teaching as a cooperative problem has not considered the problem from the perspective of the pupil.

6.1. Teacher as donor

From the perspective of a teacher, teaching may be costly in terms of (a) the effort required for teaching, and (b) future competition with skilled or knowledgeable pupils. In addition, teachers can (sometimes) be thought of as information donors (see Thornton & Raihani [2008] for review), especially if that information is otherwise costly to acquire. If there are costs of teaching, then there must be some benefit to the teacher, in order for teaching to evolve. In teaching, these benefits are indirect and due to the pupils' gains in learning – in contrast to other forms of social reinforcement. Because the costs and benefits vary across different teaching types, the ways and degree to which benefits accrue to teachers should also be quite variable. For example, teachers may be related to their pupils, or pupils may be future allies or mates.

In addition, the relative costs and benefits of teaching will matter: teaching behaviors that require little teaching effort should be the most common, both across and within species. This may have greater predictive power than considering the cognitive capacities of a species, since more than one possible psychology could enable each teaching type (see sect. 5). A priori, lower-effort

forms of teaching behavior include: teaching via social tolerance, teaching via evaluative feedback, and teaching via local or stimuli enhancement. Higher-effort forms of teaching include opportunity provisioning – because the teacher must modify the environment and transform a learning situation – and direct, active teaching, because teachers may completely cease their ongoing activities in order to verbally and/or gesturally communicate abstract, generalizable knowledge to pupils. Of course, these a priori assertions ought to be tested in terms of measurable costs, such as time, opportunity, or energetic costs to teachers. The brief review of teaching behavior given above does seem to support this prediction – all else equal, the less costly forms of teaching are apparently more common across species, and the more costly forms more rare. Observational data from Fiji show that relatedness predicts teaching between child–other dyads, and that high-cost teaching types are less common (Kline 2013). Further, Fijians are more likely to report teaching as a means of learning for domains transmitted from parents to offspring, and for domains that are highly important to success in village life (Kline et al. 2013).

If teachers are donors, they may recoup costs through indirect fitness benefits, by selectively teaching biological kin. Based on Hamilton's (1964) rule, teaching should evolve only when the cost to the pupil for independent learning, discounted by the teacher/pupil relatedness, is less than the cost to the teacher (Dewar 2002; Hoppitt et al. 2008). This suggests that teaching should be common among closely related individuals, and in species that breed cooperatively (Burkart & van Schaik 2010; van Schaik & Burkart 2010). Alternatively, it may be common where background relatedness within groups is high, and teaching happens within groups while resource competition happens between them (Taylor 1992). Where resource competition is primarily within the groups, background relatedness would have no such effect (Taylor 1992). This is consistent with the literature review above: Relatively costly *teaching via opportunity provisioning* occurs in meerkats, which breed cooperatively (Thornton & McAuliffe 2006); other forms of teaching happen in pied babblers and tandem-running ants (see sect. 4). High-cost forms of teaching, including direct active teaching, seem to be most common in humans, who have also been described as cooperative breeders (Hrdy 2008). In addition, humans often live in highly interdependent communities, which may shape caretaking, sharing, and cooperative behavior in the same ways as cooperative breeding does (Nettle et al. 2011; Roberts 2005; Tomasello et al. 2012). Such high-effort teaching is rare or absent in closely related chimpanzees (cf. Boesch 1991), which are not cooperative breeders.

6.2. Pupil as skeptic

Teaching is, in one form or another, modification of one individual's behavior by another's influence. In this sense, the pupil is vulnerable to the same pitfalls that any social learner experiences. However, pupils may be especially at risk of manipulation by "cheating" teachers who deceive pupils for their own benefit, because the benefits to the pupil depend upon some measure of credulity. This necessary trade-off suggests that pupils should practice epistemic vigilance to guard against inaccurate or deceptive teaching that harms their fitness (Sperber et al. 2010). Even when teachers are the pupil's parents, pupil and teacher interests may differ – for example, parents often prefer to distribute resources across multiple offspring, while each individual offspring may prefer not to share with their siblings. This possibility should lead to counter-strategies used by skeptical pupils to resist manipulative teachers, while maintaining receptivity to credible teachers. Some of these strategies overlap with strategies for choosing good models for social learning more generally (for a review see Henrich & McElreath 2003), while others are unique or especially applicable to teaching behavior. Pupil skepticism may be conscious and explicit, or it may be captured in learning heuristics. Heuristics may include biases based on social *context* of transmission, such as cues about the model or teacher's abilities or success (Boyd & Richerson 1985; Henrich & McElreath 2003). Alternatively, they may be based on the *content* of what is being learned, based on its plausibility or compatibility with what the pupil already knows (Boyd & Richerson 1985; Henrich & McElreath 2003; Sperber 1996).

The teaching types outlined above differ in their potential for manipulation of pupils by teachers, which will shape the type of skepticism expected to evolve in pupils. Teaching types that work by eliciting, directing, or limiting the learner's individual learning are generally least vulnerable to teacher abuse. This includes teaching via social tolerance, teaching by stimulus/local enhancement, and teaching by opportunity provisioning. In teaching by social tolerance, pupils are driven by internal motivations for social learning to seek access to another's behavior, and the "teaching" takes the form of tolerating the learner's interference. In order to achieve deception, a teacher would need to anticipate the learner's attention, and then perform the behavior in a way that would mislead the pupil to the advantage of the teacher. This type of deception would be cognitively demanding with limited effectiveness, especially if pupils have mental mechanisms for interpreting others' actions and goals, or for checking socially learned information against personal experience or observation. Similarly, teaching via stimulus or local enhancement is not prone to manipulation by selfish teachers, because teachers do not have direct influence on what pupils learn, but only facilitate pupils' individual learning by facilitating or directing their interest toward certain stimuli or sources of information. Teaching by opportunity provisioning functions similarly, as it depends on existing motives and nascent skill sets in the pupil. For example, when social predators such as meerkats provide their offspring with maimed prey, they have little effect on the pupil's motivations or the content of pupils' learning, but allow the learner to gain experience that they could not achieve safely on their own. Pure opportunity provisioning will always have these properties. Because humans often mix opportunity provisioning with other types of teaching (e.g., teaching via evaluative feedback, direct active teaching) in childhood chore assignments, opportunity provisioning contexts may be more prone to deception in humans – but this question is separate from the behavior of teaching via opportunity provisioning. For this category of teaching types, there is little benefit to pupils in being skeptical at all, as the risk of deception is very low, perhaps no greater than during any act of individual learning.

Teaching by evaluative feedback is more prone to abuse by selfish teachers, because its efficacy depends upon the teacher's modification of a pupil's behavior, in that effective teaching by evaluative feedback serves to change the likelihood of repeating a behavior that already exists in the pupil's repertoire. Detecting deception in teaching via evaluative feedback could be achieved if pupils are selectively receptive to encouragement or discouragement that is consistent with their intrinsic motivations, but only magnifies it (a content bias). Alternatively, pupils might be receptive to this type of teaching only from trustworthy teachers – for instance, close relatives who have little conflict of interest (a context bias). Teaching via evaluative feedback is unique because it is low-cost for teachers, but high-risk for pupils. As such, this teaching type should be relatively common in its use by teachers, but would be often accompanied by resistance and skepticism by pupils. Resistance may be less pronounced where content or context biases support the teacher's influence.

Direct active teaching is exceptionally vulnerable to exploitation by selfish teachers because it is the only teaching behavior that may include the direct communication of abstract knowledge, entirely independent of related behavioral observation. (Though note that gestural communication, or direct active teaching through demonstration, are both possible.) Since direct active teaching especially facilitates learning where pupils have little background knowledge to solve the frame problem, content biases will often be unhelpful. Instead, pupils may rely heavily on context biases dependent on characteristics of the teacher (Henrich & McElreath 2003).

As mentioned, learners may be more likely to trust related teachers, because inclusive fitness benefits mean they are less likely to deceive pupils. Pupils can also assume that kin have especially relevant knowledge, because they share genes and are likely to experience similar environments (Boyd & Richerson 1985; 1988). Some experimental evidence supports this conjecture: In the absence of information about accuracy, American 4–5-year-old children prefer their mothers' verbal testimony about object names and functions over a stranger's (Corriveau et al. 2009) – though when faced with accurate testimony from a stranger and inaccurate testimony from their mothers, only some children persist in favoring mother's testimony.

Without direct evidence, pupils may also choose to learn from teachers who are *known to be* accurate and reliable more broadly. Verifying teachers' claims against reality means the teacher is both knowledgeable and – at least in the past – truthful. This matters because learning from an honest-but-wrong teacher can be equally deleterious to a pupil's fitness as learning from a manipulative teacher. Studies with children in the United States suggest that 4-year-olds are capable of distinguishing teacher quality by tracking model accuracies, as well as preferring previously accurate models (Koenig et al. 2004) and knowledgeable models (Koenig & Harris 2005; Sabbagh & Baldwin 2001), and generally preferring accurate models when learning about novel object functions (Birch et al. 2008). Children also prefer accurate models over familiar ones when the models disagree (Corriveau & Harris 2009), and will accept testimony from a presently well-informed model who was previously inaccurate due to being misinformed in the past – but they will not "trust" information from a model who was both well-informed and inaccurate in the past (Nurmsoo & Robinson 2009). Children also seem to be capable of learning according to statistical evidence drawn from multiple observations of similar events, and can integrate this with information about the model (Buchsbaum et al. 2011). (For an extensive review of the developmental psychology of children's learning in pedagogical contexts, see Skerry et al. 2013). These mechanisms only apply when the pupil can evaluate teacher accuracy or gauge a teacher's reputation for being trustworthy. Outside the laboratory, accuracy and knowledge levels may be difficult for naïve learners to assess, especially when pupils depend upon teachers for learning about dangerous or causally opaque domains.

When direct verification of teacher accuracy is not possible, pupils may use alternative strategies. Some of these strategies may have evolved for social learning more broadly (see Boyd & Richerson 1985), but would also apply to cases of teaching. Simple content-based heuristics such as conformist bias (Henrich & Boyd 1998) or prestige bias (Henrich & Gil-White 2001) could be particularly important for direct active teaching when the content of what is being taught is divorced from observable outcomes. For example, conformist bias explains the believability of social gossip, where information heard from more sources is rated as more credible (Hess and Hagen 2006). Similarly, children are more likely to believe testimony endorsed by two informants in competition with a single one (Corriveau et al. 2009). Learners may also be credulous of teachers who are respected by third parties (Boyd & Richerson 1985). Prestige bias is thought to allow naïve learners to assess the quality of teachers based on the number of followers and extent of their deference (Henrich & Gil-White 2001). Consistent with this argument, 3- to 4-year-old Canadian children prefer to imitate models who were observed by others rather than models who were not watched (Chudek et al. 2011).

Finally, in some cases of direct active teaching, neither direct verification of *content* to be learned, nor properties of the learning *context* may be available to pupils. In these conditions, when teachers profess beliefs in the abstract, a pupil may avoid manipulation by learning only from teachers who seem to act in accord with their own stated beliefs (Mascaro & Sperber 2009; Sperber et al. 2010). For example, knowledge of particularly rich fishing grounds was a closely kept secret among highly competitive fishermen in pre-contact Hawaii – so much so, that if a deep-sea fisherman discovered a new productive location, he might share this information only with his children, even at the threat of physical assault (Kamakau 1976). In this situation, pupils should be skeptical of any information received; fishermen might misdirect others in order to protect their own preferred fishing grounds from becoming publicly known. Pupils should only believe fishermen who behave in ways that would be costly if their actual beliefs were in conflict with their stated beliefs – for instance, those who travel long distances to exploit particular fishing grounds. The same reasoning works for other behaviors, like not eating tasty but supposedly poisonous fruit. If such behaviors do not already exist, credibility-enhancing displays (CREDs) may culturally evolve along with beliefs, because they facilitate the spread of otherwise untestable beliefs (Henrich 2009). For direct active teaching, comparing a teacher's observed behavior against his or her

professed belief may serve as a proxy for testing the validity of their beliefs. For example, imagine a number of teachers who claim that pleasurable behaviors like sex or alcohol consumption are spiritually harmful. They could be making these claims in earnest, or could be making false claims to manipulate others' behavior. If a teacher abstains from sex and alcohol, this can serve as evidence of a teacher's credibility, since it is only worth giving up pleasurable activities if one believes the negative consequences are real. (This is not evidence that a belief is true – only that the teacher believes it). On the other hand, if a teacher engages in sex and alcohol consumption, learners can infer that the teacher does not sincerely believe that these are harmful and against his or her best interest. The evolution of credibility-enhancing displays to highlight this kind of distinction may be especially prevalent for the teaching of beliefs that are difficult or dangerous to verify directly, including beliefs about disease transmission, poisonous foods, or the supernatural.

7. Why humans teach more than other animals

The constraints of cognition and cooperation do not seem sufficient to explain why direct active teaching appears to be limited to humans, or why humans seem to be more prolific teachers in general in comparison with other species. How, then, can this be explained?

Based on the existing data and in light of the new framework proposed above, there are several possibilities. First, it may be that this is not a real difference. It could be that other species do use direct active teaching, but that because of a bias favoring the study of teaching in species with theory of mind and general cognitive capacities, researchers have been focusing on teaching in the wrong set of species. Similarly, it may be that there are simply more studies of human teaching – and a lower bar for "establishing" teaching in humans – than for any other species, so that a better sample might document teaching in nonhuman species. A related explanation is that existing operational criteria are too stringently focused on cost/benefit analyses, so that some cases of direct active teaching may go unreported. This explanation seems plausible after considering the last 20 years of studies on social learning and culture in nonhuman animals. This has changed our understanding of the varied ways in which chimpanzees – our nearest ape relative and perhaps best-studied comparison species – learn socially (see Whiten 2011). The framework presented here could be used across species and across human populations, for structured quantitative comparisons of teaching behavior (see, e.g., Kline 2013).

A second explanation of the empirical record on teaching is consistent with existing mentalistic definitions: It may be that direct active teaching is uniquely human, and that this is due to our species' derived cognitive capacities. The above-mentioned framework suggests that direct active teaching could depend upon either theory of mind or metacognition and behavior-matching capacities (or both). This suggests that researchers should not limit the study of teaching to species with forms of mind-reading or theory of mind, because it is not an a priori necessity for behavior that functions as teaching to evolve. Theory of mind and degrees of mind-reading capacities are notoriously difficult to identify even in species that are closely related to humans (see, e.g., Call & Tomasello 2008; Heyes 1998; Penn & Povinelli 2007), which makes a theory of mind–centered approach impractical, as Caro and Hauser (1992) point out. This is in part because of a focus on false belief tasks as the test for theory of mind, a practice that is itself of debatable value (Bloom & German 2000).

Rather than focus on psychological *prerequisites* for teaching, comparative researchers could gain more ground with a focus on the socio-environmental niches in which particular teaching types are likely to evolve. The framework proposed restructures the study of teaching to better link psychological mechanisms to particular teaching types, each of which is based on an informational context that poses an adaptive challenge. To study a particular psychological mechanism, researchers could focus on species where that type of adaptive challenge is common in the environment, and where the social organization suggests it is likely to evolve.

As a general direction, this might include species with cooperative breeding, interdependence, or heavy parental investment in offspring. It might also include species that depend on socially learned information for adapting to a spatiotemporally variable environment. It may be more profitable to compare humans with species that depend on complicated, socially learned behavior, for example, cetaceans (Rendell & Whitehead 2001; see also Schusterman et al. 2013) or social carnivores (Smith et al. 2012), rather than nonhuman primates. This shift in focus may lead to a change in the data researchers collect on direct active teaching, as well as other teaching types.

Finally, the most theoretically valuable explanation for why direct active teaching is observed only in humans is that ours is the only species in which it is adaptive; that is, ours is the only species in which the frame problem is fitness-relevant, and that is sufficiently cooperative for this form of teaching to evolve. I argue that this is because humans (and only humans) evolved in the "cultural niche," such that our species depends to a great degree on cumulative cultural adaptations too complex for any one individual to create on his or her own, which coevolved with species-specific cultural capacities (Boyd et al. 2011). If this is the case, then direct active teaching may be a derived form of teaching that coevolved with culture, for the purpose of transmitting hard-to-learn cultural adaptations. Testing this explanation requires an integrated, unifying framework of the study of teaching across species and societies like the one proposed in this article.

8. Conclusion

To date, the study of teaching has been conducted from three different perspectives, each of which focuses on a particular research question and tailored definition of teaching, often at the expense of integrating each study with the broader range of variation in teaching behavior across cultures and taxa. This diversity of research questions is a strength, especially when definitional disagreements are put aside in favor of an integrative framework for comparative and anthropological work, such as the one proposed here. This article refocuses the study of teaching on categorizing and studying an array of teaching types, based on a framework of adaptive problems that teaching solves for social learners. It can be used to

integrate the empirical literature on teaching in human and nonhuman animals, and highlights two major areas of inquiry in the evolution of teaching: psychological underpinnings, and cooperative dilemmas.

In light of this new framework, it makes little sense to focus research on establishing that a species or specific human population "has teaching" or "does not have teaching," because teaching – like social learning – is an array of adaptive behaviors that function to solve a set of problems for learners. Instead, researchers should identify the adaptive problem that teaching solves in a particular context or environment of evolutionary adaptiveness, and pursue research on the mental, functional, and cultural features of teaching based in this shared framework. Teaching should be distinguished from other forms of social influence on a case-by-case basis, with operational rules tied to the theoretical definitions at work, situated in the particular species and behavioral domain of study. Developing these practical methods requires differentiating among the social learning contexts in which different teaching types may evolve, because the form of teaching behavior will depend upon its specific adaptive function. This framework can illuminate the adaptive design and evolutionary origins of teaching behavior, by providing a unifying approach through which to study the form, function, and prevalence of different teaching behaviors across human and nonhuman populations.

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Open Peer Commentary

Cultural variant interaction in teaching and transmission

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Abstract: Focus on the way in which cultural variants affect other variants' probabilities of transmission in modeling and empirical work can enrich Kline's conceptualization of teaching. For example, the problem of communicating complex cumulative culture is an adaptive problem; teaching methods that manage transmission so that acquisition of some cultural variants increases the probability of acquiring others, provide a partial solution.

Much work in anthropology exhibits – or at least assumes – a significant degree of complex harmony or coherence between elements of culture within each society (e.g., Descola 1994; Richerson et al. 1997; Smelser 1993). Whether there is as much coherence as some think, it is plausible that there are many cases in which adopting certain cultural variants affects the probability that others will be adopted (Henrich & McElreath 2003; Sperber 1996; Thagard 2012; Wimsatt & Griesemer 2007). Such *transmission probability interactions* (TPIs) seem likely to play an important role in cultural transmission. For example, an individual may be more likely to adopt a belief suggested by someone else when she notices that it can be deduced from her existing beliefs, or that it has a high degree of plausibility given what she believes. More subtle kinds of inference may affect cultural transmission as well (cf. Sperber & Wilson 1995). For example, in a previous paper (Abrams 2013), I suggest that cultural transmission might sometimes be biased by analogical relations between transmitted variants and existing beliefs (cf. Gentner et al. 2001; Hofstadter & Sander 2013; Holyoak & Thagard 1995; Thibodeau & Boroditsky 2013). Although the ideas underlying the concept of transmission probability interactions are not new, I argue that a focus on TPIs as such can provide a useful enrichment to Kline's fruitful conceptualization of teaching types. Kline briefly discusses issues related to TPIs, for example, in her discussion of the role of relevance (Sperber & Wilson 1995) in teaching, in section 5.

The explicit use of TPIs in modeling is illustrated in Abrams (forthcoming), which extends one of Enquist et al.'s (2010) models. Enquist et al.'s results imply that cultural variants that are taught only by parents to same-sex children (e.g., Tehrani & Collard 2009) would eventually disappear from a population. That result is correct when there are no TPIs, but I show that a cultural variant can be maintained by such "single parent" transmission if it can be inferred with the help of cultural variants taught by others. Earlier models that incorporate effects of interactions between cultural variants have produced significant insights (e.g., Boyd & Richerson 1985; 1987; Castro & Toro 2014; Cavalli-Sforza & Feldman 1981; Fogarty et al. 2011; McElreath et al. 2003; Mesoudi & O'Brien 2008). Those models were not formulated in terms of TPIs, but can be re-described in terms of them. However, building models using explicit representations of TPIs is useful because real-world transmission probability interactions are rooted in cognitive processes within particular physical and cultural contexts. The concept of a TPI thus provides a useful abstraction from cognitive processes involving cultural transmission, while preserving a natural mapping back to them. Sperberian attractors can also be understood as biases on probabilities of inferring internal states from transmitted representations.

Explicit focus on TPIs in empirical research would emphasize the ways in which different cultural variants affect each other's spread. For example, experimental methods in which some cultural variants are used as primes for others, such as in the studies by Dehghani et al. (2009), Kashima (2000), Mesoudi and Whiten (2004), and Thibodeau and Boroditsky (2013), could be applied in a broad range of populations. Field studies of the effects of social networks on transmission by Atran and Medin (2008) and Henrich and Broesch (2011) might be adapted to tease out distinctions between the effects of network structure and effects of TPIs, as well. It may also be possible to combine such analyses with studies of cultural phylogeny (e.g., Tehrani & Collard 2009), to argue that the presence of certain cultural variants in some, but not all populations is likely to have been influenced by TPIs involving other cultural variants.

Fogarty et al. (2011), and Castro and Toro (2014) argue that teaching is particularly advantageous for complex cumulative culture, and that this is a reason for its prevalence among humans. In many cases involving cumulative culture, successful

teaching seems to depend partly on what other cultural variants the learner has already acquired (Bransford & National Research Council 2000; Wimsatt 2014; Wimsatt & Griesemer 2007), or on the presence of appropriate environmental features produced by human niche construction (Sterelny 2012; Wimsatt 2014; Wimsatt & Griesemer 2007). Therefore, one role of teaching may be to organize the transmission of cultural variants so as to increase the chance of retention, for example, by encouraging the student to begin learning simpler or more fundamental ideas or methods before others, or by providing a supporting conceptual framework (Bransford & National Research Council 2000). In other words, some kinds of teaching can be viewed as methods for *transmission probability coordination*, that is, as methods for coordinating transmission of cultural variants in such a way that early acquisition of some variants increases the probability of later acquiring and retaining other variants. We can view the problem of communicating complex cumulative culture as an adaptive problem, even if it applies only to humans (Boyd et al. 2011). Transmission probability coordination then constitutes a partial solution to this problem. Its use overlaps with other methods listed by Kline, of course, but they overlap with each other as well.

Kline suggests that direct active teaching, in particular, aids transmission of cumulative culture. Direct active teaching is the method that most obviously allows control over transmission probability coordination. However, opportunity provisioning can serve this role as well, through the choice of what experiences to provide to pupils at different stages. Evaluative feedback may also sometimes be coordinated for the same purpose, providing feedback on only those mistakes that a pupil can be expected to be able to correct. Information provided through social tolerance and stimulus enhancement is parasitic on conditions that would exist regardless, but these methods nevertheless might be used to encourage a pupil to experience only those situations that are plausibly safe or comprehensible to her.

Finally, teaching methods may themselves constitute instances of complex cumulative culture. Conceptualizing differences between teaching strategies in terms of transmission probability coordination may provide a useful abstraction for understanding interactions between transmission of teaching strategies and transmission of the variants they are used to teach.

The lowest common denominator between species for teaching behaviors

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Abstract: We propose that an underestimated albeit fundamental mechanism in teaching behavior is *perceptual resonance*. With this mechanism, many animals, including humans, are able to learn from each other by sharing and processing relevant events in the environment. For teaching, we suggest a triadic principle involving the teacher, the learner, and the events to be learned from the world.

With a very interesting theory based on several psychological dimensions (functionalist, mentalistic, and culture-based dimensions), Michelle Ann Kline proposes a functionalist approach for teaching behavior in human and nonhuman animals. Her goal is to integrate teaching mechanisms for humans and other animals into a unified theoretical framework. The author suggests several macroscopic mechanisms like "evaluative feedback," "social tolerance," or "stimulus enhancement" in order to understand teaching behaviors in animal species. However, in our view, to better understand a behavior such as "teaching," we need to first explore and to grasp the lowest common denominator among species. According to Wilson (2002), "Science is not ultimately about explaining the causality of any particular event. Instead, it is about understanding fundamental principles of organization and function" (p. 630). Consequently, without denying the importance of several macroscopic mechanisms, we stress in our commentary that it is much more important to fully understand the fundamental principle for teaching behaviors among species.

For Schütz-Bosbach and Prinz (2007), successful social interaction comes from a simple mechanism called "perceptual resonance." In this theory, and adapted for teaching skills, the learner is able to pick up and store perceptual consequences on the environment from the observation of the teacher's actions. This perceptual mechanism for perceived events might represent the basis for efficient social interaction, and teaching behaviors. For example, the perception of a relevant action can create an abstract semantic of Arabic numbers for observers (Badets & Pesenti 2010). In this study, participants had to verbally enumerate a small or large (2 or 8) number after the processing of finger movements such as a finger-grip closing. Results revealed that the perception of a finger closing movement slowed down the enumeration of large numbers. This interference comes from the different magnitudes of finger movements and numbers. Specifically, the small magnitude required for finger-grip closing toward a small object is incompatible with the large magnitude processed from a large Arabic number. In this view, the perception of a relevant action toward the environment can afford a more abstract semantic. Therefore, Badets and Pesenti (2010) suggest that: "Communication, language and conceptual knowledge related to concrete objects may rely on the sensory–motor systems from which they emerge" (p. 46).

Adapted for the theory of perceptual resonance, the perception of relevant features in the environment from a teacher's action can afford more efficiently related abstract semantics, which represent core information in human culture. To support this hypothesis, we recently revealed that the observation of a finger-grip closing enhanced the enumeration of small numbers during a random number generation task (Badets et al. 2012). For a cultural invention like arithmetic, we revealed the same perceptual mechanism (Badets et al. 2010). In this study, participants resolved simple addition more efficiently after the simulation of finger configuration from another person showing the correct answer. For Badets and colleagues, "During arithmetic learning, these outcomes (i.e., the finger–numeral configurations) overlap with the responses and are mentally activated when having to retrieve the responses of the arithmetic operations" (Badets et al. 2010, p. 21). There is a perceptual resonance between teacher and learner through the processing of relevant outcomes. In the same vein, Pickering and Garrod (2013) have recently posited a comparable perceptual mechanism for language production and comprehension. In this theory, production and comprehension are not distinct, but are intertwined throughout perceptual and simulation mechanism. Consequently, we claim that teaching does not come from dyadic behaviors between a teacher and a learner but from a fundamental triadic principle implying action for others, perception from others, and the storage of relevant events in the environment.

Studies on tool use are also consistent with the perceptual resonance hypothesis. For instance, recent neuropsychological evidence indicates that brain-damaged patients with apraxia fortool use are impaired in forming an accurate representation of the perceptual consequences of the actions performed by tools (for reviews, see Goldenberg 2013; Osiurak 2014; Osiurak et al. 2010; 2011). These difficulties are strongly associated with

lesions of the left inferior parietal lobe, a region which is specifically activated when people observe tool use actions made by others (e.g., van Elk 2014). Evidence also comes from experimental studies, wherein participants have to observe another person performing a tool action (e.g., touching a target by making a lever action) before carrying out the action themselves (see Massen & Prinz 2009). The findings stress that participants are faster and commit fewer errors when the action made by the model is congruent with the action they have to perform, independently of the congruency of the motor actions. These findings confirm that people benefit from the observed perceptual consequences of the action made by others. Interestingly, the idea that animal users such as nonhuman primates can also learn from conspecifics based on the observed perceptual consequences of tool actions, has also received great support (e.g., Horner & Whiten 2005).

Finally, for Kline's ultimate question, "Why humans teach more than other animals" (target article, sect. 7), we would like to suggest that only humans are able to efficiently reuse an old inherited perceptual mechanism for several new cultural inventions, such as numbers or tools. As suggested by Anderson (2010), a fundamental principle of the brain is to exploit well-established neuronal circuitry for various different functions. The perceptual resonance mechanism is an action-perception mechanism that might have been present in humans and nonhuman animals for millions of years (Cisek & Kalaska 2001; Shin et al. 2010). The human brain might have been able to reuse its property for new cultural inventions like spoken language (Pickering & Garrod 2013), calculation (Badets & Pesenti 2010), or tool use (Osiurak & Badets 2014). However, why only humans have been able to exploit this mechanism for other purposes such as cultural objects and teaching is an open question, and probably the most important for researchers.

Understanding teaching needs development

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Abstract: To fully understand teaching, we need to know how it develops ontogenetically. Developmental questions about the emergence of different types of teaching behaviour in young humans and the psychological capabilities that underpin them are currently overlooked. Incorporating the individual's development from learner to teacher would expand the scope and impact of Kline's useful framework.

Teaching is intrinsically a developmental issue. Most obviously, we use teaching to inform junior (typically younger) ignorant individuals of relevant information. Kline's article does much to explore the complexities of teaching behaviour and the various definitions of what counts as teaching. However, to fully understand the psychology of teaching, we need to think beyond a static system in which one individual is teacher and one learner, and also consider the process by which learners become teachers. While Kline makes good use of developmental and comparative evidence, the full potential of a developmental approach is not realized in this version of the theory.

It is recognized in the theory that teachers need psychological capacities, particularly: theory of mind, metacognition, and (what we might call) a theory of development (knowledge about children's competencies) (see target article, sect. 5.2). Kline reports evidence that children with better theory of mind (sect. 2.1, para. 2) or metacognition (sect. 5.2, para. 5) may be better teachers. But we risk neglecting some developmental issues here. First, there is significant controversy about the timing of these capacities' emergence, which is overlooked by Kline's theory (see, e.g., Baillargeon et al. [2010] and Sodian [2011] for theory of mind; Beran et al. [2012] for metacognition). In particular, theory of mind has (controversially) been ascribed to infants in their first year of life (e.g., Kovács et al. 2010), but is thought to emerge much later, in early or even middle childhood, by others (e.g., Sodian 2011). For claims about whether teaching is natural or unique to humans, it matters whether these capacities are innate or must be learned (independently or perhaps taught by others). A related question about development is whether the experiences of being teacher and learner are inter-dependent: Does one need the experiences of being a learner in order to become a teacher oneself? Kline's suggestion that perhaps "pupil and teacher psychologies should be considered separate adaptations" (sect. 5, para. 1) implies that this is not the case; however, the developmental interaction between emerging abilities and experiences has not been fully described empirically.

Furthermore, there is an implicit assumption that once these capacities are in place they will be deployed in an adult-like way. In contrast, Apperly (2011) observes that young children who pass theory of mind tests are rather different from accomplished adult theory of mind users. Fledgling abilities may need to be refined, and they need to be deployed spontaneously (without the prompting of supportive or experimenting adults). We do not know whether children who *can* identify opportunities for teaching using their cognitive capacities always *exploit* them. Another question is whether all adult individuals who "have" a theory of mind are equally good at using it. Again, one might think not (see Apperly [2011] for discussion). Overall, we lack research that brings together a sophisticated approach to the development and deployment of these psychological capabilities and the consequent relationship with teaching behaviours.

There are claims in the literature about the development of teaching and its early emergence (e.g., Strauss et al. 2002). Kline considers them, briefly, in the early part of the target article when reviewing previous accounts of teaching (e.g., sect. 2.1, para. 2). Yet, studies of the development of teaching tend to focus on only one of the teaching types that she later describes: direct active teaching (e.g., Davis-Unger & Carlson 2008). One of the main contributions of Kline's theory is that the account incorporates different types of teaching. It would be greatly enriched by consideration of the developmental emergence of these different types and by the cognitive, social, and motivational factors that influence their emergence (maturation or acquisition). For example, rarer evidence of other types of teaching comes from a cooperative task in which child participants (24- to 42-months-old) had to master complementary actions to solve a task in pairs. Evidence of demonstrations and attention-seeking is reported, as well as examples of more overt teaching directives. However, in this task, teachers gained from the learner's competence (Ashley & Tomasello 1998). We need more evidence on the emergence of different types of teaching in childhood (across different cultures) and to address how different psychological capabilities are required for each.

Kline's article ends (sect. 7) with a call to comparative psychologists to use her framework to guide their empirical work. While this is commendable, where is the complementary call to developmental psychology? As it stands, the theory is unlikely to have its full potential impact on this field. To understand teaching behaviour fully, we must engage with questions about its development more deeply: by charting the emergence of different types of teaching in the life span, by taking a more sophisticated and precise approach to the psychological capacities that may underpin (types of) teaching, and, in both cases, by considering whether these behaviours are acquired, and how.

Systematic data are the best way forward in studies of teaching

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Abstract: Functionalist approaches to teaching can be used to great effect in the study of teaching in both human societies and nonhuman species.

Integrating disparate areas of science is a noble and often productive cause, and Kline's plea in the target article – to combine the three approaches to teaching, namely functionalist, mentalistic, and culture-based – needs serious consideration. That said, the functionalist approach proposed 22 years ago (Caro & Hauser 1992) in part grew out of an attempt to break away from the burden of having to show that nonhumans could attribute mental states to conspecifics (Pearson 1989). Mental state attribution requires establishing intent to facilitate learning in another subject, and a theory of mind, and it thereby severely constrains searches for different types of teaching in nonhumans. The focus of culture-based teaching that centers on what happens in Western classrooms is, by definition, of little help in explaining how knowledge is transmitted within the huge diversity of human societies or nonhuman species. Therefore, blending approaches and hoping that something interesting will emerge, as outlined at the start of Kline's article (see also Byrne & Rapaport 2011) is unlikely to be productive.

If one is interested, as I am, in the ecology and evolution of behavior, including teaching, one needs to establish a comparative data-base of different forms of teaching, rather than focusing on a single high-bar definition. Then, these need to be related to different ecological and social variables, and examined taxonomically. Using three criteria for demonstrating teaching – namely, teachers modify their behavior only in the presence of a naïve observer; the behavior incurs costs or no immediate benefit; and, as a result, pupils acquire knowledge or skills more rapidly or efficiently than they would otherwise, or that they would not have learned at all (Caro & Hauser 1992) – enormous progress has been made in documenting the incidence of different forms of teaching (Hoppitt et al. 2008; Thornton & Raihani 2008) and its taxonomic distribution (Thornton & Raihani 2008). For example, we now know that teaching must have evolved multiple times and in several different forms (Franks & Richardson 2006; Raihani & Ridley 2008; Thornton & McAuliffe 2006). Furthermore, some progress has also been made in trying to understand the environmental conditions under which teaching is likely to be observed in nature (Richardson et al. 2007; Thornton 2008; Thornton & Raihani 2010).

I do not believe that these advances could have occurred if teaching was shackled by mentalistic or culture-based definitions, because many phenomena that are interesting (to a biologist) would have been dismissed as being unworthy of study. Kline concurs in her closing section that "researchers should not limit the study of teaching to species with forms of mind-reading or theory of mind, because it is not an *a priori* necessity for behavior that functions as teaching to evolve" (sect. 7, para. 3).

Can the study of teaching in different human cultures benefit from the functionalist paradigm in nonhumans? The second part of Kline's target article suggests that it can, and she supplies many empirical examples from humans in support of this proposal. Anthropologists might indeed benefit from systematically documenting the extent to which different forms of social learning are seen in various societies, and then relate these to patterns of kinship, subsistence activities, and ecological variables (e.g., Hewlett et al. 2011; Tehrani & Riede 2008).

Caro and Hauser (1992) wrote "we are convinced that the only way to make progress in this area is to first provide a definition of teaching which can, and undoubtedly will, be modified as empirical data accumulate" (p. 152). Others have indeed expanded on the functionalist definition of teaching (see Hoppitt et al. 2008; Thornton & Raihani 2008), but these departures never reverted to definitions centering on intent or Western-style classroom teaching. In the target article, Kline is similarly advocating a broader approach to teaching in humans by including opportunity provisioning, stimulus or local enhancement, evaluative feedback, and direct active teaching. Once systematic qualitative, semi-quantitative, and quantitative data on these and other forms of social transmission in humans accumulate, anthropologists may be able to uncover the ecological and social drivers of various forms of teaching in the same way as their biological colleagues are currently doing (e.g., Whiten 2011), and even relate different forms of social transmission, including teaching, to cultural phylogenies (Steele et al. 2010).

Questions that include whether progressive teaching (where teachers adjust their behavior as pupils' skills improve) occurs with a small number of pupils who can be monitored, whether teaching is principally found in solitary activities where there are few opportunities to learn by imitation, or whether teaching usually occurs where the costs of teaching are low in terms of lost opportunities for teachers, or where the costs of mistakes are high in terms of injury for pupils, can all be asked by anthropologists just as they can by field biologists (Thornton & Raihani 2010). Maybe commonalities about the ecology and even evolution of teaching in human societies and nonhuman species will emerge, maybe not. These are empirical issues. Kumbaya-style cross-disciplinary harmonizing will not yield progress, but systematic documentation of behavior based on cost-benefit analyses without explicit recourse to intent or classroom teaching just might.

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Does all teaching rest on evolved traits?

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Abstract: Classification schemes are useful when they elucidate common underlying mechanisms, bring together diverse examples, or illustrate gaps in knowledge for empirical investigation. Kline's scheme merges different approaches, but is orthogonal to existing schemes and overemphasizes evolved specializations, potentially at the detriment of clarifying teaching processes. Focus on underlying mechanisms, what is learned, and consequences for information transfer may provide additional utility.

Kline provides a new and adaptationist taxonomy of different types of teaching that aims to unite fields of research. Kline bases this categorization not on underlying processes or on consequences for cultural transmission, but instead on the adaptive problem that each type of teaching is proposed to solve. There is clear utility in combining knowledge from different approaches to teaching, and the new taxonomy usefully explores how teaching can result from both simple and complex processes. It also clarifies what precise knowledge or opportunities pupils lack. However, over-categorization without appropriate support risks suggesting that we understand more about underlying processes than we

do, stifling investigation: a criticism already leveled at social learning taxonomies (Heyes 1994).

Multiple mechanisms may solve the same adaptive problem and multiple adaptive problems may be solved by a single mechanism (de Kort & Clayton 2006); therefore, adaptive-problem-based categorizations will not necessarily match underlying mechanisms. However, Kline often links adaptive problems (themselves notoriously awkward to define) to underlying mechanisms, and her categories are not mutually exclusive, meaning that the new and existing schemes overlap uncomfortably. Rather than adding new categories of teaching, we may do better by incorporating classifications into existing schemes (see e.g., Hoppitt et al. 2008). For example, bringing together individual learning and social learning classifications suggested the possibility of undiscovered social learning processes (Heyes 1994).

Evolved specializations are core to Kline's definition of teaching ("behavior that evolved to facilitate learning in others"; target article, sect. 3, para. 1). We feel that this definition is overly restrictive, more restrictive than definitions used by scholars of the evolution of teaching (Caro & Hauser 1992; Thornton & Raihani 2008), and potentially unappealing to researchers whose focus is not on evolutionary processes. We prefer simply "specialization" (see our Table 1), which emphasizes that teaching processes, like other social learning processes (Heyes 2012a; Reader 2014), could be the result of genetic evolution, cultural evolution, changes within the lifetime of an individual, or interactions between these processes. For example, it is plausible that adult humans may independently develop behavior patterns that fit current functionalist criteria of at least simple modes of teaching. Much teaching may involve a mixture of evolved adaptations for teaching, evolved exaptations that facilitate the development of teaching, and experiential and culturally transmitted effects.

Table 1 also emphasizes that all social learning, including teaching, could be subdivided according to observer specialization. In tandem-running ants, for example, the learners do not appear to be specialized to promote their own learning, whereas children appear to manifest multiple specializations that promote their learning during teaching (Csibra & Gergely 2009; Franks & Richardson 2006). Similarly, learners may or may not show specializations to take advantage of inadvertent social information. Ninespine but not threespine sticklebacks use public information to learn from others, data consistent with a specialized ability having evolved in ninespine sticklebacks (Coolen et al. 2003). In contrast, growing disquiet questions the idea that all social information use rests on adaptive specializations (Heyes 2012b). Recent data show that bees can be trained to approach or avoid conspecific-marked flowers through simple associative learning, just as they might learn the value of an asocial cue (Dawson et al. 2013). Thus, at least prior to training, the bees are not specialized to utilize this social information. These data are consistent with the idea that social learning tendencies may emerge as the result of within-lifetime experience rather than adaptive specializations (Lindeyer et al. 2013).

Present classification schemes do not stress distinctions on the basis of observer specializations (i.e., dividing case 1 from 3 or 2 from 4 in our Table 1). Observer specializations are important, not least because specializations may allow inferences to be made on the costs and benefits relevant to a particular learning process. Moreover, some teaching may require observer specializations, that is, demonstrator–observer co-adaptation. However, specialized observers may be more open to exploitation and deceit (Kline's "pupil as skeptic"), potentially prompting the development of countermeasures.

Estimating the costs and benefits of teaching and social learning is complicated by the numerous direct and indirect payoffs potentially involved. For example, learning from others may carry competitive costs (Seppänen et al. 2007), but provide benefits from joint action, group cohesion, or safety-in-numbers when all perform the same act. As Grüter and Leadbeater (2014) note, high relatedness does not necessarily favor the development of high-efficacy social learning, since highly related groups may benefit from sharing the rewards of individual, independent exploration. Direct benefits may be also diverse and unexpected. In humans, for example, graduate students who teach improve their research skills (Feldon et al. 2011), thus gaining a delayed benefit rather like the superior parenting skills some cooperative helpers can acquire (Komdeur 1996). Sensitivity to the costs and benefits of teaching is expected, particularly when payoffs are variable, and evidence from several taxa suggests that teachers are indeed sensitive to costs. For example, ants abandon tandem running more quickly when teaching costs increase (Richardson et al. 2007) and superb fairy wrens trade calling at the nest against predation risk (Kleindorfer et al. 2014).

Much theory from the study of social learning, cooperation, and communication applies to teaching, although teaching also has distinctive qualities and therefore "teaching" is a useful category (Hoppitt et al. 2008). Subdividing teaching is more challenging.

Table 1. (Chouinard-Thuly & Reader). *Classification of social learning instances according to whether the individual learned from (the "demonstrator") or the learner (the "observer") show specializations in behavior.*

		Specialization in demonstrator?	
		Yes	No
Specialization in learner?	Yes	1. Teaching with specialization in learner *E.g.: children's sensitivity to ostensive signals*[1]	2. ISI with specialization in learner *E.g.: prior public information use in ninespine sticklebacks choosing feeding locations*[2]
	No	3. Teaching without specialization in learner *E.g.: route learning in tandem-running ants*[3]	4. ISI without specialization in learner *E.g.: observational learning of flowers in bumblebees*[4]

Note: Teaching occurs in cases 1 and 3, inadvertent social information use (ISI; (Danchin et al. 2004) in cases 2 and 4. We use the term "specialization" to underscore that teaching could result from both evolutionary and developmental processes, or from interactions between these processes. In italics we include possible examples, categorizing them according to current evidence. Future work may reveal specialization in learners, for example, bumblebees may preferentially learn about social cues over asocial ones. (1: Csibra & Gergely 2009; 2: Coolen et al. 2003; 3: Franks & Richardson 2006; 4: Dawson et al. 2013.)

Ideally we would determine the correspondence between different categories of teaching, their underlying mechanisms, and their consequences for information transmission. For example, we might demarcate teaching processes based on the neurocognitive mechanisms involved, and determine whether these mechanisms differ in the fidelity of social transmission achieved and the kind and generalizability of the information transmitted. Definitions and distinctions are important, but require concrete grounding to maximize productive debate.

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Learning about teaching requires thinking about the learner

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Abstract: Kline argues for an expanded taxonomy of teaching focusing on the adaptive behaviors needed to solve learning problems. Absent from her analysis is an explicit definition of learning, or a discussion of the iterative nature of the relationship between teaching and learning. Including the learner in the discussion may help to distinguish among the adaptive values of different teaching behaviors.

In an ambitious review, Kline aims to integrate literature across multiple species and theoretical perspectives. She develops a comprehensive taxonomy of teaching behaviors, arguing for distinctions to be made based on the adaptive value of the teaching behavior. I am sympathetic to her goal of developing a framework that can be used across sub-disciplines. However, focusing solely on the teacher – or on the first act of teaching between the teacher and learner – defines teaching as a rather one-sided process. I argue that a broader inspection of teaching requires a more thoughtful discussion of learning, for three reasons.

First, although Kline explicitly defines teaching according to the three different theoretical perspectives, and again according to the six different adaptive problems, she fails to focus on the to-be-learned behavior. Indeed, in some places, the learned behavior is situation-specific, whereas in others the information to be learned allows the learner to generalize to new contexts. For example, Kline highlights ants' ability to signal the location of food to a naïve learner through tandem running (Franks & Richardson 2006; Richardson et al. 2007). This example certainly fulfills Kline's definition of teaching, as well as the teaching definition widely used in studies of animal behavior (Caro & Hauser 1992). However, guiding a naïve learner to a food destination only helps that learner return to that specific destination – and not to other destinations in general. Such an act might be considered teaching, but it is also consistent with more general prosocial behavior directed towards conspecifics (Tomasello 2009), which often is directed towards a specific instance.

For an act to be considered teaching, learning must be present, and the information to-be-learned must be generic and representational. Such a definition of learning is consistent with how learning and teaching have been described in developmental science (e.g., Csibra & Gergely 2009; Gelman et al. 2013; Strauss et al. 2002), allowing teaching behaviors to be uniquely distinguishable from more general prosocial helping interactions (e.g., Warneken 2013), as well as learning behaviors to be distinguishable from imitation (Lyons et al. 2007). Based on this framework, several of the adaptive behaviors mentioned in Kline's review might not be classified as teaching (or for that matter, learning).

Second, Kline's model of teaching focuses solely on instances in which the teacher motivates the exchange of information – through ostensive cues (Csibra & Gergely 2006; 2011) or stimulus enhancement. What may distinguish human teaching from other species is the *learner's* ability to signal to the teacher that an intervention is necessary – either through nonverbal signals such as joint attention (e.g., Butterworth & Jarrett 1991; Tomasello 1995; Tomasello et al. 1993), motoric gestures such as pointing (e.g., Bates 1976), or early question-asking abilities (e.g., Chouinard 2007). Such requests for intervention have implications for cultural and interspecies variation, as well as for the speed of the transmission of information. Indeed, it is plausible that learner-motivated teaching may look very different from a teacher-directed interaction.

Moreover, the interaction between the teacher and learner does not end after the first exchange. Kline's taxonomy certainly allows for this possibility, but I would argue that the follow-up exchanges are the most interesting when exploring the relationship between teaching and learning. Kline rightly notes that even after a teaching exchange, there is likely to be a wide range of possible inferences available to the learner (e.g., Boyer 1998; Sperber 1996). True teaching is contingent teaching – that is, teaching that is adaptive to the learner's changing knowledge state.

Finally, although Kline touches on this somewhat in her discussion of the psychology of teaching, a large body of developmental research suggests that the *type* of teacher matters for learning (e.g., Harris 2012; Harris & Corriveau 2011; Sobel & Kushnir 2013). A consideration of teacher qualities should go beyond questions of honesty, to focusing on the learners' understanding of the knowledge or expertise of the teacher (Keil et al. 2008; Mills & Keil 2004) as well as their recognition that the teacher is a member of their cultural group (Corriveau et al. 2014; Richerson & Boyd 2005). Moreover, most of the examples presented by Kline involve a more senior member teaching a naïve learner, although knowledge is also transmitted horizontally, as well as vertically (e.g., Flynn & Whiten 2008, 2012). More research is needed to determine how children's learning from and teaching to peers might be different from their interacting with adults (Wood et al. 2012).

Overall, although Kline has done a commendable job in integrating literature from animal behavior and developmental science, more thought is needed in placing teaching behaviors in the context of learning.

Subjectivity may hinder the application of Kline's teaching framework in comparative contexts

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Abstract: We welcome Kline's attempt to develop an overarching framework to allow much needed collaboration between fields in the study of teaching. While we see much utility in this enterprise, we are concerned that there is too much focus on the behavior of the teacher, without examining results or costs, and the categories within the framework are not sufficiently distinct.

Kline provides us with a comprehensive and thought-provoking review of our current understanding of teaching. We particularly

welcome the focus on increasing dialogue among researchers in different disciplines studying the topic. The comparative study of teaching is still in relative infancy, with few cases of teaching in nonhuman animals having been identified (Fogarty et al. 2011; Hoppitt et al. 2008; Thornton & Raihani 2010). Increased dialogue between fields can only assist the furtherance of research in this area. By proposing a unified framework for the study of teaching, Kline aims to encourage better formalized and more constructive dialogue.

We agree with Kline that there are different mechanisms by which teaching can occur; however, we are concerned over the implementation of the framework as it currently stands. Thornton and Raihani (2010) propose a functional approach to identifying teaching, arguing that researchers need to examine the behavior of learners as well as teachers, focus on the learning outcomes, and examine the costs for teachers. By an increased focus on the behavior of teachers during a teaching event, we fear that operationalizing Kline's framework in nonhumans may depend too much on inference by the researcher about the purpose of the behavior.

Let us take as an example the category *teaching by social tolerance*. Kline proposes that adults may be tolerant of other individuals in the population, particularly juveniles, specifically in order to facilitate learning in those individuals. If "teachers" are deliberately creating a learning environment for "pupils," this clearly goes beyond inadvertent social learning and may qualify as a teaching event: "opportunity teaching" in Caro and Hauser's (1992) classification or "teaching by local enhancement" in Hoppitt et al. (2008). However, the reason for social tolerance among individuals is an empirical question itself. Tolerance varies between species (de Waal & Luttrell 1989) and within species (Burkart & van Schaik 2010), and may be influenced by the culture of the group (Sapolsky 2006). There may also be many different reasons why animals are differentially tolerant towards other individuals, including kinship bonds (Sueur et al. 2011) and strategic allegiances (Byrne & Whiten 1988), without active teaching occurring. This differential social tolerance may increase the likelihood of inadvertent social learning, as those animals that are more tolerant of one another may produce more opportunities for social learning to occur, a phenomenon known as "directed social learning" (Coussi-Korbel & Fragaszy 1995).

Care should, therefore, be taken to ensure that the behavior that is identified is due to active teaching and not inadvertent social learning, driven by the learner. Such a distinction may be relatively easy to make in human populations, where individuals may be asked why they are acting in a particular manner; however, in nonhuman species, there remains a need to rule out alternatives through empirical methods (Thornton & Raihani 2010). Functional approaches to the study of teaching, with a focus on teaching costs, learning opportunities, and learning outcomes should reduce the need for inference and subjective judgment on the part of researchers. For example, without considering these things, would Kline describe the tolerance of nut-cracking tufted capuchins for the presence of scrounging juveniles (Ottoni et al. 2005) as teaching? In reality it may be of direct benefit to individuals (and thus not "costly" teaching) to tolerate scrounging if (1) there is a chance the juveniles are their own offspring, and (2) the loss of nut-meat is less than the opportunity cost of fending off juveniles. An alternative reason why this would not qualify as teaching may be seen from the juvenile (or potential pupil's) point of view: there is conflicting evidence regarding the utility of scrounging in learning outcomes (Caldwell & Whiten 2003; Giraldeau & Lefebvre 1987). Hence, even were it to be documented that adults are more tolerant of juveniles during nut-cracking than at other times, this evidence alone is not sufficient to classify it as teaching.

The framework proposed has the advantage that it has few categories, allowing initial comparison among species, and research fields, to be more straightforward. We are concerned, however, that in studies with nonhuman species, categories may not be as intuitive as Kline has proposed. To illustrate, consider an example given by Kline for *teaching by stimulus or local enhancement*. Otters and sea lions drag their offspring into the water to ensure that they learn to swim. It is far from clear that this corresponds to stimulus enhancement, as described in the social learning literature, in which attention is drawn to an object or part of an object (Whiten & Ham 1992). While pupils will have their attention drawn to the water, placing an animal in water to ensure that it swims would equally appear to fit within Kline's *teaching by opportunity provisioning* category. In this category, teachers create the opportunities for pupils to practice, using asocial learning, which would not otherwise exist. By placing a pupil into water, it could be equally argued that the teacher is creating an opportunity that the pupil would not otherwise encounter. We propose that this represents a broader deficiency with the framework, in which categories are not exclusive and independent. The strength of a comprehensive framework is that it can provide researchers with an objective means of categorizing these mechanisms, even if multiple mechanisms are occurring in one teaching event. The framework's utility may be reduced due to the issue of the proposed mechanisms being judged differently by different researchers.

There is much to commend in Kline's attempt to construct a framework that would allow a comparative and collaborative approach to the study of teaching. However, the merit of any interdisciplinary approach must be in how applicable it is to all fields involved. We have concerns that, particularly for comparative researchers, the framework as currently proposed may prove to be overly reliant on subjective judgment and inference, reducing the comparative and collaborative utility of the exercise.

What *is* teaching? A clear, integrative, operational definition for teaching is still needed

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Abstract: The study of teaching indeed suffers from multiple approaches built upon disparate views. Kline does an excellent job in explaining the problem, but does not go all the way towards solving it. We suggest that a better *operational* definition, which could be utilized both in human studies and animal studies, is needed to integrate the field truly.

We agree with Kline that a greater dialogue between the different approaches to the study of teaching is needed to understand this aspect of behavior in an integrative manner. We further agree that the disparate views held by different research communities regarding what constitutes "teaching" have been a major stumbling block in this endeavor. However, the approach suggested here requires further development for it to be adequate for the task.

The critical component requiring development is the definition of teaching. According to Kline, "teaching is a behavior that evolved to facilitate learning in others" (sect. 1, paragraph 5). This is of course a conceptual definition, and, as such, might not be expected to be readily operationalized. But a clear operational definition is required for this framework to be useful for empirical study. The given definition does not meet this goal. Framing teaching in terms of its evolutionary sources does not help the empirical researcher to recognize it. In any case, evolutionary origins (i.e., selective histories) for a specific feature are notoriously hard to determine.

Without a clear operational definition, we have to understand the scope of what the author sees as "teaching" through the different mechanisms she details. From looking at those mechanisms, we get a definition so inclusive as to be almost meaningless. Two of the mechanisms, "teaching by social tolerance" and

"teaching by stimulus or local enhancement" are especially hard to distinguish from behaviors not evolved for the purpose of facilitating learning in others. Kline proposes that "teaching by social tolerance" could be distinguished from other forms of social tolerance by looking at the degree of tolerance by one individual towards a "pupil" in a given setting, which should be greater than the tolerance shown by that individual towards other conspecifics, or, we add, that same "pupil" in other situations. But if this pattern were observed – say, an adult chimpanzee allows a juvenile to stand very close to it as it is fishing for termites and to touch its arm, but does not allow this behavior at other times (Humle et al. 2009) – would we be justified in calling this teaching? While theoretically it is of course possible that some forms of social tolerance evolved specifically to facilitate learning, there are alternative explanations for situationally variable tolerance that do not hinge on its value to juveniles for learning which must be considered. For example, it may be that heightened tolerance by the adult in a feeding setting is associated with the adult's assessment of the social risk to itself (via agonism) from provoking a noisy protest by the juvenile if it rejects the juveniles' advances. Would we call this "teaching through coercion"? As for "teaching by stimulus or local enhancement," when the activity of an adult directs the attention of a young individual to an object, does it matter for definitional purposes if this was done with *the purpose* of teaching, or if it was an incidental consequence of the adult's ongoing activity? For example, if nut-cracking is performed by an individual in the same way with or without an audience, but when a juvenile is nearby, this activity increases the likelihood that the juvenile will explore nuts, anvils, and hammer stones (activities that aid learning to crack nuts) (Fragaszy et al. 2013), should the proficient individual's nut-cracking be identified as "teaching" when the juvenile is nearby? We cannot know if there was intention on the part of the proficient individual to influence the juvenile. It seems in this case that we can identify the learner, but we cannot identify a "teacher."

The question of when an activity is "teaching by tolerance" or "teaching by enhancement" can be answered in cases involving humans – but only by means not possible in studies with nonhuman animals. Indeed, when we look at the examples given by the author of "teaching by social tolerance" in humans, we see that the interpretation of this behavior as teaching is based on the teachers' mental state – the children are not simply tolerated, they are tolerated "with the expectation that they will learn" (sect. 4.2, para. 2). Of course, it is impossible to know what nonhuman animals expect. In the case of nonhuman animals, it seems that the author is satisfied with including *all* instances of tolerance towards young individuals as potential teaching, suspending the standard adopted for humans that an expectation of learning accompanies the tolerance. Returning to the example of nut-cracking, classifying a monkey that is proficient at cracking as "teaching" whenever it cracks when there are juveniles around it, makes the term meaningless.

This problem is not unique to this one mechanism: In the presentation of most of the mechanisms, the examples described for humans and other animals are not only different, but based on interpretation derived from different approaches. For example, one case of "teaching by opportunity providing" describes the behavior of a music teacher who plays music for his students and "expects that the students will learn as a result" (sect. 4.2, para. 3). Several cases involved verbal instructions – not just in cases of "direct active teaching," but also of "teaching by opportunity providing," "teaching by enhancement," and "evaluative feedback." This is of course a behavior that cannot be seen in nonhuman animals. As the goal of this new approach is to incorporate the mechanisms of teaching in humans and nonhuman animals into a cohesive framework, these inconsistencies present a major hurdle.

In short, the author has provided a conceptual framework, but has not yet achieved the definitional clarity needed to meet her objectives. She has identified a laudable goal and provided a stimulating set of ideas and examples; we hope that the research community can work from these to flesh out operational definitions adequate to realize the goal of an integrative understanding of teaching.

The study of teaching needs an inclusive functional definition

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Abstract: Frameworks that facilitate interdisciplinary communication on the topic of teaching are certainly needed. However, these frameworks require a solid and widely accepted definition of teaching on which to build. As Kline states, the functional definition forms a good basis for productive comparative work. I briefly discuss the most contentious aspects of the functional definition, and suggest that these issues must be resolved before more detailed frameworks become useful.

Kline correctly points out that the definition of teaching is a contentious issue. For many anthropologists, teaching is necessarily a human endeavor, while for most animal researchers functional definitions of teaching allow them to investigate the phenomenon without being shackled by assumptions of theory of mind or language use. From a theoretical evolutionary perspective, I find myself more aligned with the animal behaviorists, whose set of three simple but relevant conditions to identify teaching (Caro & Hauser 1992) lend themselves neatly to mathematical treatment (Aoki et al., in preparation; Fogarty et al. 2011). In order to identify the evolutionary roots of teaching, both comparative animal studies and mathematical modeling will be necessary.

The definition proposed by Caro and Hauser (1992) states that teaching occurs when a role model changes their behavior in the presence of a pupil, the role model suffers a cost for this change in behavior (or does not immediately benefit from it), and the pupil learns information more rapidly than their otherwise would, or learns information that their otherwise would not. This operational definition does face many challenges. For example, it is difficult to incorporate nuanced differences in teaching types into such a basic framework. As a result, it proves difficult to account for the fact that humans possess a uniquely well-developed capacity for teaching that is absent in other species. The delineations of types of teaching that the author suggests, along with previous categorizations of teaching behavior (Hoppitt et al. 2008; Thornton & Raihani 2008) allow researchers to investigate what is unique about human teaching, without claiming that nonhuman animals cannot teach.

However, new delineations of teaching types are not useful in the absence of a clear and widely accepted definition of teaching in its most basic form. In other words, we must be able to identify teaching before we can meaningfully categorize and investigate it. All suggested modes of teaching appearing in Kline's proposed framework adhere to Caro and Hauser's functional definition of teaching. As such, the same divisive problems pointed out by Byrne and Rapaport (2011) and addressed by Thornton and McAuliffe (2012), for example, remain unsolved in this framework, as in others.

The definition proposed by Caro and Hauser (1992) has certain problems. Indeed, Caro and Hauser themselves recommended that their definition be altered as more information about animal teaching came to light. For example, learning on the part of the pupil is difficult to show without experimental manipulation. Such manipulation was possible in the case of meerkats (Thornton & McAuliffe 2006) and ants (Franks & Richardson 2006), but has proven difficult in the case of large mammals and protected species in the wild with whom it may be unethical and impractical to experiment in such a way. Therefore, a definition of teaching that is applicable to such animals (and to humans) would be of great use to the community of researchers interested in animal learning.

Here, Kline accepts that the definitions of teaching currently in use are not sufficient. I agree with the author that the definitions from each field are problematic. However, I disagree that the functional approach gains from integration with the mentalistic approach, which requires discerning the intent of the teacher, or with the culture-based approach, which in extreme cases claims that only Western teaching is true teaching. Indeed, some of the criticisms leveled against the use of functional definitions in this article are the direct result of such definitions being underused ("there is a lack of systematic empirical work documenting that teaching happens across all human societies"; target article, sect. 2.4, para. 6). The functional approach allows for a standardized, scientific study of teaching in non-verbal animals as well as in humans. Whatever definition researchers eventually agree upon, this feature must not be compromised. Therefore, it seems that rather than attempting to combine functional definitions with mentalistic definitions that are essentially unusable in the identification of nonhuman teaching, a better approach might be to alter the functional definition of teaching so that the criteria can be met by close observation alone. Thornton and Raihani (2008) proposed that it might be possible to find a correlation between the extent of exposure to teaching behavior and the skill of a pupil's performance. However, as Byrne and Rappaport (2011) point out, in a case where more teaching effort is directed toward slower learners, such a correlation would not exist.

A looser set of criteria to show that learning has occurred might be that the pupil should exhibit a behavior after teaching that they did not exhibit before teaching, exhibit a behavior in a context in which it did not before teaching, or exhibit a behavior with considerably greater skill or accuracy than it did before teaching. This removes the specification that we must know what would happen in the absence of teaching, and replaces it with the specification that we must know the behavioral repertoire of each pupil prior to, and after, a teaching event. Such definitions could yield false positives. For example, if an individual is likely to improve their performance of a particular task over time, it might be difficult to disentangle the effects of teaching and the effects of experience and age.

An alternative approach could focus on the *change* in skill after bouts of learning, rather than on absolute measures of performance. It is intuitive that teaching will not be adaptive when either inadvertent social learning or asocial learning is more effective. Therefore, it may be sensible to believe that an increase in skill associated with a teaching event should be greater than an increase in skill associated with either watching a task being performed or attempting to perform it with no role model for any given individual. This difference may be identifiable through observation alone.

To investigate teaching in a meaningful way, the core aspects of the functional definition must remain intact. However, the shortcomings that exclude very probable cases of teaching in wild animals must also be carefully considered. Once this problem of a basic, workable definition by which we can identify teaching is addressed, the teaching taxonomy suggested by Kline should yield interesting insights into both human and nonhuman teaching.

Evolutionary mechanisms of teaching

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Abstract: We argue that Kline's analysis does not account for the evolutionary mechanisms that can explain the uniqueness of human teaching. We suggest that data should be complemented by an analysis of archaeological material with respect to what forms of teaching are required for the transmission of technologies over generations.

We appreciate that Kline brings out the differences in the functionalist, mentalistic, and culture-based definitions of learning. We agree that much can be gained by comparing and unifying the three approaches to learning.

We also appreciate Kline's attempt to categorize the different forms of teaching. We agree that such a categorization will be useful for animal researchers when analyzing to what extent teaching occurs in particular species. However, the transitions between different forms of active teaching may be strongly correlated with the evolution of language. From an evolutionary point of view, it is important to keep the forms of teaching that require language separate from those that do not. Kline's category "direct active teaching" is too broadly defined to take this into account, and needs to be divided into subcategories. In particular, teaching by demonstration can be accomplished without verbal instruction, whereas explaining causal relations and narrating cannot. To give two archaeologically relevant examples, teaching how to produce a simple stone tool (Stout 2011) or how to cook tubers (Wrangham 2009) can presumably be achieved without symbolic language (gestures may be required, though).

Another shortcoming in Kline's list is a lack of definition of teaching for innovation, where the pupil becomes prepared to go beyond what is taught. Kline focuses on teaching as instructions, rectifications, repetitions, and so on, with the purpose of having the learner repeat what is taught. But reducing teaching (and learning) to such a perspective results in one form of teaching vital for hominid evolution not being discussed; that is, teaching with the purpose of making the learner achieve the capacity to arrive at independent conclusions resulting in new knowledge and skills not previously known. This form of teaching has enriched the learning environment of future generations throughout human evolution, transforming human cognition and social life (Sterelny 2012).

Our main problem with Kline's article, however, is the lack of evolutionary mechanisms that can explain the uniqueness of human teaching. In section 7, she speculates about why active teaching appears to be limited to humans. Her first suggestion is that other species may actually use active teaching. In order to test this, we submit that it is necessary to more finely partition the notion of active teaching, as we suggest above. It is possible that teaching by demonstration may be found in other species, but hardly any teaching that requires symbolic communication. The only purported example of active teaching in another species is Boesch's (1991) description of chimpanzee mothers showing their offspring how to crack nuts, which indeed is an example of teaching by demonstration.

Kline's second suggestion is that teaching is uniquely human because of our capacities for theory of mind or metacognition. We find her analysis of theory of mind and its relation to teaching wanting. "Theory of mind" is not a unitary capacity, it can be broken down into understanding the emotions, attention, intentions, and beliefs (or knowledge) of others (Gärdenfors 2003; 2007). It is important to notice that the different types of teaching that Kline proposes presume different forms of theory of mind. For example, teaching by evaluative feedback requires that the pupil understands the emotions of the teacher, but it does not require understanding the beliefs of the teacher. Similarly, teaching by demonstration, which we propose as a subtype of direct teaching, presumes that the pupil understands the intentions of the teacher, but, again, not the beliefs of the teacher. The upshot is that theory of mind in the form of understanding the beliefs of the teacher (the form tested in false-belief tasks) is required only for the most advanced types of teaching.

Kline's third suggestion for why directive active teaching is observed only in humans is that "ours is the only species in which it is adaptive" (sect. 7, para. 6). Her argument for this is that humans

evolved in "the cultural niche" and that active teaching coevolved with culture. In order to evaluate this argument, it is, again, necessary to distinguish several forms of direct teaching.

The data Kline presents to illustrate the different forms of teaching come from (mainly her own) anthropological studies and from research on animals. Hominin cognition and technology have coevolved for at least 2.6 million years, and we submit that Kline's data should be complemented by an analysis of archaeological material, with respect to which forms of teaching the technologies require for their transmission over generations. For example, some forms of early lithic technology seem to require teaching by demonstration, but not symbolic communication (Stout 2011). If this is correct, several levels of "cultural niches" have existed during the hominin evolutionary line. Thus, the "cultural niche" is no unitary phenomenon, but rather something that has developed gradually in various contexts at different times, and not in a linear fashion (Lombard 2012). Kline is presumably correct when she suggests that direct active teaching coevolved with culture, but this suggestion must be fleshed out with a description of the evolutionary mechanisms that are involved.

To what adaptive problems is human teaching a solution?

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Abstract: We welcome Kline's systematic overview of teaching from a functional evolutionary perspective. However, Kline's framework does not provide satisfying characterization of the adaptive problems driving the evolution of teaching through communication found in humans, where the key function is better characterized in terms of licensing inferences to opaque generic content than in terms of overcoming shortages of access and attention.

In the target article, Kline has done a laudable job putting forward a comprehensive framework for discussing teaching from an evolutionary perspective. Her taxonomy of adaptive problems that arise in social learning is defined by two factors: insufficient attention and/or access on the part of the pupil. Using this framework, Kline identifies "active direct teaching" – which she introduces as akin to natural pedagogy (Csibra & Gergely 2011) – as an adaptation evolved in response to the problem of transferring knowledge to a pupil who "lacks both attention and access to a relevant stimulus or information" (sect. 3.1.5, para. 1).

Kline makes a convincing case for how shortages of attention/access to *stimuli* can be dealt with by the teaching mechanisms whose function it is to establish sufficient conditions for individual social-observational learning: social tolerance, opportunity provisioning, and stimulus/local enhancement. But what Kline means by the lack of access/attention to *information* is less clear. We appreciate how organizing the taxonomy along simple lines helps in presenting an integrative framework. However, we worry that in this case the simplicity comes at the cost of missing on the opportunity to specify the adaptive problems in response to which teaching might have evolved in humans, and to recognize how they relate to what humans teach about.

There are at least four types of adaptive *learnability problems* that have been identified in human social learning and hypothesized to drive, in humans, the emergence of a system of adaptations, which facilitates teaching and learning by means of communication (Csibra & Gergely 2011). All four arise from the inherent *opacity of human cultural knowledge*. First, observed behavior of the model has to be interpreted by the learner as a goal-directed action with a recognized goal. In a complex cultural environment, a learner may thus often face the problem of *teleological opacity*. For example, if the action-sequence involves many steps with individual sub-goals that provide no immediate benefits to the model and the learner (e.g., when preparation of food requires pre-processing the ingredients), its overarching goal may be difficult to grasp. Second, the learner may often face a challenge of interpreting an action despite its *causal opacity*. This issue is pertinent, for example, to learning manners of tool-use or ritual behaviors, whose causal relations to the stipulated goal may be opaque both to the learner and the model.

Third, although any observation is by necessity bounded to the observed particulars (e.g., a particular tool-item), the learner faces uncertainty as to whether the acquired information (e.g., a function inferred from the outcome of the observed action with the tool) should be treated as applying exclusively to the observed individual items (e.g., it is a dispositional property of this tool to bringing about this outcome), or whether it should be treated as generic information about the kind manifested by the particular and, therefore, generalizable to other tokens of this kind (e.g., the dispositional property to bring about this type of outcome is the function of this kind of tool). Fourth, in addition to the *uncertainty about genericity* of the acquired information, the learner may also be *uncertain about its sharedness*, that is whether, what she observed (e.g., a means action or an emotion expressed towards something) is to be attributed solely to the model or to should be treated as knowledge of a cultural practice shared by other group-members. Notably, all of these learnability problems arise *because* abstract generic representations with opaque contents, such as tool-kinds and social norms, *can* become the content of human social learning.

Admittedly, a pupil could move towards overcoming these learnability problems through a laborious process of inductive inferences based on individual social-observational learning guided by stimulus/local enhancements. During a demonstration, the model often shows and points at things for the pupil, and these behaviors may enhance the pupil's motivation and attention to stimuli. Notably, this particular function of communicative signals was singled out in Kline's examples and her depiction of natural pedagogy as a "motivational system" (sect. 2.3, para. 4).

However, numerous recent empirical results suggest an additional, different role of such ostensive-communicative signals (i.e. behaviors, from which the pupil can infer that she is the addressee of the model's communication) in human social learning. In human children, demonstrations that involve ostensive signals promote (i) acquiring causally opaque means actions (e.g., turning on the lamp with the forehead rather than the hands; Király et al. 2013); (ii) encoding kind-relevant permanent features of objects (e.g., shape) at the expense of transient episodic properties (e.g., current location or relative numerosity), that do not contribute relevant information to kind membership (Chen et al. 2011; Yoon et al. 2008); (iii) forming generic representations resilient to counterevidence (e.g., encoding a tool's function as enduring, even if the tool currently doesn't work or was temporarily put to a different use; Butler & Markman 2012; Hernik & Csibra 2015); and (iv) interpreting object-directed emotional expressions as evidence of shared knowledge applicable to interactions with other individuals (e.g., "this object is not desirable," rather than "she doesn't like it"; Egyed et al.. 2013; Träuble & Bätz 2014). According to Gergely and Jacob (2012), ostensive communication may also "fast-track" learning about kinds from statistically meager evidence by inviting in the learner an assumption of "strong," non-random sampling on the part of the demonstrator (Gweon et al. 2010).

The empirical results suggest that rather than merely shifting attention- and motivation-related parameters of individual observational learning, teaching through ostensive communication changes how the learner interprets the stimulus. Ostensive and referential signals license the pupil to engage in relevance-guided

inferences, which afford an interpretation that goes beyond the particular stimuli of the demonstration episode. In communicative demonstrations, humans use the concrete and particular to teach about the abstract and generic.

We applaud Kline's endeavor of characterizing forms of teaching through their adaptive functions. However, a comprehensive account of the adaptive problems behind teaching adaptations should recognize their relation to the types of transmitted contents. Adaptive problems in knowledge transfer arise not only because human children may lack attention or access, but critically because they often have to infer opaque contents as shared generic knowledge.

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On the persistent gray area between teaching and punishment

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Abstract: One of the challenges to a unifying framework for the study of teaching behavior will be to distinguish, if possible, between teaching by evaluative feedback and punishment.

Kline's unifying framework of teaching represents a significant advance. She proposes a broad definition of teaching as "behavior that evolved to facilitate learning in others" (target article, sect. 3, para. 1) and five typologies by which teaching occurs: (1) social tolerance, (2) opportunity provisioning, (3) stimulus or local enhancement, (4) evaluative feedback, and (5) direct active teaching. But gray areas are perhaps unavoidable. One of the challenges to an evolutionary framework for the study of teaching behavior will be to distinguish, if possible, between teaching by the fourth teaching type, evaluative feedback, and punishment.

In section 2.3, Kline cites Thornton and Raihani (2008, p. 1825), who propose three key teaching characteristics: "(1) It is a form of cooperative behavior with response-dependent fitness payoffs; (2) its function is to facilitate learning in others; and (3) it involves the coordinated interaction of a donor and receiver of information." Kline's only mention of punishment is in reference to the Thornton and Raihani (2008) definition: "A major function of these key characteristics is to distinguish teaching from other forms of social learning, communication, and social interactions like 'punishment,' which do not evolve because of the learning benefits they create for the learner" (sect. 2.3, para. 3). Kline does not describe further what punishment means, but the statement implies that teaching is something distinct from punishment. This differentiation is less clear than indicated (Kline puts the word punishment in quotation marks, which one might assume is in acknowledgement of how difficult these things are to distinguish from each other).

To get into this point a bit more: Thornton and Raihani (2008) distinguish teaching from punishment primarily through the *timing* of the fitness payoffs. They state that punishment provides immediate positive payoffs for the teacher/aggressor and immediate negative payoffs for the pupil/victim, whereas teaching, on the other hand, has delayed positive payoffs (contingent upon the learning) for both the teacher/aggressor and the pupil/victim. When payoffs to the teacher/aggressor are delayed rather than immediate, Thornton and Raihani (2008) call this "training."

However, there are many examples that show a willingness to punish without immediate positive net payoffs for the teacher/aggressor, such as the high rates of rejection for low offers in the Ultimatum Game (Henrich et al. 2006). Perhaps Thornton and Raihani (2008) would instead classify this as "training," but a subsequent paper suggests not, and seems to self-correct their definition of punishment. Raihani et al. (2012, p. 288) write, "punishment (unlike other forms of aggression) involves immediate payoff reductions to both punisher and the target, with net benefits to punishers contingent on cheats behaving more cooperatively in future interactions." This fits the more commonly used definition of punishment (as well as seems to encompass the former notion of "training") in which the costs of punishment dramatically reduce payoffs in the short run, especially for the punisher, but not in the long run (Fehr & Gächter 2002; Gächter et al. 2008; Milinski & Rockenbach 2012); and it also means the previously drawn line between teaching and punishment gets blurrier. It is also clear that the threat of punishment can provide a benefit to the group, not just the teacher/aggressor and/or pupil/victim (Fehr & Gächter 2002; Jacquet et al. 2011).

Keeping in mind this definition of punishment, let's turn to some of the examples Kline provides of teaching by evaluative feedback, including scolding children in Fiji for touching another person's head, mildly chastising boys in the Fort Normal slave culture if they answer incorrectly about which path to travel given certain ice conditions, slapping a child's hand if she tries to touch a fire or other dangerous object, and otter mothers nipping at their young if they go ahead rather than follow. It is not clear in these cases, which all seem to have immediate negative payoffs for the pupil/victim, how teaching by evaluative feedback is functionally distinct from punishment.

Perhaps the difference is in the degree of delayed positive fitness payoffs to the pupil/victim – they might be higher in the case of teaching, which is perhaps why Kline chooses to focus on the learning benefits they create for the learner (punishment can also lead to learning, but that does not mean it should be defined as teaching, nor does it mean that learning was that punishment's main motivation). Perhaps something can be called teaching when the degree of negative evaluative feedback/punishment inflicted on the pupil/victim is less for a naïve subject than it would be for other members of the society that showed the same misbehavior. We might try to distinguish between teaching by evaluative feedback and punishment by arguing that punishment exists to maintain social order and therefore is motivated by a transgression, rather than by a desire to provide benefits to the learner. But examining the four above-mentioned examples, we would find each of these definitions still inadequate for distinguishing between teaching and punishment, which is why the gray area between the two persists and is an interesting realm for future examination.

Another way to learn about teaching: What dogs can tell us about the evolution of pedagogy

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Abstract: Kline argues that it is crucial to isolate the respective roles of teaching and learning in order to understand how pedagogy has evolved.

We argue that doing so requires testing species that learn from pedagogy but that rarely teach themselves. Here, we review how one previously neglected species – domesticated dogs (*Canis familiaris*) – may allow researchers to do just that.

In the target article, Kline argues that understanding the evolution of pedagogy hinges on isolating the respective roles of teaching and learning. Though we agree with Kline that this is an important distinction, we also see one challenge for this approach: Since humans are adept at both teaching and learning, it will be difficult to disentangle the roles of teaching and learning by focusing on our species alone. As the target article makes clear, a common framework for comparing teaching behavior across species will be crucial for understanding how various aspects of pedagogy evolved, and which characteristics of teaching are unique to humans. Here, we argue that building this common framework relies on the careful consideration of *which species* offer the most valuable insights into these evolutionary questions.

We believe that one species that has previously been neglected in research on teaching – domesticated dogs (*Canis familiaris*) – may hold the key to answering some of the target article's most pressing questions regarding the evolution of pedagogy. Given that domesticated dogs are sensitive to the same ostensive cues as human children (e.g., Hare 2005; Miklósi et al. 1998; Topál et al. 2014), dogs provide a unique opportunity to directly compare human learners to nonhuman learners while holding human teaching behavior constant. Like human children, dogs must learn from human teachers how to navigate a human environment that is complex both physically and socially. In human and dog pupils, ostensive communication serves to highlight these teaching episodes and to engage the learner. This shared ability to learn from ostensive communication allows us to directly compare children and dogs by designing studies in which a human teacher demonstrates information in the exact same way for both species (e.g., Topál et al. 2009). In doing this, we can explore which aspects of human learning are unique, and which aspects may evolve jointly with sensitivity to ostensive communication.

As Kline argues in the target article, one characteristic that makes humans truly unique is their ability to transmit knowledge across multiple generations. An obvious question that remains is whether there are particular aspects of human teaching or human learning that underlie this uniquely human trait. One possibility is that humans have a unique set of expectations about communication that allow them to learn from others in a particularly efficient way. Although dogs share a general sensitivity to ostensive cues, humans may have additional expectations about information when it is provided ostensively. Supporting this idea, human children seem to expect that ostensive communication will be relevant (e.g., Lyons et al. 2007), truthful (e.g., Jaswal et al. 2010), sufficient (e.g., Bonawitz et al. 2011), and generic (e.g., Csibra & Gergely 2011). While it is possible that these expectations are unique to humans, it is also possible that dogs share some of these expectations about ostensive communication. By carefully examining the extent to which these expectations overlap in humans and dogs, we can begin to understand the selective pressures that have shaped the psychology of learners in our own and other species.

Another advantage of studying teaching in dogs is that we are able to *experimentally* compare dogs' performance with that of humans, and thus carefully isolate the roles of teaching and learning. Although ethograms and naturalistic observation have the potential to provide a wealth of information as Kline suggests, we argue that a more productive way to link these fields will be to use parallel experimental methods when possible (for a similar argument, see Skerry et al. 2013). Even in cases where a species appears to share little observable teaching behavior with humans, there may be core similarities that can only be revealed through direct empirical comparison. If one simply observed conspecific teaching behavior in dogs, it would be easy to miss core similarities between dog learners and human learners. In contrast, by designing carefully controlled experiments with human demonstrators, researchers can have a better chance of revealing any core similarities that another species might share with human learners. To investigate whether dogs have human-like expectations about ostensive communication, for example, we could test dogs experimentally in the same situations presented to human children.

In allowing us to address these questions, dogs also offer us an opportunity for even deeper exploration into the selection pressures that may have supported the evolution of pedagogy. A key advantage of studying dogs is that we know a great deal about the sorts of selection pressures that led to the development of different breeds. By examining fine-grained differences in the way dogs interpret ostensive communication across breeds, we can learn quite a bit about the potential selection pressures that shaped the evolution of pedagogy. If some dog breeds are more similar to humans than others, we may gain insight into the kinds of evolutionary pressures that shape human-like learning skills. Likewise, comparing dogs to their social canid relatives – such as wolves and dingoes – allows for a more general understanding of which aspects of teaching may be widely shared by cooperative social species, and which are unique to domestication.

Empirically comparing teaching and learning separately across species will allow us to address some of the most crucial points Kline makes in the target article. Not only will this enable us to isolate the roles of teaching and learning, but it will also allow us to begin to understand the relative uniqueness of humans as teachers and humans as learners. Dogs are an ideal species for addressing these questions, since they are sensitive to the same ostensive cues as human children, and offer an opportunity for both cross-breed comparison and cross-species comparison with other social canids. This breadth of comparison has the potential to allow us to paint a particularly rich picture of how pedagogy may have evolved in humans and across species.

The parental brain: A neural framework for study of teaching in humans and other animals

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Abstract: Parenting, conceptualized as a specific form of teaching, may inform mentalistic, culture-based, and functional definitions. Combined brain-imaging, hormone-measurement, and cognitive-behavioral analyses indicate the importance of mentalization circuits. These circuits appear to function according to culture, and cross animal species. Further, these approaches shed light on sex differences through work on fathers as well as mothers, are affected by psychopathology, and may be amenable to treatment in ways that may be applied to optimize teaching.

Parenting is a specific example of teaching that serves in the construction of infant self-representation (Fonagy et al. 2007). In this conceptualization, infants possess an innate contingency detector, which orients them towards aspects of the social world that react congruently and in a specifically cued informative manner that expresses and facilitates the learning of cultural knowledge. Thus, the infant focuses on the attachment figure – usually the parent – as a source of reliable information about the world. The infant

then is taught about the world through the caregiver's pedagogical communicative displays which focus on the child's thoughts and feelings. We argue that a number of possible mechanisms – rooted in neurohormonal systems in parents and amenable to study – inform the mentalistic, cultural, and functional definitions of teaching reviewed by Kline in the target article.

In mentalistic definitions of teaching, Kline reviews the necessity for theory of mind (ToM) capacities for teaching, which are well established to be crucial to the neurohormonal basis of parenting (Swain et al. 2011; 2012). The importance of early postpartum cry–care loops, that is, cycles of communication and response between infant and parent (Swain et al. 2004), stimulated research using poignant baby-cry stimuli to activate parent brains. This line of investigation has outlined the importance of brain circuits and key hormones involved in empathy or ToM and emotion regulation in both mothers and fathers; and suggests a framework for understanding how these circuits function or malfunction, and how they could be optimized with brain-based interventions that may be applied to improve teacher performance and student outcomes (Swain & Lorberbaum 2008; Swain et al. 2014a; Swain et al. 2014c).

One of the key conceptualizations in the neuroscience of parenting has been that of ToM (Mahy et al. 2014) – closely related to empathy, which has been a central topic in social neuroscience highlighting the insula (Decety 2015; Lamm et al. 2007). Among parents, the insula was activated while they reacted to their own babies crying (Kim et al. 2010), and was more activated among breastfeeding mothers than among formula feeding mothers (Kim et al. 2011). Furthermore, observing and actually imitating the faces of their own children revealed activations in the insula and other cortical motor imitation and mirror neuron systems (Lenzi et al. 2009), with activation correlated positively with levels of maternal empathy assessed by means of independent validated interviews. Support for the insula being part of a general system of empathy includes responses of non-parents to baby pictures (Lenzi et al. 2013) – which also involves pre-motor cortex activation in preparation for appropriate behavioral responses (Caria et al. 2012) that partially cross cultures (Bornstein et al., under review). This is in accord with the culture-based aspects of teaching discussed by Kline in the target article, and elaborated for parenting (Bornstein 2013).

In accord with the functionalist approaches mentioned by Kline, parenting in nonhuman animals may also serve as an informative model for teaching. For rhesus macaques who have recently been shown to engage in parenting activity homologous to humans (Ferrari et al. 2009), about 50% of infants engage in neonatal imitation of lip-smacking and tongue protrusion gestures (Simpson et al. 2014a). This appears to be under hormone control similar to humans (Simpson et al. 2014b), with implications for later infant capacity for eye-contact (Simpson et al. 2014a) underlining the evolutionary soundness of teaching behaviors that cross species in the instance of parenting.

Direct studies of reciprocal baby brain function in response to their parents are yet to be done; however, a recent neuroimaging study of mothers showed how perceived maternal care (a proxy for animal models' licking and grooming behaviors) affects both brain structures and functional response to their babies' cries in adult mothers (Kim et al. 2010). In this study, mothers who reported higher maternal care in their own childhood showed higher gray matter density, proportional to the number of neurons, in a range of higher cortical areas and executive function areas, including the insula, superior and middle frontal gyri, orbital gyrus, superior temporal gyrus, and fusiform gyrus. There were also increased functional responses in a number of frontal brain regions and the insula in response to their own babies' cries. This may reflect the long-term effects in humans of early-life mother–child interactions affecting adult maternal mother–infant interactions.

Recently, two studies of maternal interactions with brief video clips come closest to simulating the direct interaction of teaching for parents. In one study, mothers were scanned while observing several of their own as well as standard infant-related vignettes (Atzil et al. 2011). Beyond basic motivation/reward (nucleus accumbens [NA]) responses, the functional NA and amygdala were functionally correlated with emotion modulation, ToM, and empathy networks, including the insula. New paradigms include decision-making tasks, in which parental brain response to infant feedback tracks empathy measures inversely according to stress responsivity as indexed by cortisol measurements (Ho et al. 2014).

Positive feelings about their infants and parenting experience maybe critical in pathways engaging the dopamine-oxytocin reward circuits described in animal models (MacDonald 1992; Numan & Insel 2003; Shahrokh et al. 2010). Thus, interactions with the infant may enhance parental oxytocin and dopamine release and foster the maintenance of positive parental behaviors with associated attentiveness and sensitive caregiving – perhaps implicating future therapeutic potential (Macdonald et al. 2013). In contrast, if interactions with the infant are negative and stressful, parents may experience less brain activation in reward-motivation pathways, find the relationship less satisfying, harbor fewer positive parental thoughts, and be less willing to maintain those interactions – as may be more common with mental illnesses such as postpartum depression.

We finally touch on the issues of mental illness affecting the teaching function of parents. Postpartum depression is associated with deficits in parenting (Feldman et al. 2009) – this may be conceived as an illness of teaching. Ongoing research on the brain function in postpartum depression suggests impairments in specific empathy and emotion regulation circuits (Moses-Kolko et al. 2014) that may be amenable to intervention (see Swain et al. 2014b).

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Variations in teaching bring variations in learning

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Abstract: A unified account of teaching such as Kline's can and should accommodate facts about teaching in nonhuman animals and culturally diverse populations. But to benefit from Kline's insights, we need to understand how her taxonomy of teaching maps onto a taxonomy of learning. The crux of the problem for scientists studying humans and nonhumans is to determine not only how different models teach, but how individuals select models, and how they learn differently from different models.

Can an account of teaching go far enough? One reason that disagreement runs deep about the nature of teaching is that our concept of teaching has two closely linked but distinct aspects On the one hand, teaching is often thought of as some relevant act on the part of the teacher, and, on the other hand, teaching often emphasizes the information or knowledge that is transmitted to the learner. Kline emphasizes the first aspect of teaching without giving sufficient attention to the vast variations in learning that results. What may be needed is a fully integrated view of social transmission or exchange that adequately captures

these two complementary aspects of teaching and of learning. Accounts that strive to explain variations in teaching, along with variations in learning, may be in the best position to explain how teaching both generates and explains the knowledge that we gain from it.

Distinct forms of teaching likely lead to distinct forms of learning. Kline is right to identify the merits of functionalist, mentalistic, and cultural approaches to teaching and to point out that one type of mistake scholars make is to ignore the analogies or similarities in teaching practices across distinct human cultural groups and animal species. However, another equally significant mistake is to group together dissimilar practices under a common label of "teaching." The risk of conflating distinct teaching behaviors is that it can neglect the fact that distinct characteristics of teaching carry distinct consequences for the learner. For example, within the type "teaching by social tolerance," B can observe A, B can overhear A, and B can observe A failing to do something. In each of these cases, A plays a significant causal role in B's coming to know X or how to X. However, each of these learning opportunities can occur with more or less intentionality on the part of A, and such differences may lead to consequences for the learner (e.g., how well X is learned, understood, remembered). Without giving full attention to the consequences that such differences have for the learner, Kline leaves open important questions that concern how learning is affected by variations in the behaviors, beliefs and knowledge of the teachers.

The relevance of plain truths and falsehoods. For Kline, a central problem for teachers and learners is the need to limit information in ways relevant to the learner: She argues that only novel information which is useful or connected to the pupil's prior knowledge is relevant and useful to the learning process. In this way, Kline places demands on the teacher: "By definition, only relevant information will promote pupil learning" (sect. 5, para. 2), and on the learner: "the pupil's psychology must be sensitive to relevant information in the context of teaching" (sect. 5.1, para. 1). Learning new and relevant information certainly characterizes many teaching episodes; however, restricting pupil learning to the expression of new but "relevant" information neglects two important points. First, it underestimates (or ignores) the utility of information that is known and that fully conflicts or concurs with the prior knowledge of the learner. For example, learners come to understand and better comprehend words and sentences by experiencing them when they are plainly true; in cases when the speaker utters something that the listener can observe just as easily as the speaker can. Cases like these serve to both enrich the learner's understanding of message content and amplify the pedagogical value and reliability of the speaker. Second, in gleaning information from actions or signals that are plainly true or false, learners learn important lessons about the teacher or model who expresses them. In the case of failed actions or false messages, learners may not gain new knowledge about the expressed topic, but they certainly gain new information about the model or teacher who made the mistake, information that will prove critical in future encounters.

More generally, in cases of direct teaching as well as in cases of teaching by opportunity provisioning, learners must make assumptions and learn about the behavioral (and in the case of humans, psychological) capacities of models, such as what someone can perceive from a given viewpoint, what someone can be expected to remember over time, and what someone is likely to do in response to threat. For juveniles in a species, all of these behavioral lessons about the models are picked up along with their evaluations of the informational content that is made available to them. Thus, new information is important, but old information is important too. Old information is important because (i) it can conflict with or otherwise bear on potential new information and (ii) by evaluating the teacher against already known information, the learner can learn valuable information about the model.

Cooperation in human teaching

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Abstract: Kline's evolutionary analysis of teaching provides welcome reframing for cross-species comparisons. However, theory based on competition cannot explain the transmission of human cultural elements that were collectively created. Humans evolved in a cultural niche and *teaching-learning* coevolved to transmit culture. To study human cultural variation in teaching, we need a more articulated theory of this distinctively human engagement.

Kline's integrated theory in the target article has the potential to focus future research on species differences (and similarities) in teaching. This is welcome in a field that is peppered with controversy, sometimes unpleasantly. Focusing on the specific adaptive problems that teaching behaviors address, rather than the psychological capacities involved, Kline provides a friendly reframing for cross-species comparisons. The framework is less successful in creating a new approach to understanding human cultural variation in teaching, however.

Kline's evolutionary analysis focuses heavily on inter-individual competition, and ponders how teaching can be adaptive both for the pupil and the instructor. The theoretical assumption is that the two are independent actors, and that the behaviors of the teacher facilitate (consciously or not, intentionally or not) learning in the pupil. Certainly a large number of teaching situations across cultures are asymmetrical in this way (Tomasello et al. 1993). Either the teacher or the learner is focused on some skill or activity, some behavioral adjustment by one or the other is made, and the result is behavioral change in the learner. No coordination of intentions between the two is required. Kline's detailed typologies of asymmetrical teaching engagements like this are useful.

A problem arises. This type of social and intellectual independence will not support the transmission of human cultural elements that are highly valued, such as languages, faith, art, and science. These cultural products were collectively created through members' shared intentions and reflections on them (Tomasello 2014). Transmitting that knowledge also requires shared intentions and reflections.

Consider how a child learns an abstract cultural concept, such as a taboo. A taboo is a belief created and shared collectively and for which there often is no objective referent. To transmit this belief, teacher and learner must coordinate thinking, not just adjust behaviors (Kruger & Tomasello 1996). The teacher's knowledge of the taboo is represented in mind – and through cooperation (usually linguistic), the teacher and the learner come to a shared understanding of it. Later, the learner will evaluate his/her own behavior as conforming (or not) to the collective value that is represented in the taboo. Through this process, the learner becomes part of the collective, and the teacher and learner have jointly recreated culture. Vygotsky's compelling description (1978) of this process, *obuchenie*, is not easily translated into English. It refers to the communion (Kruger 2011) of teacher and learner. Their engagement in a *we*-centric space (Gallese 2001) is neither teaching alone nor learning alone, nor even teaching *plus* learning, but *teaching-learning*.

Teaching as cooperation is problematic (see target article, sect. 6) only when the theoretical lens is focused on inter-individual competition. If we grant that humans evolved in a cultural niche and that *obuchenie* coevolved to support culture transmission, we need a more articulated theory of this distinctively human engagement. To study cultural variation in direct teaching, an elaborated theory is needed of how and when and for what purpose teaching-learning takes place. Kline has started the process.

"Teaching is so WEIRD"

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Abstract: *Direct active teaching* by parents is largely absent in children's lives until the rise of WEIRD (Western, educated, industrialized rich, democratic) society. However, as mothers become schooled and missionized – like Kline's Fijian subjects – they adopt "modern" parenting practices, including teaching. There is great variability, even within WEIRD society, of parental teaching, suggesting that teaching itself must be culturally transmitted.

Kline has done a fine job in laying out the various disciplinary perspectives on teaching, but she fails to acknowledge that all three perspectives are mediated by culture. I find two aspects of her argument particularly problematic. First, her definition of teaching is broadened (contrast Thornton & Raihani 2008, p. 1823) to include an enormous range of behavior. In fact, the definition is so broad that it is hardly distinguishable from *social learning*: for example, "Social learning … refers to any situation in which the behavior, or presence, or the products of the behavior, of one individual influence the learning of another" (Caldwell & Whiten 2002, p. 193).

Specifically, Kline's catholic definition of teaching includes *teaching by social tolerance*, illustrated by a Fijian woman who permits her child to get involved as she prepares food (see target article, sect. 3.1.1). This is precisely the pattern of behavior that Rogoff and colleagues have been documenting for decades in rural Mexican and Guatemalan villages, and their primary conclusion is that children learn through their own initiative, observing, participating, practicing, and doing, not from being taught (Paradise & Rogoff 2009, p. 117; Rogoff et al. 2003). Perhaps the Fijian mother is simply acceding to the child's inexorable drive to learn, perhaps she's just being accommodating to head off a tantrum?

Another "type" of teaching is *opportunity provisioning* (see target article, sects. 3.1.2 and 4.2.2). This would include the frequent accounts of the provision of knives to young children. For example, a Pirahã child:

> was playing with a sharp knife … swinging the knife blade around him, often coming close to his eyes, his chest, his arm … when he dropped the knife, his mother – talking to someone else – reached backward nonchalantly … picked up the knife and handed it back to the toddler. (Everett 2008, p. 89)

Again, I would use this case as prima facie evidence of parents' *aversion* to teaching coupled with the bedrock belief – solicited in interviews – (Lancy, in press) that learning is children's business (e.g., Willerslev 2007, p. 162).

Evaluative feedback is another type of teaching discussed by Kline (sects. 3.1.4 and 4.2.4). A normative reading of the ethnographic record would stress the rarity of feedback – especially praise – from adults (Hilger 1957, p. 77). On the other hand, corporal punishment (Ember & Ember 2005) and affrightment are certainly common enough but it isn't clear that the intent is to *teach*. A Samoan mother may threaten a fretful baby by calling out "Pig! Elenoa is here, come and eat her!" (Ochs 1988, p. 183). "Evaluative feedback" is largely used to manage the child's behavior, rather than to transmit the culture.

My larger point is that, unlike *direct active teaching*, Kline's other types of teaching are more securely and parsimoniously labeled "social learning."

The second issue is that Kline fails to account for acculturation. She finds that teaching is "common" on Fiji (sect. 4.1, para. 1), but the villagers she queried had had over 100 years' exposure to Western schooling and missionary influence (Kline et al. 2013, p. 357). In my fieldwork with Kpelle children in the early 1970s where teaching was conspicuously absent, the village inaugurated its first school during my fieldwork. The Christian congregation was tiny and Muslims even rarer (Lancy 1996). Little conducted a child-focused ethnography among the Asabano, a remote and unacculturated Papua New Guinea (PNG) Highlands tribe. Schools and churches had arrived within the previous 15–20 years. In his observation of children and parents, he saw no teaching. Parents displayed no obligation to encourage children's learning; to manage their activity; or even to acknowledge, let alone reward, children's efforts. However, when "asked how their children learn anything, [parents] unanimously answered that they explicitly 'show' children in a step-by-step process. Even though they very clearly did no such thing." Probing further, Little discovered that the resolution to this contradiction lay in the consistent and explicit sermonizing of village pastors regarding the Christian duty of parents to instruct their children. Although parents had not actually changed their parenting behavior, they could parrot the credo and apply it to their own culture (Little 2011, pp. 152–53).

In comparative studies which have focused on this cultural divide, mothers and children with more schooling readily adopt the roles of teacher and student in experimental learning contexts, whereas those with little or no schooling act as if the child will learn autonomously through exploration, observation, and imitation/practice (e.g., Chavajay 2006; Correa-Chavez & Rogoff 2005; Göncü et al. 2000; Paradise & de Haan 2009). Other relevant findings come from Tahiti and Nepal, where acculturated parents adopt "modern" child-rearing practices that emphasize school readiness and developmental milestones as compared to the laissez-faire practices of their "old-fashioned" village counterparts (Levy 1996, pp. 129–30; see also Crago 1992, p. 498; Seymour 2001, p. 16). Indeed, in a recent report of a multi-site, multi-nation study, "women internalize the teacher role from their experience in Western-type schools and use it as mothers" (LeVine et al. 2012, p. 139).

Direct active teaching (sects. 3.1.5 and 4.3.1), while rare elsewhere (Lancy 2010), enjoys almost mythic status in what Henrich et al. (2010) refer to as WEIRD (Western, educated, industrialized rich, democratic) society, and is a major export – as the LeVine et al survey reveals. So important is teaching in WEIRD society, parents do it even when there is no need, such as teaching kids how to talk or how to play (Lancy 2014). Ironically, even in WEIRD society, parents and professionally trained teachers are not necessarily very good at it. In a study of WEIRD parents teaching their children the game Chutes and Ladders, some parents used effective techniques, others were quite ineffective (Bjorklund 2007, p. 158; see also Bergin et al. 1994). In a recent massive study in the United States, the level of parents' academic involvement did not predict children's grades. In fact, "helping with homework" had a negative impact because parents so often botched the job (Robinson & Harris 2014).

From the *culture-based* approach to the study of teaching, the evidence clearly shows that teaching itself must be culturally transmitted – teaching is largely a product of nurture, not nature.

Teaching interactions are based on motor behavior embodiment

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Abstract: In Kline's target article, the role of motor behavior in teaching is missing. However, it is so important that we cannot avoid taking into account the movements of another person when performing our own movements. Moreover, the state of mind is embodied. Consequently, teaching should integrate the role of motor behavior to enhance teacher/learner social interactions.

Kline focuses on social interaction in general and teaching in particular. Social interaction is obviously based on language, but 85% of any communication is based on non-verbal aspects: gesture, posture, facial expression, motor synchronization, and so forth (Mehrabian & Ferris 1967). However, in the entire target article, the word "motor" is never mentioned, while "movements" and "non-verbal" are cited only 3 times, each. I strongly believe that teaching is embodied. This commentary focuses on showing that motor synchronizations are always functionally present in any social interaction. The characteristics of interactions are based on person 1 reacting to the perception of movements from person 2 reacting to the perception of movements from person 1, *ad infinitum*. To illustrate my argument, I will use interpersonal coordination studies with healthy people and patients suffering from interaction deficits. I will first show that we are all unintentionally influenced by the movement of the person we are interacting with. Then I will indicate that such an interaction is embodied. The state of mind is directly observable in the body and the movement of the other person.

First, *movements of people we are interacting with influence our own actions*. When two persons interact together, they can be either intentionally or unintentionally coordinated. "Intentionally" is of course artificial, since people voluntarily move in perfect synchrony with each other. "Unintentionally" is what we are facing all the time as long as there is a perceptual contact. When two persons walk side by side, even if they both have different stride frequencies, as soon as they talk together, they both unconsciously change their locomotion in order to walk at the same pace (van Ulzen et al. 2008). Similarly, when an event or a show ends, the entire audience applauds. After the three first random hand claps, everyone synchronizes his or her applause at the same frequency (Neda et al. 2000). Several other examples can be found in the literature indicating that hearing, seeing, or touching someone triggers unintended synchronization. Schmidt and O'Brien (1997) were the first authors to reveal evidence of unintentional coordination when instructing two participants seated side by side to oscillate a handheld pendulum at their preferred frequency. For 30 seconds they looked at the other person's pendulum and for 30 seconds they looked in the other direction. As soon as they saw each other's pendulum, participants coordinated, revealing that even when the goal of the task was not focused on coordination, participants synchronized together. This experiment led other authors to challenge the unintended coordination phenomenon by explicitly instructing two participants to *not* take into account the movement of the other one (Issartel et al. 2007). Participants seated in front of each other were asked to move their right forearm however they wanted (improvisation task). Although all participants reported that they did not pay attention to their coactor while performing their improvisation task, they all executed movements differently from when alone. Results showed they could not avoid coordinating with their partner.

These experiments demonstrate that people's movements always influence their partner's moves even if they are not aware of such synchronization. If no one can avoid motor coordination, obviously teachers cannot either. Their motor behavior is unintentionally synchronized with that of their learner. Consequently, no matter how a teacher thinks he/she is totally independent of the students' behavior for impartiality and fairness purposes, the way students move in general affects the teacher's behavior and vice versa. Learners immediately decipher the posture, gestures, and facial expressions of their teacher, in order to react based on such a perception.

Second, *the state of mind is embodied*. Based on previous evidence, one could argue that being coordinated does not affect the core of the interaction (in this instance, the teaching behavior). Motor coordination is dissociated from the state of mind. I want to show that such a statement is wrong. Our movements reflect our state of mind and if our movements are modified by another person, then our entire interaction is altered. The most tangible support of such a claim was paradoxically revealed in the rupture of social interaction observed in patients suffering from schizophrenia and social phobia. Schizophrenics have attentional deficits, which can be directly observed in their motor interaction. For example, in the handheld paradigm these patients always had a delay (were late) within the dyad interaction in all intentional conditions (but not in unintentional conditions), expressing in their bodies their lack of attention in following the instructions (Varlet et al. 2012). Social phobics, on the other hand, are characterized as displaying inhibited behavior. They believe they are unappreciated; consequently, they are incapable of endorsing the role of leader. Therefore, in the handheld experiment, although these patients were as accurate as any other healthy participants in following the participant, they were unable to be the leader (Varlet et al. 2014). Both of these experiments indicate that the simple and neutral handheld paradigm was enough to reveal the link of mental deficit and motor coordination. Patients and clinicians are bodily influenced by each other even if they are not aware of such an interaction. Consequently, the rehabilitation of social pathologies is biased by non-verbal, body-based communication, which is rarely taken into account or controlled.

In the literature focusing on healthy participants, Wiltermuth and Heath (2009) demonstrated that cooperation and social attachment are enhanced when two people are engaged in an activity requiring motor coordination (such as walking, dancing, or singing). These authors showed that synchronization increases interpersonal rapport and pro-social behaviors (van Baaren et al. 2004) and, by extension, it reveals confirmation of a link between motor processes engaged in interpersonal coordination and the mental connectedness in social interactions. In such a context, modifying the motor synchronization between the teacher and the learner alters the rapport and mental connectedness of the dyad.

In conclusion, I believe that it should be of a particular interest to include in Kline's new integrated framework the role of the motor behavior for teaching/learner interaction. A way to control the use and the consequence of motor behavior on teaching behavior would definitely increase the efficiency of any teaching situation.

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Cognitive mechanisms matter – but they do not explain the absence of teaching in chimpanzees[1]

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Abstract: Kline's functional categories for the evolution of teaching blur some valuable distinctions. Moreover, her account provides no answer to the question of why direct active teaching seems to be a uniquely human phenomenon.

We admire Kline's attempt to illuminate the evolution of teaching via a taxonomy of different varieties, and by considering the adaptive pressures and costs that might lead to their emergence. At the same time, we doubt that Kline's theoretical distinctions are the best formulations.

Kline defines "stimulus enhancement" as occurring when "the teacher stimulates the pupil's interest in a stimulus or location" (target article, sect. 3.1, para. 4). In thereby characterising it as including cases in which a teacher *intentionally* draws attention to something, Kline departs from standard usage of this term (e.g., Whiten & Ham 1992) in comparative psychology, in which one agent's activities make salient to another some valuable information. Importantly, on this usage, enhancement can be provided even when an agent is oblivious to the presence of an onlooker – and so is cognitively undemanding. Since Kline includes as examples of stimulus enhancement cases of pointing that are typically thought to be cognitively difficult (Clark 1996; Moore 2013a; Tomasello 2008), her taxonomy glosses over cognitive issues that have been considered foundational in the evolution of human cognition. While Kline motivates her functional approach by stating that behaviour (and not cognition) is the target of natural selection, a taxonomy that lumps together behaviours supported by different cognitive abilities and appearing in only distantly related clades is not intuitively a useful tool for understanding evolution. It may lead researchers both to overestimate the relatedness of different behaviours on account of functional similarities, and to overlook the similarity of cognitively related behaviours performed with different functions.

It is also not clear to us that Kline's terminological distinctions are illuminating. For example, while she describes the flossing of teeth by long-tailed macaques (Masataka et al. 2009) as a form of stimulus enhancement, the same behaviour is also consistent with her criteria for direct active teaching – since it could well be characterised as a "non-verbal demonstration, punctuated with exaggerated movements, by an expert ... to a novice" (target article, sect. 3.1.5, para. 1). Indeed, we often engage in direct teaching by drawing others' attention to important features of objects – which suggests that Kline's categories are also not mutually exclusive. It is also hard to see why the cases of informative pointing that Kline counts as stimulus enhancement are not cases of active (albeit pre-verbal) teaching; and why the Warao father's adjustment of his son's wrist is a case of direct active teaching, and not evaluative feedback.

The confusions caused by these overlapping categories are unlikely to facilitate identification of cases of teaching in the animal kingdom. Moreover, they undermine our confidence that this new theoretical framework could be used to generate new scenarios for testing for the presence of teaching. Consequently, although Kline's categories are thought-provoking, it is not clear that they improve on the categories of social learning already described by others (e.g., Whiten & Ham 1992).

Despite this skepticism, we do not think that Kline has over-estimated cases of active teaching – at least among chimpanzees. Since chimpanzees are among our nearest living relatives, their teaching activities are of great interest for understanding the evolution of our own. Furthermore, we agree with Kline that intentional and "theory of mind" based teaching approaches sometimes overstate the social cognition that active teaching requires (Moore 2013b), and so agree that "the constraints of cognition ... do not seem sufficient to explain why direct active teaching appears to be limited to humans" (target article, sect. 7, para. 1). But then why is more active teaching not found in chimpanzees?

It seems unlikely that researchers have simply been looking in the wrong place, because several groups (Dean et al. 2012; Lonsdorf 2006; Matsuzawa et al. 2001) have tried and failed to substantiate earlier reports (Boesch 1991). Kline's emphasis on adaptive value may hold out an answer here.

Boesch (1991; 2012) has argued that chimpanzee mothers at Taï teach their children how to crack panda nuts. Because the *Panda oleasa* is particularly hard and difficult to crack, juvenile chimpanzees don't typically succeed until they are 8 years old. Because the chimpanzee interbirth interval is 5 years, Boesch argues that the demands of having two dependent offspring may push mothers to accelerate their offspring's learning. We find this explanation unlikely. Although the panda nut may be highly valued, it constitutes neither a large nor an ineliminable part of the Taï chimpanzee diet (Boesch & Boesch-Achermann [2000, p. 210] themselves describe Panda nut consumption as "rare" and "irregular"). Therefore, there is likely to be little adaptive pressure for teaching this skill. Given the scant evidence of teaching in chimpanzees, and the failure of others to find further evidence supporting Boesch's reports, it seems advisable to doubt that it is really happening. Why would this be?

One answer favoured by Kline and others (e.g., Gergely & Csibra 2005) is that behaviours that are both complex and difficult to learn through observation should lead to pressures for the emergence of teaching. Since naive captive individuals have already proven able to reinvent various wild "cultures" without social learning (Allritz et al. 2013; Huffman & Hirata 2004; Menzel et al. 2013), such opaque behaviours may not exist in chimpanzee culture. Therefore, non-teaching learning mechanisms may suffice for the propagation of contemporary chimpanzee technologies, including different forms of observational learning, individual learning, and inherited cognitive skills (Moore 2013b; Tennie et al. 2009; 2012). This may be true even for the most complex multi-tool sets (e.g., Boesch et al. 2009; Sanz & Morgan 2007).

We suspect that chimpanzees have simply faced little adaptive pressure for tools and tool-sets more complex than those that they already possess. Since they were never forced to leave their ecological niches, simpler forms of learning and social learning always sufficed for them to acquire whatever tools, tool-sets and communicative devices they needed. This would explain the lack of pressure for active teaching, not to mention the comparative absence in chimpanzees of high-fidelity learning mechanisms such as imitation. Given her closing comments about the adaptive value of teaching, we think that Kline would agree with this conclusion – but it is not clear why we needed her theoretical framework to get there.

NOTE

1. Both authors contributed equally to this commentary as joint first authors.

Eyes on the price: Human culture and its teaching

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Abstract: Kline proposes an evolutionary framework for teaching as a major base of human culture, in which she outlines how different types of teaching may solve adaptive problems with a focus on human behavior. Here it is argued that the ability to teach and the different types of teaching behavior may not only solve adaptive problems, but also create them.

In humans, a behavioral repertoire and/or cognitive patterns which significantly deviate from those of the majority and which impose a direct threat to one's own life or those of others are considered behavioral or psychiatric disorders. Virtually all psychiatric disorders are almost exclusively human, such as (endogenous) depression, schizophrenia, or drug addiction. In humans, they are highly preserved and often run in pedigrees. In fact, if one or both parents are affected by a certain psychiatric disorder, there is a significantly increased risk for its occurrence in the offspring. Despite intensive research efforts in the last two decades, only relatively minor bits of this inheritance can so far be attributed to genetic risk factors, and thus, to a genetic-based transmission and inheritance (Maher 2008). Environmental factors do play a

role too, such as stressful life events; but the interaction of genetic with environmental risk factors may not sufficiently explain the high rate of inheritance (Caspi & Moffitt 2006). The lack of a shared genetic base, which may explain behaviorally complex psychiatric disorders (Fanous & Kendler 2005), might suggest a cultural transmission of maladaptive behaviors and cognitive patterns (Koopmans & Boomsma 1996). This transmission may, at least in part, be driven by various forms of teaching.

The propensity for psychoactive drug use, abuse, and addiction may, for example, not only be genetically inherited (Kendler et al. 2003; Müller & Homberg 2015), but specific abuse-related behaviors may be taught by parents, by other family members, or by members of the peer group (Eissenberg & Balster 2000). Children who are exposed early on to parents who drink alcohol, for example, in order to cope with work stress or to solve relationship problems (Müller & Schumann 2011), instead of being taught non-drug–incorporating problem-solving strategies, may simply copy these behaviors (Alexander 1990). But parents and peer groups do also actively teach maladaptive behaviors and, thereby, preserve them as a behavioral complex and a part of human culture. They may also teach these behaviors and cognitive patterns, not being aware that they serve as teachers. Teachers may subsequently positively reinforce these newly copied drug-use behaviors in the pupils (Heath 2000).

Even more problematic is that these maladaptive behaviors are not only preserved in pedigrees as non-shared cultural knowledge, but may also become shared cultural knowledge when they are "outsourced from human brains" by behavioral storage, copying, and teaching mechanisms. A crucial mechanism for human cultural development is the continuous establishment/creation of new behaviors and their accumulation. Each individual human brain has as a behavioral storage medium only a limited capacity and is unable to store all behaviors and cognitive patterns (including semantic information) that are available in a culture. A major difference to nonhuman species is that humans developed the behavior of coding, storing, and teaching behaviors *ex vivo*, that is, in other media than the brain. Importantly, these media are virtually unlimited in their storage capacity and may serve as a crucial teaching resource in terms of a shared environment (Müller et al. 2012). This includes mechanisms of retrieval and re-incorporation into the actual behavioral complexes of an individual. I argue here that this works also for maladaptive behaviors, which may well lead to psychiatric disorders when copied. As an example, one may consider movies that idealize drug consumption and instrumentalization as behavioral problem-solving strategies (Gibbons et al. 2010; Hanewinkel et al. 2012). Being exposed to them facilitates learning in others in the sense that it provides a behavioral or cognitive scheme that is "authorized" for copying. *Ex vivo* storage and teaching works for behavioral sequences as well as for cognitive patterns, which constitute behavioral response predispositions. Thereby, the definition of teaching behavior should be expanded – only as regards humans, though – to *ex vivo* sources of behavior and cognitive patterns, including behaviors such as "writing/reading books" or "producing/watching movies" (Wilhite et al. 2010). Schizophrenia-associated cognitive patterns may, for example, be found in movies with the "hero" displaying violent paranoid behavior but still serving as a sort of role model. An important feature of this cultural transmission (and accumulation) of maladaptive behaviors and cognitive patterns is that it can be preserved ex vivo and, thereby, jumping several generations, before it is re-activated and actively re-incorporated *in vivo* into individual behavioral repertoires. Here, one may think about lost ideologies that are rediscovered after centuries and shape new cognitive repertoires and behavior.

One may readily assume that not only adaptive cultural behaviors, but also large parts of the human maladaptive behavioral and cognitive repertoire is transmitted by various types of teaching as outlined by Kline in her excellent article. Thereby, the teaching may be performed at an age before disadvantages of the taught behavior affect biological reproduction. This may explain why the capability of teaching is genetically (and culturally) passed on to the next generation. The negative consequences of the taught behavior only manifest later in life for the teacher. Thus, the maladaptive character may, for example, result in reduced offspring care. Alcohol-addicted parents have fewer resources to actively teach their offspring and to take care of them, because of the development of addiction-related physical and psychological problems (Ward et al. 2009). At the same time, they teach them significantly more drug-related behaviors to solve everyday problems (e.g., stress drinking). This may constitute a cultural bias towards maladaptive behavior in a pedigree.

Considering these seemingly exclusively human phenomena, I suggest that when discussing teaching as an adaptation in humans which is essential to transmit culture, pleiotropic effects need to be considered in an integrative framework as the individual "price of culture" and its transmission by teaching.

Childhood and the evolution of higher-effort teaching

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Abstract: Kline presents an excellent synthesis of teaching theory and research, with cogent arguments regarding its prevalence. In this, she claims that "active teaching" is human specific, and presents tangible reasons why. But in doing so, she overlooks a critical aspect of the human condition that may have arisen only recently in our evolutionary history: Childhood as a life stage.

The Oldowan knapped stone industry appeared around 2.6 million years ago. Given a lack of evidence for trial and error in Oldowan knapping (De La Torre 2004; Delagnes & Roche 2005) some teaching may have underpinned the transmission of this technology. However, the technology and shape of Oldowan artefacts was largely controlled by the properties of the raw materials used, rather than by stylistic traditions (De La Torre 2004; Toth 1985). If teaching were to have occurred, it likely only needed to be what Kline defines as "lower-effort forms." It is not until 1.75 million years ago, with the emergence of the Acheulean industry, that we see a shift in lithic construction hinting at the onset of Kline's "higher-effort forms of teaching."

Acheulean technology involved the ability to strike large stone flakes and bifacially shape stone artefacts into hand-axes and cleavers (Beyene et al. 2013; Lepre et al. 2011). Consider cleaver manufacture from the 1.21 million year-old site of Isampur Quarry in South India (Shipton 2013). Cleavers are U-shaped bifaces with a broad bit as their principal cutting edge, manufactured by setting up platforms on thick slabs of limestone from which large flakes could be struck obliquely to the bedding plane, then retouched into the requisite shape (Petraglia et al. 1999; Shipton et al. 2009). The manufacturing sequence involves several hierarchically organized stages, such as removing thick flakes from the slab perimeter to set up suitable platforms from which to strike the large blank flakes; and to a novice it would be unclear how some of these relate to the finished product (Shipton 2013). To understand why the platform is necessary requires sufficient experience to accurately identify the angles and surfaces that are good for striking large flakes. It is also important to note that Acheulean hand-axes and cleavers are deliberately shaped to be symmetrical, often in

two planes (Wynn 2002), yet butchery experiments suggest that this symmetry may not greatly improve their utilitarian value (Machin et al. 2007). In other words, they feature unnecessary characteristics and were probably made using unnecessary processes. Demonstrating the requisite skills may have required one of Kline's higher forms of teaching in order to steer novice knappers to the same, somewhat arbitrary, outcomes.

But it is here that we are confronted with a conundrum that highlights a key aspect of the human condition missed by Kline. The Acheulean period stands out for its unparalleled homogeneity: The industry persists for around 1.5 million years (Shipton et al. 2013). Compare this to a state-of-the-art personal computer purchased 10 years ago that is now so obsolete it is probably best employed as a piece of kitsch sculpture. Signs of cumulative culture in the Acheulean are, therefore, fleeting. What, then, is missing? The answer is hidden in Kline's target article. She is rightly at pains to point out that her examples of teaching are just that, and should not be taken as prescriptive. But note a key aspect of each example where humans are involved: All feature adult to child transmission, something that cannot occur if there are no children.

Due to the large size of our brain, but relatively narrow birth canal, humans are born in a state of altriciality where they depend on their parents for nourishment for longer than most animals (Bogin 1998). With the high metabolic demands of a brain that is still growing rapidly, humans have evolved "childhood," a new life history stage in which older members of the social group provide specially prepared foods that are high in energy and nutrients for the young whose brains are growing rapidly, but whose bodies are growing slowly (Kaplan et al. 2000; Locke & Bogin 2006). No other living species has this. Indeed, it may not have appeared until relatively late in our evolutionary history.

Reconstructions of extinct hominin life history using dental development, body mass, and brain growth point to a short or absent childhood in the earlier Acheulean hominin *Homo erectus* (for summaries, see Nielsen 2012b; Robson & Wood 2008). Childhood as we know it thus post-dates the emergence of Acheulian stone tools (Hopkinson et al. 2013). In contrast, there is evidence of a childhood in *Homo neanderthalensis* (Smith et al. 2007) who are, along with early *Homo sapiens*, associated with the establishment of Middle Paleolithic technology around 300,000 years ago. It is during the Middle Paleolithic that, under the right demographic circumstances, we begin to see instances of cumulative cultural evolution (d'Errico & Stringer 2011; Powell et al. 2009). Notably, by the Late Acheulean period a handful of technological advances, such as the use of soft-hammers, had accrued (Stout et al. 2014), and there is evidence that the Late Acheulean hominin *Homo heidelbergensis* had childhood lengths more similar to our own than *Homo erectus* (Nowell & White 2012; Robson & Wood 2008).

Childhood enables ample opportunity for play and discovery, and for entertaining the kinds of creativity that later in life undergird the imaginative endeavours that may bring new technological advances (Nielsen 2012a; 2012b). Childhood also affords multiple opportunities for extensive learning and for sophisticated cultural behaviors to arise (Bogin 1990) – and hence for more complex and detailed approaches to teaching. Childhood is necessary both because humans are born with brains that still have a long growth trajectory, and because it takes extra teaching investment to develop complex behaviours. Indeed, it may be argued that it was the combination of creativity, teaching, and learning that typifies childhood, which took us from being a cultural animal to being a cumulatively cultural one.

Kline's approach provides a new framework through which hitherto divided disciplines can find common ground for debating the phylogenetic and ontogenetic foundations of teaching, and promises to lead to new insights into one of the most critical of all social learning mechanisms. In it, she is right to ask why humans teach more than other animals. But the answer may be simpler than is outlined. It is because, unlike any other animal, we have children to teach.

Play to learn, teach by play

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Abstract: The synthesis provided by Kline in the target article is noteworthy, but ignores the inseparable role of play in the evolution of learning and teaching in both humans and other animals. Play is distinguished and advantaged by its positive feedback reinforcement through pleasure. Play, especially between adults and infants, is probably the platform from which human learning and teaching evolved.

> *Play is older than culture, for culture, however inadequately defined, always presupposes human society, and animals have not waited for man to teach them their playing.*
>
> — from *Homo Ludens* (Huizinga 1938/1949)

Kline provides a commendable synthesis, valuable for designing future research on learning and teaching both cross-culturally and across species. Kline ties teaching and learning to the cognitive, social, and cultural evolution of humans. However, although Kline claims to have incorporated "all known teaching mechanisms in humans and other animals into a cohesive theoretical framework" (sect. 3, para. 2), the role of social play is virtually ignored.

Play only *seemingly* serves no function and has no apparent, immediate benefits, but the incredible phylogenetic depth of play strongly suggests that play is a functional and adaptive behavior (Burghardt 2005). It is well appreciated that play facilitates learning in humans, and it is thought that learning is a key explanation and function of play across the animal kingdom (Pellegrini 2011; Pellis & Pellis 2009).

Many lines of evidence point to social play as a prime building block for the evolution of both learning and teaching. Play, in human and nonhuman infants, provides opportunities for the acquisition of relevant stimuli, for the diffusion of social and environmental knowledge, and for the development of fundamental cognitive and communicative capacities (Power 2000). Play reduces spatial separation between individuals (*Macaca tonkeana*, Palagi et al. 2014) and increases cooperation and empathic proclivity (*Pan paniscus*, Demuru & Palagi 2012; *Theropithecus gelada*, Palagi et al. 2009). Play renders individuals more competent in the emotional domain (Pellis & Pellis 2009), thus creating favorable conditions for learning and teaching (Ciani et al. 2012). In brief, play cannot be separated from learning, and is a ready-built platform from which to launch teaching.

What differentiates play from other forms of teaching and learning is the positive reinforcement arising from its pleasurable nature (Lewis & Barton 2006; Rilling et al. 2011). Play between adults and infants, in particular, is a behavioral setting in which a "teacher" and a "learner" can be clearly recognized. While benefits always outweigh costs for immature learners, costs for adult teachers are generally high and strongly dependent upon the type of play and on the social environment. In order for teaching to evolve, there should also be benefits for the teacher. For example, teachers may be related to their pupils, or pupils may be future allies or mates (Mancini & Palagi 2009). In species characterized by a complex sociality, such as human and nonhuman primates, play between adults and immature subjects can be an important bridge to broaden and strengthen social networks of the adults (Palagi et al. 2004; 2006).

Social play is a multifaceted behavior with various typologies (Cordoni & Palagi 2011; Palagi 2014; Palagi & Cordoni 2012), which come in succession in early stages of life and then integrate into one another. Information gathered and lessons learned by playing can later be recruited and tinkered to cope with many other aspects of life. Long-standing data show that the longer the period of development and learning, the more pervasive the social play (Fagen 1993).

Play between mother and offspring is probably both ontogenetically and phylogenetically the first means of teaching and learning. In primates, the role of mothers in the playful exchanges with newborns is fundamental. For example, great ape mothers are responsible for initiating and ending play sessions with offspring in their very first months of life. Later, infants spontaneously become more interactive in initiating new playful interactions with their mothers (Hoff et al. 1981; van Lawick-Goodall 1968). Gradually, newborns are introduced into the social network of the mother (Berman 1982). During this period, the mother actively monitors her infant's play sessions and often modifies their content (Power 2000). The direct, active interventions of the mother decrease as the infant learns to self-regulate and acquires social and emotional competence (Govindarajulu et al. 1993; Pellis & Pellis 2009). The provision of positive or negative reinforcements by the mother is a form of evaluative feedback (*sensu* Kline) because it leads to the appropriate management of play by infants.

Over time, the infant's sphere of play extends outward to other kin adults and, in tolerant social systems, even to non-kin adults (Ciani et al. 2012). In despotic societies, cultural and social knowledge gained by playing is therefore mainly vertical, limited to close kin, whereas in tolerant societies, transmission can also spread horizontally, involving unrelated individuals. Moreover, because unrelated subjects can use different play schemes and modules compared to related subjects, social tolerance enhances the diffusion of behavioral and cultural innovation (Fagen 1993; Huffman et al. 2010). Hence, play is an engine fostering a positive feedback linking tolerance to teaching and learning.

According to Kline, teaching includes specific communicative capacities as behavioral markers or ostensive cues. Similarly, play requires intensive, constant exchanges of ostensive signals and can be actively stimulated. Nonhuman primate research is rich in examples of the capacity of mothers and adults to adapt their communicative schemes to infants. When addressing infants of other females, macaque females (*Macaca mulatta*) use specific vocalizations to communicate their benign intent, a form of metacommunication ("vocal motherese"; Whitham et al. 2007). Gorillas (*Gorilla gorilla*) use a higher rate of repetitions and sequences of tactile gestures (Luef & Liebal 2012) when playing with infants. This form of "nonvocal motherese" sustains the development of infant gorillas in the learning process of nonvocal signals, and meets the criteria defining direct active teaching (*sensu* Kline).

As Kline notes, "the prevalence of teaching in humans and other animals is a contentious issue" (sect. 4.1, para. 1). However, the existence of play in all human societies and across mammalian species is not. This lends credence to our hypothesis that play may be one of the most basal building blocks from which human learning and teaching evolved.

Mind, brain, and teaching: Some directions for future research

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Abstract: In line with Kline's taxonomy, highlighting teaching as an array of behaviors with different cognitive underpinnings, we advocate the expansion of a specific line of research on mind, brain, and teaching. This research program is devoted to the understanding of the neurocognitive mechanisms and the evolutionary determinants of teaching skills, with the ultimate goal of helping teachers improve teaching quality.

In cognitive science, although progress has been made in dissecting the neurocognitive mechanisms underlying learning, little is known of those supporting teaching. This has become especially untenable in the light of mounting evidence that teachers have an important, long-lasting impact on their pupils; for example, econometric studies on the "teacher effect" extending into real life indicators of socio-economic status, including: retirement plans, salary, and house ownership (Bressoux & Bianco 2004; Bressoux et al. 2008; Chetty et al. 2011; Kane & Staiger 2008; Konstantopoulos 2007; Nye et al. 2004; Rivkin et al. 2005). Educational research and the mind and brain sciences have strengthened their cooperation during the last decade, to the extent that a new field of research is developing (Brabeck 2008; Fischer et al. 2007; Pasquinelli 2011; 2013a; 2013b). In this commentary, we advocate the development of a specific line of research on mind, brain, and education, with a translational aim and an evidence-based attitude at its core, devoted to the understanding and betterment of teaching skills (see also: Battro 2010; Rodriguez 2012; Strauss & Ziv 2012).

Kline's framework for going beyond traditional sector-honed definition theories to observe teaching practices, across species and across cultures, provides a base from whence we can ask the questions that have historically driven a wedge between nonhuman and human teaching debates: (1) Whether there is something like a "teaching instinct" in humans (teaching as a natural cognitive ability, as hypothesized in Csibra [2007], Csibra & Gergely [2009], and Strauss [2005]); and (2) whether and how the teaching instinct relates to or interacts with other cognitive functions (Barnett 1973; Olson & Bruner 1996; Pearson 1989; Premack 1984; Tomasello et al. 1993).

In order to answer these questions, we believe that a promising approach would be to use the experimental toolkit of cognitive psychology and neuroscience and implement quantitative studies. First, we should develop solid psychometric measures for evaluating teaching abilities, and then run correlational studies (based on inter-individual differences), assessing whether the success of professional as well as non-professional individuals in complex teaching tasks is related to their skills in the cognitive domains that are classically thought to be relevant for teaching (Theory of Mind [ToM], empathy, metacognition, general intelligence). This research should also compare kin versus non-kin use of Kline's taxonomy types in adult–child interactions, and include individuals with atypical development. One interesting population would be that characterized by a non-severe form of autism, Asperger syndrome: a neurodevelopmental disorder characterized by poor ToM and cognitive empathy, but with preserved metacognition, affective empathy, and general intelligence (Charman et al. 2011). Studying teaching abilities under different neurocognitive constraints could help refine the role of specific cognitive skills in teaching. Another method used in cognitive psychology to assess the relation between different cognitive functions is that of training. In order to isolate the cognitive determinants of the "teaching instinct," this research program

should, therefore, include training studies aiming at improving either Theory of Mind, or empathy, or metacognition, and measuring to what extent a transfer can be observed to teaching skills. Finally, comparing the data from objective studies with the subjective views of teachers, their folk theories of teaching and learning (Dekker et al. 2012; Olson & Bruner 1996; Pasquinelli 2012; Strauss 2001) and one's own self-assessment, could be key for gaining valuable insights on discrepancies between facts and intuitions about teaching.

It also seems reasonable that research on teaching should broaden its view so as to account for mechanisms that do benefit the teacher as much as the learner, by considering that teaching allows the teacher to gain cognitive advantages, and perhaps also prestige, leadership, and/or social status. Historically, the functional characterization of teaching in animal studies (Caro & Hauser 1992) explicitly excludes behaviors benefiting the teacher. However, as Kline states, "If there are costs of teaching, then there must be some benefit to the teacher, in order for teaching to evolve" (target article, sect. 6.1, para. 1). Kline suggests that the benefits of teaching are indirect, the pupil being a gene carrier, protector, or mate (see also Fogarty et al. 2011; Hoppitt et al. 2008; Skerry et al. 2013). However, it is our belief that teaching also serves purposes that are advantageous to the teacher himself (beyond indirect gains and kin selection). For example, it has been observed that learning in order to teach (i.e., preparing for teaching) enhances content understanding and retention as compared to studying for pure learning (Bargh & Schul 1989), and research on peer teaching suggests that both teacher and learner show benefits (Brown & Palincsar 1989). More research that focuses specifically on the teacher's gains is required.

Furthermore, a respected view in evolutionary biology characterizes communication and signaling as serving both altruistic and egoistic aims, namely: influence upon the addressee, that is, manipulation of conspecifics and prey behavior. The view predicts the coevolution of skills for persuading and for resisting persuasion when detrimental (Dawkins & Krebs 1978; Krebs & Dawkins 1984; Fernald 1992). The prediction seems to be confirmed, in the case of humans, by the observation that persuasion skills coexist with a complex of vigilance mechanisms that act upon the information given as much as the information giver (Harris & Corriveau 2011; Sperber et al. 2010). If teaching behavior also proffers advantages to the teacher, a cost-based calculus might not be enough to predict when more complex (and costly) forms of teaching will spontaneously appear. A set of questions then follows:

1. Which are the specificities of the persuasion-related displays that teachers commonly employ, in comparison with sales-persons' and leaders' techniques aimed at persuading their audience?
2. What is their impact on learning outcomes (understanding, retention)? Are there other measurable effects upon the teacher's prestige, status, and position?.

Answering these questions, and more generally acquiring a better understanding of the cognitive underpinnings of teaching behaviors, is a necessary condition for explaining, and taking advantage of, the "teacher effect." This will benefit education by enhancing the efficacy of professional development (Harris & Sass 2011; Yoon et al. 2007) and the development of strategies and technologies that exploit and supplement "natural" teaching.

Clarifying the range of social-cognitive processes subserving human teaching

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Abstract: An evolutionary framework on human teaching is not well equipped to explain the nature of human teaching unless it specifies the subserving cognitive and motivational mechanisms. Only a theory that speculates on the psychological processes provides testable predictions and stimulates further empirical research.

We applaud Kline's effort in providing a unifying framework on the social-cognitive mechanisms subserving human teaching behavior. Her approach may be seen as one of the very few attempts that not only systematize the different ways of teaching, but also examine underlying psychological mechanisms. Kline discusses the mentalistic approach in her framework. In particular, she notes that theory-of-mind (ToM) abilities are important prerequisites for human learning and teaching (see also Sodian & Frith 2008). Although we agree on the author's evaluation of the role of ToM in teaching, we think that the discussion of the psychological mechanisms remains too sketchy to generate novel research and, therefore, needs further extension. We will demonstrate this with the following two points: First, the mentalistic approach does not fully capture teaching behaviors in young children. Second, teaching, even by adults, at times can be unconsciously and implicitly employed in human interactions. We discuss these points in more detail next.

As Kline points out well in her article, according to the mentalistic approach theory of mind plays an important role in human teaching. Yet, recent empirical studies provide some evidence that – even in situations that require an understanding of others' knowledge state –ToM abilities may not be sufficient enough to explain children's selective teaching behaviors (Kim & Spelke 2013; Kim et al., in press). For example, Kim and Spelke (2013) reported that 4- to 8-year-old children were presented with two characters: one, knowledgeable and, the other, ignorant. In one task, they had the chance to ask one of the characters for information. As expected from the ToM literature, by 4 years – the age at which children already have an understanding of the difference between knowledge and ignorance – children did selectively consult the knowledgeable person. By contrast, when children were asked to teach one of the characters about the information they knew, it was only at around 7 and 8 years old that children reliably chose to teach the ignorant person. These findings suggest that ToM abilities are *not sufficient* for the development of selective teaching. Rather, an understanding of another's knowledge states needs to be complemented by additional, and perhaps even independent, psychological processes, in order to produce selective teaching behaviors. Together, although Kline reserves a place for mentalistic processes in her framework, it seems to lack a deeper appreciation of the specific psychological mechanisms involved in selective and efficient teaching.

In other circumstances, teaching can be rather automatically and naturally enacted in human interactions in which psychological mechanisms other than mentalistic ones are responsible for adaptive teaching behavior. One recent approach, also mentioned by Kline, assumes teaching to be an evolutionary adaptation that operates on the basis of non-mentalistic and subconscious processes (Csibra & Gergely 2009). Another, even more parsimonious approach with respect to the cognitive prerequisites subserving teaching, originates from the study of parent–infant interactions. Developmental literature has provided ample evidence that caregivers automatically demonstrate novel actions in a way that allows infants to recognize and process the central elements of observed behaviors. More specifically, the concept of "motionese" has been used to describe parents' inclination to demonstrate actions with greater enthusiasm, a slower motion rate, simplified sequences, and in a more punctuated manner (e.g., Brand et al.

2002). These demonstrations by caregivers have been shown to facilitate imitative learning in young children (Williamson & Brand 2013). Further support for these findings comes from studies demonstrating how mothers' sensitivity relates to infants' understanding of others' behaviors (Licata et al. 2014). It is likely that, via this kind of simplified action demonstration, parents actually tune into their infants' motor system, that is, they demonstrate the actions that resemble how infants themselves might perform these actions. This might help infants to relate the observed behavior to their own restricted motor repertoire (Paulus 2014), subsequently supporting imitative learning (Paulus et al. 2011, 2013). Given that these behaviors seem to be quite automatic and not based on mentalistic reasoning, these findings provide further evidence for the claim that mentalistic reasoning may not be necessary for all forms of teaching. Yet, Kline's proposal does not specify the exact psychological processes that subserve these implicit forms of teaching behavior.

In short, although we applaud Kline for taking up the challenge and for presenting a theoretical framework of human teaching, we believe that her account must be elaborated by specifying the exact psychological mechanisms subserving human teaching. Such a model would provide testable predictions that could stimulate further research.

Multiple dilemmas of help and counteraction to teaching in complex social worlds

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Abstract: Human civilization has a system of different social tools, institutions, and types of positive and negative work with teaching/learning determined by different interests of many actors. Negative work is more hidden and less studied. A paradoxical adaptive problem for teachers with good intentions is design of teaching/learning that equips pupils for learning in future environments unknown to the teachers.

My commentary is aimed at broadening Kline's reasoning about social dilemmas, deceptive teaching, and pupils' resistance to that teaching.

In comparison with nonhuman animals, many more actors with different interests and aims are involved in human teaching and education. Humans create more and more social tools to manage and control others' teaching and education. As a result, human civilization has a well-differentiated and permanently developing system of special social tools, institutions, and types of positive and negative work with teaching/learning (Poddiakov 2012). Positive work, or stimulation of teaching/learning, is more explicit and better studied. Negative work is usually more hidden.

The negative work includes three subtypes: denying teaching to another subject, aggressive counteraction to others' teaching/learning, and "Trojan horse" teaching. Counteraction or denying teaching is often prompted by the need to defend – either pupils, or other people *from* the pupils. Humans counteract teaching and learning activities that seem dangerous, abusive, or inappropriate. (Naturally, some people are skeptical about it and try to teach and learn these activities.) Trojan horse teaching is caused by the wish to get benefits from the ignorance and mistakes of pupils perceived as either prey (i.e., sources of benefits) or as potential competitors who must be stopped. For if "the ability to learn faster than your competitors may be only sustainable competitive advantage" (De Geus 1988, p. 3), then a blow at the ability to learn and master new types of activity is an effective means of weakening the competitor (Poddiakov 2004).

Trojan horse teaching with evil intent has some analogies with host manipulation by parasites: Many brain parasites change the behavior of their hosts (insects, fishes, mammals, etc.) so that the hosts behave in a way harmful for themselves but favorable for the parasites (Cézilly 2005; Hughes et al. 2012; Lafferty 2006). Naturally, the parasites act on the hosts' nervous systems and brains via physical and chemical influences, not via social ones as in humans' Trojan horse teaching, which was invented later. Yet, both kinds of manipulation are, to use Kline's terms, "modification[s] of one individual's behavior by another's influence" (sect. 6.2, para. 1) working at different levels.

Not only teachers, but pupils themselves may seek to impede other pupils' learning. Moreover, a pupil can try to stop competitors' learning via influencing a teacher. Alexander the Great wrote to his teacher, Aristotle, that the latter should not publish his doctrine to preserve Alexander's pre-eminence over all the others (Plutarch 2000, pp. 218–19). However, in some situations, pupils may help each other to learn.

There are complex interplays of positive and negative aims, and different kinds of assistance and counteraction in teaching/learning – without one-to-one matches between selfish behaviors and counteractions or between altruism and help in teaching. Both counteraction to teaching and Trojan horse teaching are realized not only because of actors' selfish interests but also to help pupils. For example, Trojan horse teaching with good intentions (i.e., with a hidden agenda of developing the students) is used when organizers believe that the content of education that the student needs would cause the student's resentment or would not be assimilated properly if presented upfront. Some educators consider educational computer programs as good Trojan horses helping students to master those disciplines (e.g., mathematics, logic, etc.) which they are unwilling or unable to learn in the traditional way (Bailey 1999; Boyle 2001; White 2004). The need for such teaching with hidden aims and content arises from the divergence of the goals and interests of the organizers and the students, which leads to a kind of manipulative strategy of teaching.

On the whole, humans support and stimulate teaching and learning towards definite directions, in definite domains, in definite periods (e.g., historical or professional or age development periods), often in a certain group of people, and so forth; and, conversely, humans counteract teaching and learning in certain areas (e.g., dangerous and/or competitive ones), in certain periods, and among some people. Such stimulation and inhibition takes place at the micro-, meso-, and macro-social levels – from a level of informal interpersonal relations to a level of state laws and foreign relationships.

In contrast to nonhuman animals, this complex positive and negative work includes meta-teaching: explicit knowledge of whether to teach or not to teach in different areas (Barnes & Cavaliere 2009; Poddiakov 2004); how to conduct Trojan horse teaching; how to detect deceptive teaching and resist it; how to study teaching and learning; and so forth. And the target article, "How to learn about teaching…," along with the multiple commentaries on it, is a part of this explicating work.

I do not know of analogies to such systems of tools and activities in nonhuman animals, but in any case one should try to reveal their evolutionary and cultural foundations and mechanisms.

A crucial, and paradoxical, adaptive problem for teachers is that, rather than the simple copying of necessary knowledge and behaviors by pupils while learning, there should be a creative design of *developing* education, teaching, and learning, of the kind that equips pupils for learning and acting in future environments – which are more or less unknown and unpredictable for the teachers, and in which the teachers may not be sufficiently competent.

Let me introduce a formalism describing constructiveness of teaching/learning strategies:

$$Constr = N'C' - NC$$

where *Constr*=constructiveness of the teaching/learning strategy; *N* and *C*=novelty and complexity of problems which an agent (a being, an organization, etc.) can raise and solve before teaching/learning; *N′* and *C′*=the parameters after teaching/leaning.

If *Constr* > 0, the teaching/learning strategy is constructive (positive), and if *Constr* < 0, it is destructive (negative). It seems that the constructiveness-destructiveness of teaching/learning is related not only to educational technologies per se, but also to some general properties of a social system in which teaching/learning is realized. It would be interesting to compare the constructiveness of teaching/learning strategies in societies with different Global Peace Indexes (Estes 2014) or Moral State of Society Indexes (Iurevich & Ushakov 2010).

The cognitive and educational paradoxes of developing constructive teaching/learning cannot be solved without solving cooperative, psychological, social, and moral dilemmas – an important part of which Kline has started to analyze.

Is tolerance really teaching?

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Abstract: Kline succeeds in demonstrating the value of an approach that integrates information from various scientific and social disciplines, but her framework does not uniformly provide clarity. Specifically, inclusion of situations in which knowledgeable individuals do not actively donate information is misguided. Passive tolerance by demonstrators should continue to be excluded from definitions of teaching, in order to focus on situations in which selection has favored behaviors that are specifically geared to promoting learning in others.

Kline's attempt to bring together the various disciplines that study teaching behavior, and their disparate perspectives, is commendable. The target article's central theme – that a synthesis of comparative and cross-cultural research on the topic could move our understanding significantly forward – is well taken. Although most researchers would agree with the definition of teaching "as behavior evolved to facilitate learning in others" (target article, sect. 1, para. 5), vigorous debate has reigned beyond this most basic point. Fueling much of the controversy has been a proliferation of terminology without enough attention to consistency, as well as a penchant to disregard the complementarity of different levels of explanation (*sensu* Tinbergen 1963). Psychologists have tended to exclusively focus on the proximate cognitive mechanisms that may serve to support teaching; this is what Kline terms the "mentalistic" approach. Kline's "functionalistic" approach, which is taken by many evolutionary anthropologists and biologists, is an ultimate-level perspective. Unfortunately, the functionalistic framework has not encouraged a nuanced exploration of either the potential variation in teaching behavior that may be exhibited across nonhuman species or of the cognitive processes that may be involved (Byrne & Rapaport 2011; Rapaport & Byrne 2012). Instead, much of the emphasis of this approach has centered on cataloguing species that fit Caro and Hauser's (1992) narrow operational definition (Thornton & Raihani 2008; 2010).

Such single-minded attention has left uncontested the potentially erroneous argument that teaching in nonhumans is merely analogous to teaching in human. Consequently, the claim that comparative study cannot not inform us as to the evolutionary sequence that led to intentional teaching in humans (Csibra & Gergely 2011) remains untested. This humans-only perspective may well be premature. Therefore, I agree with the need for synthesis but would argue that there is little justification for introducing new terms for these various approaches, given the already vast terminology that plagues the field and the enduring utility of Tinbergen's (1963) levels-of-explanation paradigm.

More importantly, I question the justification for expanding the characterization of teaching to include situations in which the knowledgeable partner does not actively promote learning but simply tolerates close and intrusive observation by a naïve individual ("teaching by social tolerance" in Kline's parlance). Young nonhuman primates often share feeding sites with and forage in close proximity to adult conspecifics, especially close relatives, who also are feeding and foraging. True, tolerance may be costly when the young interfere with adult feeding efficiency, but when adults do not actively assist immatures, any food-related information they gain from these activities is realized through efforts initiated by the young (reviewed in Rapaport & Brown 2008). When the presence of another individual leads an observer behave in a similar way or to focus its attention on a location or object, without active assistance from the knowledgeable partner, the social learning that occurs is thought to be inadvertent on the part of the demonstrator. Only when the knowledgeable individual alters its behavior in order to demonstrate relevant environmental cues or behavior has the interaction been considered to be "teaching" (Hoppitt et al. 2008).

Alternatively, Kline proposes that teaching by social tolerance can be recognized when "the degree of tolerance … is greater than species-typical tolerance toward other conspecifics" or by "heightened social tolerance in situations … when the potential gains in learning for the young are especially high" (sect. 3.1.1). The problem is, adult primates are noticeably tolerant of closely related young in many different situations. When a mother macaque allows her juvenile to use her back as a springboard as she rests in the midday heat or when her infant hangs from her arm as she attempts to groom another adult, is the mother engaged in teaching? One could argue that immature primates learn adaptive lessons in social etiquette or acquire physical training through these activities (Bekoff & Byers 1998; Byers & Walker 1995), and that adults suffer energetic or opportunity costs from intrusions by the young, but these situations appear to be cases in which immatures are exhibiting an adaptive propensity to take advantage of adult tolerance in order to facilitate individual learning. Thus, the learning that occurs is likely to be less socially based than that which may occur during co-feeding and co-foraging, and yet, the behavior of the adult – that is, tolerance – is not measurably different.

Likewise, "teaching by opportunity provisioning" appears to not always incorporate active involvement by the putative demonstrator. This category comprises situations in which the knowledgeable partner allows access to information that is otherwise too difficult or too dangerous for the naïve pupil to acquire by individual means. Yet the human example that Kline provides – that of a music teacher who "plays music for his students without modification" (sect. 4.2.2.) – evinces no behavioral adjustment on the part of the teacher. Kline's overly broad definitions open the door to a host of social-learning situations in which the demonstrator simply goes about his or her normal activities, inclusion of which may only muddy the waters, rather than contribute to a greater understanding of what it means to teach. Hoppitt and colleagues (2008) have provided a scheme that is similar to Kline's, which recognizes that the social learning processes from the perspective of the pupil may not substantially differ in situations that involve or do not involve active teaching by a knowledgeable partner. However, Hoppitt et al.'s scheme more clearly defines teaching as incorporation of active demonstration. On the other hand, the present article offers the valuable addition of a category, *direct active teaching*, which thus far has been convincingly reported only in humans. The most valuable contribution, however, may be Kline's emphasis that social learning in general, and teaching specifically, form overlapping continua in which multiple strategies

may be employed at any given time. This is one of the characteristics of teaching behavior that creates difficulties for investigators, but makes the behavior so endlessly interesting.

Measuring teaching through hormones and time series analysis: Towards a comparative framework[1]

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Abstract: Arguments about the nature of teaching have depended principally on naturalistic observation and some experimental work. Additional measurement tools, and physiological variations and manipulations can provide insights on the intrinsic structure and state of the participants better than verbal descriptions alone: namely, time-series analysis, and examination of the role of hormones and neuromodulators on the behaviors of teacher and pupil.

We welcome Kline's emphasis on comparing behavioral measurements between learning episodes, and suggest including novel measures applicable to taught/learnt behaviors across species and tasks.

Hormonal or neuromodulatory states are well known to affect learning, for example, in bird-song acquisition (Ball et al. 2002). So far, little research has been undertaken on the role of hormonal states of teachers and learners in teaching episodes, although such examination offers promise for intraspecies and interspecies comparisons. The few animal studies linking endocrine parameters with social learning show that oxytocin and arginine-vasopressin mediate the social transmission of food preferences and that oxytocin plays an important role in mate-choice copying (Dore et al. 2013). Until more direct evidence is available, predictions on the endocrinology of teaching can be established by linking hormonal measures to behaviors that are essential to teaching. For instance, oxytocin and vasopressin mediate social approach and aversion (Porges 2001). Arguably, increased approach motivation and decreased social aversion are essential in teaching contexts. Other relevant behaviors, such as social motivation, affiliation, individual recognition, aggression, anxiety, and stress are associated with and regulated by oxytocin, vasopressin, testosterone, estrogens, and progesterone (McCall & Singer 2012; Mehta & Josephs 2012). These hormones also regulate and are influenced by trust, prosociality, empathy (empathic concern, perspective taking), reward sensitivity, and status seeking (Bos et al. 2012; Crockford et al. 2014; Heinrichs et al. 2009; Insel 2010; Mehta & Josephs 2012; van Anders et al. 2011). To what extent these behaviors play a role in teachers or pupils may depend upon the teaching type. Therefore, we propose that Kline's teaching types can be mapped to hormonal variations in teachers and learners via social and cognitive building blocks (Fig. 1). This approach parallels existing frameworks for the study of cooperation (Soares et al. 2010), and according to Kline, teaching is a cooperative behavior.

Kline proposes to conduct comparative research with emphasis on socio-environmental niches in which teaching and specific teaching types evolve. In cooperatively breeding New World monkeys, after the birth of an infant, fathers experience changes in vasopressin, oxytocin, and testosterone (Kozorovitskiy et al. 2006) and siblings show increases in oxytocin (Ragen & Bales 2012), suggesting physiological adaptations to infants and juveniles (the individuals who are usually taught). Rearing conditions influence later oxytocin balance and social behavior (Fries et al. 2005; Winslow et al. 2003), and altruistic behaviors, sibling

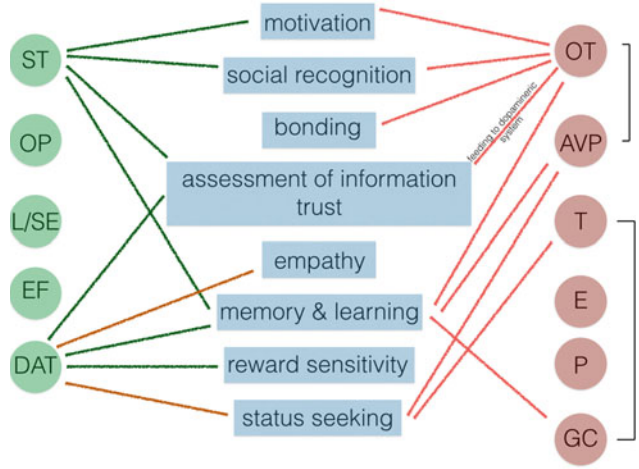

Figure 1. (Ravignani & Sonnweber). Exemplary mapping of teaching types to hormonal measures via behaviors. The "building blocks" of teaching (in the middle with blue background) are mediated by and fed back to different hormones (right with pink background), such as oxytocin (OT), vasopressin (AVP), testosterone (T), estrogens (E), progesterone (P) or glucocorticoides (GC) (actual although incomplete results on behavior–hormone interactions are indicated with red lines). Hormonal measures allow the investigation of motivational and emotional changes in teaching contexts and can be linked to cognitive processes and behavioral modifications associated with teaching. Kline distinguishes five teaching types based on the adaptive problem they solve: (i) teaching by social tolerance (ST), (ii) opportunity provisioning (OP), (iii) local or stimulus enhancement (L/SE), (iv) evaluative feedback (EF), and (v) direct active teaching (DAT). A precise mapping between building blocks and different teaching types needs to be investigated: Predictions on possible connections are indicated on the left (brown lines for teachers and green lines for pupils). Mapping teaching types to hormones and behaviors may help us understand basic processes and mechanisms of teaching across and within species.

relationships, or decision making are genetically associated with different vasopressin-receptor types (Israel et al. 2008; Knafo et al. 2008). Parental investment and siblings' infant care predict changes in vasopressin and oxytocin in cooperatively breeding monkeys (Ragen & Bales 2012). Hence, developmental and epigenetic forces might contribute to the evolution of teaching behavior (Bjorklund 2006; Soares et al. 2010). Future comparative data will elucidate the epigenetics of teaching.

While hormones elucidate internal states, Kline's focus is on external, observable behaviors. She claims that the only example of direct active teaching in nonhuman animals comes from anecdotes of chimpanzees learning to crack nuts (Boesch 1991). Building on recent work on synchrony and motor mimicking in chimpanzee dyads (Fuhrmann et al. 2014), we propose additional tools to measure teaching and learning over time *across species* and *behaviors*.

A chimpanzee performing quasi-periodic movements to crack nuts can be tracked over time, for example, via video coding (Fuhrmann et al. 2014) or movement sensors (Nagasaka et al. 2013; Ravignani et al. 2013). This produces, for each individual, evenly spaced samples (time series) of rhythmic, learnable behaviors. Behaviors can be movements, fundamental frequency of vocalizations, or any other possible recordable semi-repetitive behavior within short time scales (few seconds). Kline stresses the importance of comparing behaviors in teaching and non-teaching contexts, and argues that finding differences in rates of behaviors between baseline and teaching contexts suffices to

conclusively demonstrate teaching. Time series of teachers and pupils can be plotted together and statistically related to test hypotheses on teaching types.

Autocorrelation (correlation of a series with itself at different time lags) can be employed to investigate practice and self-consistency in learning movement patterns. Increased learning can be shown via an increase in between-trial autocorrelation (i.e., increased predictability of the pupil's next step once the action is almost completely learned).

Faithfulness of action copying and individual learning performance can be investigated using cross-correlations: the higher the correlation between teacher and pupil, the more accurate the learning. A cross-correlogram provides a measure in the delay of copying: A high cross-correlation (near zero lag) provides evidence for simultaneity of actions (high cross-correlation at a short lag is predicted in stimulus/local enhancement). Alternative methods, originally developed to infer similarity between geometrical curves, can measure resemblance between taught/learnt behaviors, such as Fréchet distance (Alt & Godau 1995), procrustes analysis (Gower 1975), and dynamic time warping (Verhoef et al. 2014).

Granger-causality (Granger 1969; Seth 2010) enables investigation of directionality of information transmission in the teaching process; a teacher's time series causes a pupil's time series (sensu Granger-causality) if past teacher's data significantly improve the prediction of future pupil's data (when compared to forecasts based on past pupil's data alone). Granger-causality can be used to show that teacher–pupil synchrony is unilaterally driven by one of the two (Fuhrmann et al. 2014). Alternatively, two time series Granger-causing one another constitute evidence for bilateral information transmission: not only does the pupil's series depend upon the teacher's series, but the teacher's behavior will also be triggered by a pupil's (imperfect) behavior (as needed in evaluative feedback). An alternative for measuring the amount and directionality of information transmission is partial directed coherence (Baccalá & Sameshima 2001; Ghazanfar et al. 2012).

The proposed quantitative tools can serve to analyze behaviors in teaching contexts. Hormonal measures allow for conclusions about motivational and emotional states or reward mechanisms. Controlled correlation studies measuring relevant hormones (i.e., via saliva, urine, or feces) or experimental administration studies can help shed light on basal processes involved in teaching and social learning. The tools we suggest here will hopefully contribute to a more empirical and quantitative approach to teaching, transcending verbal descriptions alone.

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NOTE

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The benefits of an evolutionary framework for the investigation of teaching behaviour: Emphasis should be taken off humans as a benchmark

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Abstract: We agree with Kline that a lack of unification is preventing progress in understanding the occurrence of teaching behaviour and the selective pressures influencing its presence. However, we feel that the proposed framework, which incorporates mentalistic and cultural approaches, continues to overlook cases of teaching in nonhuman animals. We advocate the comparative functionalist framework to identify the proximate causes of teaching behaviour in both humans and other animals.

Teaching is a behaviour, or array of behaviours, that has provoked considerable debate (see Csibra 2007; Hoppitt et al. 2008; Premack 2007; Thornton & Raihani 2008). Much of this debate comes from the belief that teaching is a behaviour that requires uniquely human cognitive abilities, such as theory of mind, and therefore occurs only in humans (Premack 2007). A number of supporters of the mentalistic and culture-based approaches to teaching argue that there is remarkably little evidence for teaching in nonhuman animals, and supporters of the functionalist approach agree (Byrne et al. 2013; Thornton & Raihani 2008; 2010). However, the way that teaching is defined is likely to be a primary cause for the relative absence of it in nonhuman animals (Thornton & Raihani 2010). Indeed, a recent surge in research claiming to show teaching in nonhuman animals has benefited strongly from the functionalist definitions proposed by Caro and Hauser (1992) and updated by Hoppitt et al. (2008). By providing a definable criteria for what constitutes teaching, within a quantifiable and comparative framework, teaching has now been discovered in a number of animals (for recent examples, see Franks & Richardson 2006; Kleindorfer et al. 2014; Raihani & Ridley 2008; Thornton & McAuliffe 2006; and see Maestripieri et al. [2002] and others reviewed in Thornton & Raihani [2008] for anecdotal examples of teaching in animals that have not yet been experimentally proven).

Teaching, if we are to follow the functionalist definition, may therefore not be as rare as originally supposed. Indeed, Byrne et al. (2013) argue that "the old idea that cultural learning through teaching is how we do things, while trial-and-error fumbling is how *animals* do them has now been thoroughly discredited" (p. 51 [emphasis in original]).

Even from the perspective of human-based studies it has become increasingly acknowledged that the mentalistic and culture-based definitions of teaching are overly restrictive. For example, recent research into the occurrence of teaching behaviour in humans has used nonhuman examples to explain the different types of teaching that exist (Dean 2011; Niedermeyer 2014). The famous philosopher John Dewey wanted to ground our understanding of teaching in evolutionary theory, and hence came up with a definition of the two types of teaching – which is very similar to that of Thornton and Raihani (2008). However, Dewey failed to make the explicit link between the evolutionary bases of teaching behavior and human education (Niedermeyer 2014). Thus, Kline's article provides welcome recognition of the need for a unification of the definition of teaching in her call for a new, evolutionary framework for teaching.

Previously, it has been suggested that teaching must be defined in the absence of environmental and genetic influences (reviewed in Dean 2011). However, increasing opposition to this idea identifies that environmental factors are likely to influence behavioural patterns in all animals, and to exclude them would result in false negatives (Laland & Janik 2006). Therefore, while we agree with Kline that a new framework for the definition and measurement of teaching behaviour is required, we disagree with the following statement:

> [A]ny framework for understanding the evolution of teaching should be tested against the human case. (target article, sect. 2.4, para. 6)

This suggests that humans act as the benchmark for understanding the occurrence of teaching in other animals. While it may be the case that humans are abnormally prolific teachers for certain *types* of teaching behaviour, this does not explain why teaching behaviour may be present in other animals. In all cases, if teaching creates a benefit for both teacher and pupil (albeit a delayed benefit for the teacher), if the cost of teaching is not prohibitively high for the teacher, and learning would not have occurred (or occurred less efficiently) in the absence of teaching, then teaching may be expected to occur (Fogarty et al. 2011). It is therefore unclear to us why the occurrence of teaching in humans should be used as a benchmark to explain teaching in nonhuman animals. Indeed, even those opponents to the evidence of teaching in nonhuman animals suggest that the key differences are in the *type* of teaching that occurs, rather than the existence of teaching at all (Csibra 2007; Premack 2007).

Kline suggests that without a common framework to compare between humans and other animals, the functionalist framework (the framework primarily used in nonhuman animal studies) may only provide part of the explanation for why teaching evolves in many species. While we understand Kline's point of view here – that the apparently atypical and sophisticated teaching behaviors in humans are an interesting case – it does not mean that we should assume that the factors that promoted this apparently "abnormal" teaching in humans explains the occurrence of teaching in other species. Instead, we suggest it is highly likely that teaching has arisen as a survival and/or fitness benefit according to the prevailing ecological and social conditions that species are exposed to. If we start at a point where we agree upon a clear definition of teaching that does not require uniquely human behaviours, but instead focuses upon what really constitutes teaching behaviour, then we may truly create a framework where a unified, operational definition for teaching can be quantified and thus compared between studies.

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Human teaching and learning involve cultural communities, not just individuals

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Abstract: Cultural accounts of how people facilitate learning extend beyond the five types of teaching outlined by Kline's target article. Rather than focusing so exclusively on individual teaching, cultural accounts examine the mutually constituting efforts of individuals who are teaching, together with those who are learning. Further, cultural research emphasizes the community contexts of people's arrangements for learning and their teaching/learning interactions.

In this commentary, I argue that we need to move beyond studying only individual or dyadic aspects of teaching to a broader, cultural view of interpersonal and community ways of fostering learning, at least for humans.

Kline seems to have overlooked the depth of the available cultural research on what she defines as teaching: "behavior evolved to facilitate learning in others." Because of her focus on the definition of teaching as schoolish instruction, she erroneously claims that cultural researchers say that teaching does not exist in non-Western communities. (In addition, her account misrepresents cultural work as claiming that learning occurs through observation and not participation and that the process is automatic, natural, and simple.)

Many people reserve the term *teaching* for the kind of instruction that is common among schoolteachers. Even Guatemalan Mayan mothers who had not been to school seemed to use the term teaching in this way when I asked them many years ago how they taught their daughters to weave. They often responded that they do not teach them to weave; the daughters learn. Over the past decades, my work and that of a number of other cultural scholars has focused on finding out how adults facilitate children's learning, when they are not doing schoolish teaching.

Kline's misrepresentations may stem in part from her focus on individuals in competition with each other. Her framework does not take into account either the mutually constituting nature of teaching and learning, or the contributions of cultural communities themselves. An example of community contribution is the inclusion of children as contributors to a broad range of activities of the community. This is common in many communities but would be difficult in many middle-class communities, for reasons well beyond the actions of any individual.

Children's inclusion in the range of activities of their family and community subsumes Kline's first type of teaching: *social tolerance,* in which the teacher does not stop the pupil's close and intrusive observation. (Interestingly, Kline found that in Fiji, an impressive 100% of children's physical intrusions into others' activities were tolerated.) In many communities, children's presence and involvement is not just tolerated, but expected and encouraged by individuals and the community as a whole. For example, in some Mexican communities, children's presence in important events is seen as a contribution to the group, to learn how to maintain the culture (Corona & Pérez 2007; Pérez Martínez 2011). And adults' willingness to allow toddlers to help with chores may be regarded as an important contribution to development of the next generation's character and skill.

Inclusion of children in family and community endeavors also subsumes Kline's second type of teaching: *opportunity provisioning*, in which a teacher creates opportunities for practice that would otherwise not exist. Kline gives an example of an uncle facilitating the help of a 4-year-old in carrying water, although the uncle could have carried more water without the child's involvement. Oddly, Kline refers to this as "asocial learning," which may be connected with her focus on individuals.

Cultural research has often discussed Kline's third type of teaching: *by stimulus or local enhancement*, in which a teacher stimulates the pupil's interest in a stimulus or location, such as pointing or verbally calling the child's attention to observe. Further, if children are included in community activities, their interest can be stimulated by others' interest, and they are often encouraged to be generally observant. In such contexts, Kline's fourth and fifth types of teaching have also been extensively studied – *evaluative feedback*, such as scolding or teasing, and *direct active teaching* (verbal or nonverbal or both).

The cultural literature has for decades examined all 5 types of teaching in Kline's framework. In addition, the cultural research goes beyond a focus on teaching by an individual. It calls attention to the mutually constituting, complementary contributions of teachers and learners, who always operate in the context of cultural communities' ways of facilitating learning. These themes are central to the articles that Kline cites as exemplars of cultural research (e.g., Gaskins & Paradise 2010; Lancy & Grove 2010; Lave & Wenger 1991; Paradise & Rogoff 2009; Rogoff et al. 2003). Such themes have also been central to the cultural research of many other scholars for more than four decades (e.g., Bolin, Cole, Erickson, Fortes, Goodnow, Greenfield, Gutiérrez, Heath, Jordan, Lee, LeVine, Maynard, Nasir, Ochs, Philips, Saxe, Schieffelin, Scollon, Scribner, Serpell, and the Whitings).

To take a specific example from my own work, ever since those Mayan mothers challenged my way of thinking about teaching and

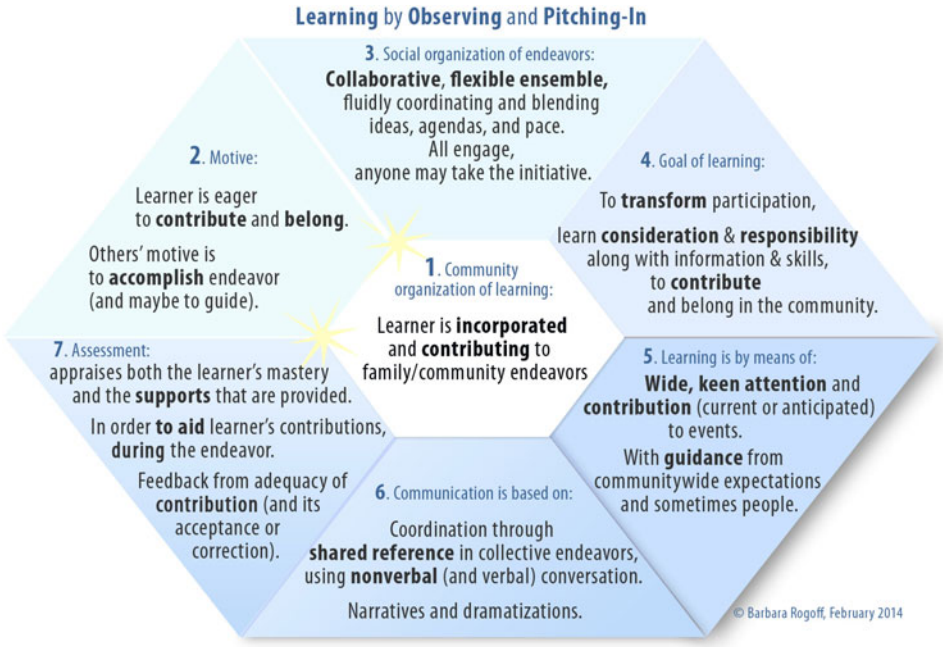

Figure 1 (Rogoff). The facets defining Learning by Observing and Pitching In: a cultural tradition for fostering learning that integrates community processes with individual and group processes.

learning decades ago, I have written about the role of community arrangements and practices in facilitating learning, and the mutually constituting nature of teaching and learning (e.g., Rogoff 1990; 2003). Over more than a decade, I have published articles articulating a way of learning that appears to be common in Indigenous-heritage communities of the Americas.

This way of facilitating learning emphasizes the community's role. It is the central feature of the seven features that define this cultural tradition for fostering learning. In addition, all the facets of this learning tradition include complementary teaching/learning roles (Rogoff 2014). Figure 1 shows a prism defining the facets/features of Learning by Observing and Pitching In (LOPI). The prism's seven facets can be seen as broader versions of Kline's 5 teaching types; in addition, they form part of a cultural tradition for fostering learning that involves individual, interpersonal, and community processes.

Kline's laudatory aim to integrate developmental, cultural, and ethological studies of teaching would benefit from a more in-depth cultural view of the integrated manner in which individuals, small groups, and communities foster the learning of the next generation.

The active role played by human learners is key to understanding the efficacy of teaching in humans

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Abstract: The early developing capacity of human learners to seek out reliable informants, initiate pedagogical episodes, and monitor and redirect ongoing instruction is critical to understanding humans' remarkable capacity for cumulative culture.

Kline categorizes teaching types according to their ability to address different social learning problems. However, the learning problems that she identifies all assume an attentive teacher. Absent from her discussion are situations in which the learner must direct the attention of the teacher in order to obtain relevant information. We argue that the early developing capacity of human learners to seek out reliable informants, initiate pedagogical episodes, and monitor and redirect ongoing instruction is critical to understanding humans' remarkable capacity for cumulative culture.

In order for instruction to be effective, it must be relevant: its content must be novel and useful and/or connected to the learner's prior knowledge (Sperber & Wilson 1995). From the learners' perspective, one way to ensure that instruction is relevant is to select informants who are likely to be reliable. Recent research has shown that preschoolers are astute social learners who do not simply trust what they are told but selectively learn from informants (Harris 2012). Remarkably, even infants display selective learning capacities (Harris & Lane 2013). When presented with a novel toy in a laboratory setting, 12-month-old infants preferred to look at the experimenter for clarifying information rather than at their caregiver, even when the caregiver presented the novel toy (Stenberg 2009; see also, Stenberg 2013).

In addition to seeking out "local experts," infants actively recruit informants to obtain relevant information by redirecting the attention of their caregivers to personally relevant stimuli and by initiating pedagogical episodes through information requests. For example, 10- to 13-month-old infants are more likely to combine pointing with vocalizations when mothers are not paying attention, or fail to respond to the target of the point (Wu & Gros-Louis 2014), and 16-month-old infants are more likely to point to request information about novel objects when interacting with a knowledgeable experimenter rather than an ignorant experimenter (who had previously named familiar objects incorrectly and appeared unsure of the names of the novel objects) (Begus & Southgate 2012).

Preschoolers' language abilities give them additional tools to shape the instruction they receive. They frequently ask questions

(Chouinard 2007) and monitor informants' responses to their questions, often restating their questions or providing their own explanations when given unsatisfactory explanations (Frazier et al. 2009). Thus, young children not only initiate but also monitor and influence pedagogical exchanges.

Human leaners' early developing capacity to initiate and influence pedagogical situations has a catalyzing effect on the effectiveness of the teaching behaviors identified by Kline, because it makes human teaching more responsive and relevant to individual learners. In turn, this increases the quality and quantity of information that can be exchanged through instruction. Therefore, it will be important for future research to not only study the occurrence of the teaching behaviors identified by Kline across and within species, but to also study the occurrence of learner behaviors that direct and redirect instruction.

In conclusion, the remarkable human capacity for cumulative culture seems attributable not only to the human capacity for teaching, but also to the active role played by human learners in the teaching process.

More examples of chimpanzees teaching

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Abstract: Darwinism is a principle of biological continuity. This commentary argues against any claim of discontinuity between humans and other animals that must be based on absence of evidence. Instead, we offer additional examples of active teaching by chimpanzees.

Wisely, in our view, the only evidence for spontaneous teaching that Kline accepts is from professional records of field observations. Christophe Boesch, for example, is a veteran primatologist who has been publishing reports of wild chimpanzee behavior in respected scientific journals for more than 40 years. Boesch is best known for discovering that wild chimpanzees in Ta'i National Park, Ivory Coast, crack nuts by striking them with stones and branches that the chimpanzees specially select for use as hammers, and carefully place the nuts on rocks specially selected for use as anvils. In the course of intensive studies, he discovered that mothers of dependent infants engage in behavior much like teaching:

> After successfully opening a nut, Sartre replaced it haphazardly on the anvil in order to attempt access to the second kernel. But before he pounded it, (his mother, Salome) took it in her hand, cleaned the anvil, and replaced the piece carefully in the correct position. Then, with Salome observing him, Sartre successfully opened it and ate the second kernel. Here, the mother demonstrated the correct positioning of the nut. (Boesch 1991, p. 531)

In a second example:

> Ricci's daughter, 5-year-old Nina, tried to open nuts with the only available hammer, which was of an irregular shape. As she struggled unsuccessfully with this tool, alternately changing her posture, hammer grip, and the position of the nut, Ricci was resting. Eventually, after 8 min of this struggle, Ricci joined her and Nina immediately gave her the hammer. Then, with Nina sitting in front of her, Ricci, in a very deliberate manner, slowly rotated the hammer into the best position with which to pound the nut effectively. As if to emphasize the meaning of this movement, it took her a full minute to perform this simple rotation. With Nina watching her, she then proceeded to use the hammer to crack 10 nuts (of which Nina received six entire kernels and a portion of the other four). Then Ricci left and Nina resumed cracking. Now, by adopting the same hammer grip as her mother, she succeeded in opening four nuts in 15 min. Although she still had difficulties and regularly changed her posture (18 times), she always maintained the hammer in the same position as did her mother. She whimpered whenever encountering difficulties, to attract her mother, but Ricci did not return to her even when she threw a temper-tantrum after unsuccessfully attempting to open a fifth nut for 3 min. (Boesch 1991, p. 532)

We are curious to see how Kline, or others, might apply her framework to the wild chimpanzees at Gombe featured in this Animal Planet video (available at: http://www.animalplanet.com/tv-shows/jane-goodall/videos/almost-human-chimps-human-tools.htm); or to Fouts et al.'s (1982) report of active teaching by the captive chimpanzee, Washoe. Washoe had begun to appropriately use signs of American Sign Language as an infant of about 10 or 11 months (Gardner & Gardner 1969). When Washoe was approximately 14 years old, Roger Fouts introduced Washoe to a 10-month-old infant chimpanzee, Loulis. During the first few days after Loulis arrived, Washoe often turned toward him signing COME, approaching him, and finally grasping his arm and drawing him close. During the next five days she signed COME and only approached without touching him. After about a week, Washoe only signed COME as she turned towards Loulis, and faced him until he came to her. Washoe also molded Loulis' hands to form signs. In one observation, as a human friend was bringing candy, Washoe repeated the FOOD sign, jiggling about and grunting with excitement. Loulis was watching her. Abruptly, Washoe stopped signing, molded Loulis' hand into a FOOD sign, and moved his molded hand to his lips. Washoe formed the GUM sign with her hands, but placed it on Loulis' cheek. She also formed DRINK with her own hand and brought it to Loulis' lips, and formed HAT with her own hands and brought it to Loulis' head. In still another observation, Washoe placed a small chair in front of Loulis and repeated the CHAIR sign while watching him intently.

Other examples of direct active teaching among nonhuman animals may be relatively rare because, as Kline points out, "there are simply more studies of human teaching – and a lower bar for 'establishing' teaching in humans – than for any other species" (sect. 7, para. 2). The framework in the target article promises to set common standards across cultures and species, thereby permitting comparative studies that might establish functional relationships between learning problems and teaching types. We wholeheartedly agree with this approach. If teaching is a product of biology, then it is a function of variables – a highly complex function, yes; many variables, doubtless; but a function of variables, nevertheless. Logical divisions between human and nonhuman and between teaching and nonteaching seem plausible only because divisions of this kind agree with Aristotle's law of the excluded middle.

Historically, philosophers claimed that humans were unique because only humans used tools, or later, because only humans made tools (e.g., Edman 1920, p. 15; Grzimek 1977, p. 357). Each claim was eventually discredited by observations. Perhaps, Kline's framework will stimulate more reports of direct active teaching by other animals. In the meantime, we are cautious about accepting still another claim for discontinuity between humans and other animals.

The mutual relevance of teaching and cultural attraction

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Abstract: As Kline envisages, there is an important relationship between cultural attraction and teaching. The very function of teaching is to make the content taught an attractor. Teaching, moreover, typically fulfills its function by exploiting a variety of factors of cultural attraction that help make its content learnable and teachable.

In the Introduction to her excellent target article, Kline raises the question of what mechanisms and processes facilitate the faithful transmission of cultural knowledge. She considers the possibility that "cultural attractors" might play an important role. She suggests, however, that factors of attraction, in particular evolved psychological mechanisms, that make specific contents more attractive, do not change fast enough "to keep pace with culturally evolving mental representations" (sect. 1, para. 2), and, for this reason, she does not pursue the matter further. This, we fear, is an inaccurate interpretation of the theory and amounts to missing an opportunity of particular relevance to Kline's own agenda.

Actually, cultural attraction theory (henceforth CAT: Sperber 1996; cf. Claidière et al. 2014) considers not only psychological but also biological and environmental factors of attraction, and not only factors that act throughout the whole cultural evolution of a species, but also factors narrowly situated in time and space. To give but one example, Imo, the female macaque who, in 1953, had initiated the practice of cleaning sweet potatoes in water, started a second tradition among her conspecifics on the island of Koshima, that of making potatoes tastier by dipping them in sea water. Two factors of attraction help explain the cultural success of this second practice: the existence of the earlier tradition of cleaning potatoes in water, which limited the learning involved in acquiring the second practice – a local factor – and the macaques' biologically evolved taste for salt – a general factor.

In most current approaches to cultural evolution, it is assumed that cultural variants (mental representations, practices, and artefacts) propagate by being copied within and across generations. Cultural evolution, in such a perspective, is the effect of various forces, the interplay of which determine the differential success of cultural variants in eliciting copies of themselves.

From the viewpoint of such approaches, many culturally evolved active teaching practices present if not a paradox, at least a serious challenge. Active teaching involves a continuum of variants that go from performing the behavior to be transmitted in the usual way and instructing the learner to copy it, to merely giving verbal instructions describing the behavior without performing it at all. Most typical cases of actively teaching a skill fall somewhere in between these two extremes. A teacher teaching a learner how to, say, tie a knot, is likely to *demonstrate* the action, which involves slowing down the regular process of tying a knot, exaggerating some gestures, making pointing movements, and engaging in a verbal explanation of what she does. The learner isn't at all intended to copy this complex teaching behavior but to use the information provided in a mix of preservative and constructive ways to work out how to tie a knot. Needless to say, practices of active teaching themselves are generally transmitted not by the learner copying a teacher teaching, but, here too, by a complex mix of preservative and constructive processes.

The idea that cultural transmission is not – and not even principally – a matter of imitation or copying, but instead involves the systematic use of preservative and constructive processes is what lies at the center of the CAT approach. CAT thus proposes that propagation by copying should be treated as a special case of a more general phenomenon of causal impact and attraction: In general cultural items of any given type at time step t may have an impact on the frequency not only of items of the same type but also of items of any other type at time step $t + 1$. In particular, when items of type A asymmetrically have a positive impact on the frequency of items of type B, B is an attractor relative to A. Teaching is a case in point. Teaching any given cultural variant has a greater positive impact on the frequency of the variant taught than the variant has on the frequency of its teaching: Teaching, in other terms, not only contributes to making some variants cultural attractors, but also, it is its function to do so. In short, the abilities to teach, and to learn from teaching, are important factors of cultural attraction.

To be effective, most teaching practices – the rare exceptions being cases of teaching purely by rote – must take advantage of other factors of cultural attraction, only a few of which have been previously described in the literature (typically under the label "biased transmission" – Richerson & Boyd 2005, p. 69). Consider, for instance, ballroom dancing as a cultural skill. Much of what gets taught in dance classes are classic steps and rhythms that are highly characteristic of a given dance and that have contributed to its cultural success. As such, the form these steps take is in large part the consequence of a range of underlying factors of attraction, which are variously cognitive, biological, or environmental in nature, and which include, in particular, physical affordances of the human body that make certain steps easier to teach and learn, the (highly locally situated in time and space) repertoire of dance steps already known to the learners, pan-human or culture-specific aesthetic preferences, and of course the rhythms being danced to (rhythm and dance being a glaring example of the way in which one type of cultural item may have an impact on the frequency of another).

Cultural attraction theory is not meant as a radical alternative to evolutionary approaches to cultural evolution that have been developed in the past 40 years or so. It is, rather, a generalization of these approaches that provides novel tools to describe the causal impact of cultural items of a given type on not only the success of that same type, but also on the success of other types. Teaching as a cultural practice illustrates this essential dimension of cultural evolution in two ways. First, it is a practice that is aimed at increasing the frequency of practices other than itself. Second, to do so successfully, it relies on other factors of cultural attraction. This mutual relevance of the case of teaching and of CAT makes us particularly grateful to Kline for providing such a useful "evolutionary framework for the study of teaching behavior," and encourages us to encourage her and anybody interested in the evolution of teaching to take advantage of the tools and hypotheses that CAT provides.

Teacher and learner: Supervised and unsupervised learning in communities

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Abstract: How far can teaching methods go to enhance learning? Optimal methods of teaching have been considered in research on supervised and unsupervised learning. Locally optimal methods are usually hybrids of teaching and self-directed approaches. The costs and benefits of specific methods have been shown to depend on the structure of the learning task, the learners, the teachers, and the environment.

In a bilingual public school classroom near Silicon Valley, one can observe a variety of teaching and learning practices occurring simultaneously. The teacher has a queue of five students at her desk, and she helps them individually. Thirteen other students are working "quietly" at their desks, and two are being tutored by adult volunteers, focusing on reading in English and Spanish. Perhaps the most striking observation in this classroom is the

irrepressible tendency of the students to request and receive help from each other. Another is the participation of volunteers, many of whom work at Google, NASA, and Stanford. In addition, there is a broad range of unsupervised and tacit learning, including Spanish pronunciation and grammar, beliefs about the supernatural, entry-level soccer skills, gender roles, Minecraft, and so on. This suggests that teaching and learning are far richer phenomena than depicted in the target article. Who is a teacher and who is a learner, and does teaching require intention?

We suggest that useful contributions to Kline's framework may follow from examining the extensive work in the field of cognitive science, especially in the subfields of machine learning (ML) and intelligent tutoring systems (ITS). This research has addressed teaching in terms of four major types of variables: learner, environment, teacher, and content. The results demonstrate the limits of "what works" for effective human learning and teaching (though other work addresses artificial agents and nonhuman animals as well). By avoiding discussion of research on formal instruction, the Kline framework limits the landscape of what we know about teaching.

In the field of cognitive science – especially in the subfields of ML and ITS –theories and models of teaching have been characterized in terms of supervised and unsupervised learning. In the case of *unsupervised* learning, the learner has some means of encoding input from the environment. In the case of *supervised* learning, environmental input is selected, filtered, or otherwise enhanced by a teacher (Duda et al. 2000). The teacher may choose to apply a wide range of different strategies in order to increase the learner's rate of progress. Settles (2010) and Zhu (2008) review work on (hybrid) semi-supervised learning, which focuses on the effectiveness of specific combinations of methods.

These notions have been made precise in recent work on machine learning. They have been subjected to extensive empirical evaluations. In general, the effectiveness of various teaching strategies – mainly hybrids of supervised and unsupervised approaches – depends strongly on the structure of the environment and of the learning task (content). As a starting point for continuing interdisciplinary dialogue among cognitive science, anthropological, and evolutionary perspectives (cf. Atran & Medin 2008; Beller et al. 2012; Kline's target article), we present a few informative examples from the ML and ITS literature.

Kline discusses a child cooking alongside her parent, whereas research in cognitive science examines teaching in adult learning. Hutchins' (1995a; 1995b; 2005) research has emphasized the universal importance of teaching by apprenticeship. His work on navigation tasks has included Micronesian small boats, piloting of large naval vessels, and crew-automation interaction in advanced aircraft. Apprentice learning appears to work best in small teams where less experienced members learn by performing less demanding aspects of real tasks while supervised by expert members (Seifert & Hutchins 1992). For example, Hutchins (1995b) suggests the importance of the "horizon of observation," or access to visual information about other activities occurring around the learner. Participation through "overlooking" (as in "overhearing") may play an important role in preparing for future learning.

Cooperative learning is also raised by Kline, and recent work (Resendes et al. 2013) suggests that its benefits begin accruing early in life. Resendes et al.'s study of second-grade students claims that "the continual give and take of ideas to advance community knowledge is a foundational principle upon which knowledge building communities operate" (p. 396). In the study, they designed and evaluated tools to support behaviors like sharing information and word learning. In classrooms with team-based learning among 7-year-olds, they found that individual vocabulary and community (shared) knowledge both increased. Peers are important sources of knowledge for human learners in both informal and formal educational settings (Boud et al. 2014).

One-on-one tutoring is such an obviously optimal teaching strategy that a good teacher will implement it (even with a 20:1 student–teacher ratio, as seen in our opening example). Clearly, 1:1 tutoring out-performs regular classroom or textbook-based instruction. And ITS have been found to perform as well as human tutors (VanLehn 2011). But does it matter *which* strategies a teacher uses during tutoring? Studies show very little evidence that different tutoring approaches significantly affect learning outcomes (Chi et al. 2011). However, using an ITS for college-level physics (very advanced, abstract content), Chi et al. were able to demonstrate that theoretically superior tutoring strategies actually do out-perform others when analyzing at a micro-step level (2011). These results, along with some of the examples in the target article, suggest that humans have evolved to be good teachers, but not *optimal* ones. Optimization may require detailed monitoring, decision-making, and control that lies beyond the cognitive capacities of the unaided tutor.

In closing, we raise an issue that may not surface in cognitive science without the benefit of an anthropological or evolutionary perspective. Much of the discussion of teaching and learning in humans focuses on providing basic skills, broadening horizons, or talent-scouting. But much actual teaching, in both Western and non-Western cultures, aims at instilling *conformity* by building resistance to change and maintaining conventional customs. Teaching can be aimed not at "utility by truth" (technology, nature, geography, etc.), but rather, at "utility for solidarity," as in folklore, kinship, history, and mythology (cf. Roberts [2013], for a contemporary Western example). Content may be quite tenuously linked to reality, yet it is often taboo to question this. From a cognitive perspective, this type of teaching seems anomalous; however, from an anthropological perspective, it may seem routine, and scarcely merit comment. It is clearly a key element in considering the (culturally) adaptive value of teaching.

Robot teachers: The very idea!

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Abstract: Insufficient attention has been paid to the use of robots in classrooms. Robot "teachers" are being developed, but because Kline ignores such technological developments, it is not clear how they would fit within her framework. It is argued here that robots are not capable of teaching in any meaningful sense, and should be deployed only as educational tools.

According to Kline, teaching behaviour is found in Western and non-Western human societies and in some nonhuman animals. Could robots also be said to teach?

Recent technological developments mean that robots are being used in classrooms as intermediary tools to explain concepts in mathematics and science, and as a means of involving students in technology by building and programming robots (Mubin et al. 2013). There is also interest in the idea of robots actually doing the teaching. Kanda et al. (2004) report a field trial in a Japanese elementary school in which two "Robovie" robots spoke English to children who approached them. A test showed improvements in the English skills of children who frequently interacted with the robots. Movellan et al. (2009) report a study in which a robot operated in an early education centre for 2 weeks was found to have improved toddlers' knowledge of targeted words. Other robot "teachers" have been remote-controlled by humans, sometimes under Wizard of Oz conditions, in order to explore robot capabilities that are not yet available. The Saya robot has a female appearance and an emotionally expressive

face, and can be operated remotely. Hashimoto et al. (2011) describe how it was used to deliver material about the principles of leverage to elementary school pupils. EngKey robots are deployed in South Korean classrooms to teach students English, delivering automated scripts for practicing pronunciation and conversation, and enabling telepresence communication between students and remote instructors in the Philippines. Yun et al. (2011) report that they improved student performance.

Robots may be able to help second language learners, but should their behaviour be described as "teaching"? Could a robot ever be said to offer *good* teaching? Also, should such developments be seen as progress, or as something that we would do better to avoid?

Kline's article sheds some light on these questions, although she does not consider robot teachers, nor discuss the use of indirect forms of teaching and teaching tools such as books, or computer-aided instruction. In her framework, robot teaching seems to fall within the category of "direct active teaching," and clearly it would be possible for a robot to convey new information to a pupil. However, Kline also claims that direct active teaching requires the teacher to have the ability to "identify and communicate the relevant information to the pupil" (sect. 3.5.1, para. 1). Could a robot have such an ability?

Presumably a robot that delivered the same material regardless of the presence or composition of its audience could not be said to be actively teaching. For nonhuman animal behaviour to be counted as teaching, Caro and Hauser (1992) required that it should occur only in the presence of a naïve observer, and at some cost, or at least no immediate benefit, to the teacher.

There are measures that can enable a robot to detect the level of interest or engagement shown by a pupil. For instance, Mutlu and Szafir (2012) programmed a humanoid robot to tell a story to individual students, and used an electroencephalographic (EEG) signal to monitor the student's attention. When brain signals indicated that the student's attention had dropped, the robot would raise its voice or use arm gestures to regain the student's attention.

A robot that could adapt its instructional behaviour depending upon the response of its pupils might be said to be exhibiting a form of teaching, as is the case for some examples of nonhuman animal behaviour. The idea that a robot could identify what a pupil needs to know seems more challenging. As nonhumans, how could they determine what human children need to know, or have the intention to pass on the information that is needed to accomplish the tasks required in human culture? Similarly, because robots are not subject to evolution in the way that living entities are, they cannot evolve the knowledge of the material that needs to be taught to solve an adaptive problem.

Kline's framework moves away from the requirement for teachers to have a theory of mind and particular mental capacities. She is more concerned to encompass teaching behaviours found in both nonhuman animals and in humans, and to unify different approaches to the study of teaching. A consequent problem is that her framework loses sight of the specialised human requirements for *good* teaching, and might even be seen as opening the door to an acceptance of the idea of robot teachers. However, there are many requirements for being a good teacher that a robot is unlikely to be able to fulfil. As acknowledged by educational theorists with a mentalistic perspective, a good teacher will identify the zone of proximal development for a child based on a detailed understanding of that child's capabilities, and will be able to teach them just what they need to know, just when they need to know it (Pelissier 1991). Good teachers also help to socialise their pupils, acting as attachment figures and as role models, and inspiring an empathetic view of fellow humans (Verschueren & Koomen 2012). A robot teacher is not going to have the social understanding to be able to perform such functions, and even if it did, it surely would not be a good idea for children to model themselves on robots, however lifelike they were.

Robots in the classroom may be able to function as educational tools: for instance, offering the opportunity for the individualised practice of skills such as speaking a foreign language. At the same time, we need to guard against using them too much or imagining that they could replace skilled human teachers.

The very idea of developing and using robots for teaching could be viewed as positive evidence of the crucial role that teaching plays in the development and maintenance of human culture. It could also be seen as an unhappy development that moves us further away from the evolutionary roots of teaching behaviour in humans towards a scenario in which teaching is automated and outsourced to machines.

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Teaching as an exaptation

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Abstract: We appreciate and endorse Kline's ethological taxonomy and its application. However, the definition of teaching she presents is problematic, as it replaces mentalistic intent with intention on the part of natural selection. We discuss problems with the strict adaptationist view and suggest instead that the five forms of teaching presented in the taxonomy may constitute exaptations rather than adaptations.

> *Natural selection built the brain; yet, by virtue of structural complexities so engendered, the same brain can perform a plethora of tasks that may later become central to culture, but that are spandrels rather than targets of the original natural selection.… Surely, for something so complex and so replete with latent capacity as the human brain, spandrels must vastly outnumber original reasons, and exaptations of the brain must greatly exceed adaptations by orders of magnitude.*
>
> — Stephen Jay Gould (1991, p. 57)

The target article is an important contribution toward an integrative understanding of teaching and its place in the broader field of social learning. The consilient integration of the human social sciences with the biological study of behavior is a desirable result, and we commend Kline for making headway regarding the study and classification of teaching. That said, we also believe that the adaptationist definition of teaching presented in the target article is problematic. Kline suggests that what separates teaching from other types of social learning is dependent upon the evolution of the behavior *for teaching*, defining teaching as "behavior that evolved to facilitate learning in others" (sect. 3, para. 1). This definition was designed to avoid one of the limiting characteristics of mentalistic approaches, that of intent on the part of the teacher. However, the definition eschews mentalistic intent only to replace it with intention on the part of natural selection.

It is important to exercise caution in proposing adaptationist explanations of behavior (Gould & Lewontin 1979). We are concerned that viewing teaching as an adaptation – that is, a trait that was explicitly selected for – obscures deeper truths about the social and psychological nature of our species and others. Many of the traits that enable social species to successfully cooperate and interact might give rise to the behaviors described as teaching in Kline's taxonomy *without being directly selected for*. Indeed, the emergence of social behaviors that involve coordinated differentiation of roles is not easy to explain, particularly when those roles involve responsive learning and may result via other adaptive mechanisms (Smaldino 2014). We propose that at least

some of the teaching behaviors falling under each taxonomic category described by Kline may be better explained as *exaptations*, defined as "features that now enhance fitness, but were not built by natural selection for their current role" (Gould & Vrba 1982, p. 4). Specifically, many of the adaptations that facilitate sociality across species – for example, attraction, tolerance, and so on – combined with adaptations for parental and alloparental care may produce teaching without being explicitly selected for. Here we consider each type of teaching in Kline's taxonomy and discuss problems for the adaptationist argument.

Teaching by social tolerance. While tolerating observation or intrusion by a youngster may allow him or her to learn, it also allows the adult or teacher to supervise offspring or other wards while simultaneously completing a necessary task. Moreover, high levels of social tolerance often occur when no direct lesson is being taught. For example, parents often allow toddlers to climb on them, and this may increase the mother–child bond or facilitate exploration of bodies and reactions. In these ways, learning may be a byproduct of social tolerance, but social tolerance is unlikely to have evolved specifically for the facilitation of learning.

Teaching by opportunity provisioning. Even very young children will work to provide opportunities for others, such as when a toddler opens a cabinet when she sees an adult with his arms full trying to put things inside (Newton et al. 2014; Warneken & Tomasello 2006). Although opportunity provisioning may be co-opted as a teaching mechanism, we suggest that it emerges from more general prosocial tendencies.

Teaching by stimulus or local enhancement. The behaviors involved in stimulating another's interest in something, be it through pointing at a target, physically moving a pupil, or using verbal communication, could have evolved for many reasons, including the immediate identification and communication of danger (Skyrms 2010). This applies to Kline's example of human mothers using pointing or "motherese" to manipulate a child's attention. For example, Falk (2004) has proposed that motherese emerged in order to encourage juveniles to behave and follow their mother, which suggests that it likely became exapted only later as a teaching tool.

Teaching by evaluative feedback. Reinforcement learning is evolutionarily ancient, providing a ready-made structure that can be co-opted for social influence. Any sort of manipulation can therefore tap into that rudimentary structure for general learning, including incidental behaviors that benefit the teacher. Consider Kline's example of primate mothers encouraging their offspring to walk by setting them down and then looking/calling for them to join. This could functionally free the mother's hands for other work, while incidentally facilitating and rewarding self-locomotion in the child. In general, behaviors incorporating evaluative feedback can benefit both teachers and learners in multiple ways, making it unlikely that these behaviors evolved specifically to facilitate learning. Instead, these behaviors likely evolved for other purposes, and capitalize on a general sensitivity to reinforcement and punishment.

Direct active teaching. Direct teaching in humans requires joint attention and theory of mind, corresponding to complex adaptations related to communication and coordination. While one of the purposes of communication is the transmission of new knowledge or skills (i.e., teaching), there are others. For example, Tomasello and colleagues have proposed that communication, both verbal and nonverbal, evolved largely to solve cooperation and coordination problems, and not initially for teaching (Tomasello et al. 2012).

It is our supposition that many of the behavioral and cognitive aspects of teaching, in both humans and other animals, are best characterized as exaptations, calling into question a strictly adaptationist definition of teaching. Although understanding the evolution of teaching behaviors is an important research topic, incorporating a reliance on those behaviors' evolutionary histories into the definition of teaching is counterproductive.

We agree with Kline in rejecting constrained definitions of teaching, such as those that rely exclusively on mentalizing. It may not be possible, in the end, to produce a single all-encompassing definition of teaching. Indeed, Kline's taxonomic categories may constitute a piecemeal but exhaustive definition, with each instantiation having qualitatively different evolutionary and emergent origins.

Cognitive universals and cultural variation in teaching

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Abstract: We address three issues: (1) There is a need for a comprehensive multidisciplinary understanding of teaching; (2) teaching is a natural cognitive ability for humans; and (3) there is a need to incorporate the mentalistic and cultural approaches to teaching. We suggest certain research studies that can help deepen our understanding of the cognition of teaching.

Teaching involves bidirectional communication (Strauss et al. 2014), which is inherently social. Learning, the complement of teaching, has been studied extensively in the cognitive sciences. As important as teaching is for humans, it has been largely neglected in the cognitive sciences. Kline's target article is a beginning attempt to redress this problem.

To explain and describe teaching, Kline casts her net wide to include phylogeny, cultural anthropology, and nonhuman animal teaching. But as important as it is to include these domains, there is a need to have an even broader study of teaching. Other cognitive areas could include the brain sciences (Hasson et al. 2012; Holper et al. 2013), artificial intelligence (Dessus et al. 2008), psycholinguistics (Bartsch et al. 2010), philosophy (Scheffler 1965), intelligent tutoring systems (Kopp et al. 2012), cognitive archeology (Morgan et al. 2015) and computer–human interface systems in robotics (Vollmer et al. 2014) among others. (See Strauss [2013] for a call for such a comprehensive, multidisciplinary view.) Part of this enlarged view of teaching includes cognitive development. In that domain, Strauss et al. (2002) were the first to suggest that teaching may be a natural cognitive ability for humans. Of the support that can be harnessed to bolster this claim, here we slightly elaborate only one: teaching is developmentally reliable among humans. The nub of the argument is that teaching is complex and opaque, and that, although toddlers are exposed to teaching, they are not taught to teach. Nonetheless, teaching appears early (Strauss 2005).

Developmental research conducted in different industrialized countries with different tasks indicates convergent paths of teaching strategies (Strauss & Ziv 2012). Strategies proceed from teaching precursors in infancy, to teaching via demonstration among 3-year-olds, to explanation and contingent teaching among 5-year-olds. Strauss and Ziv (2012) constructed a taxonomy of teaching strategies culled from research with children from industrialized societies.

In contrast, there is a dearth of developmental research on teaching in non-industrialized societies. We propose that there is room for such studies. The result will likely be an extension of Strauss and Ziv's (2012) taxonomy, which will help us better understand the scope of human teaching.

In the target article, Kline proposes a framework based on a functional approach for integrating three research traditions regarding teaching: mentalistic, culture-bound, and functional. However, it may be that by contrasting these traditions and determining the different kinds of teaching they identify, they could yield a more fine-grained taxonomy. For example, Frye and Ziv (2005) argued that functional definitions cannot identify failed teaching as teaching because they incorporate changes in the recipient's (learner's) behavior as a part of the definition.

In the mentalistic approach, teaching is identified by its goal, so failed teaching is still teaching even if the goal is not fulfilled. This example illustrates that mental states are not just epiphenomena in teaching but make possible different actions. It also shows that if mental states are not considered, then entire categories of teaching will be absent from our taxonomies and not studied.

We suggest that incorporating mentalistic and culture-bound definitions of teaching could be beneficial for understanding human teaching. What is at stake here is the nature of the relations between the cultural view and the mentalistic, cognitive substrate. This question is akin to issues in the debate between adherents of cultural niches (Boyd et al. 2011) and cognitive niches (Pinker 2010).

As Kline notes, modern industrialized-type teaching has been found to be rare in non-Western small-scale societies. Some ethnographers (Lancy 2010; Paradise & Rogoff 2009) have noted little vertical teaching (parent to offspring); however, the application of evolutionary theory to cultural transmission in non-industrialized cultures predicts vertical and oblique (non-family adult to child) teaching. Both were found when adults reported who gets taught by whom, for what tasks and at what age (Kline et al. 2013; see also Hewlett et al. 2011).

It is possible that children come into the world with similar cognitive abilities that allow them to teach in culturally relevant ways. This claim is neutral to the ways in which children learn teaching behaviors, such as Bayesian learning or Chomskian-type universals and acquisition devices. If, as we claim, there are universal human teaching abilities, an explanation is needed for how they get expressed differently in various societies. There are two main kinds of explanations.

First, we might expect similar cognitive origins and developmental trajectories of teaching among children from different societies. Regarding origins, research on Western preverbal infants indicates that they correct others' mistakes and even anticipate errors and act to ward them off (Knudsen & Liszkowski 2012a; 2012b). These are at the foundation of teaching. It would be of interest to see if infants from, say, small-scale subsistence and hunting and gathering societies show the same abilities. If so, we could argue that at their inception, cognitive prerequisites for teaching are not cultural. Nevertheless, teaching is not uniform across cultures. A developmental route from common infant precursors of teaching to diverging teaching in adults in various cultures could be that teaching develops along a similar pathway until it parts ways at a certain juncture, in directions that are culturally based. This would suggest that cultural variations of teaching may need a certain developmental level of cognitive substrates before these variations appear.

Second, infants from modern industrialized and small-scale societies may be cognitively different from the earliest points when cognitive prerequisites for teaching can be detected. This possibility suggests that teaching's cognitive precursors may be cultural in nature even before actual teaching appears.

Choosing between these two alternative explanations is an empirical question. Neither of these alternatives has been studied experimentally, and we believe they should be.

In summary: We propose that a more comprehensive multidisciplinary approach to teaching is in order. It could include cognitive development. We argue that teaching may be a natural cognitive ability among humans. If so, we would need to explain relations between a possibly common cognitive beginning point in infancy and cultural variations of teaching.

Learning in and about opaque worlds

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Abstract: We argue that direct active teaching in humans exhibits at least two properties (open-endedness and content opacity) that make the recognition of teaching episodes without ostension untenable. Thus, while we welcome Kline's functional approach to the analysis of teaching, we think that she ignores important features of the socio-environmental niche in which human teaching likely evolved.

We applaud Kline's explicitly functionalist approach to the topic of teaching. Somewhat reminiscent of the model proposed by Hoppitt et al. (2008), the classification of the types of teaching that Kline charts out in the present article is primarily dependent on the range of adaptive problems that social learners may face. This allows the author to discuss the design features that each teaching type exhibits in terms of the adaptive problem that it purportedly evolved to solve (e.g., limited motivation to attend to relevant information). A rigorous application of this genuinely Darwinian approach could indeed bridge the study of the taxonomical distribution of teaching behaviors and that of the socio-environmental niches where particular types of teaching are observed and likely evolved.

We think, however, that Kline's characterization of "direct active teaching" (DAT) in humans may fall short of adequately describing the mutual evolutionary dependency between species-typical psychology and adaptive niche that her framework rightly champions. As Kline notes, DAT "does not require ostensive cues (at least by definition)" (sect. 3.1.5, para. 1) – in other words, it does not require the teacher to explicitly mark her demonstration as a teaching attempt, addressed to a specific pupil. This could indeed be the case when there is some "shared background knowledge" that the pupil could rely on to interpret the teacher's demonstration as communicating to-be-learned information. Articulating Kline's intuition, one could imagine such background knowledge as consisting of species-typical sensitivity to fitness-relevant action outcomes, whose causal relations the pupil is unable to entertain and appropriately reconstruct via asocial learning mechanisms. Alternatively, this background knowledge could also be established by explicit linguistic communication, for example, by informing the putative pupil that a subsequent demonstration would constitute a teaching episode. In either case, the function of DAT could be potentially realized without the need of ostensive communication. Tellingly, however, these hypothetical scenarios could dispense with ostension only by assuming (in the first case) that the set of fitness-relevant information that a given species needs to acquire is narrow in scope and fixed in content; or, alternatively, (in the second case) that the pupil's expectations could complement the pedagogical stance of the teacher only if both parties are capable of linguistic communication. Neither of these trade-offs seems to constrain DAT in humans: The domain of teaching is clearly open-ended, and its receptivity, as a large volume of developmental evidence shows, well predates the understanding of language. How could this be?

Klein is keenly aware of the learnability challenge that this open-endedness poses: "the pupil … has no way to solve the 'frame problem' by observing others' behavior" (sect. 3.1.5) and "the pupil's only indication that information is relevant comes from the teacher" (sect. 5.1, para. 3). Therefore, given that DAT is fundamentally characterized by "(a) manifestation of relevant information by the teacher to the pupil, and (b) interpretation of this manifestation in terms of knowledge content by the pupil," and that – at least in humans – the second condition could not be satisfied by simply recovering pedagogical intentions from the

(perceived) fitness relevance of the demonstrator's behavior, something else is required.

As argued elsewhere (Csibra & Gergely 2009; 2011), a candidate solution to this problem is ostensive communication. The design features that ostension exhibits in terms of the cognitive effects it produces in the pupil are tailored to solve the problem of communicating about the occurrence of relevant, to-be-learned knowledge content. Rather than merely attracting the attention of the pupil towards certain objects, actions, or locations, together with making manifest to the pupil that she is the intended addressee of the demonstration, ostension restructures the relevance assumptions governing the pupil's learning in more fundamental ways. It allows the pupil to acquire the content of a culturally transmitted behavior that may to a large extent remain cognitively opaque in terms of its underlying causal and teleological structure. Similarly to epistemic deference (Gergely & Jacob 2012; Sperber 1997), ostension allows for the acquisition of (generic) knowledge contents that are not only functionally non-transparent, but also do not seem to have any perceivable fitness value. This prima facie puzzling susceptibility, which clashes against a cognitive economy rarely prioritizing the encoding of opaque information in non-communicative contexts, is revelatory of the type of evolutionary challenge that favored the selection of this mechanism.

As Kline writes, "our species depends to a great degree on cumulative cultural adaptations too complex for any one individual to create on his or her own" (sect. 7, para. 6). Our fundamental reliance on opaque (material and social) kinds cries out for an explanation of how human cognition succeeded in stabilizing the transmission of cultural items such as artifacts and conventions, which are opaque through and through. This unprecedented evolutionary challenge was partly overcome, we believe, by evolving cognitive adaptations that would allow for the interpretation of communicated information as being applicable beyond its local and episodic use. This is precisely the type of inference that ostensive signals license about demonstrated content. Therefore, if human teaching is to be portrayed as a glaring exception in the animal kingdom, this is not, or not solely, because of its frequency and breadth of use, but rather because of its capacity to perpetuate cultural kinds that are causally and teleologically opaque. To emphasize this aspect is to highlight the irreplaceable role that ostension plays in DAT for humans.

Thus, while endorsing and strongly encouraging the application of the framework that Kline laid out, we also think that more weight should be assigned to ostensively grounded teaching. This, if anything, could only enrich Kline's functionalist agenda by adding a further adaptive problem – learning in and about, and in spite of, a culturally opaque environment – to her articulated classification, while doing proper justice to the idea of "cultural niche" (Boyd et al. 2011).

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The proximate-ultimate confusion in teaching and cooperation

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Abstract: Kline does an admirable job of extending the functionalist framework developed by comparative researchers to help understand the function and form of human teaching. Functionalist approaches consider the adaptive value and underlying mechanisms of behaviour as separate but complementary questions, avoiding the conflation of ultimate and proximate explanations that has long hindered research on teaching and other forms of cooperation.

Teaching is fundamentally cooperative: teachers, be they ants or psychology professors, invest time and energy in helping others to learn. The proximate mechanisms by which they do so may be many and varied, but ultimately all are likely to result in fitness benefits for both pupils and teachers (Thornton & Raihani 2008). Here we argue that the debates that have stifled our understanding of the evolution and diversity of teaching mirror those in the broader literature on cooperation and stem largely from confusion between proximate and ultimate explanations.

Historically, most approaches to the study of teaching have conflated proximate mechanisms and ultimate function by specifying a priori psychological mechanisms without which behaviour cannot be classified as teaching, even if it demonstrably helps others to learn. Thus, what Kline terms "culture-based definitions" stipulate a need for formal, Western classroom techniques, mentalistic definitions insist on the use of theory of mind, and the natural pedagogy approach (which Kline places within the functionalist school) specifies that teaching must involve ostensive cueing and metacognition. By imposing restrictive mechanistic pre-requisites, these approaches automatically exclude the possibility of teaching not only among most animals but also among many in human groups including non-Western societies or people with socio-cognitive impairments such as autism. Consequently, they are of limited value for understanding how teaching evolves and is implemented across human and nonhuman societies.

The comparative functionalist framework (Caro & Hauser 1992; Hoppitt et al. 2008; Thornton & Raihani 2008), which Kline builds on in her article, provides a solution to this problem by following in Tinbergen's footsteps to consider adaptive value and proximate causation as separate but intertwined questions (see Tinbergen 1963). Here, teaching is treated as a functional category of behaviour that serves to promote learning in others and can be underpinned by a variety of different mechanisms (Thornton & Raihani 2008). Comparative research has not only demonstrated that taxonomically diverse animals, including invertebrates, birds, and mammals, perform behaviour that functions to help others learn but has also revealed the psychological mechanisms by which this is achieved. Thus, we now know that diverse mechanisms, including reflexive responses to observable cues of pupils' competence (as in meerkats; Thornton & McAuliffe 2006) and active Pavlovian conditioning (as in pied babblers; Raihani & Ridley 2008), may underpin teaching in different species. As Kline highlights, a similar functionalist framework to study human teaching is now essential to uncover the variety of psychological mechanisms employed across cultures and to understand how these evolved.

Like the teaching literature, the study of cooperation has suffered from confusion over proximate and ultimate levels of explanation. For instance, some researchers have treated seemingly cooperative behaviour in nonhuman animals as diagnostic of psychological mechanisms known to be prevalent in humans. In one highly publicised example, laboratory rats learned to open a door to release a trapped conspecific and were duly credited by the authors with empathetic concern (Ben-Ami Bartal et al. 2011). Although the trapped animal clearly benefitted from being liberated, the study provided little direct evidence that its rescuers were motivated by psychological representations of the unfortunate captive's distressed emotional state (Vasconcelos et al. 2012). Indeed, the assumption that rescue behaviour necessarily involves empathy is akin to assuming that teaching behaviour requires theory of mind. Proximate mechanisms cannot be assumed but rather must be identified through experimentation. For example, a recent follow-up to the rat empathy study found that rescue behaviour could be explained by a motivation for

social contact on behalf of the rescuers (Silberberg et al. 2014). In work on teaching, playback experiments show that adult meerkats deliver age-appropriate hunting lessons to their pups not by reasoning about pups' knowledge states, but by responding reflexively to age-related changes in their begging calls (Thornton & McAuliffe 2006). Similar experimental scrutiny of human psychological mechanisms is critical if we are to understand not only the role of seemingly computationally complex processes such as theory of mind, but also lower-level cognitive responses and hence the minimal cognitive constraints on the evolution of human cooperation and teaching (Thornton & McAuliffe 2012).

Just as we cannot infer psychological mechanisms from the existence of seemingly helpful behaviour, we must also be cautious in extrapolating adaptive functions from proximate mechanisms. This issue is particularly prevalent in literature on strong reciprocity, which is often presented as both a proximate and an ultimate explanation for human cooperation (see Scott-Phillips et al. 2011). Strong reciprocity is defined as a psychological predisposition to reward cooperators and punish cheats (Fehr & Fischbacher 2003). People often exhibit such tendencies in anonymous, one-shot laboratory games in which there is no obvious scope for direct reciprocity or reputation-based benefits. Consequently, some theorists argue that this psychological altruism implies evolutionary altruism – that is, that actors derive no fitness benefits from their helpful actions – and that therefore these predispositions must evolve as a result of group-level rather than individual-level benefits (e.g., Bowles & Gintis 2004). However, like mentalistic views of teaching, this argument conflates psychological and evolutionary goals. The comparative functionalist framework illustrates the need to analyse these goals separately: ants, meerkats, and babblers may not be driven by the psychological goal of helping others to learn, but their behaviour is nevertheless favoured by selection because it achieves this goal and consequently benefits both teachers and pupils (Thornton & Raihani 2008). Conversely, humans' psychologically altruistic preferences may be selected because they ultimately benefit the actor, for instance through increasing perceived attractiveness or prestige (Hardy & Van Vugt 2006; Sylwester & Roberts 2013; Van Vugt & Iredale 2012). Thus, just as neural and hormonal mechanisms mediating parents' love for their offspring are ultimately self-serving, psychological altruism may also yield self-serving benefits, even if we are not consciously motivated by them.

Kline neatly illustrates the need for functionalist frameworks that consider the adaptive function and proximate mechanisms of teaching as distinct but complementary questions. If other researchers follow her lead, we will be well on our way to a truly integrative understanding of the proximate and ultimate drivers of teaching and cooperation across species and cultures.

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Author's Response

Much to learn about teaching: Reconciling form, function, phylogeny, and development

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Abstract: The collection of commentaries expands an already extensive field of research on teaching, and contributes new questions, techniques, and strengths to the evolutionary approach proposed in the target article. In my response, I show how reconciling multiple levels of explanation – mechanistic, ontogenetic, phylogenetic, and functional – enables researchers to build a more integrated, interdisciplinary approach to the study of teaching in humans and other animals.

R1. Introduction

I thank the authors of all 38 commentaries for their thoughtful extensions and critiques of the target article on the study of the evolution of teaching, in humans and other animals. The breadth of responses from anthropology, biology, psychology, and beyond attests to the wide-ranging relevance of research on teaching. Due to the large number of commentaries, I am unfortunately not able to address the entirety of points made in each commentary. Instead, I address the major concerns of each, and structure my response according to levels of explanation, in order to further an integrated, interdisciplinary approach to the study of teaching in humans and other animals.

The range of commentaries highlights ontogenetic, phylogenetic, or proximate psychological explanations of teaching behavior as important research areas not covered in the target article. In some cases, the commentators suggest that the lack of such explanations in the target article renders the proposed framework insufficiently broad to motivate comparative work in disparate disciplines. However, the commentary by **Thornton & Raihani** anticipates how these foci fit with the proposed framework. They argue that working from a functionalist framework allows for the much-needed distinction between ultimate explanations of teaching behavior and proximate ones – and indeed that the study of cooperation more broadly could be improved by a similar frame of analysis.

The collection of commentaries would benefit from taking this one step further: The ultimate/proximate levels of analysis can be split into dynamic (explaining processes of change) and static (explaining present form), such that there are four categories of explanations available to us – mechanistic, functional, ontogenetic, and phylogenetic (see Table R1; derived from Tinbergen 1963). Whereas the target article discusses existing definitions of teaching based on disciplinary convention, in this response research problems are addressed according to the type of explanation they offer. Note that a key to the enduring usefulness of Tinbergen's levels of analysis is that these levels are consilient: each explanation must be reconcilable with explanations at other levels of analysis. It therefore does not make theoretical or practical sense to argue that one kind of explanation is better or more correct than another – their validity is mutually dependent.

R2. Mechanistic explanations

R2.1. Psychological and neural mechanistic explanations

I first address the commentaries that propose extensions to the target article's framework in ways that would explain how teaching works in terms of proximate, causal

Table 1. *A grid showing Tinbergen's levels of analysis applied to static and dynamic explanations of traits.*

	Static	Dynamic
Proximate	*Mechanistic*: explains how a trait works, in causal terms	*Ontogenetic*: explains how a trait comes to function, over developmental time
Ultimate	*Functional*: explains the function or adaptive value for which a trait was selected	*Phylogenetic*: explains the evolutionary history or descent of a trait, often through comparative reasoning

Table Note: Most non-evolutionary disciplines focus mainly within one of these categories. One advantage of an integrative evolutionary framework is that it relates proximate/ultimate and static/dynamic explanations to one another in a theoretically meaningful way.

mechanisms. These include mental, cognitive, neural, hormonal, and behavioral mechanisms.

Commentaries by **Ronfard & Harris**, **Koenig**, **Kruger**, and **Corriveau**, each, respectively, argue for greater coverage of a topic not covered in detail in the target article: the behavior of pupils as learners. I agree that this is an important topic underserved in the target article, and I thank these commentators for highlighting it. Ronfard & Harris as well as Corriveau emphasize that among humans, pupils may solicit teaching, may monitor or direct ongoing instruction, and may seek out reliable informants (see sect. 6.2 in the target article for brief coverage of these ideas). Ronfard & Harris even nominate pupil's behavior as another important piece of the puzzle in understanding human cultural capacities, and cite a broad body of work showing that children seek out adult attention. This raises the question of whether such a practice occurs in nonhuman pupils, as well. In some cases, I argue that we know it does: *teaching via social tolerance* depends by definition upon pupil initiation, and seems to be relatively common among nonhuman animals. The question of pupil behavior extends even beyond the suggestions made by Ronfard & Harris, and could inspire comparative work in the future.

In addition, **Corriveau** and **Kruger** argue that teacher and pupil should not be envisioned as independent actors. Both these commentators take issue with the target article's asymmetrical treatment of teacher and pupil behavior. They make an important point in recognizing how humans (and other animals) coordinate, and that this may be observable in teacher–pupil interactions. It may be especially interesting to describe how the behavioral and psychological mechanisms for coordination do or do not differ across human populations, where social hierarchies may restrict the entreaties of young learners (see, e.g., Lancy 2008), or where norms about verbal communication and eye contact mean coordination is more subtly communicated, as is common in Pacific societies (Watson-Gegeo & White 1990). Explaining the communicative mechanisms by which teachers and pupils jointly interact is not mutually exclusive with tracking the fitness costs and benefits separately. Even for a public good created through cooperation, and even if all parties benefit equally, the reproductive or fitness consequences of behavior must be tallied individually, since it is their fitness relative to each other, rather than absolute reproductive fitness, that predicts the outcomes of natural selection. It is this practical concern that drives the target article's focus on the evolution of *teacher* behavior over questions regarding pupil behavior. In the context of the target article, this is as a parallel line of inquiry into a mechanistic explanation of teacher and pupil behavior that benefits from the proposed functional framework, even as it requires shifting focus toward pupil behavior.

Pasquinelli, Zalla, Gvodzic, Potier-Watkins, & Piazza (**Pasquinelli et al.**) discuss how little is known about the neurocognitive mechanisms of teaching, and make a worthwhile appeal for translational, applied research using established methods in cognitive psychology and neuroscience. Similarly, **Kim, Torres-Garcia, & Swain** (**Kim et al.**) focus on the neurocognitive and hormonal bases of teaching. These are growing fields, and better integration of their techniques may advance the study of teaching. Both commentaries, however, treat teaching behavior as a unitary phenomenon rather than a set of behaviors. Kim et al. even subsume "parenting" under teaching, which is either a narrow definition of parenting, or a loose definition of teaching that does not coincide with the one proposed in the target article. While Pasquinelli et al.'s focus is a valuable and promising research direction, I urge researchers to step away from the entrenched questions their commentary highlights: whether humans have a "teaching instinct," and its dependence on theory of mind. A central tenet of the target article is that teaching *behaviors* are not monolithic in their form and mechanism – and as a result we should not assume that proximate teaching *psychologies* are uniform, either. This demands that we take a more textured look at the variety of teaching behaviors used by a given study species, by linking the proximate psychological mechanisms to their ultimate functional explanations.

Pasquinelli et al. also suggest that teaching behavior might directly benefit teachers in two ways. First, that "learning in order to teach" creates direct benefits to the teacher, through enhancing the teacher's own learning. The evidence cited in favor of this idea is based on grade-school children and on undergraduates asked to learn in order to teach in a classroom context. This cannot distinguish between the impact of teaching versus the impact of preparing-to-teach, on the teacher's comprehension. Thus, while this research may impact in-classroom teaching techniques, it seems unlikely to affect functional explanations of the cost/benefit structure of teaching behavior. After all, learning for the anticipated purpose of teaching is a special case in human teaching, and almost certainly non-existent other animals. Second, Pasquinelli et al. suggest that teachers might manipulate others for their own direct gain, and that manipulation in a broad sense may be considered teaching. Communicative behaviors used in persuasion and manipulation are superficially similar to those displayed in teaching. Further, it may be that the two share a proximate psychology: The same

psychological features that make learners receptive to teaching also make them vulnerable to manipulation, and manipulators may use the same communication techniques that can be useful for teaching. This is a broader problem in human communication, and demands epistemic vigilance among communicators (for deeper discussion, see Sperber et al. 2010). However, integrating mechanistic psychological descriptions with functional explanations makes it clear that manipulative influence should not be categorized as teaching. Teaching, as functionally defined, is a cooperative behavior in which the teacher benefits only indirectly, through the learning benefits the pupil derives. This illustrates why a multi-level approach to the study of teaching is important. For further discussion, see deceptive teachers and skeptical pupils (sect. 6.2) in the target article.

Ravignani & Sonnweber make an ambitious proposal to dissect the proximate mechanisms of the full range of teaching behaviors through hormonal and neuromodulator evidence, as well as time-series analyses. They argue that studying the physiological mechanisms will help scientists to identify the motivations and emotions involved in teaching behavior. While this is one promising tool scientists may use to study teaching, I caution against relying too heavily on proximate mechanisms to diagnose teaching. It poses the same sort of problem discussed above – and repeats the same stumbling blocks for using theory of mind capacities as a measuring stick. In the target article (sect. 5), I argue that there is more than one possible psychological mechanism that could reliably produce a given type of teaching behavior. This suggests that using a single proximate mechanism as a heuristic for identifying teaching runs the risk of excluding behavior that fits the functional definition of teaching.

This same critique applies to the use of teacher–pupil synchrony to diagnose teaching behavior. **Marin** states that motor movement synchrony (and indeed a wide range of mutual influence between pupil and teacher) can happen during teaching. However, this does not mean it is particularly diagnostic of all types of teaching behavior in all species. For example, for teaching types that promote pupils' independent exploration of novel stimuli (teaching via *stimulus enhancement* and via *opportunity provisioning*), behavioral synchrony would not be expected. It also does not establish that synchrony is unique to teaching, as opposed to being common in communication more generally. Similarly, **Badets & Osiurak** state that perceptual resonance is common across animals, but it is not clear that it is especially relevant to the evolution of teaching, as opposed to perception or social interaction more broadly.

Finally, **Palagi, Stanyon, & Demuru** (**Palagi et al.**) highlight play as one of many "forms of teaching and learning." I think this is a mistake. Although play certainly facilitates learning, and although teaching behavior may happen in the context of play, behaviors commonly accepted as "play" can fall outside of any of the definitions of teaching discussed in the target article. For example, solitary play cannot possibly be categorized as teaching, since it takes (at least) two to teach. While some kinds of teaching may resemble some kinds of play, behaviors sharing proximate mechanisms do not necessarily share an ultimate function. For this reason, a functional explanation of teaching behavior makes an ideal structure upon which to build a framework for comparative research. For example, not all displays of ostensive cues constitute teaching, and not all teaching relies upon ostensive cues. Some behavioral cues, like "motherese," may be teaching-specific, but this is an empirical question requiring further study. Palagi et al. describe gestural motherese in gorillas as being "direct" and "active," but this does not categorize it as *direct active teaching* as defined in the target article. Instead, teaching behaviors should be categorized based on the learning problem they are thought to solve, with consideration of the learner's access and attention. Within the target article, I explicitly classify *motherese* as a form of teaching via stimulus enhancement (see sect. 3.1).

R2.2. Social, cultural, and other contextual mechanistic explanations

Another group of researchers focuses on a proximate description of the social, cultural, or other contexts of teaching behavior. **Rogoff** begins by pointing out that cultural anthropologists and others have been richly describing a broad array of teaching and learning behaviors for decades, and that this includes behaviors that fit into my five teaching type categories. This is right – and in the target article I credit such researchers for their achievement (see sect. 2.2), while drawing heavily on their descriptions in the empirical review of teaching in humans (sect. 4.2). To clarify, I do not argue that culture-based approaches are without descriptions of the range of behaviors I discuss in the target article. In fact, there is a richness in that literature that I could not begin to address in the target article. This includes one-to-many and many-to-one teaching, which Rogoff discusses, and questions that draw on social theories of power, knowledge-making, modes of communication, and meaning, to name a few. It also includes aspects of teaching behavior featured in Rogoff's graphic, ranging from community organization, to learning goals, learner and others' behavior, and the mental state or motivation of the learner and others (see Rogoff's Figure 1). These are all valid domains of study, at the level of describing sociocultural contexts. However, descriptions and analyses made without a shared framework do very little to integrate the study of teaching behavior across levels of explanation. Further, much of this qualitative data is exclusive to human teaching and is analyzed without respect to the features we do share with other animals.

This is a problem for an integrative framework for use across human and animal populations. Drawing categories of social learning and teaching in terms of social meaning and cultural context can work as a coherent mechanistic-level analysis. These categories have affordances for discussing the questions that cultural psychologists, for example, are interested in. However, it is incompatible with functional and phylogenetic analyses, and with any comparison with nonhuman animals. This incompatibility limits the usability of data from the culture-based approach by other researchers. In turn, this confines the questions one can ask from a culture-based approach to the mechanistic level. For instance, only a shared framework allows the combination of evidence from cognitive developmental and ethnographic descriptions for a better understanding of how humans, as a single biological species, can demonstrate so much behavioral variation in teaching, across the lifespan. This variation can be described in detail from a

culture-based approach, and its subjective meaning can be examined. However, if we want to know how humans came to be this way, or to shift the goals of educational systems towards creativity and away from uniformity, then ontogenetic and functional perspectives are key. Since developing these explanations depends in part upon comparison with other species, a multi-level approach grounded in phylogeny is the best option. This is not a call for cultural psychologists and anthropologists to abandon their questions – it is merely a call to integrate their questions, and their very valuable data, with complementary work on teaching from other approaches.

In many ways, the culture-based approach can be compatible with the functional framework proposed here, so long as we recognize it is a different level of explanation, and seek to reconcile those levels of explanations. **Lancy** argues that the definition of teaching used in the target article is too broad, and that researchers should persist in the culture-based approach to the study of teaching. However, the breadth of a functional definition is only problematic if one interprets the framework as obligating researchers to use functional definitions exclusively, and to use these definitions without operationalizing criteria for identifying teaching behavior. I am not persuaded, and refer readers to the target article's discussion of the benefits of integration (sect. 2.4). A key consideration is that the functional framework would not prevent researchers from focusing on specific contexts or genres of teaching should they have the intellectual motivation to do so. The teaching typology means research focused on a particular kind of teaching – for example, direct active teaching – can be fitted into the framework with minor adjustments. In fact, the functional framework is perfectly open to the study of when and how learners may solicit teaching – a concern Lancy highlights. Further, distinctions between what **Koenig** calls "mode" of learning – hearing, watching, seeing – are compatible with a functionalist approach as a mechanistic explanation. Finally, the framework also does not require granting privileged status to teaching as a means of learning, so it can be integrated into the ethnographic and theoretical study of social learning more broadly. Research on social learning has itself benefited from the kind of integrative framework I propose here, and has allowed for cross-species studies. As is clear from my own empirical work (e.g., Kline et al. 2013), teaching is but one of many kinds of social learning.

Lancy also suggests that the illustrative examples I use from my field work in Fiji are irrelevant, because (as I explain in the target article and elsewhere in my published work) the indigenous Fijian people I work with do attend British-style formal schooling. However, I include these details precisely because I think they are important for contextualizing my qualitative observations and quantitative data (see, e.g., Kline et al. 2013). Moreover, the presence of formal schooling does not render these examples useless, nor does it undermine the overarching goal of the target article, which is to propose a synthetic framework. These ethnographic examples are single events, chosen specifically to illustrate teaching types. Examples like this cannot be used to generalize about a population, and disregarding these examples would not topple the proposed framework. The target article includes a range of examples of teaching behavior from the broader ethnographic literature (see sect. 4.2). Further, argument by example cannot tell us whether Western education correlates with (let alone causes) teaching behavior outside of the classroom. To test this kind of relationship would require a large-scale cross-cultural comparative study with quantitative measures of Western schooling and the prevalence of teaching types per population. Alternatively, we might test whether *within* populations, exposure to Western schooling for the learner or the teacher predicts likelihood of teaching. For the Fijian population in which I work, the answer is that it does not (see Kline 2013). Still, Lancy's question highlights the need for a broad, quantitative comparative study of teaching behavior across human populations. The target article has outlined the framework that makes this kind of study possible.

R2.3. Applied uses for mechanistic explanations

Several commentaries have discussed human socio-cultural institutions, such as classrooms, apprenticeships, or styles of parenting, that can affect the performance of teaching. While the target article focuses on kinds of teaching *behavior* rather than on the human socio-cultural institutions that structure and influence teaching behavior, the study of those institutions is not in conflict with the approach I propose. In fact, this focus on context is one of the most valuable contributions of the culture-based approach can contribute to the study of teaching more broadly. While socio-cultural institutions can be analyzed at other levels, most of the commentaries on these topics focused on how it is that teaching happens, and in what contexts. In this way, they make use of mechanistic accounts of teaching behavior and its contexts in humans.

Shafto & Seifert take an applied approach, asking how we might optimize learning through a combination of teaching and self- and peer-directed learning. In an example regarding peer-directed learning, they contrast peers with teachers as important sources of knowledge. However, in the analysis in the target article, teachers and pupils are not separate, mutually exclusive populations: they are fluid roles that are shorthand ways of describing behavior. A classroom in NASA or at Google may contain only one person employed as a teacher, but within the framework I propose, students can just as easily be performing teaching behavior, and a single individual can be both a learner and teacher. Like a classroom, an apprenticeship is a social arrangement and a context, and not a type of behavior.

Similarly, a syllabus or overarching goals of an educational system are social institutions designed by humans in order to shape teaching behavior to reach a given end – for example, conformity or creativity. **Poddiakov** likewise describes a number of contexts in which teaching may happen, for example, when a teacher's interests are in conflict with a pupil's. Because teaching evolved as a cooperative behavior, this context poses a cheater-detection problem for pupils, discussed at length in the target article (sect. 6.2). Despite this, what Poddiakov terms "negative work" in teaching, and the kind of false-information that **Koenig** discusses, are not separate kind of teaching behavior – both are contexts in which teaching behavior happens, and may be examples of teacher-pupil conflict where the pupil's role as skeptic could be studied. For example, **Müller** suggests a specific domain in which

teaching and social learning may proliferate unhealthy behavior: psychiatric disorders.

Researchers whose goal is to define and create strategies for teaching that maximize a given outcome – be it creativity or conformity – would do well to consider teaching from more than one level of analysis. **Shafto & Seifert** point out that humans are good teachers but not optimal ones. This makes sense from a functional perspective because natural selection produces traits that are best-suited to maximize actors' reproductive success. This is not the same as optimizing teaching for the best possible learning outcome, because there are cost/benefit tradeoffs that affect teachers and pupils. We should not assume that evolved teaching behaviors are optimal teaching behaviors; instead, we can think of them as tendencies or biases that should be taken into consideration in attempts to optimize the teaching process.

R3. Ontogenetic explanations

Another cluster of commentaries focuses on developmental explanations of teaching and learning, particularly in humans. **Chouinard-Thuly & Reader** put forth developmental specialization as an alternative to evolutionary specialization. As with mechanistic explanations, this only highlights another level of analysis and a shift in focus. I agree that understanding variation and the processes that generate it is important – variation is the engine of change in natural selection. However, development and learning are themselves evolvable, such that ontogenetic explanations are part of an evolutionary explanation rather than a mutually exclusive alternative (see Barrett 2006). Examples of flexible social learning behaviors, whether in sticklebacks, bees, or humans, can be indicators of *prepared* learning (see Barrett & Broesch 2012) in that the cognitive features of the learning mechanism are functionally specialized to a set of contexts (Cosmides et al. 2010).

In this view, empiricists ought to probe the contexts and conditions under which teaching happens, to understand the flexibility and boundaries of teaching behaviors (Barrett 2014). This is in keeping with Heyes' (1994; 2012a) critiques of the divisions between social and individual learning, because it treats teaching and other forms of social learning as continuous and complementary strategies. While it is still a useful analytical and practical exercise to categorize learning and teaching types, note that a number of the teaching types I propose effect learning through the combination of teacher intervention and the learner's independent exploration of stimuli. From the learner's perspective, this is a seamlessly integrated process of learning. Likewise, from the perspective of a runner, locomotion and respiration are united – yet it is useful to create abstract categories for the purpose of analysis and quantification. Practically, explaining teaching behavior at any level requires cataloguing and comparing sources of variation in teaching behavior across individuals, societies, and species. To do so, we need a comprehensive framework like the one proposed here; linking developmental accounts to the functional framework, and revising the framework when we find it does not account for the data.

I am encouraged that so many additional commentaries call for a focus on the ontogeny of teaching and learning, including **Beck** as well as **Paulus, Kim, & Sodian** (**Paulus et al.**), and **Strauss, Ziv, & Frye** (**Strauss et al.**). However, each of these commentaries emphasizes theory of mind (ToM) or mind-reading as a definitional criterion for identifying teaching. In some cases the commentators mistake the target article's outline of the mentalistic approach (sect. 2.1) as evidence that I endorse this view. In contrast, I argue in the target article (sect. 5) that some combination of metacognitive capabilities along with some degree of mind-reading or ToM capacities might be sufficient *but not necessary* for direct active teaching, and that other types of teaching might require neither. For example, Strauss et al. argue that because teaching sometimes fails to effect learning, we can only identify teaching by its goal as captured in a mental state rather than by its result. In addition to the theoretical problems with this strategy as discussed in the target article, its practical challenges have been roundly criticized since Caro and Hauser (1992) first outlined a functional definition of teaching. I will not recapitulate those critiques here.

As discussed by **Strauss et al.,** the study of teaching behavior is in need of cross-cultural data on the ontogeny of teaching behavior, especially from non-Western samples. However, their argument for how to interpret cross-cultural variation is based on a misunderstanding of evolution and developmental flexibility. They suggest that uniformity in the early psychology and development of teaching behavior would indicate that teaching is "not cultural," whereas variation early in the trajectory would suggest that the cognitive underpinnings of teaching are "culturally determined." This link does not hold, because it depends upon a false dichotomy. Universality of a phenotype can result from convergent development in a system evolved to be developmentally plastic and sensitive to cultural and environmental inputs, just as it can result from a system evolved to be insensitive to such inputs (Jablonka & Lamb 2014). Adaptive plasticity – the potential for a developmental system to produce a variety of phenotypes depending on context – can also be selected for, and produce a "norm of reaction" across contexts. In this case, while cultural variation might be linked to variation in phenotype, the resulting variation is nonetheless a product of the evolved developmental system and the environment in which it develops, not necessarily cultural learning. The question we ought to be asking is one of degree of influence. Our empirical efforts, then, should focus on the flexibility of the ontogeny of teaching behavior in a range of environmental contexts.

R4. Phylogenetic and evolutionary historical explanations

Several of the commentaries argue for a focus on the historical nature of the evolutionary process. **Smaldino & Newton** in particular object to the idea that teaching behaviors are adaptations as opposed to being exaptations. They have a point, in that I take a straightforward adaptationist approach in basing my inquiries on a functional definition of teaching. However, it is not clear how this critique changes the usefulness of the framework as a tool for exploring and understanding the functionality of teaching behavior. An exaptationist program would likely be identical to an adaptationist one in that it would focus on evidence (or lack thereof) of functionally specialized design

(see Andrews et al. 2002). In either epistemological context, the framework I propose should be viewed as one full of hypotheses; as illustrated by the range of commentaries discussed here, a functionalist explanation is only one of many integrated levels of analysis open for exploration.

If **Smaldino & Newton** have ideas about how to generate new hypotheses or research questions based on an exaptationist program, they do not share them in their commentary. Instead, they provide a partial alternative explanation for each teaching type, tying features of the teaching behavior described in each type to some underlying feature of human behavior. This critique goes off track in that it mischaracterizes my argument, supposing disagreement where there is none. To clarify: I do not argue that every aspect of teaching behavior evolved *de novo* because of selection for teaching. On the contrary, I think the best explanation for human-specific forms of teaching is that it evolved alongside a suite of other social and cooperative behaviors. The same reasoning applies to other teaching types. Similarly, I do not argue that social tolerance *in general* evolved because of selection favoring teaching behavior. My argument applies only to *teaching via social tolerance*, which might be thought of as a *secondary adaptation*[1] derived from those traits Smaldino & Newton discuss (Gould & Vrba 1982). Future work based on the proposed framework should seek to test whether there is evidence of design specialization for the teaching types I outline. In this sense, testing the adaptationist hypotheses I lay out is the same exercise as testing the exaptationist hypotheses.

Smaldino & Newton's account provides a useful description of the adaptations in humans that likely predate and underlie the emergence of teaching behavior. Such a phylogenetic or comparative approach, combined with evidence for special design, can provide some of the best evidence for adaptation (see Andrews et al. [2002] for kind of evidence for special design, and Gervais & Wilson [2005] for an example of this tool applied to laughter). Rather than ask whether teaching should be called either an adaptation or an exaptation, or a secondary adaptation, we would be better off characterizing the observable functions of teaching behavior and, where possible, quantifying its effects on fitness. Adaptationism generates hypotheses in this context.

In an alternative historical approach, **Gärdenfors & Högberg** suggest that the emergence of teaching types in humans might be reconstructed from the archaeological record. While this would be data worth having, this endeavor may prove intractable both because of the nature of teaching behavior, and because of the practicalities of the archaeological record. The typology I propose in the target article does link teaching types to adaptive problems to be solved, but this is only in terms of the proposed selection pressures. It does not follow that, once a flexible teaching behavior is within a species' repertoire, that teaching type was subsequently applied to only that learning problem. In fact, much of the ethnographic literature attests to the broad use (some call it over-use) of direct active teaching in white, upper and middle-class American populations, in comparison to societies where children are expected to learn predominantly in more self-directed ways (Lancy 2008). In light of the present-day range of variation it seems tenuous at best to link particular artifacts or technologies in the archaeological record to specific teaching behaviors. The relationship between teaching behaviors, cognitive capacities, and archaeologically observable artifacts is further muddied by the fact that human technologies result from population-level processes. These processes are affected not only by method of transmission, but also by demographics like population size (e.g., Kline & Boyd 2010) and spatiotemporal population structure (Powell et al. 2009). In light of these complications, specifics about the timing of emergence of types of teaching behaviors may be beyond what archaeological data in general can tell us (Smith 1998).

Nielsen & Shipton also suggest archaeological data, but with a focus on the emergence of childhood as a necessary precursor to the evolution of teaching. This is an interesting suggestion, but it need not be true: Children are not the only recipients of teaching, though they are overrepresented in the ethnographic literature. In fact, my own fieldwork has focused on children because of doubts from the *culture-based* school of thought that young children are taught anything at all in non-Western societies (for review, see Hewlett et al. 2011). Other examples in the target article are drawn from an ethnographic literature that is specifically focused on how children learn. This should not be misconstrued as a representative sample of teaching and learning across human life history in any sense. However, the proposed framework may lead to the creation of such a sample in the future.

In addition to sampling issues, there is some empirical evidence against **Nielsen & Shipton**'s assertion of the relationship between childhood and teaching behavior. First, high-skill tasks for which teaching would be especially useful are learned later in life (Kline et al. 2013). In addition, in at least some domains, children's skill outpaces their physical ability to complete a task, suggesting that teaching would serve little purpose (Bliege-Bird & Bird 2002). Childhood and human teaching behavior may both have evolved as part of the human cultural niche (Boyd et al. 2011), but there is presently little evidence to suggest that teaching requires an extended juvenile period, or vice versa. Further, as reviewed in the target article, teaching has been documented in a range of other species (see sect. 4.3), none of which have the same dramatic extended juvenile period as do humans.

Ridley & Ashton as well as **Scheel, Shaw, & Gardner** (**Scheel et al.**) focus on the power of the comparative approach, and express concern that highlighting humans as exceptionally prolific teachers skews the study of teaching behavior by using "humans as a benchmark" by which to measure teaching in other animals. I agree that human exceptionalism is not a theoretically sound approach to comparative studies of teaching. I argue in the target article that although humans are particularly prolific and extensive teachers, any framework we use should account for human *as well as* nonhuman animal teaching behavior with a single explanatory framework. I do not think humans teach as a result of human-specific mental capacities (see sect. 5), or because of some other inexplicable discontinuity between humans and other animals. Instead, I anticipate human teaching is at the extreme end of the distribution of teaching and that, like other apparent exceptions that in fact prove the rule, explaining teaching in humans will inform our understanding of teaching across species.

This is why an explicit goal of the framework I propose is to enable researchers to collect equivalent data on human and nonhuman animals. Data equivalency is crucial because, while most humans (though not all scientists) will interpret the ethnographic examples provided in the target article as clear evidence of teaching in humans, very few would do the same for Boesch's, or **Scheel et al.**'s, similarly descriptive accounts of what they argue are cases of teaching in chimpanzees. An integrative framework like the one I propose is needed for this endeavor, because if we are to seek continuity in our explanations we must also have equivalency in our data.

R5. Functional explanations

R5.1. Extensions within a functionalist approach

Commentators have also made suggestions for extensions of the functional analysis offered in the target article. For example, **Johnston, McAuliffe, & Santos** (**Johnston et al.**) make a compelling argument for how dogs may serve as a useful study species, because they have evolved to learn from humans, and to attend to ostensive cues. Their proposal is intriguing and novel – though, as with any cross-species comparison, caveats apply. For example, basic differences in dog and human cognitive and communicative capacities mean that the study of human direct active teaching with dogs as pupils is probably not possible.

Scott-Phillips & Sperber contribute richness to the theoretical foundations of the target article, highlighting the importance of psychological, biological, and environmental factors of cultural attraction. **Abrams** details *transmission probability interactions* as a system that makes it possible to build abstract mathematical models of teaching and of cultural attractors. No matter their origins, attractors can preserve and construct what is to be learned – and may work in concert with or against what is being taught. A future analysis might delve deeper into the importance of attractors for the range of different teaching types. For example, for teaching that enables individual learning, attractors may play a major role in determining learning outcomes, while teaching affects whether learning is possible. These authors also point out that the study of teaching behavior is especially compatible with cultural attraction theory because teaching (a) functions to influence the frequency of practices or variants other than itself, and (b) the impact of teaching is in part dependent on other sources of cultural attraction. In the context of cross-species comparisons, a major caveat is that not all teaching promotes cultural learning in particular, and only some forms of teaching may be culturally learned. Cultural attractors may be especially relevant for the study of direct active teaching, and for applications of this theory to improving the effectiveness of teaching methods.

Tatone & Csibra argue that despite the synthetic value of the framework, *ostension* must still be key to understanding human teaching. While I agree that in some contexts, ostension is a key part of human teaching behavior, I think it does not cover the range of teaching behaviors that exists. The goal of the framework above is not to rule out ostension as a feature of a subset of teaching behavior, but it does include a range of teaching behaviors that do not necessarily rely upon ostension. I also do not see ostension as a reliable cue to teaching, as distinct from other kinds of communication.

Hernik & Gergely argue that teaching fills the function of enabling a naïve individual to learn content that is *opaque* and *generic*. Their commentary questions the validity of basing the target article's framework in a learner's access and attention, and redirects the focus to four problems of opacity. These indeed do pose problems for learners, but the identification of these problems is relative to the learner and the context (i.e., to the learner's access and attention). The framework in the target article explicitly captures this, by taking the learner's access and attention into account. In this sense, opacity is not treated as an objective feature of the world, because it depends upon the learner's existing store of relevant knowledge. Considering the attention and access of the learner can characterize the learning situation as more or less opaque, rendering particular types of teaching useful or irrelevant. Conceptualizing the pupil's access and attention are not in conflict with identifying kinds of opacity, and in some ways these concepts are addressing the same problem: Why is it the pupil cannot learn, or will learn more slowly, without aid from a teacher?

Finally, while **Caro** endorses the need for a broadly comparative database, he is not interested in friendly campfire tunes, instead arguing that the mentalistic and culture-based approaches require constraints that make the kind of synthesis I outline impossible. I maintain that a functionalist approach can benefit from integration with the research questions and the empirical observations made across specialized fields (sect. 2.4). Further, I think the application of multiple levels of explanation in this response makes that compatibility explicit rather than hypothetical. In the end, I propose we employ the framework from the target article and evaluate its usefulness empirically.

R5.2. Operational definitions

Another group of commentaries generally approves of the functionalist approach, but expresses doubts about the practical application of the proposed framework, given that operational definitions are only addressed briefly in the target article.

Dean & Kendal argue that the framework focuses too heavily on teacher behaviors as opposed to learner behavior. However, a key component to the framework is to match teacher behaviors to learning problems. These learning problems are defined from the perspective of the learner – whether the learner lacks access or attention to information. From a practical standpoint, this may mean that observational and experimental studies will need to focus on the learner. From a theoretical perspective, it means that the adaptive problem is always with respect to the learner's status. For this reason, learner behavior is indeed an important source of information in arguing for or against alternate explanations of candidate teaching behaviors. In fact, learner behavior can serve both as evidence of an existing learning problem that might be solved by teaching, and as a measure of the fitness-relevant effects of teaching should it be observed. Both kinds of evidence are important in identifying cases of teaching behavior.

Alternatively, **Dean & Kendal** return to the cost/benefit criteria first proposed by Caro and Hauser (1992). Caro and Hauser's criteria are admirably simple and should serve as

one of many kinds of evidence for the function of behavior as teaching (see target article, sect. 2.3, para. 1). However, it does not follow that these criteria are an objective rule by which to identify teaching. Take, for example, the criteria that there is a cost, or at least no immediate benefit to the teacher: applied without a researcher's inference or subjective interpretation, this would neatly rule out all instances of (adaptive) teaching as cases of teaching. This is because, for teaching to evolve, there must be some fitness benefit to teachers as opposed to non-teachers. The fact that Caro and Hauser's criteria *have* been used to identify and confirm cases of teaching is evidence that researchers (quite rightly, I think) apply it in selective ways that make sense within the context of their studies. This is not to say we should do away with Caro and Hauser's criteria. Instead, we should regard it as only one of many lines of evidence for specialized design: that the *form* of the behavior fits the proposed *function* of teaching. Further, we should aim to show a behavior fits this proposed function better than it does an alternate function.

In their argument against the adoption of the target article's framework, **Dean & Kendal** do not consider the discussion of learning problems upon which the framework rests. Specifically, they do not consider that teaching types correspond to a learner's access and/or attention. As a result, they suppose that when otters and sea lions drag their offspring into the water, this fits the framework's definition of either teaching by stimulus/local enhancement or teaching by opportunity provisioning equally well. They take this as an indication of broader problems with the framework. Ironically, given their suggestion for greater focus on learners, the distinction between these two forms of teaching is in the learning problem, from the perspective of the learner. In these examples, the pups are not prevented by circumstances or by conspecifics from entering the water. This means there is no *access* problem for the pups. However, they only seem to learn to swim as a result of being forced into the water by their mothers. This suggests that they lack *attention* to the water, and only engage in swimming when their attention is forced. We can imagine that pups who are never pulled into the water by their mothers might never learn to swim, or might learn much later without interference. In either outcome, opportunity provisioning does not fit the scenario, since it corresponds to cases where learners lack *access* to a stimulus, and do not lack attention. Opportunity provisioning would apply if, for example, otter pups consistently attempted to enter the water but were not able to do so because they were physically prevented from accessing it by their small size, and could only reach the water through assistance in gaining access by their larger-bodied mothers.

Similarly, commentators **Moore & Tennie** and **Eschar & Fragaszy** favor an evolutionary approach focused on adaptive problems, but take issue with the framework's categories. First, Moore & Tennie suggest my definition of *teaching by stimulus enhancement* is meant to be a new definition of *stimulus enhancement* more generally. As discussed above, I am not arguing for a new definition of stimulus enhancement and would not categorize *all* learning by stimulus enhancement as teaching. They go on to argue that lumping teaching behavior by function rather than by cognitive difficulty is "not intuitively a useful tool for understanding evolution." This is demonstrably untrue, since evolutionary reasoning is regularly and fruitfully applied according to functional definitions. For example, the reproductive habits of soapbox bugs and of humans rely upon wildly different cognitive mechanisms, yet we can understand frequency-dependent mating strategies in both species with the same kind of cost/benefit rationale. On the other hand, a functional framework is just one level of analysis. This shared functional analysis does not prevent us from studying the cognitive complexity of each teaching type, or of teaching behaviors that cut across functional categories. On the contrary, it facilitates phylogenetic comparisons, which help researchers to understand the details of how and when individuals in each species do or do not adjust their behavioral strategies. This gives us insight into the behavior's proper domain and the constraints on its flexibility, including cognitive constraints.

Moore & Tennie go on to argue that the flossing behavior of Japanese macaques, as discussed in the target article, could fit the definition of "direct active teaching." In contrast, they make the suggestion that Warao fathers' repositioning of their sons' hands during canoe carving should fall under evaluative feedback rather than direct active teaching. This is only possible because they substitute their own intuitive definition of what constitutes "direct teaching," for the one I propose, stating "we often engage in direct teaching by drawing others' attention to important features of objects." In asserting this, Moore & Tennie step away from the definition of direct active teaching proposed in the framework above, such that these specific critiques cannot apply in a meaningful way. The source of confusion here seems to be similar to **Dean & Kendal**'s, in that the focus is on apparent behavioral similarity (i.e., something can be described as "direct" and "active" in lay terms) rather than how researchers might tease apart behaviors based on their function in facilitating learning. This problem is not unique to the evolution of teaching behavior. For example, researchers have had to create ways to discriminate mounting behaviors that function to establish dominance from those that function as reproductive sex. As in the framework I propose above, distinctions are made by contextual indicators, including others' behaviors, rather than by a distinguishing feature of the actor's behavior alone.

Eshchar & Fragaszy state that "[f]raming teaching in terms of its evolutionary sources does not help the empirical researcher to recognize it." I strongly disagree. Observed teaching behaviors should, all else equal, represent a specialized functional match to the context of the adaptive problem, and, if functioning in its proper domain, should have fitness-enhancing consequences for the teacher and pupil. This form–function fit can generate insights into the ways cognition can operate to reliably produce teaching behavior in teachers and pupils.

Mapping conditions under which the behavior's functionality breaks down can serve as evidence of the adaptation's proper domain, and experimental methods may help us to probe that landscape to better understand the flexibility of an adaptation (Barrett 2014). Similarly, ontogenetic evidence can be used to infer a trait's function and further detail its flexibility or lack thereof. Phylogenetic analyses can temper adaptationist reasoning with an understanding of the evolutionary origins of underlying traits, as suggested by **Smaldino & Newton**. Further, comparative studies based on phylogenetic analyses may help us to identify recurring social learning problems that can be solved by

teaching, for a set of socio-ecological niches. All of this comes with a better understanding of the evolutionary sources of teaching behavior, and these multiple lines of evidence can be used to design better operational criteria for distinguishing among alternative explanations for potential teaching behavior.

As **Rapaport** discusses, there are a range of criteria that can and should be used to identify and characterize teaching behaviors. This is directly addressed in the target article (sect. 3). This section of the paper makes clear that, contrary to **Eshchar & Fragaszy**'s assertions, the framework in the target article is not designed to include any and all learning that happens in any social context as teaching. Eschar & Fragaszy's critique is that the framework does not come with a generalizable operational rule to distinguish teaching behavior from all alternative explanations of behavior, so it must be impossible to differentiate between teaching and other kinds of learning under this framework. This argument is flawed. Our operational definitions are necessarily going to be variable and piecemeal, because we are studying a selection of behaviors spread across a range of species and contexts. Creating operational criteria will not be simple or easy, and I do not provide a universal operational criterion because I believe there is none that will apply across all study contexts. Again, this does not mean that researchers should subjectively judge what seems to be teaching and what is not. Instead, it means they should design tools of measurement and experimental and field methodologies to distinguish teaching from other forms of social learning and from other forms of communication. These methodologies should enable researchers to provide evidence that a behavior likely functions *as* teaching, and to collect evidence of functional specialization *for* teaching, as opposed to some alternate function.

As **Fogarty** highlights, this is a challenging problem for researchers, especially those conducting observational work without the option for experimental manipulation of their subjects. In mathematical modeling, Caro and Hauser's (1992) criteria may be the easiest and therefore most fruitful to apply. However, this represents a tradeoff, since those models will only be able to tell us about a subset of socio-ecological contexts that the underlying assumptions accurately describe. To explore the evolutionary dynamics that could have given rise to the full range of teaching behaviors, a more differentiated set of models is needed. Nonetheless, this kind of model can be a powerful tool for generating theoretical insight beyond what verbal reasoning can tell us.

Rapaport meets the difficult question of what operational criteria we might use head on. She proposes we use Hoppitt et al.'s (2008) standard of only including "active" demonstration as teaching. However, this approach struggles with precisely the same questions as the framework proposed in the target article. Hoppitt et al.'s "active" or "advertent/inadvertent" distinction is simply another way of weighing alternative explanations of behavior against one another. Rapaport rightly notes that distinguishing social tolerance that evolved as teaching from social tolerance more generally is a difficult challenge in primate species that have reached ceiling-high levels of social tolerance. I agree with Rapaport's assertion that it is not scientifically sound to categorize all types of social tolerance as instances of teaching by social tolerance; I also agree with similar assertions made by **Moore & Tennie** with respect to teaching by stimulus enhancement, and by **Eshchar & Fragaszy** about the teaching types in general. However, these objections are somewhat surprising since they echo the argument made in the target article, in the very introduction to the framework itself (see sect. 3). In each of these cases, the commentators misinterpret some of the examples of teaching and as a result infer that the framework equates social learning with teaching. Here I discuss these misinterpretations in turn.

First, **Rapaport** notes that, in the example of the Balinese music teacher who plays for his pupils without adjusting his style of play, there is no behavioral adjustment whatsoever by the teacher. In fact, in this example, the music teacher puts on a performance exclusively for the pupils to observe – were the pupils not present, he would not play. The modification is *that* he is playing, not *how* he plays. Aside from the specifics of interpreting ethnographic examples, there is a broader point. The practical difficulty of identifying teaching by social tolerance does not necessarily lessen its theoretical validity. Because of the minimalist nature of teaching by social tolerance, it may predate the evolution of other, more derived forms of teaching. The conceptual role of teaching by social tolerance in this framework may be important in considering the socio-ecologies in which we would expect teaching to evolve, even if we are unable to reach a consensus on how to quantify and observe cases of teaching by social tolerance.

Eshchar & Fragaszy provide their own examples, presenting them as problematic for the framework. These examples are worth discussing in that they highlight some important misunderstandings. First, they propose that in a case of chimpanzee termite fishing, when a juvenile physically intrudes upon a foraging adult, it will be impossible to tell the "purpose" of the adult's social tolerance. They argue that teaching by social tolerance will be indistinguishable from the social tolerance that evolved because intolerant adults would incur direct costs. This is a testable hypothesis, provided the researchers can come up with a proxy measure of the cost or threat of costs (e.g., presence and rank of the juvenile's kin). This question can be settled by testing the competing hypotheses against each other, using measures developed for the study species and context. In fact, it is difficult to see why Eshchar & Fragaszy think this problem is specific to the framework described in the target article, as the same kind of challenge exists for all studies of teaching behavior, and more broadly for the measurement of behavior in general.

Eshchar & Fragaszy also suggest that under the proposed framework, teaching would include any behavior done in proximity to juveniles, even if there is no behavioral modification contingent on the learner's presence. This directly contradicts the target article's discussion of distinguishing teaching behavior from baseline behavior (sect. 3). These commentators also highlight the need to know whether a behavior is "for the purpose" or with the "intention" of teaching. This is not a reliable standard, for reasons discussed throughout the target article, and has been discarded by functionalists since Caro and Hauser's (1992) critique. On the other hand, some of the ethnographic examples I draw upon in the empirical review section (sect. 4.2) do give accounts of the mental states of human teachers. As discussed in that same section, I include these examples because

ethnographic data are necessarily impoverished of quantitative data on behavioral details, and the ethnographer's qualitative interpretation of the actor's intention can lend valuable insight when applying quantitative criteria is not possible. Using these examples as an act of necessity is not the same as endorsing intentionality as a criterion for identifying teaching.

Jacquet raises punishment as an example, asking how punishment can be distinguished from teaching by evaluative feedback and suggesting that this may necessarily be a grey area. Jacquet notes that others have distinguished punishment from teaching according to the timing of the fitness payoffs, reasoning that behavior that results in an immediate benefit to the actor should be considered to function as punishment, rather than as teaching (see, e.g., Thornton & Raihani 2008). Evident in Jacquet's commentary are a range of definitions of what actually constitutes punishment, and I suspect this topic could inspire a review piece of its own. For the sake of clarity, I conceptualize punishment here as "negative feedback" in which the actor creates and imposes a cost on its recipient. The specific definition of teaching by evaluative feedback (sect. 3.1) is not as relevant here as the definition of teaching more generally as a cooperative behavior between teacher and learner (sect. 6). With these definitions, teaching via evaluative feedback is neither equivalent with punishment nor mutually exclusive with it. That is, some punishment may function as teaching by evaluative feedback, and some may not. Differentiating between these cases will require considering the costs and benefits to the candidate teacher and pupil in a particular context.

A defining feature of teaching as discussed in the target article is that the benefit to the teacher is indirect, derived from benefits to the pupil. In this sense, teaching is a cooperative behavior. This means punitive behavior that benefits the actor/punisher at the expense of the recipient/punished – for example, parking tickets or reputational damage – does not function as teaching. This is more precise than timing of costs and benefits since, in reality, teachers must benefit at some point regardless of timing, and punishers can accrue delayed benefits. Likewise, punishment that is not teaching can still create direct benefits for the punisher, as a result of the punished individual modifying her behavior. To continue the example, if those who receive parking tickets learn not to park in permit-only zones, the punisher gains parking availability. In this case, punishment is not equivalent to teaching because it is not cooperative: the punisher (the permitted parker) benefits at a cost to the punished individual (the ticketed, unpermitted parker). Where punishers derive indirect benefits from the modified behavior of the punished individual, *and* the punished individual also benefits, punishment is a form of teaching by evaluative feedback, albeit a relatively costly form. Of course, these questions become more complex when we consider that teaching, like other cooperative behaviors, is open to manipulation for selfish means by teachers. The waters are further muddied by considerations of how to measure the scale and flow of benefits and costs – but these are matters of methodological rather than theoretical distinctions and are beyond the reach of this response.

Sharkey provides an outside-the-box commentary, asking whether robots are teachers. Since robots are not living, reproducing creatures, they do not evolve or behave in the way that organisms do. Thus, in an evolutionary approach, robots are best characterized not as being teachers themselves, but as culturally evolved tools that humans use for teaching. This is because robot actions are not shaped by natural selection on robot behavior and reproduction, but instead are the result of natural and cultural selection on human behavior and culture. So, for example, where robots are deployed to provide an English-speaking companion for students studying English as a second language, this is an example of humans teaching via opportunity provisioning. Humans may even undertake direct active teaching via a robot, by equipping a robot with a pre-planned lecture or demonstration. Likewise, some book-based teaching may fall into this category since, like robots, books are cultural artifacts created by humans. Similarly, the online quizzes with feedback that are common in large university courses at the present can be considered teaching via evaluative feedback. From an applied perspective, the important difference between teaching that uses robots as tools and teaching that happens between two humans face-to-face, is the relatively poor ability of a robot to tailor its actions to the context and the learner's status. As noted in other commentaries, this reactivity between teacher and pupil (or more broadly, in acts of human communication) is important for the effectiveness of communication. This has implications for the use of robots as teachers-by-proxy: Teaching types that are more dependent on adjustment and tailoring may be less effective through the use of robots. This poses a problem for the use of robots in the classroom, because direct active teaching can be tailored, intensive, and quite common in a typical Western-model classroom.

R6. Conclusion

The commentaries expand an already extensive field of research on teaching, and contribute new questions, techniques, and strengths to the evolutionary approach proposed in the target article. The various commentaries have touched on a wide range of subjects, from the neurobiology of teaching, to the receptivity of domestic dogs to human teaching and the roles of robots as teachers, as well as the finer points of how to operationally define teaching in the laboratory and in the wild. As several commentators have suggested, the proposed framework would benefit from additional emphases on mechanistic, ontogenetic, and phylogenetic research problems. I have used the response here to demonstrate how these research questions are not in conflict with the functionalist approach I outline, but should be regarded instead as multiple lines of evidence that may improve and modify the framework in the future. Students of the evolution of teaching have thus far lacked a comprehensive framework that is open to this kind of input, and this has been a source of miscommunications across disciplinary divisions.

The breadth of commentaries in response to this framework is in itself evidence that this approach is accessible to researchers pursuing questions across levels of explanation. Further, it provides a platform on which to integrate research questions and data at the core of the mentalistic, culture-based, and functionalist approaches to the study of teaching. The proposed framework defines teaching from a functionalist perspective, as behavior that evolved

to facilitate learning in others. The categories of teaching are based on learning problems derived from a learner's lack of access or attention to relevant stimulus. Because these represent general adaptive problems for learners, these categories capture the full range of teaching behaviors that have been described so far in the qualitative and quantitative literature on teaching behavior in humans and in other animals. The application of this framework will allow for a more integrated, interdisciplinary treatment of questions and data across populations of humans and other animals.

NOTE

1. I do not use the term *secondary adaptation* in the target article because it is tautological – for the most part all adaptations are built upon other adaptations. As a result, I find it confuses the argument without contributing any new inferences.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively]

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