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The Cognitive Foundations of Teaching

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ABSTRACT

The propensity to teach is vital to human cultural evolution and to our ecological dominance of the planet, but its cognitive foundations remain poorly understood. Traditional explanations argue that teaching hinges on particular cognitive pre-requisites, such as Theory of Mind. However, such explanations conflate the function of teaching—promoting learning in others—with how it is achieved, and overlook the role of comparatively simple mechanisms like the heuristics known to underpin teaching in some non-human animals. We propose a novel framework integrating evolutionary and psychological perspectives to understand the diversity of teaching by focusing on the cognitive requirements for flexibility and sensitivity to pupil needs. Synthesizing theory and evidence across disciplines, our framework evaluates the contributions of different mechanisms in determining who and what is taught, and how teaching is achieved. This allows us to understand the cognitive foundations of teaching across different species, in diverse human societies, and neurodiverse populations.

1 | Introduction

The ecological dominance of the human species is often ascribed to our ability to innovate, retain, and build upon cultural traits [1–3]. The progressive improvement in the efficacy of human cultural products, such as tools and technologies, commonly termed Cumulative Cultural Evolution (CCE) [4], is unmatched in the animal kingdom and has allowed our species to colonize and transform the globe [5]. Explanations for the human capacity for CCE commonly focus on our use of high-fidelity forms of social learning that allow cultural traits to be transmitted and built upon in a ratchet-like manner [2, 6, 7]. In particular, the flexibility and sensitivity of human teaching are often thought to be critical for CCE, allowing us to pass on information to differing audiences across a vast range of contexts, enabling the acquisition of skills and knowledge that would be difficult to learn alone [1, 8–12].

The definition of teaching has long been contentious. Traditionally, psychologists have tended to favor definitions that impose a priori requirements for particular cognitive mechanisms (see [13]). For instance, Tomasello et al. [2] argue that teaching requires joint attention and representations of others' mental states (i.e., Theory of Mind [ToM]). However, definitions that specify cognitive pre-requisites risk conflating what the behavior is for (the function), with how it is achieved (the mechanism) (*sensu* [14]). Moreover, such definitions are typically based on forms of teaching prevalent in Western, industrialized societies and necessarily preclude potential examples of teaching in other human societies, neurodiverse human populations, and non-human animals [15]. Definitions that hinge on specific mechanisms also exclude the possibility that multiple mechanisms may be involved in teaching behavior and that these mechanisms may differ across species, individuals, and contexts. We therefore favor a functional definition which classifies teaching as a form of cooperative behavior that functions to promote learning in others [13, 16]. Following Caro and Hauser [17], we identify teaching operationally according to

three criteria: (1) an individual (teacher) modifies their behavior in the presence of naïve observers (pupils), (2) the teacher incurs some cost, or derives no immediate benefit, and (3) the pupil develops a new skill or knowledge that they would otherwise not have learned, or that they would have learned more slowly or less efficiently. This view of teaching is neutral with regard to the underlying mechanisms and, therefore, facilitates unbiased investigation of the cognitive foundations of teaching within and across species.

Viewed from this functional perspective, there is now strong experimental evidence of teaching in a number of non-human animal species. For example, meerkats (*Suricata suricata*) teach naïve pups prey-handling skills by gradually introducing them to live prey. Very young pups are typically provisioned with dead prey items, but as they grow older, adults increasingly provide them with live, modified prey (e.g., scorpions with the sting bitten off) or fully intact prey. Giving away live prey that may escape is costly for adults, but provides pups with otherwise unavailable opportunities to handle live prey, resulting in improvements in pups' hunting skills [18]. Similarly strong experimental evidence for Caro and Hauser's [17] criteria has also been reported in a handful of other species. In pied babblers (*Turdoides bicolor*), a cooperatively breeding bird (where, like in meerkat societies, non-parents contribute to raising young), adults produce distinctive "purr" calls while delivering food to nestling chicks. This behavior is of no immediate benefit to the adult, but causes chicks to learn to associate these calls with food. Adults later exploit this association to encourage chicks to fledge the nest and lead fledglings away from danger [19, 20]. In tandem-running ants (*Temnothorax albipennis* [21]), knowledgeable individuals returning to the colony from a newly discovered food or nest site will recruit any available worker and gradually lead it, via a process known as tandem-running, to the resource, providing opportunities for the recruit to learn the route by exploring landmarks along the way. Superb fairy wrens (*Malurus cyaneus* [22]) sing "vocal passwords" to chicks in the egg; after hatching, this then allows genetic offspring to distinguish themselves from parasitic cuckoo nestlings. Finally, zebra finches (*Taeniopygia guttata* [23]) modify their song in the presence of young chicks, aiding their vocal learning. Further, albeit not fully conclusive, evidence for teaching comes from observational studies across a range of bird and mammal species in contexts ranging from the development of vocal communication (e.g., [24, 25]), to navigation [26], migration routes [27], and foraging techniques, including tool use [28]. See Arbon and Thornton [29], Lee et al. [30], and Thornton and Raihani [16, 31] for reviews of these behaviors. This body of evidence makes clear that, from a functional perspective, teaching is not a uniquely human behavior.

Nevertheless, it is clear that there are substantial differences between teaching in humans and that seen in other species. In particular, whereas non-human teaching is typically restricted to narrow functional contexts, with limited adjustment to different pupils, human teaching spans a far broader range of domains and appears more responsive to variation in pupil characteristics. In the following section, we consider how these differences allow us to structure variation in teaching along lines of contextual breadth and responsiveness to pupils.

2 | A Framework for the Cognitive Foundations of Teaching

We propose a two-axis Flexibility/Sensitivity (F/S) framework to conceptualize the cognitive requirements of different forms of teaching across and within taxa (see Figure 1) and shed light on mechanisms that are shared across species or are unique to humans. Specifically, we focus on the cognitive "toolkits" that underpin the ability to teach flexibly across different contexts and with a high degree of sensitivity to pupil needs.

Under our framework, flexibility can be operationalized as the number of contexts in which teaching occurs. For example, adult meerkats only teach pups how to handle difficult-to-catch prey [18]. Other skills, like selecting where to search for food [32], what types of food to eat [33], or how to respond to predators [34] are not taught: instead, pups acquire them through individual experience and inadvertent social learning. Indeed, all firm examples of teaching in non-human animals are restricted to a single adaptive context closely linked to survival or reproductive success. Some anecdotal and observational studies do hint at more flexibility some in non-human species, for example in foraging and communication contexts in dolphins [25, 35] and in the development of different forms of tool use in chimpanzees (for nut-cracking [36]; and termite-gathering [37]. However, current evidence remains inconclusive. By contrast, though some teachers may specialize in particular subjects, the potential flexibility of human teaching is clearly almost unbounded.

Sensitivity in teaching may be operationalized as the degree of plasticity in teacher behavior in response to the characteristics, behavior, and knowledge of pupils. In pied babblers, this is highly limited: adults use the same, relatively stereotyped behavior (purr-calling) to teach all young [20]. Meerkats, on the other hand, modify their presentation of prey as pups get older [18]. There are suggestions that some species may go further and adjust their teaching according to individual pupils' skills or informational needs: chimpanzees have been reported to provide greater help to offspring learning about complex rather than simple tools [37], though whether teaching is involved remains open to debate [38]. Meanwhile, in humans, the degree of sensitivity can vary between teachers and between contexts: for instance, compared to a one-on-one tutorial, an academic lecturing in a public forum is likely to show less sensitivity to pupil needs.

Thus, teaching varies continuously along the axes of flexibility and sensitivity, with non-human examples typically clustering at low values and human teaching occupying the upper range (Figure 1). This pattern is likely to be underpinned to a substantial degree by genetic variation shaped by natural selection. However, this does not imply that the mechanisms underpinning human teaching arose de novo in the hominin lineage as discrete cognitive "instincts," as is sometimes proposed (e.g., [39]). Rather, natural selection may have fine-tuned domain-general mechanisms of perception, attention, learning, and memory [40], which are subsequently shaped by developmental influences, including cultural norms, within and across [41]. Although such gene–environment interactions remain

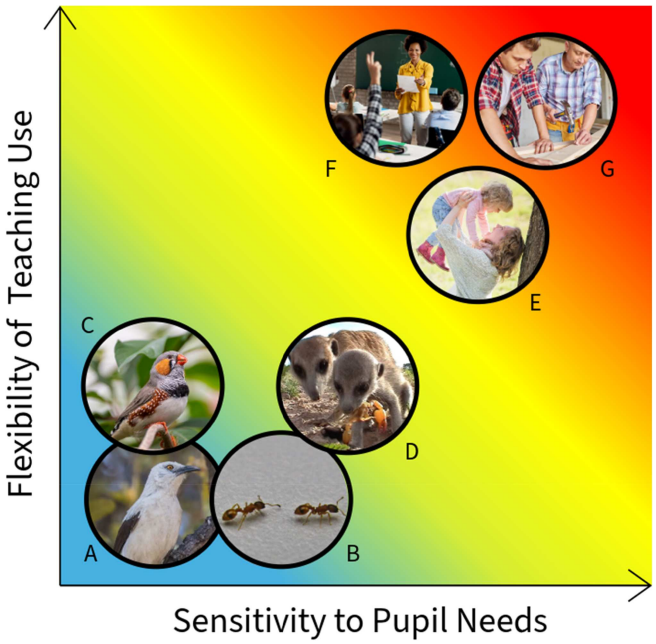

FIGURE 1 | The Flexibility/Sensitivity (F/S) framework for the cognitive basis of teaching. The use of differing cognitive mechanisms is reflected in the cross-contextual flexibility of teaching and the degree of sensitivity to pupil needs within and across species. Known cases of teaching in non-human animals all occur in a single, adaptive context, showing limited flexibility and sensitivity. Pied babblers and tandem-running ants use relatively fixed action patterns to teach declarative information. Pied babblers (A) condition chicks to associate distinctive "purr" purr calls by pairing calls with food delivery. (B) *Temnothorax albipennis* ants use "tandem-running" to teach nestmates routes to foraging and nest sites, sensitively modifying their speed in response to their pupils' progress and the value of the goal. Other animals teach procedural information: (C) Adult male zebra finches produce visual displays and modify their song in the presence of naïve chicks, thereby promoting chick song learning, while (D) adult meerkats are sensitive to cues of vocal cues of pups' age, flexibly modifying their prey-provisioning behavior to promote learning of hunting skills. Human teaching shows greater flexibility and sensitivity, but this varies across contexts. In humans, infant-directed speech (E) serves as a form of teaching in the specific context of infant vocal development. This is similar to zebra finches and pied babblers where pupil need is not adjusted for, whereas humans show sensitivity to a range of infants' responses (e.g., ostensive cues, facial expression, infant vocalizations). (F) Class-room teaching and (G) one-on-one tuition may cover an almost infinite range of topics, but the former may be tailored toward group-level needs while the latter may involve greater sensitivity to individual pupils' changing competence or knowledge. Further details of examples, including references, are given in the main text. Figure produced in Adobe Express, all embedded images reused with permission. *Image permissions: A and D from Alex Thornton, B and C from Wikimedia Commons, E from Pixabay, F and G from Freepik. Descriptive caption: A two-axes graph is shown. The *X*-axis is increasing degrees of sensitivity to pupil needs, and the *Y*-axis is increasing flexibility of teaching use. Within the body of the graph, seven examples are given as depicted by images of non-human or human teaching, placed according to their relative degrees of flexible and sensitive teaching in contrast with other examples. The background color is a gradient spectrum, proceeding from blue (bottom left, least flexibility and sensitivity), to yellow and then red (top right, most flexibility and sensitivity).

poorly understood, we suggest that higher levels of flexibility and sensitivity reflect greater developmental plasticity, including a likely role for culturally transmitted variation in shaping teaching. Indeed, it is notable that compared to other animals, human teaching remarkably responsive to conditions encountered throughout life, including experience with younger siblings, social norms within families and communities, and institutional expectations [41, 42]. Such plasticity likely underpins the exceptional scope of human teaching, facilitating the transmission and accumulation of complex cultural knowledge [11, 13, 43], and so supporting cumulative culture.

In sum, the F/S framework moves us away from a priori assumptions about the mechanisms required for teaching and instead provides a broader perspective. This allows us to consider the range of cognitive processes that may underpin teaching behavior and to design studies that test their contributions. For example, by manipulating opportunities to teach across contexts or the availability of cues about pupil age, skill, or competence, we can evaluate how different mechanisms enable or constrain observed levels of flexibility and sensitivity. Throughout this paper, we use the F/S framework to analyze contrasting examples of teaching across taxa, drawing on research from a wide range of fields. Specifically, we examine the mechanisms that shape decisions about who to teach, what to teach, and how to teach.

3 | Who to Teach?

Across a population, individuals' knowledge and skill levels will vary. Consequently, potential teachers must be selective in deciding whom they should invest time and effort into teaching. Known examples of teaching in non-human species are typically directed toward dependent young or close kin. In contrast, humans regularly teach both kin and non-kin across a wide range of ages and competencies, implying important differences in the mechanisms used to select potential pupils. Given the goal of teaching is to facilitate learning (criterion 3 of the functional definition of teaching), one rule any teacher might follow is to teach those who lack knowledge. How might a teacher identify where there is a knowledge gap to be filled?

In all known examples of teaching in non-human vertebrates, the recipients of teaching are exclusively immature individuals. Theory predicts that teaching will be favored by selection when the costs of teaching are outweighed by the fitness benefits gained when pupils learn [10, 16]. Young vertebrates generally have the most to gain from teaching due to their lack of experience, so related adults may benefit by helping them to learn vital knowledge and skills. In contrast, among *T. albipennis* rock ants, where relatives work together to raise the queen's offspring, teaching serves to facilitate information transmission among adult workers [21] and is determined not by age but by experience in tandem-running [44].

In stark contrast to the forms of teacher–pupil selection seen in other species, human teaching frequently occurs not only between non-related individuals but also between individuals of similar ages and experience. This apparent chasm between human and non-human teachers points to cognitive mechanisms

that allow humans to reliably identify suitable pupils, going beyond teaching only juveniles or kin. Arguably the most influential view is that ToM—inference of the beliefs, desires, and knowledge of others (e.g., [45])—is crucial to identifying who to teach. From this perspective, ToM is often seen as a necessary pre-requisite for teaching: unless we can recognize and intentionally correct a lack of knowledge or understanding in others, we cannot teach [2, 12, 46–53]. Indeed, following the seminal paper by Tomasello et al. [2], ToM has commonly been treated as a fundamental component of our ability to acquire and transmit cultural information. Tomasello et al. [2] argued on the basis of evidence that children diagnosed with Autism Spectrum Disorder exhibit impoverished ToM [54], stating "Autistic children thus show little or no evidence of cultural learning: we believe that this is due to the absence, or seriously diminished quality, of human social cognition in this population" (p. 503). Tomasello et al. [2] further cite observations of a lack of interest in joint attention (i.e., sharing another person's focus on external stimuli [55]), symbolic play (e.g., simulating adult roles [56]), and an atypical conception of others as independent mental agents [54] in young autistic people, as crucial elements that hinder the absorption of culturally relevant information such as shared social rules or language use [57]. Tomasello et al. [2] went as far as to argue that autistic people may be viewed as "acultural" (p. 504) beings (see [58] for a response). Similar views have since become embedded in the discourse around the uniqueness of human teaching. For instance, Strauss et al. [53] claim that "recognition of the learner's lack of knowledge seems to be a necessary prerequisite for any attempt to teach" (p. 1484). Reflecting this perspective, Knutsen et al. [59] report that 6–8-year-old autistic children are impaired in their recognition of teaching as an intentional effort to address gaps in knowledge between teachers and learners. The implication, therefore, is that those with non-neurotypical ToM will struggle to identify where naïve members of their group are lacking in knowledge and, therefore, will be unable or unmotivated to teach.

The notion of ToM as an a priori requirement for teaching is clearly undermined by the evidence for teaching in non-human animals. We would argue that it has also led us to neglect the potential role of other mechanisms in human teaching. Indeed, cross-cultural developmental evidence reveals substantial variation in the degree to which people take others' knowledge status into account when teaching [60], implying that teaching does not rely on a single, universal ToM-based mechanism. One possibility is that decisions regarding who to teach might, in some instances, rely on the use of simple heuristics, or rules of thumb [61]. Among non-human vertebrates, evidence indicates that pupil selection is determined not by knowledge attribution, but through a simple heuristic of "teach dependent young," based on salient cues of pupil age. For example, adult zebra finches modify their songs specifically in the presence of juveniles to aid song learning [23]. Similar acoustic parallels have been observed recently in greater sac-winged bats [24] and bottlenose dolphins [25]. Here, teachers are not known to track the progress of competency or their pupils' skills/knowledge, but instead their teaching behavior is triggered merely by the presence of young.

Chen et al. [23] highlight the striking parallel between zebra finch song teaching and human infant-directed speech (IDS). In humans, IDS is characterized by a simplified and tonally exaggerated speech, is used cross-culturally [62] and seemingly reflexively by adults when speaking to young infants [63], or even robots with infant-like features [64]. Much as zebra finch song tutors promote song-learning in juveniles, human IDS has been linked closely to speech development in infants [65, 66]. Indeed, in cases of post-partum depression where IDS use is impaired, a lack of prosodic exaggeration is linked to poorer associative learning in infants [67], which Sohr-Preston and Scaramella [68] speculate may be a factor in delayed language acquisition amongst this group, but this warrants further investigation. From a functional perspective, therefore, IDS is a form of teaching, fulfilling Caro and Hauser's [17] criteria. From a cognitive perspective, the fact that people use IDS reflexively when speaking to infants, robots, and even, to some degree, to pets [69] implies it may not be contingent on attribution of ignorance. Instead, humans may follow simple heuristics to determine whom to target with this form of teaching: for example, a rule like "use this speech pattern in response to infant-like stimuli" may be sufficient to support infants' acquisition of key communication skills. However, as we will see in Section 5, precisely how humans deploy IDS may be fine-tuned through experience and show great sensitivity to pupils' needs.

Beyond IDS, age-based heuristics may also influence decisions as to whom to target in other forms of human teaching. In BaYaka foragers, for example, older pupils received less teaching of spear-hunting skills and more opportunities to lead hunts, but teachers' behavior does not appear to be related to individual pupils' level of experience [70]. In other contexts, heuristical approaches to teaching may involve the integration of multiple heuristics into super-heuristic structures. Smith and Trainor [71] demonstrated how mothers dynamically raised the pitch of their voice when observing their infant responding positively to speech, as opposed to a negative response. Here, parents may be operating on a heuristic of "during talk, raise pitch when my infant smiles." The integration of multiple heuristics may also be relevant when handling multiple pupils with varying teaching needs. For instance, social norms and institutional obligations govern much of our behavior, including expectations about the likely behaviors and needs of others [72]. In formalized classroom teaching, human cultural norms may act as a broad heuristic, but we may then adopt multiple additional heuristics where necessary when deciding who to target with different forms of teaching. For example, a teacher might follow one heuristic structure for a typical group of adolescent pupils (e.g., "teach year nine classes in this way"), or modify the teaching approach for variations on this group with other heuristics ("teach more able students in this way," "teach unruly students in this way") depending on the perceived need of the group. In combining heuristics, a teacher might efficiently generate greater sensitivity to pupil need (see Figure 1), without necessarily needing to deploy more complex cognitive tools. A more deliberated teaching approach may be deployed for pupils who do not fit the status quo, where the utilization of other cognitive mechanisms, such as ToM, might then be favored.

Contemporary observations of autistic people and other neurodivergent populations have further highlighted the viability of alternative cognitive styles and mechanisms to contribute to teaching. Far from being "acultural" [2, 58], autistic people can be highly accomplished teachers [73]. Indeed, in Crompton

et al. [74], groups of autistic adults were just as effective as non-autistic groups at retaining information about a story when that information was passed from one individual to the next in a diffusion chain. Further still, when groups featured "mixed" pairs (i.e., autistic participants communicate only with non-autistic participants and vice versa), a significantly steeper decline in information retention was found. These findings suggest that any difference in intuitive reasoning is not necessarily a barrier to effective teaching, and highlight an urgent need for research to determine how teaching approach may be shaped by one's cognitive skillset.

Crucially, decisions about who to teach could be based not on an understanding of what potential pupils know, but on what they do—that is, on behavior-reading rather than mind-reading. Mistakes and a lack of competence are often observable, so behavior can provide a valuable indicator of the need for teaching. Here again, heuristics could play an important role (e.g., "teach those who make mistakes"), but teachers may also acquire experience about the characteristics of potential pupils who are likely to benefit from teaching, both through direct interaction with pupils and through exposure to cultural or institutional norms. This is not to imply that ToM is unimportant—the ability to think about what others know or believe is likely to allow greater sensitivity to pupils' needs and to pre-empt the need for teaching. However, the role of ToM (or indeed any mechanism) cannot be assumed, but must be tested through careful experimentation.

4 | What Should Be Taught?

As we have noted, examples of teaching in non-human are restricted to essential, fitness-related skills [16, 18, 31]: meerkat pups are taught to hunt [18], pied babbler chicks are taught to follow adults [20], and tandem-running ants are taught foraging routes [21]. Given that teaching entails inherent costs [17], knowledgeable individuals are only expected to invest in teaching information or skills that are of high fitness value and would be difficult or impossible to acquire through trial and error or observational learning alone—that is, where the "utility" of teaching [16] is high (see also [10]). This allows us to understand the distribution of teaching in the animal kingdom. For instance, observational reports of teaching are common in felids, which, like meerkats, hunt alone but are absent in pack-hunting canids [16]. Crucially, juvenile solitary hunters like cheetahs lack opportunities to handle live prey unless provisioned by adults [75], whereas pack hunters can gain direct hunting experience by joining hunting parties without the need for adults to modify their behavior, so the utility of teaching is relatively low [16]. The relatively restricted range of conditions under which the benefits of teaching outweigh the costs may also explain why non-human teachers teach only in a single adaptive context [10, 34]: that is, the flexibility of teaching is low (see Figure 1).

In contrast, humans teach across an almost limitless range of contexts—how to speak, read, and write, how to kick a football or sharpen a spear, how to cooperate with or deceive others, how gravity works, and so on. Thus, more or less every crumb of attainable knowledge may, in principle, be passed between humans, in part or whole, through teaching. Theoretical modeling by Fogarty et al. [10] suggests this gulf in flexibility and application of teaching compared to other animals is a consequence of human cumulative culture. According to this model, as the ratchet effect cranks up the complexity of cultural artefacts, teaching becomes more necessary to maintain the faithful replication of traits between individuals. Empirical evidence for this conclusion is provided by Lucas et al. [11], who observed the effect of different learning conditions (teaching, imitation, emulation, or asocial) in transmission chains of people tasked with building tools of differing complexity. Across all conditions, the tools became increasingly effective as people learned from one another, implying that teaching was not strictly necessary for CCE to arise. However, teaching became advantageous over other forms of learning when the assembly process for the tool was causally opaque (see also [43]). This is consistent with the argument that growing reliance on tools of increasing complexity generated selection for cognitive mechanisms enabling flexible teaching [10, 11, 43, 76]. We suggest that this greater flexibility is likely to co-evolve, through both genetic and cultural processes, with increased sensitivity to pupil needs, enhancing the efficiency of information transfer and supporting the retention and refinement of innovations needed for cumulative culture.

Given the wealth of opportunities for teaching, human teachers may need to decide precisely what should be taught, evaluating when it is worth investing time and effort in helping others to learn [10]. While simple heuristics may suffice in some cases (e.g., teaching infants to talk), successful information transmission will often be determined by a teacher's capacity for considering the costs and rewards associated with the lesson to be taught—that is, the utility value for their pupil. Jara-Ettinger et al. [77] frame this decision-making process as a "utility calculus": a cognitive framework that incorporates behavioral observations and inferences into assessments of the value of engaging in teaching, which, they argue, emerges rapidly in early childhood. Bridgers et al. [78] illustrate how utility calculus may be applied in a pedagogical context, where 5- to 7-year-olds chose which of two toys an adult experimenter should select for teaching to a naïve learner, and which should be left to be learned through exploration alone. The choice of toys varied in how difficult it was to discover how they worked ("discovery cost") and in their appeal ("discovery reward") as toys. The behavioral results were then compared to various predictive models of behavior based on whether the children incorporate cost, reward, both, or neither when making decisions. The results supported a model in which children factor in both cost and reward, as compared to models that incorporate only one or the other. This outcome suggests that such cost-benefit reasoning plays an important role in enabling flexible human teaching. Nevertheless, further work is needed to understand how the use of this framework varies across cultures and developmental backgrounds. Moreover, a potential limitation of the utility calculus account is that it leans heavily on social reasoning as the driver of utility value assessments and does not address another skill which may have a significant role: technical reasoning.

Technical reasoning describes our ability to understand how systems or mechanisms work. Some researchers (e.g., [79, 80]) have argued that this skill forms the bedrock for the ever-increasing

complexity of human cumulative culture, and by extension may therefore contribute to our evaluations of utility value. In the Bridgers et al. [78] study, young children had been given hands-on experience with different toys before evaluating whether teaching was necessary on the basis of causal opacity—that is, whether or not the method to "activate" the toy was immediately obvious from casual observation. The decisions of these young children may therefore have hinged on their technical understanding of the toys, that is, the children could compare the methods of activation between the toys and mentally simulate the complexity of the task at hand. Some authors suggest that the capacity for understanding the abstract relations between representational objects and physical ones is a fundamental cognitive difference between the minds of humans and other animals [80]. Whether this difference is one of degree or of kind remains a matter of great debate [81], but the versatility of human technical reasoning is likely to facilitate not only the ability to solve complex problems flexibly across different contexts, but also to determine when others need to be taught.

In addition to technical reasoning abilities, utility value assessments may also be facilitated by a suite of other cognitive abilities. One such candidate contributor is our ability to engage in "mental time travel," that is to mentally recreate one's past experiences and use them to anticipate what may happen in the future [82]. Vale et al. [83] suggest that mental time travel allows us to predict the potential needs of pupils, allowing us to adjust our "teaching capabilities" (p. 226) and prepare pupils for future probable events based on our own experiences. A parent who had used tools to obtain hard-to-obtain foods during times of famine might, for example, teach their offspring to use the same tools in anticipation of future times of need. Evidence for mental time travel in non-human animals is contentious and typically restricted to narrow ecological contexts (see [81, 84] for reviews). For instance, Western scrub-jays (*Aphelocoma californica*) will cache food in locations where they anticipate they will be hungry the next morning [85, 86]. Similarly, apes will choose a tool that can be used to access a highly preferred reward in the future over one that will provide a less prized reward immediately [87]. However, of the species for which there is evidence of mental time travel, none unequivocally fulfill the criteria for the functional definition of teaching ([16, 17]; see also [38]). Perhaps, as Laland and Seed [81] suggest, the distinctiveness of human mental time travel arises through interaction with other abilities such as metacognition (reflecting on one's own mental states) and language.

Together, all of these abilities (i.e., social, technical reasoning, and mental time travel) are likely to contribute to the flexibility of human teaching. Further work is now needed to understand how experience of teacher–pupil interactions, social norms, and institutional expectations shape their development, the potential interplay between reasoning about the functional utility of teaching (enabling flexible teaching across contexts) and social reasoning about the desires or knowledge states of pupils (potentially enhancing the sensitivity of teaching to pupil needs).

5 | How to Teach?

Humans and non-humans also differ in what teachers must do to facilitate learning. A key determinant of teaching method is the type of knowledge the teacher imparts upon their pupil. Thornton and Raihani [16] distinguish between two forms of teaching in non-human animals: fixed and progressive (see Figure 1). In fixed teaching, teachers perform a single kind of behavior to promote learning of declarative knowledge of content or facts ("knowing that") as seen in pied babblers, where teaching consists solely of conditioning chicks to follow purr-calling adults after fledging (see sidebar [19]). In contrast, to facilitate learning of procedural knowledge ("knowing how") teachers must alter their behavior as pupils' skills develop, as occurs when meerkats provide dead prey to young pups and increasingly intact prey to older pups [18]. Playback experiments show that meerkats' sensitivity to their pupils' changing needs is based on responsiveness to age-related changes in pups' begging calls: adults tend to bring dead prey if they hear the calls of young pups and live prey if they hear older pups. Through this simple heuristic decision rule, they thus provide pups with age-appropriate opportunities to learn to handle potentially dangerous prey. In both fixed and progressive teaching, there must be a degree of feedback between teachers and pupils [16, 88]. Pied babbler chicks will not learn unless they attend to the purr calls adults produce in their presence [19]. Similarly, meerkat teaching depends not only on adults' sensitivity to changes in the acoustic structure of pups' calls but also on pups' responsiveness to the sight of adults with food. Nevertheless, the heuristic mechanism underpinning meerkat teaching behavior allows for only limited sensitivity (see Figure 1); adults respond to acoustic cues of pup age, but there is no evidence that they track the changing skill levels of individual pupils and adjust how they teach accordingly [18, 89].

In the literature on human teaching, mechanisms underpinning the interplay between teacher and pupil behavior are at the core of the influential theory of natural pedagogy. Csibra and Gergely [90] propose three communicative tenets that teaching dyads (teacher and pupil) must abide by as a minimum to engage in what they term "natural pedagogy": ostension, reference, and relevance. In brief, dyads require mechanisms to establish a mutual understanding that teacher and pupil are ready to engage in a communicative exchange (ostension), that they have a shared recognition of the teaching subject (reference), and that the subject concerns novel and relevant information for the pupil (relevance). Some examples of these behaviors include eye contact, gaze-shifting, pointing [90], but also IDS [91]. Observational work illustrates how these communicative cues translate into pedagogical interactions. For example, in an analysis of parent–child play sessions, Sage and Baldwin [92] identified three components: "demonstrative actions" (e.g., performing an action with a new toy in view of the child), "information provision" (e.g., testing their child's knowledge of a toy with questions), and "joint attention" (e.g., playing with the same item as the child). Critically, such interactions are thought to promote the acquisition of generalizable knowledge, sometimes from a single interaction [91, 93]. Consistent with this, 18-month-olds not only learn an adult's preference for a novel object but also generalize this preference to others if it is communicated with ostensive cues like gaze, pointing, and IDS [94]. A recent meta-analysis further suggests that pedagogical contexts elicit distinct teaching-oriented behaviors, with children becoming more informative when prompted to teach compared to non-pedagogical contexts [95].

The benefits of the generalization biases for ostensive cues are twofold. First, it may help to minimize the expenditure of teaching effort by enabling learners to apply acquired knowledge across contexts. Second, it expands opportunities for learning by decoupling teaching from specific environmental conditions. Unlike non-human systems, where teaching is typically tied to particular contexts and conditions (e.g., meerkats only teach if they have appropriate prey to provision [18]), humans can deploy teaching flexibly according to the demands or opportunities presented by the environmental context (see Figure 1). For example, if a parent points at a cow in a field and tells their child "Cows go moo," the child will recognize that this rule applies not just to the cow they can see, but all other cows. Similarly, a parent might show their child a picture of a cow, tell them that "cows go moo," and still reliably expect the child to understand the generalization.

Anthropological evidence lends further support to the widespread occurrence of behaviors consistent with natural pedagogy across diverse societies, including in small-scale hunter-gatherer groups (e.g., [96–98]). However, developmental and cross-cultural research indicates that reliance on such pedagogical cues varies across populations, with some cultures placing greater emphasis on learning through observation and participation rather than explicit instruction [13, 99]. This suggests that while the mechanisms underlying natural pedagogy may be widespread, their expression and relative importance are shaped by cultural context (see also [41]). Taken together, these findings indicate that natural pedagogy provides a powerful, though not exhaustive, account of the mechanisms underpinning human teaching, helping to explain why its sensitivity and flexibility far exceed those observed in other animals.

Another crucial element that distinguishes human teaching from that of other animals is our ability to improve and refine how we teach by learning from pupil feedback. Returning to the meerkat example, adults do monitor pups' prey-handling efforts and will retrieve prey that escapes or further incapacitate the prey if the pup is struggling [18]. They do not, however, change how they teach as they gain experience of caring for pups. In other words, meerkats do not learn to teach: regardless of age, adults who have previously cared for (and taught) pups behave no differently to those serving as teacher for the first time [89]. By contrast, human teaching is typically shaped by experience from teacher–pupil interactions, even when teaching decisions are governed by relatively simple heuristics. More generally, this suggests that human teaching behavior is largely co-created through social interactions between teachers and learners. For instance, although the production of IDS appears to be a reflexive response to infant-like stimuli, adults modify the way they use IDS based on feedback from infants [71]. Parents also adjust their IDS across the first 6 months of infant life [100], and to dynamically fine-tune it to their child's developing language skills [101], suggesting a role in facilitating the incremental improvements in infants' abilities. Experience further shapes these behaviors: having younger siblings [102] or previous children [103] changes IDS profiles, raising the possibility that people learn from their caregiving experience to shape their speech for the benefit of language development more effectively. The feedback between teachers and pupils may also help to explain variation in infant learning: for example, Kuhl et al. [104] show that developmental delays in language acquisition by autistic children are linked to reduced attention and neural responses to IDS (for review, see [105]). One possibility is that reduced responsiveness disrupts the feedback loop between infant and caregiver, leading to lower levels of IDS input. However, this hypothesis remains to be tested directly.

Humans also appear to be unique in our pedagogical use of social tools by exploiting the effectiveness of reward and punishment in modulating the behavior of others. Ho et al. [106] frame this as building on the propensity to assign positive and negative values to actions based on their outcomes. They suggest that humans use "evaluative feedback" during social interactions to assign value to actions, through a process of "reward feedback" and "value updating." The fundamental basis of this feedback likely lies in reinforcement learning, a phylogenetically ancient process through which organisms assign value to actions based on reward and punishment, with evolution and development fine-tuning the extent to which social cues, such as approval or disapproval, function as reinforcers. For example, human teachers communicate their perceived value of an action (e.g., a toddler eating a disliked vegetable for dinner) by using social cues as feedback (e.g., smiling and clapping) to trigger a reward in their pupil (e.g., delight), leading to a change in behavior. A distinctive feature of this form of pedagogical action is the capacity for teachers to guide learners toward potentially valuable outcomes, even if the benefits of the preceding actions are not immediately apparent to the pupil. This supports the great flexibility of human teaching, facilitating access to a wide range of otherwise difficult-to-acquire skills (Figure 1). Building on these reinforcement processes, Ho et al. [106] highlight the role of inferring others' mental states (i.e., ToM) in enabling effective evaluative feedback. In their view, limited or absent ToM in pupils would constrain their ability to infer pedagogical intent (i.e., ostension) and to interpret the action values of others, thus reducing the likelihood of adopting new behaviors (e.g., sharing) that lead to instrumental and intrinsic rewards (e.g., peer approval). Consistent with this, evaluative feedback methods seem to be widespread in human societies [107, 108], whereas comparable evidence in non-human remains is limited and support for ToM is equivocal (see [109]). However, because Ho et al. [106] focus mainly on the cognition of learners rather than teachers, further research is necessary to ascertain how diverse teachers deploy evaluative feedback and the extent to which this relies on ostensive cues and ToM-based inferences.

Humans' uniquely flexible pedagogical approach clearly harnesses a diverse and versatile cognitive toolkit, but the effectiveness of all these tools is greatly enhanced by our use of language. While many animals have sophisticated systems of vocal communication, true language, where a finite number of elements are recombined to generate an infinite number of meanings, is unique to humans. Language is, therefore, an intrinsic component of human teaching. Indeed, some scholars argue that language may have evolved to enable the teaching of causally opaque information [11, 43,

76, 110]. As our reliance upon language grew, so too would our necessity for a mechanism to promote language acquisition. In this vein, IDS can be seen as a central mechanism for the perpetuation of teaching as a key driver of CCE. Critically, language unlocks a range of potential learning outcomes that would otherwise be unobtainable with other communicative strategies. Recent empirical work has highlighted the efficacy of language over social learning via imitation and emulation in promoting the development of complex skills [11, 43]. One crucial advantage of language over other communicative methods may be in the ability to convey both positive and *negative* instruction ([11]; see also [111]). In other words, language enables a teacher to communicate instruction relating to what *not* to do. Through discouragement, a teacher gains the ability to steer pupils away from negative outcomes (e.g., "do not eat the berries from this plant, they will make you unwell") or increase the efficiency of their pupil's learning (e.g., "do not use this kind of stone, it will blunt your spearhead").

Language has a number of further advantages to teachers beyond enabling the teaching of what not to do. Much of human behavior is governed by social norms and institutional expectations and, according to cultural-evolutionary models, explicit conceptualizations about the actual and expected behavior of others are represented through the medium of language [72]. For instance, social rules and conventions can be taught through conversation. To elaborate on a descriptive example used in Ho et al. [106], a father trying to encourage his daughter to share might shower her with verbal praise if she allows other children to use her toys or verbally scold her if she refuses. In addition, anthropological evidence suggests that storytelling, another deployment of language, plays a crucial role in the transmission and maintenance of generalizable social knowledge and customs [112]. Lastly, the deployment of recorded or written language on human teaching cannot be ignored. This capacity solidifies the fidelity of transfer of cultural artefacts and thus enables enormous potential for the transmission of information and behavior within and across generations, and thus for cumulative culture change. In the context of the range of pedagogical mechanisms discussed in this review, it is not difficult to see how a scribe might sensitively target their pupils' or readers' needs when committing information to text. Furthermore, language deployed in this way enables teaching to occur for an infinite range of topics and across both live (e.g., classroom or presentational teaching to live audiences) and remote (e.g., through books or online videos) contexts. Ultimately, the levels of teaching flexibility and sensitivity achieved by humans are only accessible through the advent of language.

6 | Conclusion

Historically, researchers have tended to overestimate the complexity of cognitive processes involved in human behavior, a phenomenon Buckner [113] terms "anthropofabulation." Previous assessments of the cognitive foundations of human teaching fall foul of this assumption, tending to ignore evidence from non-human animals which show that simple heuristics can allow effective teaching without the need for sophisticated cognitive processes. Nevertheless, non-human teaching appears to exhibit minimal degrees of flexibility and sensitivity when compared to humans. Research on the cognitive underpinnings of human teaching is still in its infancy, but in some cases (e.g., IDS), relatively simple heuristics may also play an important role. For this reason, we advocate a "minimal cognition" approach to understanding human teaching. That is, there is much to be gained by first examining the value and limitations of relatively simple mechanisms before then considering the role of additional mechanisms. In Tables 1 and 2 below, we summarize the contributions of mechanisms discussed in the course of this review and illustrate how these tools may enable various degrees of flexibility and sensitivity. Accordingly, we seek to move away from "silver bullet" explanations for the uniqueness of human teaching, which typically cite the utilization of complex cognitive mechanisms such as ToM (e.g., [53]) as critical prerequisites for any type of teaching to occur.

Future research on human teaching should examine the variety of cognitive mechanisms at the teacher's disposal, and how these enable flexible and sensitive teaching. One potentially fruitful avenue of investigation here would be to investigate differing approaches to teaching in neurodiverse and neurotypical populations (e.g., as demonstrated in [74]). Studies of the cognitive basis of teaching often focus on comparing children at different developmental stages, often between the ages of 2 and 4 [47, 48, 53]. However, this approach risks confounding the development of a variety of teaching-relevant traits (e.g., language, social norms) with key mechanisms of interest (e.g., ToM). A useful complementary approach may be to investigate the role of ToM in teaching by contrasting neurotypical and autistic populations. According to previous interpretations (e.g., [58]), autistic teachers may struggle to anticipate the needs of their pupils due to an impoverished ToM. In contrast, the F/S framework for teaching proposes that a teacher may rely on tools such as single or integrated heuristics in lieu of ToM-supported pupil need assessment. If this were the case, one may expect deployment of behaviors primarily governed by heuristics, such as IDS, to be similar in neurotypical and autistic teachers, despite differences in ToM. The F/S framework provides a starting point for comparative, developmental and cross-cultural research, helping to reveal the diversity of teaching mechanisms and their relative strengths and limitations. This may also help to shed light on key debates around the role of genetically based adaptations [39, 90] versus culturally evolved mechanisms ("cognitive gadgets" [40, 115]) in the origins of human teaching. Rather than viewing these as competing explanations, we suggest that a key task is to understand how genetic, cultural, and developmental processes interact to shape the flexibility and sensitivity of teaching. In this sense, mechanisms of teaching may best be conceived not as fixed traits but rather as emergent phenotypes influenced by evolutionary processes but further co-constructed through interactions between teachers and learners within broader social and cultural environments. As this review makes clear, there is no single way to teach. The challenge now is to understand the origins and functions of the multitude of mechanisms that make an effective teacher.

TABLE 1 | A visualization of how different strategies for pupil need assessment provide increasing sensitivity and tailoring of teaching to pupil need.

Sensitivity to pupil need				
Pupil assessment strategy	**Species-specific observed example of teaching**	**Pupil information**	**Teaching response mechanism**	**Pupil knowledge or skill gain**
Simple heuristics	Tandem-running ants [1]	Olfactory cues of colony membership.	Olfactory stimulus-response cues teaching behaviour, towards colony members.	Foraging/nesting routes.
	Zebra finches [2], Greater sac-winged bats [3]* Bottlenose dolphins [4]*	Characteristic features of infancy (e.g. vocalisations, relative body size, relatively large head and eyes).	Visual/auditory cue prompts vocal adjustments addressed to dependent juveniles.	Vocalisation skills (singing). Vocalisation skills (vocal signatures). Vocalisation skills (signature whistles).
	Meerkats [5]	Characteristic features of infancy (as above).	Adults direct teaching towards dependent pups; changes in pup begging calls trigger changes in adult behaviour (provisioning prey dead or alive).	Prey handling.
	Humans –infant directed speech [6, 7]	Characteristic features of infancy (e.g. small size, relatively large head and eyes, chubby cheeks, babbling).	Visual/auditory cue prompts vocal adjustments addressed to target or misdirected towards targets with infantile characteristics (e.g. pets).	Vocalisation skills (language).
	Humans - natural pedagogy (e.g. toy function and value)	Ostensive gesture to teacher (e.g. eye-contact/pointing). [8]	Teacher provides preference information, through language or body language.	Understanding of object value.
		Pupil-expressed interest in the function of an object (e.g. playing). [9]	Teacher engages in joint attention on the object and demonstrates its function.	Understanding of object function.
↓				
Additional heuristics	Humans –infant directed speech	Infantile characteristics AND knowledge of infants through shared environment (e.g. siblings).[10]	Visual/auditory cue prompts vocal adjustments addressed to target, characterised by greater variation of fundamental frequency.	Vocalisation skills (language).
		Infantile characteristics AND prior experience of childcare provision. [11]	Visual/auditory cue prompts vocal adjustments addressed to target, accompanied by enhanced energy in production of vowel sounds.	
		Infantile characteristics AND active positive response to speech. [12]	Visual/auditory cue prompts vocal adjustments addressed to target, accompanied by dynamic increase in pitch when additionally cued by infant response.	
	Meerkats [9]	Observable cues of pupil competence – e.g. pups fumble prey or allow it to escape.	Teacher recaptures or further incapacitates prey and returns to pupil.	Prey handling.
	Humans – basket building [13, 14]	Observations of pupil performance.	Teacher assesses whether action is performed correctly, modifies behaviour to address observable pupil mistakes.	Basket manufacture/motor skills.
↓				
Group or individualised approaches	Humans – group teaching (e.g. University students)	Teacher is presented with groups of pupils with key shared characteristics and similar teaching need (e.g. year group and module).	Integration of multiple heuristics, experience of individual teacher, social norms and customs.	All pupils gain an approximately optimal degree of knowledge (e.g. information that will be in the exam).
	Humans – one-to-one tuition (e.g. driving lesson)	Teacher observes gaps or errors in knowledge/skill that pupil needs to attain (e.g. how to safely navigate a roundabout).	Teacher utilises theory of mind to interpret mental state, beliefs and knowledge of pupil. This information is used to address perceived gaps in knowledge/skill.	Pupil acquires skills specific to individual need (e.g. which lane to be in at a roundabout).

Note: Rows at the top of the figure reflect a more generalized, one-size-fits-all approach, and descending rows reflect progression toward individualized approaches to pupil need. Note that examples of utilization are non-exclusive; that is, this is just one ecological context in which that strategy may be used. Examples are complimented with numbered supporting evidence where possible; non-referenced human examples are hypothetical. References marked with an asterisk in the text highlight that current evidence is partially suggestive of teaching, as conclusive experimental evidence is lacking: 1 = [21], 2 = [23], 3* = [24], 4* = [25], 5 = [18], 6 = [62], 7 = [68], 8 = [92], 9 = [90], 10 = [100], 11 = [101], 12 = [70], 13 = [94], 14 = [11].

TABLE 2 | A visualization of how different mechanisms may enable teaching about an increasingly flexible range of topics.

Flexibility of application				
Application range	**Species-specific observed example of teaching**	**Ecological context(s)**	**Teaching response mechanism**	**Pupil knowledge or skill gain**
High utility fixed skills/behaviours.	Tandem-running ants [1]	Member of colony returns from nesting/foraging site.	Experienced members automatically and reflexively liaise with naïve members and carefully lead to nesting/foraging sites.	Foraging/nesting routes.
	Pied babblers [2]	Adult birds are raising fledglings and providing food.	Adults automatically and reflexively sing (purr call) when feeding fledglings.	Conditioned response to attend to purr call.
↓				
High utility progressive skills/behaviours.	Zebra finches [3]	Adults in the presence of dependent young.	Adults automatically and reflexively modify temporal structure of vocal production only when young are present. It remains unclear whether adults alter their pupil-directed vocalisations as young pupils get older, but male zebra finches direct more singing towards young that pay more attention, suggesting there may be progressive changes in teacher behaviour[3].	Vocalisation skills (singing).
	Greater sac-winged bats [4*]			Vocalisation skills (vocal signatures).
	Bottlenose dolphin [5*]			Vocalisation skills (whistles).
	Meerkats [6]	Adult meerkats forage and can hear begging calls of pups in the group.	Hearing begging calls triggers adults to bring captured prey to pups; the acoustic structure of begging calls (a cue of pup age) determines whether adults kill the prey before presenting it to pups.	Prey handling skills.
	Humans – infant directed speech [7, 8]	Adults in the presence of young and can observe cues of developmental stage (e.g. baby, toddler, young child).	Adults automatically and reflexively modify speech in the presence of young but modify the characteristics of IDS progressively with target age[8].	Vocalisation skills (language).
↓				
Fixed and progressive skills, cultural customs, and conceptual knowledge.	Humans	Experienced adult has identified a learning need specific to their pupil(s). Domain may include: • Technical skills (e.g. basket weaving). • Procedural skills (e.g. guitar playing). • Social norms (e.g. sharing). • Conceptual knowledge (e.g. maths).	Experienced adults will vary in teaching response to pupils, dependent on input from various mechanisms. This will include consideration of importance of the skill (e.g. utility calculus[9]), perceived ability/understanding of the pupil (e.g. heuristics[10], theory of mind[11]), and the knowledge possessed by the teacher (e.g. mental time travel[12], technical reasoning[13]), as well as the optimal mode of delivery (e.g. story-telling[14], direct/guided instruction[15], evaluative feedback[16], negative instruction[17]).	Pupils receive knowledge of teacher experience, in which ever domain the teaching occurred in.

Note: High-utility fixed skills and behaviors represent the least flexible applications of teaching (as determined by the specific ecological conditions under which they occur). High utility progressive skills represent greater flexibility because teachers modify their behavior as pupils' skills develop, but the plasticity of teacher behavior may be underpinned by simple, reflexive responses. Thereafter, the widest degree of flexibility is accessible only to humans, where teaching is deployed for any perceived learning need in the pupil(s). References are provided to highlight documentation of their occurrence in the species (1–8) and of the various factors that have input to ultra-flexible deployment of teaching (9–17). References marked with an asterisk in the text highlight that current evidence is partially suggestive of teaching, but further evidence is needed: 1 = [21], 2= [20], 3 = [18], 4 = [23], 5* = [24], 6* = [25], 7 = [62], 8 = [98], 9 = [77], 10 = [60], 11 = [2], 12 = [82], 13 = [78], 14 = [110], 15 = [114], 16 = [104], 17 = [11].

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no data sets were generated or analyzed during the current study.

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