Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis

Esther Herrmann,[1]* Josep Call,[1] María Victoria Hernández-Lloreda,[2] Brian Hare,[1,3] Michael Tomasello[1]

Humans have many cognitive skills not possessed by their nearest primate relatives. The cultural intelligence hypothesis argues that this is mainly due to a species-specific set of social-cognitive skills, emerging early in ontogeny, for participating and exchanging knowledge in cultural groups. We tested this hypothesis by giving a comprehensive battery of cognitive tests to large numbers of two of humans' closest primate relatives, chimpanzees and orangutans, as well as to 2.5-year-old human children before literacy and schooling. Supporting the cultural intelligence hypothesis and contradicting the hypothesis that humans simply have more "general intelligence," we found that the children and chimpanzees had very similar cognitive skills for dealing with the physical world but that the children had more sophisticated cognitive skills than either of the ape species for dealing with the social world.

Humans have brains roughly three times larger than those of their nearest primate relatives, the great apes (1, 2), and of course have many cognitive skills not possessed by other primates as well, from language to symbolic mathematics to scientific reasoning. The questions from an evolutionary point of view—especially given the enormous energetic expense of a large brain (3)—are how and why humans have evolved such powerful and distinctive cognitive abilities requiring so much neural tissue.

One hypothesis is the general intelligence hypothesis. Larger brains enable humans to perform all kinds of cognitive operations more efficiently than other species: greater memory, faster learning, faster perceptual processing, more robust inferences, longer-range planning, and so on. The alternative is the adapted intelligence hypothesis (4). Cognitive abilities evolve in response to relatively specific environmental challenges, and so we may see caching birds with exceptional memory skills, homing pigeons with marked skills of spatial navigation, bees with complex systems of communication, and so forth (5). In the case of primates, some theorists have proposed that the distinctive aspects of primate cognition evolved mainly in response to the especially challenging demands of foraging for seasonal fruits and resources embedded in substrates [the ecological intelligence hypothesis (6, 7)], whereas others have proposed that the distinctive aspects of primate cognition evolved mainly in response to the especially challenging demands of a complex social life of constant competition and cooperation with others in the social group [the social intelligence hypothesis (8–11)].

In the case of humans, one reasonable hypothesis involves extending the primate social intelligence hypothesis to reflect the fact that humans are not just social but "ultra-social" (12). That is, whereas primates in general have evolved sophisticated social-cognitive skills for competing and cooperating with conspecifics, humans have also evolved skills that enable them to actually create different cultural groups, each operating with a distinctive set of artifacts, symbols, and social practices and institutions. To function effectively in the cultural world into which they are born, human children simply must learn to use these artifacts and tools and to participate in these practices, which require some special social-cognitive skills of social learning, communication, and "theory of mind" (13). Some other ape species transmit some behaviors socially or culturally (14, 15), but their species-typical cognition does not depend on participating in cultural interactions in the same way as it does in humans, who must (i) learn their native language in social interactions with others, (ii) acquire necessary subsistence skills by participating with experts in established cultural practices, and (iii) (in many cultures) acquire skills with written language and mathematical symbols through formal schooling (16). In the end, human adults will have all kinds of cognitive skills not possessed by other primates, but this outcome will be due largely to children's early emerging, specialized skills for absorbing the accumulated skillful practices and knowledge of their social group (so that a child growing up outside of any human culture would develop few distinctively human cognitive skills). Humans' especially powerful skills of social-cultural cognition early in ontogeny thus serve as a kind of "bootstrap" for the distinctively complex development of human cognition in general. We may call this the cultural intelligence hypothesis.

There have been no direct tests of the cultural intelligence hypothesis, nor any direct comparisons of it with other hypotheses of human cognitive evolution. The social intelligence hypothesis for primates in general is supported by positive correlations between relative brain size (i.e., neocortex size) and social variables such as group size or grooming clique size [as an index of social complexity (11, 17–20)]. This evidence provides support for the general social direction of the cultural intelligence hypothesis, but overall correlations do not tell us the basis of the brain size differences in terms of particular cognitive skills, nor do they help us to identify which cognitive skills humans may have that other primates lack. There have also been some experimental studies that directly compared the performance of several primate species on a few cognitive tasks, but in the only meta-analysis of those studies, none of the tasks targeted social cognition and humans were not represented (21). Several other experimental studies have directly compared some individual cognitive skills of humans (mostly children) and nonhuman primates (mostly apes), but each of these studies has been conducted with different individuals, and indeed the ages of the children and the members of the nonhuman primate species are inconsistent across studies (22).

What is needed to test the cultural intelligence hypothesis is a systematic comparison of a representative range of cognitive skills among a single set of human and nonhuman primate individuals, which has so far not been done. In such a comparison, the cultural intelligence hypothesis predicts that there should be an age in early human ontogeny (specifically, an age before children have been seriously influenced by written language, symbolic mathematics, and formal education) at which humans' skills of physical cognition (concerning things such as space, quantities, and causality) are very similar to those of our nearest primate relatives but at which their skills of social-cultural cognition (specifically those most directly involved in cultural creation and learning, such as social learning, communication, and theory of mind) are already distinctively human. This is in stark contrast to the general intelligence hypothesis, which predicts that human cognition should differ from that of other primates uniformly, with no difference between physical and social cognition.

In the current study, therefore, we sought to identify any distinctive features of human cognition that may exist at an early stage of ontogeny and, in this way, to assess and directly compare the cultural intelligence and general intelligence hypotheses of human cognitive evolution. We did this by administering a comprehensive battery of cognitive tests to a large number of chimpanzees (Pan troglodytes) (one of humans' two closest living relatives), orangutans (Pongo pygmaeus) (a more distantly related great ape), and human children (Homo sapiens) at 2.5 years of age. Of crucial importance to our analysis were

[1]Max Planck Institute for Evolutionary Anthropology, Leipzig, D-04103, Germany. [2]Departamento de Metodología de las Ciencias del Comportamiento, Universidad Complutense de Madrid, Spain. [3]Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27705, USA.

*To whom correspondence should be addressed. E-mail: eherrman@eva.mpg.de (E.H.)

the following: (i) all subjects from all three species were naïve to the tests from the test battery; (ii) the apes lived in rich, semi-natural environments; and (iii) there was a sufficient number of subjects to properly test, as virtually no previous studies have done, the role of gender, age, and temperament (measured in a separate test) as possible mediators of cognitive performance on the tasks.

Methods: the test battery and its administration. The Primate Cognition Test Battery (PCTB) was constructed based on the theoretical analysis of primate cognition by Tomasello and Call (22). In this analysis, the primary division is between physical cognition and social cognition. Although primates in their natural habitats regularly use skills of physical and social cognition together [e.g., foraging for food while competing with groupmates (23, 24)], in theory the two sets of skills are distinct because physical cognition deals with inanimate objects and their spatial-temporal-causal relations, whereas social cognition deals with other animate beings and their intentional actions, perceptions, and knowledge.

More specifically, in this analysis, primate cognition of the physical world evolved mainly in the context of foraging: To locate food, primates need cognitive skills for dealing with "space"; to choose wisely among multiple food sources, they need cognitive skills for dealing with "quantities"; and for extracting food from difficult places, they need cognitive skills for understanding "causality" (including, for some species, the context of tool use). In this analysis, primate social cognition evolved because of the tension between cooperation and competition among group members: To manipulate the behavior of others, primates need skills of "communication"; to learn things vicariously from observing others, they need skills of "social learning"; and to predict the behavior of others in competition, they need cognitive skills for understanding psychological states such as goals and perceptions ("theory of mind"). The PCTB therefore comprised the two domains of physical cognition and social cognition, each of which comprised three cognitive scales (the six terms enclosed in quotes above), with each scale being constructed with one or more specific tasks composed of several items each. Most of the items were derived from previously published studies of primate cognition (table S2), whereas others were created for the PCTB and validated before use with the chimpanzees and orangutans at the Wolfgang Köhler Primate Research Center

in Leipzig, Germany. Table 1 briefly summarizes the structure of PCTB (25) (movies S1 to S32).

The PCTB was administered to three groups of participants. First were 106 chimpanzees (53 males and 53 females; 3 to 21 years of age; mean age: 10 years) that lived either at the Ngamba Island chimpanzee sanctuary, Lake Victoria, Uganda, or at the Tchimpounga chimpanzee sanctuary, Republic of Congo. Second were 32 orangutans (17 males and 15 females; 3 to 10 years of age; mean age: 6 years) that lived at the Orangutan Care Center and Quarantine in Pasir Panjang, Kalimantan, Indonesia. All of these apes live in the richest social and physical environments available to captive apes and have grown up in close contact with humans who feed and care for them. Third were 105 human children [52 males and 53 females; 2.5 years of age (±2 months)] from a medium-sized city in Germany. All children had been using language for ~1 year (25) (table S1).

Participants were individually tested by a human experimenter, with the same experimenter testing a subject throughout the entire battery. Each participant completed all tasks in the PCTB, which took from 3 to 5 hours altogether, generally in the same order across several days of testing (table S3). The human children were

Table 1. The PCTB, including domains, scales, and tasks (25).

Domain	Scale	Task	Description
Physical	Space	Spatial memory (1 item, 3 trials)	Locating a reward.
		Object permanence (3 items, 9 trials)	Tracking of a reward after invisible displacement.
		Rotation (3 items, 9 trials)	Tracking of a reward after a rotation manipulation.
		Transposition (3 items, 9 trials)	Tracking of a reward after location changes.
	Quantities	Relative numbers (1 item, 13 trials)	Discriminating quantity.
		Addition numbers (1 item, 7 trials)	Discriminating quantity with added quantities.
	Causality	Noise (2 items, 6 trials)	Causal understanding of produced noise by hidden rewards.
		Shape (2 items, 6 trials)	Causal understanding of appearance change by hidden rewards.
		Tool use (1 item, 1 trial)	Using a stick in order to retrieve a reward which is out of reach.
		Tool properties (5 items, 15 trials)	Understanding of functional and nonfunctional tool properties.
Social	Social learning	Social learning (3 items, 3 trials)	Solving a simple but not obvious problem by observing a demonstrated solution.
	Communication	Comprehension (3 items, 9 trials)	Understanding communicative cues indicating a reward's hidden location.
		Pointing cups (1 item, 4 trials)	Producing communicative gestures in order to retrieve a hidden reward.
		Attentional state (4 items, 4 trials)	Choosing communicative gestures considering the attentional state of the recipient.
	Theory of mind	Gaze following (3 items, 9 trials)	Following an actor's gaze direction to a target.
		Intentions (2 items, 6 trials)	Understanding what an actor intended to do (unsuccessfully).

tested on 5 days within a 2-week period, and the apes were tested on consecutive days, averaging a total of 8 days. Chimpanzees and orangutans were tested in a familiar room, and human children were tested in a child laboratory and accompanied by a parent who was told not to influence or help in any way. To measure the comfort level of participants in the test situation (because this could be a mediator of their performance in the PCTB), we also gave subjects (within the first 4 days of testing) a temperament test designed to assess their reaction to novel objects, people, and rewards (*25*) (tables S6 and S7). All testing was videotaped.

For most of the tasks, a human experimenter (E1) sat behind a table facing the subject through a Plexiglas window (children and some apes) or a mesh panel (apes only). The window had three holes at different positions, through which subjects could insert a finger to indicate their choice when necessary (figs. S1 and S2). On all trials, E1 always waited until the subject was facing her before beginning a trial. For trials requiring a choice, the position of the reward was counterbalanced across either two or three locations (depending on the task) but the reward was never hidden for more than two consecutive trials in the same place. In a few tasks, subjects were tested in other setups, requiring them to do such things as to use a simple tool, follow gaze direction, or gesture to E1 (*25*).

Subjects' responses were initially coded live by E1 except for gaze-following trials, which E1

coded from videotape after the test. A second observer independently scored (from videotape) 100% of the trials for human children and chimpanzees and 20% of the trials for orangutans. The inter-observer agreement for all tasks combined was 98% for orangutans, 99% for chimpanzees, and 99% for human children (table S4).

Results. Figure 1 presents the results at the most general level of analysis. Averaging across all of the tasks in the physical domain, humans and chimpanzees were correct on ~68% of the trials, whereas orangutans were correct on ~59% of the trials (the absolute values are not especially meaningful because some tasks had a 50 or 33% chance of success by guessing, and some tasks had no possibility for guessing). Statistically, the humans and chimpanzees did not differ from one another in the physical domain, but they were both more skillful than the orangutans ($P < 0.001$ in both cases). In the social domain, a very different pattern emerged. Averaging across all of the tasks in the social domain, the human children were correct on ~74% of the trials, whereas the two ape species were correct about half as often (33 to 36% of the trials). Statistically, the humans were more skillful than either of the two ape species ($P < 0.001$ in both cases), which did not differ from one another.

Figure 2 presents the results at the level of the six scales. In the physical domain, there were no differences among species on the quantities scale. On both the space and causality scales, however, humans and chimpanzees did not differ from

one another, but both were more skillful than orangutans ($P < 0.001$ in all cases). The difference between chimpanzees and orangutans remained even after controlling for age (*25*). In the social domain, the pattern was again different from the physical domain and the same for all three of the scales. Human children were more skillful than either of the ape species in each of the three social scales ($P < 0.001$ in all cases), and the apes did not differ from one another.

Table 2 lists species' performance on the 16 different tasks within each of the scales (note that social learning is a scale and a task). The overall pattern is that within the physical domain, human children and chimpanzees each were better at some tasks than the other, with orangutans often representing an outlier. Within the four spatial tasks, children were better than chimpanzees at one task (object permanence), whereas the chimpanzees outperformed the children at another task (transposition). In terms of quantities, all three species were similar at judging which of two quantities is larger, but chimpanzees were better than both of the other species at combining quantities in order to make a judgment. Children were better than both ape species at the three causality tasks in which a judgment must be made before manipulation or choice, whereas chimpanzees were better than children and orangutans at the one causality task involving active tool use. Within the social domain, again the pattern was very different. As predicted, the human children were consistently more skillful than both of the ape species (at five

Fig. 1. Physical domain (**A**) and social domain (**B**). The box plots show the full distribution of the proportion of correct responses for physical and social domains of the PCTB for each species: median, quartiles, and extreme values. Boxes represent the interquartile range that contains 50% of values (range from the 25th to the 75th percentile). The line across the box indicates the median. The whiskers represent maximum and minimum values, excluding outliers [indicated by circles, at least 1.5 times the interquartile range (i.e., 1.5 box lengths from the upper or lower edge of the box)] and extremes [indicated by asterisks, at least 3 times the interquartile range (i.e., >3 box lengths from the edge)]. Statistical comparisons on each domain were made by multivariate analysis of variance (MANOVA), followed by analysis of variance (ANOVA) tests for each domain. Post-hoc tests (the Bonferroni correction was used when the equality of variances assumption holds, and the Dunnett t3 correction was used otherwise) followed in case a significant effect was detected. Performance on the PCTB as a whole differed significantly across species (MANOVA with species and gender as between-subject factors and performance in both domains of the PCTB as the dependent variables; Wilk's Lambda: $F_{4,472} = 123.965$, $P < 0.001$, $\eta^2 = 0.51$). No statistically significant differences were detected between genders, but there was an interaction between species and gender (Wilk's Lambda: $F_{4,472} = 2.815$, $P < 0.025$, $\eta^2 = 0.02$). Univariate analyses (ANOVA) showed that the differences across species were significant for both
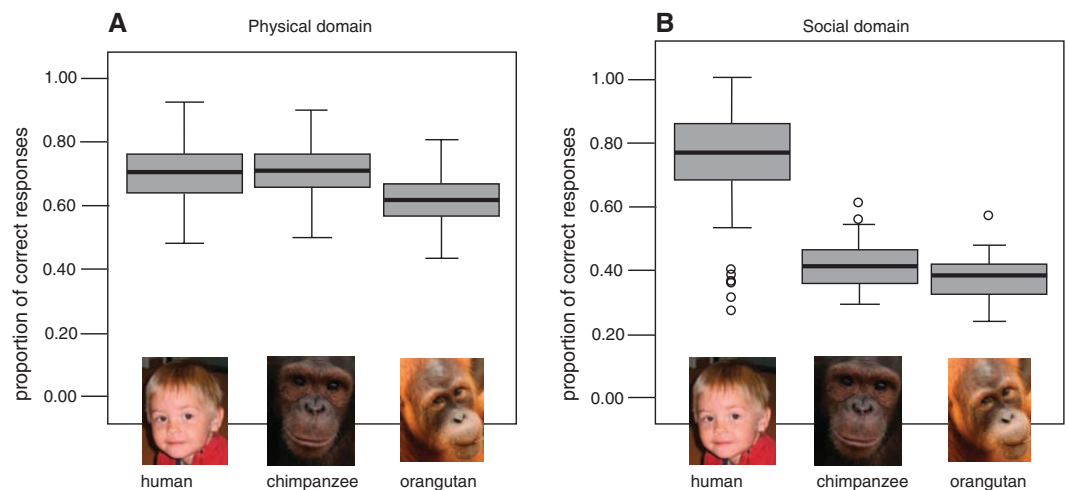
domains: physical ($F_{2,237} = 19.921$, $P < 0.001$, $\eta^2 = 0.14$) and social ($F_{2,237} = 311.224$, $P < 0.001$, $\eta^2 = 0.72$). Univariate analyses for the interaction between species and gender revealed that there was a significant interaction for the physical domain ($F_{2,237} = 5.451$, $P = 0.005$, $\eta^2 = 0.04$) but not for the social domain ($F_{2,237} = 0.224$, $P = 0.799$). Post-hoc tests (Dunnett t3 correction) revealed that humans and chimpanzees performed better than orangutans in the physical domain (for both $P < 0.001$, with no difference between humans and chimpanzees). However, post-hoc tests (Dunnett t3 correction) showed that human children outperformed both chimpanzees and orangutans in the social domain (both $P < 0.001$). Post-hoc tests for the interaction between species and gender in the physical domain showed that female children were better than male children ($P = 0.001$). No other gender differences were found.

out of six tasks), and the two apes did not differ from one another on any task.

To test for possible species differences in individual variability, we computed a coefficient of variation and a 95% two-sided exact confidence interval for both domains for each of the three species (table S5). There were no significant species differences in variability. For two of the three species (humans and chimpanzees), there was more individual variability in the social than in the physical domain (the trend for orangutans was in the same direction but not significantly so), but this may be due to the larger proportion of

tasks with the possibility of chance success in the physical domain (90% in the physical domain and 33% in the social domain), which provides a higher baseline for unskillful individuals (25).

There was no effect of gender for any of the species on any of the social scales. On the physical scales, chimpanzee males outperformed chimpanzee females on the scale space, whereas human females outperformed human males on the scale quantities. Human females also outperformed human males at the level of the physical domain as a whole (although this was not so for the two ape species).

In terms of temperament (operationalized as approach behavior to novel objects, people, and rewards), the human children were shyer or less interested in the novel items in the test situation than were the two ape species, which were bolder or more interested ($P < 0.001$ in both cases) [(25) and tables S6 and S7]. Also, children's temperament measures did not correlate with any aspect of their cognitive performance. For the two ape species, there was also no correlation of temperament with any of the social scales, but ape individuals that approached novel situations more quickly (i.e., were bolder and more in-
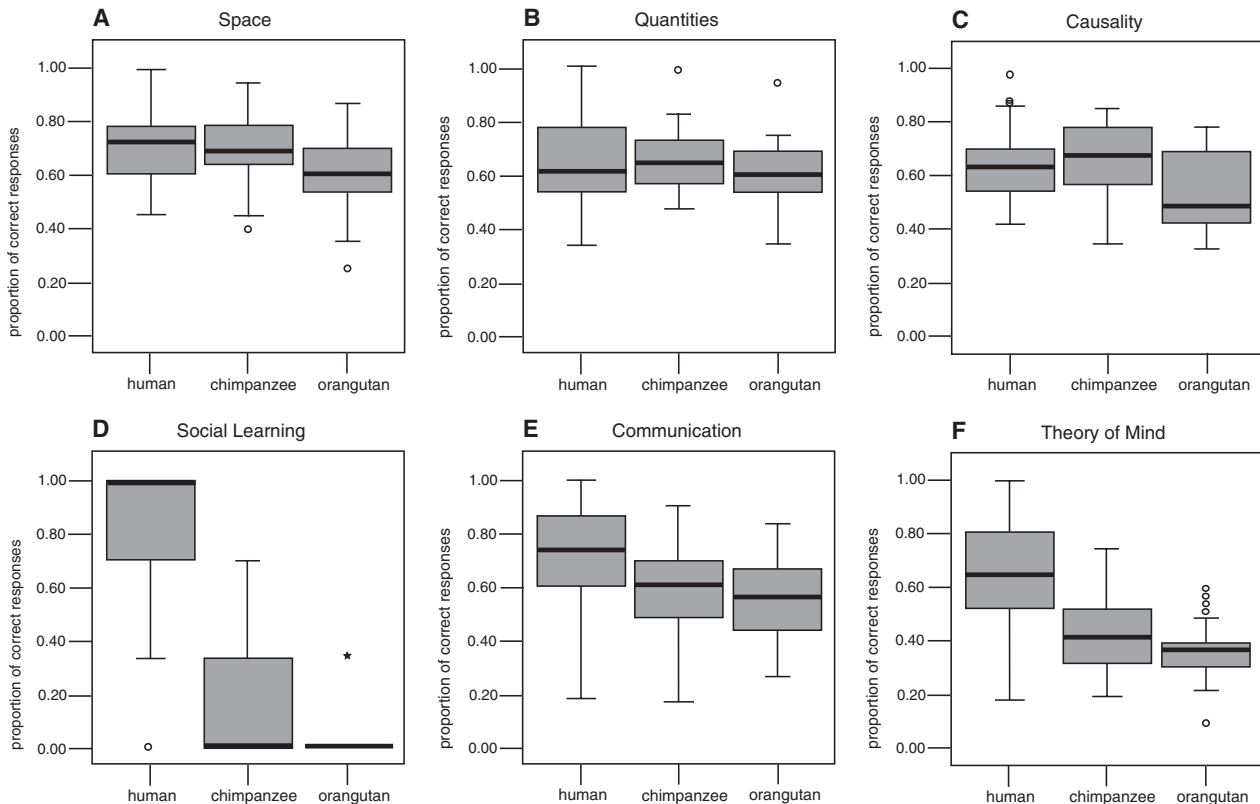

Fig. 2. Space (**A**), quantities (**B**), causality (**C**), social learning (**D**), communication (**E**), and theory of mind (**F**). The box plots show the full distribution of the proportion of correct responses on the six scales of the PCTB for each species: median, quartiles, and extreme values. Boxes, lines, whiskers, outliers, and extremes are as described in Fig. 1. Statistical comparisons on each scale were made by MANOVA, followed by ANOVAs for each scale. Post-hoc tests (the Bonferroni correction was used when the equality of variances assumption holds, and the Dunnett t3 correction was used otherwise) followed in case a significant effect was detected. Performance in the physical domain differed significantly across species (MANOVA with species and gender as between-subject factors and performance in the three scales of the physical domain as the dependent variables; Wilk's Lambda: $F_{6,470} = 6.934$, $P < 0.001$, $\eta^2 = 0.08$). No statistically significant differences were detected between genders. However, there was a significant interaction between species and gender (Wilk's Lambda: $F_{6,470} = 2.393$, $P = 0.027$, $\eta^2 = 0.03$). Univariate analyses (ANOVA) showed that the differences across species were significant for the scales space ($F_{2,237} = 11.033$, $P < 0.001$, $\eta^2 = 0.09$) and causality ($F_{2,237} = 8.617$, $P < 0.001$, $\eta^2 = 0.07$). No species difference was found for the scale quantities ($F_{2,237} = 1.970$, $P = 0.142$). Univariate analyses for the interaction between species and gender revealed that there was a significant interaction for the scales space ($F_{2,237} = 4.095$, $P = 0.018$, $\eta^2 = 0.03$) and

quantities ($F_{2,237} = 3.147$, $P = 0.045$, $\eta^2 = 0.03$) but not for causality ($F_{2,237} = 0.199$, $P = 0.820$). Post-hoc tests (Bonferroni correction) revealed that humans and chimpanzees performed better than orangutans in the scales of space and causality (for all $P < 0.001$), with no difference between chimpanzees and humans on these scales. Post-hoc tests for the interaction between species and gender for space showed that chimpanzee males outperformed females ($P = 0.047$). Post-hoc tests showed that human females outperformed males on the quantities scale ($P = 0.004$). No other gender differences were found. Performance in the social domain differed significantly across species (MANOVA with gender and species as between-subject factors and performance in the three scales of the social domain as the dependent variables; Wilk's Lambda: $F_{6,470} = 96.846$, $P < 0.001$, $\eta^2 = 0.55$). No statistically significant differences were detected between gender, and no significant gender-species interaction was found. Univariate analyses (ANOVA) showed that the differences across species were significant for the all three scales: social learning ($F_{2,237} = 382.145$, $P < 0.001$, $\eta^2 = 0.76$), communication ($F_{2,237} = 24.717$, $P < 0.001$, $\eta^2 = 0.17$), and theory of mind ($F_{2,237} = 70.646$, $P < 0.001$, $\eta^2 = 0.37$). Post-hoc tests (Dunnett t3 correction) revealed that humans outperformed chimpanzees ($P < 0.001$) and orangutans ($P < 0.001$) in social learning, communication, and theory of mind. The performance of chimpanzees and orangutans in all three scales did not differ.

Table 2. Proportion of correct responses on each of the tasks across species. Statistical comparisons on each scale were made by MANOVAs (with species and gender as between-subject factors and performance on the different tasks within each scale as dependent variables), followed by ANOVAs (with species and gender as between-subject factor) for each scale and task. Post-hoc tests (the Bonferroni correction was used when the equality of variances assumption holds, and the Dunnett t3 correction was used otherwise) followed in case a significant effect was detected. In case of important deviations of the model assumptions, a Kruskal-Wallis test with post-hoc Mann-Whitney U tests with the Bonferroni correction was performed. The tool-use task was analyzed separately with a chi-square analysis because it consisted only of one trial with a yes or no response. Space: Performance in the scale space differed significantly across species (MANOVA, Wilk's Lambda: $F_{8,468} = 11.273$, $P < 0.001$, $\eta^2 = 0.16$). No significant differences were detected between genders, and there was no significant interaction between species and gender. Univariate analyses (ANOVA) showed that the differences across species were significant for each spatial task: for spatial memory ($F_{2,237} = 3.329$, $P = 0.038$, $\eta^2 = 0.03$), object permanence ($F_{2,237} = 27.911$, $P < 0.001$, $\eta^2 = 0.19$), rotation ($F_{2,237} = 3.564$, $P < 0.030$, $\eta^2 = 0.03$), and transposition ($F_{2,237} = 14.038$, $P < 0.001$, $\eta^2 = 0.11$). There was a statistically significant effect for spatial memory, but post-hoc tests (Dunnett t3 correction) revealed no significant difference across the three species. Pair-wise comparisons (Bonferroni correction) for object permanence showed that humans performed better than chimpanzees ($P < 0.001$) and orangutans ($P < 0.001$). Chimpanzees performed significantly better than orangutans on the task rotation ($P = 0.028$). Post-hoc tests for transposition revealed that chimpanzees outperformed humans ($P < 0.001$) and orangutans ($P < 0.001$) [see (25) for age effect]. Quantities: Performance in the scale quantities differed significantly across species (MANOVA, Wilk's Lambda: $F_{4,472} = 3.994$, $P = 0.003$, $\eta^2 = 0.03$). No statistically significant difference between genders was detected, and there was no significant interaction between species and gender. Because the model assumptions for an ANOVA were not met for both tasks within the quantities scale, nonparametric tests were performed. Kruskal-Wallis one-way ANOVA showed that the differences across species were significant for addition numbers ($\chi^2_2 = 9.574$, $P = 0.008$) but not for relative numbers ($\chi^2_2 = 4.149$, $P = 0.126$). Post-hoc tests, with Mann-Whitney U tests for addition numbers, revealed that chimpanzees performed better than humans ($U = 4462.00$, $z = -2.556$, $P = 0.011$) and orangutans ($U = 1192.50$, $z = -2.638$, $P = 0.008$). The species difference in addition numbers between chimpanzees and orangutans remained even after controlling for age by matching the age of chimpanzees and orangutans and comparing the performance of these individuals ($U = 735.50$, $z = -2.540$, $P = 0.011$). Causality: Performance in the scale causality differed significantly across species (MANOVA, Wilk's Lambda: $F_{6,470} = 33.093$, $P < 0.001$, $\eta^2 = 0.30$). No

statistically significant differences were detected between genders, and there was no significant interaction between species and gender. Univariate analyses (ANOVA) showed that the differences across species were significant for each causality task: for noise ($F_{2,237} = 74.163$, $P < 0.001$, $\eta^2 = 0.39$), shape ($F_{2,237} = 29.335$, $P < 0.001$, $\eta^2 = 0.20$), and tool properties ($F_{2,237} = 20.211$, $P < 0.001$, $\eta^2 = 0.15$). Post-hoc tests (Bonferroni correction) revealed that humans performed better than chimpanzees ($P < 0.001$) and orangutans ($P < 0.001$) on the noise task. The same difference was found for the shape task (chimpanzees, $P < 0.001$; orangutans, $P < 0.001$) and for tool properties (chimpanzees, $P < 0.001$; orangutans, $P = 0.003$). Performance in tool use was significantly different across species ($\chi^2_2 = 55.815$, $P < 0.001$). Pair-wise comparison revealed that chimpanzees outperformed humans (Fisher's exact test, $P < 0.001$) and orangutans (Fisher's exact test, $P < 0.001$). The species difference in tool use between chimpanzees and orangutans remained even after controlling for age by matching the age of chimpanzees and orangutans and comparing the performance of these individuals (Fisher's exact test, $P = 0.018$). Social Learning: The social-learning scale was analyzed with a Kruskal-Wallis one-way ANOVA. A significant difference between species was found ($\chi^2_2 = 183.301$, $P < 0.001$). Post-hoc tests, with Mann-Whitney U tests, revealed that humans performed better than chimpanzees ($U = 255.00$, $z = -12.593$, $P < 0.001$) and orangutans ($U = 56.50$, $z = -8.935$, $P < 0.001$), which did not differ from one another. Communication: Performance in the communication scale differed significantly across species (MANOVA, Wilk's Lambda: $F_{6,470} = 24.462$, $P < 0.001$, $\eta^2 = 0.24$). No statistically significant differences were detected between genders, and there was no interaction between species and gender. Univariate analyses (ANOVA) showed that the differences across species were significant for the comprehension ($F_{2,237} = 67.021$, $P < 0.001$, $\eta^2 = 0.36$) and attentional-state tasks ($F_{2,237} = 19.155$, $P < 0.001$, $\eta^2 = 0.14$). However, there were no species differences in the pointing-cups task ($F_{2,237} = 0.087$, $P = 0.916$). Post-hoc tests (Bonferroni correction) revealed that humans performed better than chimpanzees ($P < 0.001$) and orangutans ($P < 0.001$) on the comprehension task. The same difference was found in the attentional-state task (chimpanzees, $P < 0.001$; orangutans, $P < 0.001$). Theory of mind: Performance in the theory-of-mind scale differed significantly across species (MANOVA, Wilk's Lambda: $F_{4,472} = 44.868$, $P < 0.001$, $\eta^2 = 0.28$) No statistically significant differences were detected between genders, and there was no interaction between species and gender. Univariate analyses (ANOVA) showed that the differences across species were significant for both the gaze-following task ($F_{2,237} = 23.096$, $P < 0.001$, $\eta^2 = 0.16$) and the intentions task ($F_{2,237} = 87.129$, $P < 0.001$, $\eta^2 = 0.42$). Post-hoc tests (Bonferroni correction) revealed that humans performed better than chimpanzees ($P < 0.001$) and orangutans ($P < 0.001$) on the gaze-following task. The same difference was found for the intentions task (chimpanzees, $P < 0.001$; orangutans, $P < 0.001$).

	Human	Chimpanzee	Orangutan
Physical	0.68[O]	0.68[O]	0.59
Space	0.71[O]	0.71[O]	0.60
Spatial memory	0.91	0.95	0.85
Object permanence	0.79[C,O]	0.64	0.60
Rotation	0.55	0.56[O]	0.46
Transposition	0.57	0.70[H,O]	0.47
Quantities	0.67	0.68	0.63
Relative numbers	0.71	0.66	0.64
Addition numbers	0.64	0.69[H,O]	0.61
Causality	0.65[O]	0.66[O]	0.55
Noise	0.85[C,O]	0.61	0.56
Shape	0.83[C,O]	0.68	0.64
Tool use	0.23	0.74[H,O]	0.38
Tool properties	0.71[C,O]	0.61	0.63
Social	0.74[C,O]	0.36	0.33
Social learning	0.86[C,O]	0.10	0.07
Communication	0.72[C,O]	0.57	0.55
Comprehension	0.84[C,O]	0.63	0.65
Pointing cups	0.72	0.74	0.73
Attentional state	0.59[C,O]	0.34	0.26
Theory of mind	0.65[C,O]	0.40	0.36
Gaze following	0.45[C,O]	0.22	0.17
Intentions	0.85[C,O]	0.59	0.56

Superscripts indicate that values are significantly higher than human (H), chimpanzee (C), or orangutan (O) values.

terested) performed better in the physical domain. In terms of inhibitory control, children showed a greater ability to inhibit than either ape species, and chimpanzees inhibited more readily than orangutans. There was a positive correlation for all three species of inhibitory control and cognitive performance in the physical, but not in the social, domain (*25*).

Discussion. The current results provide strong support for the cultural intelligence hypothesis that human beings have evolved some specialized social-cognitive skills (beyond those of primates in general) for living and exchanging knowledge in cultural groups: communicating with others, learning from others, and "reading the mind" of others in especially complex ways. Young human children who had been walking and talking for about 1 year, but who were still several years away from literacy and formal schooling, performed at basically an equivalent level to chimpanzees on tasks of physical cognition but far outstripped both chimpanzees and orangutans on tasks of social cognition. This was true at both the most general and the most specific levels of analysis, for individuals never before exposed to these tests, and across the most comprehensive test battery ever given to multiple primate species.

The current results provide no support for the general intelligence hypothesis that human cognition differs from that of apes only in general cognitive processes such as memory, learning, or perceptual processing, which should have led to children differing from apes in both the physical and social domains to an equal degree. However, we should note that because the children were somewhat more skillful than the apes in the causality tasks not involving active tool manipulation, as well as in the tasks of social cognition, it is possible that what is distinctively human is not social-cultural cognition as a specialized domain, as we have hypothesized. Rather, what may be distinctive is the ability to understand unobserved causal forces in general, including (as a special case) the mental states of others as causes of behavior (*22, 23, 26*). Even in this case, however, it is a plausible hypothesis that understanding hidden causal forces evolved first to enable humans to understand the mental states of other persons, and this generalized only later to the physical domain (*22*).

We may thus think of 2-year-old children's cognitive development in the physical domain as still basically equivalent to that of the common ancestor of humans and chimpanzees some 6 million years ago (with perhaps a little more sophisticated understanding of causality outside the context of tool use) but their social cognition as already well down the species-specific path. As one example, the finding that 2.5-year-old children's quantitative skills are basically equivalent to those of apes suggests a great ape "starting point" for human mathematical skills before serious instruction from adults (using written numerals) has begun (*27*).

Also, another recent study found that young human children have preferences for spatial orientation similar to those of great apes, but older children have preferences that align with those of their culture, presumably as a result of experiencing their culture's ways of dealing with space, including the use of particular kinds of spatial language (*28*). This provides one example of the kind of cognitive transformation that may result from children using their specialized social-cognitive skills to participate in the cultural practices around them.

In terms of human evolution, it is likely that the crucial developments in skills of social-cultural cognition probably had not yet occurred in *H. erectus* 1 to 2 million years ago, because (i) their rapid pattern of brain growth during ontogeny was more similar to that of chimpanzees than to that of modern humans (*29*) and (ii) there are few signs in this early hominid of elaborate cultural differences between groups (*30*). The ecological conditions within which post–*erectus* humans' special skills of social-cultural cognition evolved are not known, but one hypothesis is that those skills evolved in support of especially complex forms of collaborative activity, such as hunting or gathering, supported by special skills of communication and social learning (*31*). These skills presumably grew out of earlier evolved primate skills of social cognition and learning in general, such as those that nonhuman primates display in their everyday interactions with groupmates in the wild, involving an understanding of the intentions, perceptions, and motivations of others (*24*).

It is certainly an issue that the test battery was both constructed and administered by humans. But in previous studies with these same tasks from the social domain, there is no evidence that the use of human versus conspecific interactants had any significant effect on performance (table S2) (*25*). And our temperament measures did not correlate with performance on the social domain of the test battery, which is where there were the largest differences among species (and indeed the children were more shy or less interested in general in the temperament task), providing no support for the notion that the apes related less well to the testing situation. In terms of test construction, we of course could have obtained different results with a different test battery. But the PCTB was constructed from a comprehensive theory of primate cognition based on the ecological tasks that primates face most commonly in both their physical and social environments. In general, we suspect that there would be more consensus among experts about the appropriateness of our tasks of physical cognition, whereas there might be more controversy about the social tasks. But a major factor in the choice of the social tasks was our focus on humans and the cultural intelligence hypothesis, and this meant testing those social-cognitive skills relevant to participation in culture by young

children and then seeing the degree to which closely related species have these skills as well. It is perhaps relevant, in this regard, that domestic dogs (*Canis familiaris*) (which, in some sense, have been selected to live in human cultures) do not perform as well as chimpanzees on tasks of physical cognition but outperform them on tasks of social cognition (*32, 33*).

The role played by individual variability and gender in our results requires further investigation. The finding that, at a very general level of analysis, there were no species differences in cognitive variability is somewhat unexpected, given that apes are much more genetically variable in general than are humans (*34*). Gender did not play a large role either. The one finding for gender with the apes (that male chimpanzees were better than female chimpanzees at space) fits with previous research. But our finding that human females were better than human males at tasks of physical cognition in general (and quantities in particular) does not fit so well with previous research (*35*), though not so much research has been done with children this young, and so there may be developmental differences involved.

The past few years have seen the sequencing of both the human and the chimpanzee genome (*36–38*) [the orangutan and bonobo (*P. paniscus*) genomes are currently being sequenced], with a major goal being to identify domains of human genetic distinctiveness. But to do this with specific reference to behavior and cognition, what is needed first are comprehensive and detailed comparisons among humans and closely related primates at the level of the phenotype, in terms of the actual behavioral and cognitive skills that have promoted survival and reproduction (*39*). A major avenue of future research is thus to use the PCTB to characterize the behavioral-cognitive phenotype of a wide variety of primate species. This could be done through systematic testing of carefully chosen representatives of the more than 50 genera of primates, which should then enable us to map out cladistically the evolution of primates' most important cognitive skills at the level of both the phenotype and, ultimately, the genotype.

References and Notes

1. H. J. Jerison, *Evolution of the Brain and Intelligence* (Academic Press, New York, 1973).
2. P. Harvey, R. Martin, T. Clutton-Brock, in *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (Univ. of Chicago Press, Chicago, 1987), pp. 181–196.
3. L. C. Aiello, P. Wheeler, *Curr. Anthropol.* **36**, 199 (1995).
4. J. Tooby, L. Cosmides, in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, J. H. Barkow, L. Cosmides, J. Tooby, Eds. (Oxford Univ. Press, New York, 1992), pp. 19–136.
5. S. J. Shettleworth, *Cognition, Evolution, and Behavior* (Oxford Univ. Press, New York, 1998).
6. K. Milton, in *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*, R. W. Byrne, A. Whiten, Eds. (Clarendon Press, Oxford, 1988), pp. 285–306.
7. R. W. Byrne, in *Modelling the Early Human Mind*, P. Mellars, K. Gibson, Eds. (McDonald Institute Research Monographs, Cambridge, 1996), pp. 49–56.

8. N. K. Humphrey, in *Growing Points in Ethology*, P. P. G. Bateson, R. A. Hinde, Eds. (Cambridge Univ. Press, Cambridge, 1976), pp. 303–321.
9. F. B. M. de Waal, *Chimpanzee Politics: Power and Sex Among Apes* (Harper and Row, New York, 1982).
10. R. W. Byrne, A. Whiten, Eds. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans* (Clarendon Press, Oxford, 1988).
11. R. I. M. Dunbar, *Annu. Rev. Anthropol.* **32**, 163 (2003).
12. R. Boyd, P. J. Richerson, *Proc. Br. Acad.* **88**, 77 (1996).
13. L. S. Vygotsky, *Mind in Society: The Development of Higher Psychological Processes* (Harvard Univ. Press, Cambridge, MA, 1978).
14. A. Whiten *et al.*, *Nature* **399**, 682 (1999).
15. C. P. van Schaik *et al.*, *Science* **299**, 102 (2003).
16. M. Tomasello, *The Cultural Origins of Human Cognition* (Harvard Univ. Press, Cambridge, MA, 1999).
17. R. I. M. Dunbar, *J. Hum. Evol.* **22**, 469 (1992).
18. R. I. M. Dunbar, *Behav. Brain Sci.* **16**, 681 (1993).
19. R. I. M. Dunbar, *Evol. Anthropol.* **6**, 178 (1998).
20. H. Kudo, R. I. M. Dunbar, *Anim. Behav.* **62**, 711 (2001).
21. R. O. Deaner, C. P. van Schaik, V. E. Johnson, *Evol. Psychol.* **4**, 149 (2006).
22. M. Tomasello, J. Call, *Primate Cognition* (Oxford Univ. Press, New York, 1997).
23. D. L. Cheney, R. M. Seyfarth, *How Monkeys See the World: Inside the Mind of Another Species* (Univ. of Chicago Press, Chicago, 1990).
24. D. L. Cheney, R. M. Seyfarth, *Baboon Metaphysics: The Evolution of a Social Mind* (Univ. of Chicago Press, Chicago, 2007).
25. See supporting material on *Science* Online.
26. A. Whiten, in *Theories of Theories of Mind*, P. Carruthers, P. K. Smith, Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 277–292.
27. M. D. Hauser, F. Tsao, P. Garcia, E. S. Spelke, *Proc. R. Soc. London Ser. B* **270**, 1441 (2003).
28. D. B. M. Haun, C. Rapold, J. Call, G. Janzen, S. C. Levinson, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 17568 (2006).
29. H. Coqueugniot, J.-J. Hublin, F. Veillon, F. Houët, T. Jacob, *Nature* **431**, 299 (2004).
30. R. G. Klein, *The Human Career: Human Biological and Cultural Origins* (Univ. of Chicago Press, Chicago, ed. 2, 1999).
31. M. Tomasello, M. Carpenter, J. Call, T. Behne, H. Moll, *Behav. Brain Sci.* **28**, 675 (2005).
32. B. Hare, M. Brown, C. Williamson, M. Tomasello, *Science* **298**, 1634 (2002).
33. J. Bräuer, J. Kaminski, J. Call, M. Tomasello, *J. Comp. Psychol.* **120**, 38 (2006).
34. A. Fischer, J. Pollack, O. Thalmann, B. Nickel, S. Pääbo, *Curr. Biol.* **16**, 1133 (2006).
35. D. Voyer, S. Voyer, M. Bryden, *Psychol. Bull.* **117**, 250 (1995).
36. J. C. Venter *et al.*, *Science* **291**, 1304 (2001).
37. E. S. Lander *et al.*, *Nature* **409**, 860 (2001).
38. The Chimpanzee Sequencing and Analysis Consortium, *Nature* **437**, 69 (2005).
39. M. Hauser, *Nature* **437**, 60 (2005).
40. We thank L. Pharoah, R. Atencia, K. Brown, and the Jane Goodall Institute USA and staff of Tchimpounga Sanctuary, as well as L. Ajarova, D. Cox, R. Ssunna, and the trustees and staff of Ngamba Island Chimpanzee Sanctuary, for their enthusiasm, help, and support. We also thank B. M. Galdikas and the staff of the Orangutan Care Center and Quarantine in Pasir Panjang for their great help and support. In particular, we appreciate the hard work of the animal caregivers from the three sanctuaries: J. Maboto, B. Moumbaka, A. Sitou, M. Makaya, B. Bissafi, C. Ngoma, W. Bouity, J. A. Tchikaya, L. Bibimbou, A. Makosso, C. Boukindi, G. Nzaba, B. Ngoma, P. Kibirege, I. Mujaasi, S. Nyandwi L. Mugisha,

REPORTS

Muscular Thin Films for Building Actuators and Powering Devices

Adam W. Feinberg,[1] Alex Feigel,[2] Sergey S. Shevkoplyas,[2] Sean Sheehy,[1] George M. Whitesides,[2]* Kevin Kit Parker[1]*

We demonstrate the assembly of biohybrid materials from engineered tissues and synthetic polymer thin films. The constructs were built by culturing neonatal rat ventricular cardiomyocytes on polydimethylsiloxane thin films micropatterned with extracellular matrix proteins to promote spatially ordered, two-dimensional myogenesis. The constructs, termed muscular thin films, adopted functional, three-dimensional conformations when released from a thermally sensitive polymer substrate and were designed to perform biomimetic tasks by varying tissue architecture, thin-film shape, and electrical-pacing protocol. These centimeter-scale constructs perform functions as diverse as gripping, pumping, walking, and swimming with fine spatial and temporal control and generating specific forces as high as 4 millinewtons per square millimeter.

Muscle cells are microscale linear actuators driven by the activation of actin-myosin motors, coordinated in space and time through excitation-contraction (EC) coupling (*1*, *2*). Structure-function relations are conserved over several orders of spatial magnitude, from the sarcomere to the muscle bundle, by virtue of a hierarchical architecture. These architectures are achieved by morphogenesis programs that are responsible for coupling a broad range of processes, from sarcomeregenesis to the integration of the biochemical and electrical networks that support muscle function (*1*). Muscle actuation occurs over a wide range of frequencies (0 to ~100 Hz), spatial dimensions (5 μm to ≥1 m), and force regimes (~5 μN to ≥1 kN) (*3*, *4*). Artificial muscles can match certain temporal, spatial, or force regimes typical of biological muscle (*5*, *6*), but they cannot fully replicate all of these capabilities, nor can they use the same high-density energy sources. Thus, engineered muscle remains an attractive method for building actuators and powering devices from the micro to macro scales.

Device design with engineered tissues faces many of the same technical challenges as therapeutic cardiac tissue engineering [reviewed in (*7*)], the most difficult of which is proper replication of morphogenetic coupling schemes in three dimensions. Tissue-engineered myocardium based on cardiomyocytes seeded into gels (*8*), rolled up from sheets (*9*), or released from surfaces (*10*) has demonstrated the potential to produce actuators (*11*), tissue grafts (*12*), and power microdevices (*13*). The utility of these techniques is limited by the geometry of the device, but recent work in soft lithography (*14–16*) has provided new techniques to replicate cell and tissue microenvironments in vitro, suggesting an alternative means of achieving the functionality of a three-dimensional (3D) device with a 2D tissue.

[1]Disease Biophysics Group, School of Engineering and Applied Sciences, Harvard University, Cambridge, MA 02138, USA. [2]Department of Chemistry and Chemical Biology, Harvard University, Cambridge, MA 02138, USA.

*To whom correspondence should be addressed. E-mail: gwhitesides@gmwgroup.harvard.edu (G.M.W.); kkparker@seas.harvard.edu (K.K.P.)