

Review

Social learning and evolution: the cultural intelligence hypothesis

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If social learning is more efficient than independent individual exploration, animals should learn vital cultural skills exclusively, and routine skills faster, through social learning, provided they actually use social learning preferentially. Animals with opportunities for social learning indeed do so. Moreover, more frequent opportunities for social learning should boost an individual's repertoire of learned skills. This prediction is confirmed by comparisons among wild great ape populations and by social deprivation and enculturation experiments. These findings shaped the cultural intelligence hypothesis, which complements the traditional benefit hypotheses for the evolution of intelligence by specifying the conditions in which these benefits can be reaped. The evolutionary version of the hypothesis argues that species with frequent opportunities for social learning should more readily respond to selection for a greater number of learned skills. Because improved social learning also improves asocial learning, the hypothesis predicts a positive interspecific correlation between social-learning performance and individual learning ability. Variation among primates supports this prediction. The hypothesis also predicts that more heavily cultural species should be more intelligent. Preliminary tests involving birds and mammals support this prediction too. The cultural intelligence hypothesis can also account for the unusual cognitive abilities of humans, as well as our unique mechanisms of skill transfer.

Keywords: social learning; intelligence; brain size; enculturation; cross-fostering; social deprivation

1. INTRODUCTION

Intelligence is the ability to respond flexibly to new or complex situations, to learn and to innovate [1]. This ability is anchored in genetic predispositions towards faster reaction times, greater working memory, inhibitory control and greater response to novelty [2]. However, intelligence poses an evolutionary puzzle. What is heritable, and therefore malleable by natural selection, is the ability to invent effective solutions. But what contributes to fitness is not the ability to learn *per se* but rather these innovative solutions: the learned skills. Rare, serendipitous inventions may make major contributions to fitness, yet they are not heritable because their acquisition depends on many additional factors, such as the constellation of environmental conditions and sheer serendipity. Thus, selection to favour increased cognitive abilities beyond mere conditioning, towards innovative solutions to problems, i.e. true intelligence, must face a high threshold.

Nonetheless, many species are intelligent. Here, we argue this is largely because socially mediated learning (henceforth: social learning, for short) by offspring or

other relatives makes inventions heritable, thus lowering the threshold for selection on intelligence. Opportunities for social learning allow an individual to acquire many learned skills during development that it could not acquire on its own. If the social system is such that such opportunities are frequent over many generations, selection may favour increased individual learning ability, i.e. intelligence, but it should certainly favour improved social-learning ability, which, as an inevitable by-product, will improve intelligence.

The 'Vygotskian intelligence hypothesis' [3] considers cultural effects on cognitive development, and assumes them to be unique to humans [4,5]. However, several scholars have highlighted the presence of similar developmental effects in apes (e.g. [6–8]). Allan Wilson [9] went further and suggested that these cultural effects could also have affected the evolution of intelligence in our lineage and others (see also [10,11]), an idea called the cultural intelligence hypothesis by Whiten & van Schaik [12]. This hypothesis builds on a long tradition suggesting that social learning, and thus culture, may affect evolution (e.g. [13]), and can also be linked to Reader & Laland's [14] hypothesis that general behavioural flexibility, which includes social learning, may have favoured the evolution of intelligence. Here we examine both the developmental and evolutionary aspects of the cultural intelligence hypothesis.

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This hypothesis was motivated by observations on great ape cultures. Maturing chimpanzees and orang-utans would not have acquired these cultural variants, which are complex learned skills, on their own, if it were not for social learning [15–18]. This is evident for tool-assisted nut cracking in chimpanzees [19] or seed extraction from *Neesia* fruits in orang-utans, which improves fitness by bringing unusual energetic benefits but which is rarely invented and hence patchily distributed [20]. However, numerous less spectacular examples [21,22] may also contribute to fitness and may also be difficult to invent, as suggested by their patchy geographical distribution [23]. Their acquisition should, therefore, also be dependent on social learning. Comparisons across populations indicated that the set of learned (cultural) skills, in particular difficult tool-using skills, is larger where opportunities for social learning are more abundant [11,24]. But the importance of social learning may extend beyond the acquisition of cultural skills and also include non-culturally varying (i.e. universal), learned skills [18,25]. Indeed, there is little exploration and learning by maturing apes in nature that is not socially guided, suggesting they prefer social learning when possible [18]. All this suggests that they acquire their repertoire of learned skills less through individual exploration and invention (arrow labelled 1 in figure 1) than through social learning (arrow 2; see also [26]). Similar processes may occur in capuchin monkeys [27,28], and possibly to some extent in other non-primate lineages (cf. [29]). After having reviewed this developmental evidence in more detail, we will examine the evolutionary consequences of this reliance on social inputs for skill acquisition.

2. THE CULTURAL INTELLIGENCE HYPOTHESIS

Social learning can be defined as learning influenced by observation of, or interaction with, another animal [30]. It thus encompasses two rather different processes. Learning through social interaction, including social play and agonistic interactions, generally involves the acquisition of social skills. Learning via social information is essential for the acquisition of non-social skills, although it may also be used in the acquisition of social skills (e.g. through eavesdropping: [31]). This second kind of social learning can take different forms of varying complexity, ranging from mechanisms as simple as local or stimulus enhancement to complex forms of imitation (e.g. summarized in [32]). It must be pointed out, however, that most social learning in animals is not direct copying. Indeed, along with a variable involvement of dedicated cognitive mechanisms [33–35], social learning almost invariably includes an important element of individual evaluation [36], and may indeed largely rely on existing asocial-learning mechanisms [37].

Social learning is not necessarily adaptive [38]. However, whereas horizontal social learning (i.e. from peers) to acquire perishable information about the state of the biotic or social environment can sometimes be maladaptive, vertical and oblique social learning (i.e. from parents or others in that generation) of cognitively demanding skills by naive immatures is

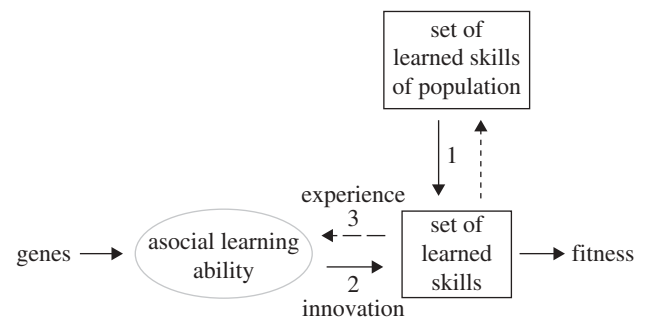


Figure 1. The sources of an individual's set of learned skills as acquired during development: (1) the skills learned through social learning from the population's pool of learned skills, and (2) the skills acquired through innovation from its own asocial (individual)-learning ability. The dashed arrow 3 reflects the effect of experience on asocial-learning ability.

most likely to be adaptive (cf. [39]). Throughout, we will focus on these adaptive forms.

The cultural intelligence hypothesis assumes that social learning is more efficient than individual, or asocial, exploration and learning, and that individuals in practice tend to rely on social learning to acquire skills, i.e. prefer it to asocial learning. We expect higher efficiency for social learning because asocial learners face the fundamental problem of identifying which environmental stimuli they should attend to, forcing them to explore in a less directed fashion. Thus, the signal-to-noise (relevant versus irrelevant) ratio of stimuli encountered by immatures is higher for those relying on social learning, making it more likely that they acquire a skill through either socially directed trial-and-error learning (enhancement effects) or observational forms of social learning (i.e. copying of actions, goals or results). Asocial learners, on the other hand, have a far lower signal-to-noise ratio since social inputs do not help them to filter out irrelevant stimuli (cf. [40]). Thus, at constant cognitive abilities, they will on average be less likely or take longer to find a solution to a problem than social learners.

A test of the assumption that social learning is more efficient requires that social learning be operationalized. A commonly used definition is that subjects acquire particular behaviours or skills faster when exposed to skilled role models than they do in a control situation, in which they can independently explore and eventually learn the skill individually. This assumption has been validated in many taxa, and especially in primates [34], although success rates vary across lineages [41], as do known mechanisms [35]. It is also supported by experiments in humans [39]. Thus, social learning acts to speed up the acquisition of behaviour patterns that are universal in the species concerned and thus probably have an innate component [42–44], such as nest building in great apes. It also improves their adult deployment, as shown for nest building in chimpanzees [45,46]. However, social learning also allows acquisition of novel behaviours (innovations) that the animals would not learn at all otherwise. In many experiments, the control animals fail to find the solution (e.g. [47,48]), a finding supported by

the patchy geographical incidence of learned skills in wild populations [21,22].

A second critical assumption is that animals able to learn socially do so preferentially rather than rely on individual exploration to acquire skills (as humans should do: [39]). Field observations show that infants in several primate species show relatively little independent exploration, but strongly increase selective exploration of potential food items after mothers fed on them [25], to the point that among orang-utans their diets have become identical with those of their mothers by weaning [18], which cannot be attributed to genetic predispositions, because mothers from the same population differ with regard to their feeding repertoires from each other. Vertical inheritance of foraging specializations in dolphins suggests the same process [49]. Experiments similarly show that infants of some species avoid novel foods until their mothers or others have tried them (e.g. *Daubentonia*: [44]). Rats likewise avoid foods not eaten by others, focusing instead on those eaten by others [50].

Interspecific cross-fostering experiments are the most powerful tool to demonstrate a preference for social learning, if they produce a bias towards the behaviour of the adopting species. Although most examples in rodents and birds refer to sexual imprinting [51], a few experiments have examined the effects of more long-term exposure to heterospecific parents. They found powerful effects on diet, foraging, movement and even styles of social behaviour in birds [52–54] and mammals [55,56], suggesting that social learning (through social information and social interaction) prevails over asocial learning in these domains. Enculturation studies, reviewed below, show equally powerful effects. Overall, these findings support the assumption that especially the young and naive of various species actually show a preference for social learning over individual exploration, although the exceptions (e.g. [57]) might provide a useful testing ground for the cultural intelligence hypothesis.

3. TESTING THE DEVELOPMENTAL PREDICTION

The main prediction of the developmental version of the cultural intelligence hypothesis is that the number of learned skills acquired by a maturing individual depends on its opportunities for social learning during this period. While we already noted that observational data from wild apes support this prediction, we now discuss experiments that artificially reduce access to role models for social learning (deprivation) or provide better role models with larger skill repertoires (enculturation).

(a) *Deprivation effects*

For several decades following World War II, many deprivation experiments were conducted in which infant monkeys or apes were reared without access to their mothers or other adult conspecifics. Monkeys and apes reared in partial social deprivation (i.e. with peers only) tend to have near-normal sexual and social competence, which can largely be learned through social interaction, but clearly reduced maternal competence [58–61]. For physical skills,

learned through social information, the effects are stronger. Infant chimpanzees reared without adult role models show much reduced competence in many physical skills, such as nest building [45,46] and tool use [62], or fail to develop them altogether, despite showing otherwise normal behaviour. Thus, primates, especially apes, deprived of adult role models acquire a smaller set of learned skills (see electronic supplementary material for more details).

(b) *Enculturation studies*

Enculturation is interspecific cross-fostering, in which an animal is reared by humans and treated more or less like a human child, thus exposed to human artefacts and rules through joint attention and active teaching. Enculturation thus provides increased opportunities for socially guided learning, including in domains not present in normal conspecific individuals (e.g. complex artefacts, language). Usually, the cross-fostered individuals were apes, but where monkeys were studied, the results were in the same direction (e.g. [63]). Enculturation brings about more rapid behavioural and motor development [8] and an increased number of learned skills (reviewed in e.g. [64–66]), including more interest in objects and more sophisticated object manipulation [66,67] and more skilful tool use [63,68]. Perhaps most strikingly, some great apes developed unusually elaborate comprehension and some use of human language systems despite the complete absence of such symbolic signalling in the wild [6]. Further details are provided in the electronic supplementary material. Thus, enculturation studies not only show the strong preference for socially guided learning and interest in role models' actions of infant primates, but also the remarkable potential for apes to acquire learned skills well outside the range of acquisition during normal development if appropriate role models are available.

(c) *A stronger version of cultural intelligence*

A stronger version of the cultural intelligence hypothesis is that social learning not merely increases the set of learned skills, as examined so far, but also affects the asocial-learning ability (intelligence) itself. Where an individual has a greater set of learned skills, it may become a better asocial learner through the experience it has gathered in learning the other skills, either because affordance learning has increased its scope of possible innovations or because learning has produced transfer of experience and abilities to new situations. This experience effect is ubiquitous in humans [69] and has long been known for captive primates [70], but also explains why wild primates generally show poor performance on cognitive tasks requiring familiarity with human artefacts or tasks [16,71,72]. Thus, where the population has a large pool of skills and social learning is possible, this should allow the individual not only to increase its set of learned skills, but also, through experience, to improve its asocial-learning ability (arrow labelled 3 in figure 1).

The critical prediction of this stronger version is that the frequency of opportunities for social learning

during development affects asocial-learning ability, i.e. intelligence. Indeed, social deprivation reduces learning ability in rodents [73] and probably primates [74,75]. On the other hand, enculturation effects improve it [67,76,77]. For instance, only enculturated individuals master delayed imitation. However, because the exact nature of enculturation effects remains unclear (see detailed discussion in the electronic supplementary material) and systematic cognitive tests of primates deprived only of adult role models have not yet been conducted, this conclusion is preliminary. If further, systematic tests support this prediction, the evolutionary effects envisaged by the cultural intelligence hypotheses, reviewed below, are even stronger.

4. THE EVOLUTIONARY VERSION OF THE CULTURAL INTELLIGENCE HYPOTHESIS

The observations and experiments reviewed above show that individuals with more opportunities for social learning systematically acquire a larger set of learned skills and also become better asocial learners. This effect of social learning may have two opposing evolutionary consequences. If individuals in lineages with systematically increased opportunities for social learning can more efficiently acquire the minimum number of skills to survive and reproduce, but derive no fitness benefit from enlarging the set of learned skills, then selection would favour smaller brains in these lineages than in less sociable ones. However, given that relative brain size has consistently increased over evolutionary time [78], the opposite outcome is more likely. Thus, if the number and complexity of skills acquired through social learning positively impact survival and/or reproduction, lineages with more opportunities for social learning can more readily respond to selection for an increased set of learned skills than lineages with limited contact between the generations or tolerant independent animals.

The increased set of learned skills is actually achieved through selection on improved social-learning ability. However, this can lead to improved asocial-learning ability, i.e. intelligence, in two distinct ways (figure 2). First, better social-learning performance automatically improves asocial-learning processes [26], owing to the high overlap of the cognitive processes involved in social and asocial learning [37]. For instance, at the simplest level, selection on enhancement learning favours the causal understanding of agent–object relations. All forms of observational social learning benefit from increased inhibitory control, attention and memory—components of executive functions that enhance individual learning [2]. Emulation critically requires goal understanding; production imitation requires inhibitory control and working memory. In the extreme case, social-learning abilities may merely function as input channels for the asocial-learning mechanisms [37]. Thus, selection for more effective social learning indirectly or directly improves asocial-learning abilities. A second way in which improved social-learning ability can improve asocial-learning ability is direct. It arises whenever the experience effect operates and the increased set of

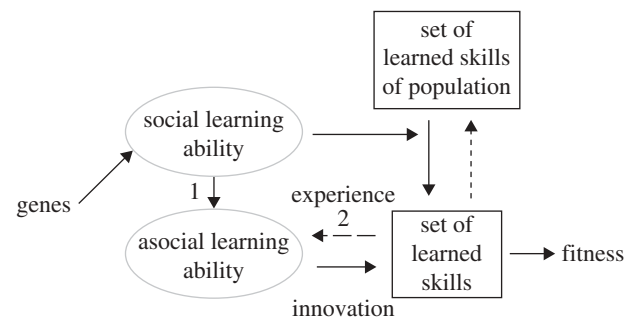


Figure 2. The evolution of intelligence through cultural feedback. Selection on an increased set of learned skills is achieved by improved social learning. Owing to the high cognitive overlap, social learning improves the asocial (individual)-learning ability (i.e. intelligence; shown by arrow 1). More learned skills also improve the latter through stronger experience effects (arrow 2).

learned skills leads to a direct improvement of the asocial-learning ability.

In lineages with opportunities for social learning, a positive coevolutionary process between social-learning ability and brain size may ensue, until increases in brain size no longer provide sufficient additional pay-off in survival or reproduction in the current environment. Different lineages are expected to go different distances in this eco-evolutionary process, with the position of the equilibrium depending on where the fitness costs of continued investment in neural structures begin to balance the benefits.

The cultural intelligence hypothesis therefore makes two evolutionary predictions, which can be tested comparatively. The first prediction is that social-learning abilities and asocial-learning abilities show correlated evolution. The second is that intelligence and frequency of opportunities for social learning show correlated evolution.

(a) *Coevolution of social and asocial learning*

The prediction of a positive interspecific relationship between the abilities for social and asocial learning is a strong one because under other hypotheses for the evolution of intelligence (see §5), greater individual intelligence is not necessarily accompanied by greater ability for social learning.

Reader & Laland [14] and Reader *et al.* [79] provided comparative support for this prediction by showing that among primates, reports of social learning, regardless of mechanism, show a significant positive correlation with reports of innovation, and both show significant positive correlations with the executive brain ratio, i.e. (neocortex + striatum/brain-stem). Similarly, Lefebvre [80] reviewed evidence for a positive interspecific correlation between performance in social learning and individual learning experiments among birds.

A more detailed test compares the asocial-learning ability with the cognitive complexity of social learning across a set of taxa. We compared four primate grades: prosimians (lemurs, galagos and lorises, and in principle tarsiers), monkeys (i.e. both Old and New World monkeys), great apes (i.e. leaving out the

gibbons and humans) and humans. While these grades do not correspond to actual clades, they are fairly homogeneous with respect to lifestyle and relative brain size (e.g. [81]). The summary of table S1 in the electronic supplementary material shows that the performance in both social and asocial learning increases systematically from prosimians, to monkeys, to great apes and finally humans. It is generally assumed that observational forms of social learning, including all forms of emulation and imitation, involve more complex cognitive mechanisms than the non-observational forms, such as facilitation and enhancement. There is no evidence for observational learning in prosimians [34]. Almost all the observational forms of social learning documented so far among monkeys refer to contextual imitation [33] or imitation of species-typical actions [11], whereas among great apes, we see evidence for copying of novel actions, complex action sequences (also production imitation) or deferred imitation (see also electronic supplementary material). Subiaul [35] argues that this distinction is supported by neurobiological differences between these latter two lineages, with production imitation requiring neural adaptations that mediate the planning and coordination of gross and fine motor patterns. In support, human children can copy known motor acts before they can copy novel actions or action sequences [82].

(b) Opportunities for social learning and brain size

The second prediction is that selection would be most likely to favour the evolution of improved domain-general cognitive abilities where opportunities for social learning are present, and should do so more when such opportunities are systematically more abundant. This is a *ceteris paribus* prediction. Thus, not all lineages satisfying the condition need to have evolved greater intelligence, but conversely all highly intelligent species should have excellent opportunities for social learning. In short, prediction 2 is that the most intelligent species should all be highly cultural species.

A proper test of the second prediction requires knowledge of the distribution and extent of culture among taxa in the wild. This information is woefully incomplete, forcing us to use indirect estimates of the amount of social learning in the wild as a first approach to testing this prediction. Opportunities for social learning correlate with a number of non-exclusive variables that can therefore be used as proxies for it: presence of stable social units containing overlapping generations, a long period of close association with one or more parents, the presence of cooperative breeding and extent of social tolerance in social units [24,83]. Because the effect of social tolerance outweighs that of group size, in both theoretical [26] and empirical studies [14], group size is not a relevant variable, although group living *per se* probably is.

Intelligence must likewise be assayed indirectly, using neuro-anatomical measures, although theoretically there is no obvious best measure [84]. Results obtained with different measures are often the same (e.g. [85]) or similar (e.g. [14]), but not always [86].

As yet, no systematic analyses have been done for mammals, but among birds, several patterns are consistent with the cultural intelligence hypothesis. First, young of altricial species generally have far longer and more intensive contact with parents than precocial ones, and thus more opportunities for social learning. Accordingly, altricial birds have far larger average relative brain size than precocial ones [87]. Second, among altricial birds, the duration of post-fledging parental care, a period during which various skills improve [88], is positively correlated with relative brain size [89], as predicted. Third, among bowerbirds, learning of bower building has been argued to be socially mediated [90], and the species that build bowers are larger brained than either non-bower-building relatives or ecologically similar but unrelated species [91]. Finally, among precocial birds, post-hatching care consists largely of protecting and less of provisioning, allowing a test of the effect of opportunities for social learning without being confounded by that of direct energy inputs to the young. This care is highly variable, but largely homogeneous within families (because most variation is at the higher taxonomic levels, we therefore consider patterns at the level of family). As predicted, the number of caretakers in a family strongly predicts relative brain size (K. Isler & CvS 2010, unpublished data).

5. DISCUSSION

(a) The evolution of intelligence

The cultural intelligence hypothesis makes plausible assumptions that were empirically supported: (i) social learning is more efficient than individual learning, and (ii) animals appear to rely on it preferentially. The developmental effects on skill repertoires it predicts were found as well, whereas we also found preliminary support for the predicted evolutionary effects: interspecific correlation between individual and social-learning abilities and a relationship between opportunities for social learning and cognitive abilities across taxa. Future tests should focus on aspects not yet sufficiently evaluated. For instance, species with high social tolerance, as well as species with demonstrated traditions in natural conditions, should have a larger relative brain size than sister taxa lacking these features. If future tests remain favourable, then cultural intelligence should be part of the explanation for variation in intelligence and brain size across species.

Unlike the cultural intelligence hypothesis, currently popular hypotheses for the evolution of intelligence emphasize specific benefits. For the lineage that gave rise to humans, the primates, the most popular idea is that the challenges and opportunities of living in individualized, stable social groups have provided the strongest selective pressure towards increased cognitive abilities (social brain hypothesis), but ecological pressures, such as foraging demands, have probably contributed as well [92]. More specific benefits may have applied in particular lineages (e.g. acoustic foraging in aye-ayes: [93]). All of these hypotheses enjoy some support from comparative tests using brain size as a proxy for cognitive

performance (e.g. [94]), although all hypotheses positing domain-specific benefits must explain how more generalized cognitive abilities, i.e. intelligence, subsequently arose from these specific cognitive adaptations. An alternative approach assumes domain-general benefits in the form of general problem-solving abilities, bringing fitness-enhancing behavioural flexibility [14,79]. This idea is supported by the high correlations among performance measures on various and sundry cognitive tasks, suggesting the existence of general intelligence in animals, at least primates [95,96]. There is also a good relationship between this general intelligence and aspects of brain size [79,86].

Such benefits alone may not be sufficient to explain patterns in the evolution of brain size and intelligence. Brain tissue is metabolically more costly than many other tissues in the body, and consequently larger brains lead to developmental delays in precocial species [97] or require species to have higher metabolic turnover [98]. Therefore, benefits owing to increased brain size must be greater than those owing to equal changes in the size of most other tissues. Indeed, variation in the strength of these costs or ability to bear them explains much interspecific variation in brain size [97,99]. By arguing that social learning leads to a more efficient use of brain tissue than individual exploration, the cultural intelligence hypothesis explicitly acknowledges these costs.

The efficiency argument holds regardless of the exact nature of the benefits or whether the benefits are domain-general or domain-specific, provided learning of skills is involved. Thus, the cultural intelligence hypothesis complements the benefit hypotheses mentioned above by specifying the conditions in which these benefits are likely to be cost-effective enough to be favoured by natural selection. The cultural intelligence hypothesis is therefore not meant to replace the benefit hypotheses because intelligence will not be favoured by natural selection merely because the costs are low, but only if it also provides clear improvements in survival or reproductive success. Rather, the cultural intelligence hypothesis specifies the conditions in which these potential benefits can be realized, namely whenever the social conditions allow sufficient social learning.

The complementarity with the benefits hypotheses makes it difficult to independently test the cultural intelligence hypothesis, at least until information on the taxonomic incidence of the expression of culture and oblique and vertical social learning is available. However, the cultural intelligence hypothesis correctly predicts the interspecific correlation between asocial and social learning, which is not predicted by the benefit hypotheses. It can also account for correlated evolution between opportunities for social learning and relative brain size, independent of living in stable groups.

(b) Cultural intelligence and human evolution

Species vary dramatically in cognitive abilities. Much of this variation should be linked to the extent to which social learning is possible and improves survival and/or reproductive success. The equilibrium reached

in a particular taxon will depend on (i) its social system and life history, i.e. its aggregate measure of opportunities for social learning, and (ii) the degree to which the possession of any skills or knowledge will improve survival or reproductive success. The latter need not be true for organisms in habitats with high unavoidable mortality. Some species will therefore end up relying more on social learning and on more sophisticated forms of it than others, even if opportunities for social learning are similar. Evidently, taxa with highly tolerant social systems, slow development and low rates of unavoidable mortality are expected to have evolved the most extensive forms of social learning. Great apes, capuchin monkeys, dolphins and toothed whales, elephants, corvids and parrots, all lineages with known social-learning abilities [100,101], fit these conditions.

The evolution of uniquely human cognitive abilities is entirely consistent with the cultural intelligence hypothesis. Although the term cultural intelligence had been proposed earlier [11] to apply to animals generally, Herrmann *et al.* [5] soon thereafter used the term cultural intelligence to specifically refer to humans (i.e. the Vygotskian intelligence hypothesis [3]). Their comparison of adult chimpanzees and orang-utans with human toddlers showed that human infants outperformed apes in the social, but not the physical domains of cognition, suggesting that socio-cognitive abilities (including social learning) and physical cognition have become dissociated in humans. This may seem inconsistent with the broader cultural intelligence hypothesis, but note that human *adults* clearly outperform all great apes in both social and physical cognition, indicating the social cognitive abilities simply mature earlier than the physical cognitive abilities. Herrmann *et al.* [5] version of the cultural intelligence hypothesis thus is that humans show specific adaptations fostering social learning that become apparent early in ontogeny and enable a further, socially constructed amplification of cognitive skills. This position is paralleled by the concept of pedagogy proposed as a specifically human adaptation by Gergely *et al.* [102], which encompasses specialized communicative acts on the part of the role model and specific sensitivity to these acts on the part of the infant. These human-specific adaptations are entirely consistent with the broad cultural intelligence hypothesis developed here (cf. [103]), and probably arose after humans adopted cooperative breeding [104,105].

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