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Human and chimpanzee shared and divergent neurobiological systems for general and specific cognitive brain functions

Martijn P. van den Heuvel[a,b,1], Dirk Jan Ardesch[a], Lianne H. Scholtens[a], Siemon C. de Lange[a,c], Neeltje E. M. van Haren[d,e], Iris E. C. Sommer[f], Udo Dannlowski[g], Jonathan Repple[h], Todd M. Preuss[i,j], William D. Hopkins[k], and James K. Rilling[j,l,m,n,o]

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A long-standing topic of interest in human neurosciences is the understanding of the neurobiology underlying human cognition. Less commonly considered is to what extent such systems may be shared with other species. We examined individual variation in brain connectivity in the context of cognitive abilities in chimpanzees (n = 45) and humans in search of a conserved link between cognition and brain connectivity across the two species. Cognitive scores were assessed on a variety of behavioral tasks using chimpanzee- and human-specific cognitive test batteries, measuring aspects of cognition related to relational reasoning, processing speed, and problem solving in both species. We show that chimpanzees scoring higher on such cognitive skills display relatively strong connectivity among brain networks also associated with comparable cognitive abilities in the human group. We also identified divergence in brain networks that serve specialized functions across humans and chimpanzees, such as stronger language connectivity in humans and relatively more prominent connectivity between regions related to spatial working memory in chimpanzees. Our findings suggest that core neural systems of cognition may have evolved before the divergence of chimpanzees and humans, along with potential differential investments in other brain networks relating to specific functional specializations between the two species.

connectome | brain | intelligence | MRI | evolution

Significance

Understanding the neurobiology of human behavior and cognition is a central theme in neuroscience. The present study integrates individual cognitive performance and brain connectivity data in chimpanzees and humans and shows that overlapping anatomical circuitry is involved in cognitive ability in both species. Differential investments in specialised brain networks may relate to functional specializations, such as language and working memory, in humans and chimpanzees. The identification of a conserved structural backbone for cognition has important implications for our understanding of the evolution of human intelligence and other highly developed brain functions.

The study of the neurobiology underlying cognitive abilities has a long history in neuroscience (1, 2). One focus has been the question of whether individual variation in brain systems is associated with individual differences in cognitive abilities and intelligence (3).

This relationship between brain structure and cognition is most often investigated in humans. Less commonly considered is the possibility that individual variation in brain organization may be similarly linked to individual differences in cognitive performance in other animals. While human brains differ markedly from those of our closest living evolutionary relatives [including a 3 to 4 times larger brain size than chimpanzees and bonobos (4)], human and chimpanzee brains display many similarities due to their shared evolutionary history, as evidenced by an extensive list of comparable topological features and systems ranging from a similar left–right asymmetric organization (5), overlapping morphological features (6, 7), and comparable structural and functional macroscale networks (8, 9). Similarly, like humans, chimpanzees display a rich variety of cognitive skills and live in large social groups with complex social relationships and interactions (10, 11). They display for example advanced visual spatial working memory skills (12–15) and show complex behavior in competitive strategic interactions (14). Mounting evidence suggests that also individual variation in brain size and organization among chimpanzees is related to individual differences in general intelligence (16), tool use (17), and the strategic use of vocalization behavior (18). Examining to what extent individual variation in brain systems related to shared cognitive abilities such as problem solving and relational thinking overlap in both species can increase our understanding of the origin of neural systems underlying cognitive abilities.

Since humans and chimpanzees diverged from their common ancestor an estimated 7 to 8 Mya (19), both species evolved in their respective ecological niches (20, 21). Building upon evolutionary adaptations from a shared ancestral phenotype, comparative brain studies have noted divergence in, for example, frontal, temporal, and visual cortical areas (22–24), morphological properties of neurons (25, 26), and cross-species variation in large-scale brain wiring of specific networks (27, 28). Besides potentially shared systems, these differences point toward a tuning of other brain networks and their function in support of each species' own behavioral repertoire and cognitive specializations. Cross-species variation in the insula and amygdala for example has been related to differences between primate species in social behavior (29, 30) and adaptations in frontotemporal connectivity

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[1]To whom correspondence may be addressed. Email: martijn.vanden.heuvel@vu.nl.

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in humans have been suggested to be foundational to the development of language (28, 31, 32). Similarly, the chimpanzee brain may have experienced changes to facilitate their own rich variety of cognitive skills (33), such as supporting their advanced spatial working memory skills (12–14) (see also refs. 15, 34, and 35) for discussion).

Taken together, these comparative observations tend to suggest the existence of human–chimpanzee shared cognitive brain systems, along with species-specific adaptations in brain organization that support the cognitive domains most crucial for each species. We examined this hypothesis with two lines of analysis. We first examined whether, and if so how, networks of brain connectivity associated with nonsocial cognitive skills such as problem solving and relational reasoning overlap between humans (Fig. 1 *A* and *B*) and chimpanzees (Fig. 1*C*). We further investigated whether there are brain circuits involved in specific brain functions and cognitive domains that are relatively well developed in each of the two species.

Results

Human Brain Systems Related to Cognitive Abilities. We began by examining the relationship between white matter connectivity and cognition in humans. We focused our analysis on aspects of nonverbal and nonsocial cognition (NIHTB-CB tasks testing for executive functioning, relational reasoning, processing speed, see *Materials and Methods*) to best match the cognitive tasks in the chimpanzee population (see for chimpanzee test-battery below). We correlated the individual composite cognitive scores of these tasks with connection strength for each reconstructed brain connection using a CWAS approach in a human discovery dataset of n = 480 subjects of the Human Connectome Project (HCP Q3 release, Fig. 1*A*) (37, 38). Fitted regression coefficients denoted the strength of the association between intersubject variation in strength of that connection and cognitive performance, with connections showing the highest coefficients indicating the subset of connections that were most strongly related to cognition (*SI Appendix*, Fig. S1, see *Materials and Methods*). The most strongly correlated connections included connections between the superior frontal cortex and pars opercularis (b = 0.59, $P = 1.39 \times 10^{-3}$), between the superior frontal and precentral cortex (b = 0.46, $P = 0.0170$), and between the insula and inferior temporal cortex (b = 0.43, $P = 7.89 \times 10^{-3}$, all uncorrected), brain systems indeed hypothesized to relate to human cognition (39). Statistical significance of the most strongly correlated subset of connections was assessed using Network Based Statistics [NBS (40)], confirming a cognitive network of connections spanning areas of the inferior parietal, middle temporal, inferior temporal, insula, lateral occipital and superior frontal cortex (NBS $P = 0.0104$, NBS P-threshold = 0.05, 1,000 permutations).

Human Polyconnectomic Scores (PCS). The predictive power of the identified connections was validated by applying the edgewise summary statistics to the second part of the HCP (n = 572, HCP Q4 S1200 release, Fig. 1*B*). PCS [(41), see *Materials and Methods*] were computed for each individual in the HCP test dataset, multiplying the normalized top highest connection-wise regression coefficients (Fig. 2*A*) by the matching connection strength values for the subjects in the test dataset. PCS showed a significant correlation with the cognitive scores in this dataset (PCS threshold 29%, see *Materials and Methods*: $r = 0.091$, $P = 0.0294$) indicative of PCS computed on the basis of brain circuitry to have significant predictive power for cognitive performance (Fig. 2*B*). Results were validated in external datasets, showing similar effects of PCS consistently capturing a proportion of individual variation in cognitive scores in humans (validation dataset 1: n = 69, $r = 0.26$, $P = 0.0301$; AOMIC validation dataset 2: n = 885, $r = 0.084$, $P = 0.0129$, MACC (Marburg–Muenster Affective Disorder Cohort) validation dataset 3: n = 468, $r = 0.10$, $P = 0.0263$, see *Materials and Methods* and *SI Appendix* for details).

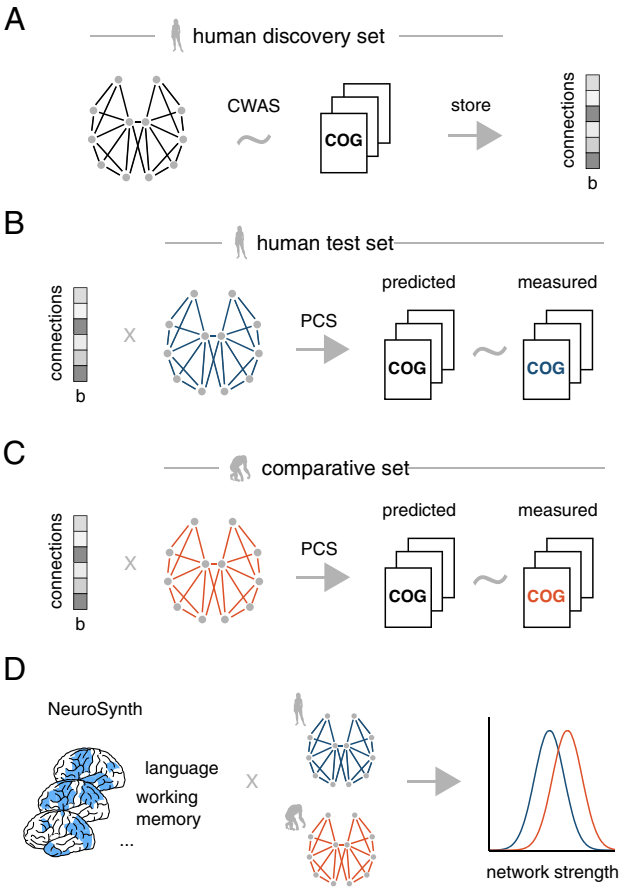

Fig. 1. Study overview. (*A*) Human Connectome Project (n = 480) data were used to perform a connectome-wide association study (CWAS), correlating the strength of connections in the connectome with a summary score of cognitive performance of the individuals. The regression coefficients of the most strongly associated connections were stored as summary statistics. (*B*) The stored regression coefficients were multiplied by the corresponding connection strengths of a separate human test set (HCP, n = 572 nonoverlapping subjects) to calculate a polyconnectomic score (PCS), reflecting a predicted cognitive score for every subject in the test set. Predicted scores were correlated with the measured empirical cognitive scores to evaluate the performance of the CWAS analysis in humans. (*C*) Human CWAS summary statistics were applied to a sample of chimpanzee subjects by multiplying the stored (human) coefficients by the corresponding connection strengths of a chimpanzee dataset. The predicted chimpanzee cognitive scores based on the human CWAS data were correlated with the measured empirical cognitive scores in chimpanzees to evaluate whether strength of connections associated with cognition in humans also predicts individual variation in cognitive performance in chimps. (*D*) Functional cognitive systems (161 in total, among others, "language" and "working memory") were mapped by taking functional activation maps from the NeuroSynth database mapped to the DK-114 cortical atlas. Normalized connection strength for the examined functional systems was calculated based on the human and chimpanzee connectome, and compared across species to identify brain functions that displayed a more prominent role in the human versus the chimpanzee brain network. Icons from phylopic.org. Brain plots visualized with Simple brain plot (36).

Human Cognitive Networks Predictive for Cognition in Chimpanzees. We continued with our main topic of investigation, examining whether the networks that predicted cognitive performance in humans were also associated with cognitive variation in chimpanzees. Individual scores relating to aspects

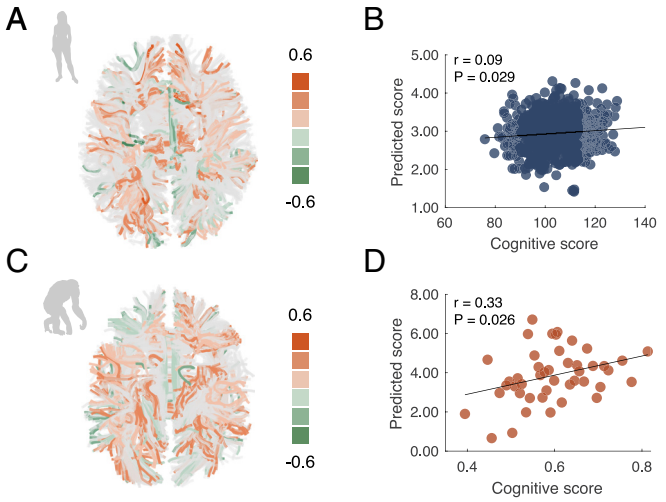

Fig. 2. Human-based polyconnectomic scores (PCS) predict cognitive performance in both humans and chimpanzees. (*A*) Network plot of the top most strongly associated connections visualized on an example human subject. Color corresponds to regression coefficients of the top most strongly associated connections; gray denotes remaining connections. (*B*) Empirical cognitive scores vs. PCS-predicted cognitive scores in humans (PCS threshold = 29%). (*C*) Network plot of the top most strongly associated connections visualized on an example chimpanzee subject. (*D*) Normalized empirical cognitive scores vs. PCS-predicted cognitive scores in chimpanzees (PCS threshold = 29%).

of physical cognition were derived from items from the Primate Cognition Test Battery [PCTB (42), measuring cognitive skills related to causality, spatial cognition, and quantity discrimination, collectively referred to as "physical cognition" (43), see *Materials and Methods*]. We used the human edge-wise summary statistics to compute PCS, but now computed on the normalized connectivity data of the sample of chimpanzees (n = 45, Fig. 1*C*, see *Materials and Methods*). Chimpanzee PCS for physical cognition significantly predicted the cognitive scores in the chimpanzees (r = 0.33, P = 0.0259, Fig. 2 *C* and *D*), suggesting that brain networks related to cognitive variation in humans are potentially shared and similarly associated with variation in cognitive performance in chimpanzees. We validated this effect to be specific to connections linked to cognition: Computing PCS based on connections outside of the network of connections linked to cognitive performance in the human population as a null condition showed no significant effect in the chimpanzee population (P = 0.43).

Differential Investment in Language and Working Memory Networks. We next addressed our second main question: To what extent do brain networks involved in specific functions differ across the two species (Fig. 1*D*). We tested this by means of computing normalized network strength of brain systems related to two brain functions suggested to be relatively well developed in each of the two species, being language in humans (32) and visual spatial working memory in chimpanzees (12–14). We began by examining brain connectivity between two extensively studied, a priori defined, brain networks related to language and spatial working-memory (*Materials and Methods*). In line with previous comparative observations (31), normalized connection strength of the language network was found to be significantly higher in humans, as compared to chimpanzees (two-sample t test $t(78) = 3.78$, $P = 3.02 \times 10^{-4}$, Fig. 3*A*). In contrast, normalized connectivity strength of the working memory network was found to be relatively high in the chimpanzee brain compared to the human brain ($t(78) = 2.77$, $P = 0.007$, Fig. 3*B*). We further examined these brain systems by means of using data-driven functional brain maps derived from the extensive NeuroSynth database (44) (*Materials and Methods*). Normalized connection strength between regions involved in language processing (NeuroSynth term "language") was similarly found to be significantly higher in humans as compared to chimpanzees (two-sample t test $t(78) = 3.37$, $P = 0.0012$, *SI Appendix*, Fig. S2) and normalized connectivity strength between regions involved in working memory (NeuroSynth term "working memory") was found to be higher in chimpanzees compared with humans ($t(78) = 3.32$, $P = 0.0013$, *SI Appendix*, Fig. S2).

Comparison of a Broad Range of Functional Brain Networks. We next performed a data-driven exploratory analysis in which we examined connectivity strength among the broad set of brain functions included in the NeuroSynth database, including a total of 161 terms (*SI Appendix*, Table S1, see *Materials and Methods*) related

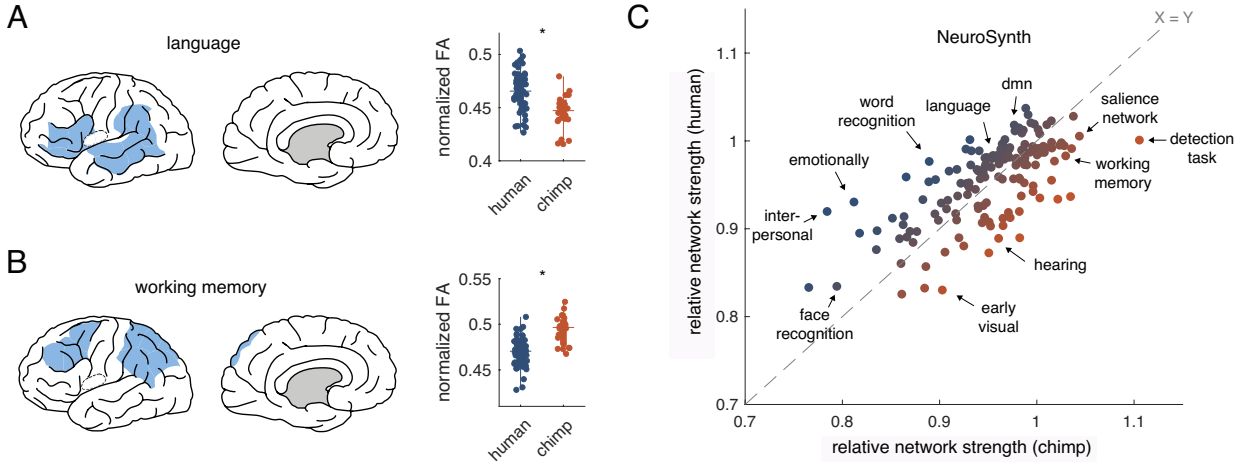

Fig. 3. Cross-species comparison of network investment in brain functions. (*A*) Cortical regions included in the language network (*Left*) and strength of connections between these language regions in humans vs. chimpanzees (*Right*). (*B*) Cortical regions included in the working memory network (*Left*) and strength of connections between these working memory regions in humans vs. chimpanzees (*Right*). Results of *A* and *B* were consistent when using brain maps derived by means of the NeuroSynth database (*SI Appendix*, Figs. S2 and S3). (*C*) Relative network strength of all 161 included NeuroSynth terms in humans vs. chimpanzees. Dashed line indicates equal relative strength in humans and chimpanzees. NeuroSynth terms above the dashed line represent brain functions with relatively high network prominence in humans compared with chimpanzees (blue color), while terms below the line represent functions with relatively high network prominence in chimpanzees compared with humans (orange color).

to a wide range of cognitive brain functions ranging from primary brain functions (e.g., terms such as "auditory", "sensory", "motor") to multimodal cognitive functions (e.g., "social cognition", "working memory"). Connectivity strength was computed for each network relative to the rest of the brain, with networks ranking high in relative connectivity strength occupying a relatively prominent role and networks ranking relatively low occupying a lesser role in total brain connectivity. We compared normalized relative connectivity strength between these functional networks between chimpanzees and humans in a cross-species comparative analysis. Consistent with the notion of strong overlap in overall connectome layout between humans and chimpanzees (8, 27) network connectivity strength correlated across the two species when considering all functional brain networks together ($r = 0.69$, $P = 6.90 \times 10^{-24}$, Fig. 3*C*). Nevertheless, some cross-species differences could be observed: Functional brain networks with relatively high connectivity in humans compared with chimpanzees included networks related to terms "emotionally", "visuo", "word recognition", "decision task", "default mode network", and "linguistic" (Bonferroni-corrected $P < 0.05/161$, Fig. 3*C*, see *SI Appendix*, Table S1 for a full list). In contrast, functional brain systems potentially relating to functions such as "memory tasks", "working memory", "decision-making", "hearing", and "salience network" (Bonferroni-corrected $P < 0.05/161$) were found to show a relatively more prominent role in brain connectivity in the chimpanzee population compared to humans (Fig. 3*C* and *SI Appendix*, Table S1). These exploratory data-driven results suggest a relative divergence in investment in brain connectivity in the language system in humans and systems related to more sensory and visual spatial working memory skills in chimpanzees.

Discussion

Our study makes two observations regarding individual variation of brain systems and their role in cognition. First, our findings suggest that brain systems related to various aspects of physical cognition (problem solving, relational reasoning, timing) are shared between humans and chimpanzees, and may similarly explain variation in physical cognitive skills in both species. Second, comparative analysis of relative brain connectivity suggests that brain networks that have diverged in relative connection strength align with specialized cognitive brain functions in one species compared to the other. Networks supporting functions such as language and the default mode network may have adapted toward relatively high levels of brain connectivity in humans, while brain networks related to working memory, salience processing, and auditory processing occupy a relatively more prominent position in the chimpanzee brain.

Great apes have highly developed cognitive skills (45). Bonobos and chimpanzees are believed to be capable of understanding aspects of social causality (29, 46, 47), and to have components of theory of mind (47, 48). Yet, their ability to engage in high-level theory of mind such as inferring false beliefs or understanding others' perspectives well enough to deliberately teach others, may be limited (49, 50). Like chimpanzees, orangutans possess advanced cognitive skills, particularly in interaction with humans (51), and gorillas are capable of complex social and spatial learning (52, 53). Such shared cognitive abilities are hypothesized to be products of a shared evolutionary history and suggest the existence of a general neurobiological substrate for cognition and intelligence among great apes (43, 51). Indeed, shared neurobiological systems for cognition are supported by experimental studies suggesting that variation in brain volume, connectivity, and function are important factors to explain cognitive abilities among both humans (54) and chimpanzees (46). Shared macroscale circuitry and functional brain systems may be a key factor in these cross-species shared cognitive skills, with overlapping networks underlying intersubject cognitive variation among at least humans and chimpanzees, suggesting that their role in cognition may be phylogenetically much older than the human lineage (55).

Comparative results suggest that human and chimpanzee brain circuits have evolved to adapt each species to their own specific niche. Humans show relatively strong investments in white matter connectivity between areas of the language system compared to chimpanzees and macaques (31), and previous comparative studies point toward a distinct hub architecture across primate species (8) with potentially more and more developed structural and functional connectivity around higher order networks, including the default mode network in humans (8, 56). Chimpanzees may have potentially benefited more from investments in connectivity among brain networks involved in aspects of visuospatial attention and salience processing (12, 57, 58). Comparative studies have underscored the importance of physical cognitive skills for the extractive foraging behavior of chimpanzees, and their ability to use a large variety of tools when foraging in their natural habitat (42). Comparative studies have further suggested that visual spatial working memory skills (12–14) and object-based attention (59) may have been important for survival in the competitive social environment of wild chimpanzees, with competitive interactions and situations being a central part of their juvenile development and adult life (14, 60). It may be that a combined investment in networks related to visuospatial attention and networks related to monitoring and reacting to external events were of importance for their success. Such theories are supported by behavioral studies showing that adult chimpanzees perform relatively better in competitive than in cooperative tasks (61) and that chimpanzees outperform bonobos in cognitive tasks testing for physical causality and tool use (42). This may contrast with the observation of human enhancements for language and the default mode network, suggesting advantages to language and self-reflection activity in human evolution. In humans, advanced language skills have been hypothesized to allow them to more easily switch to cooperative cognitive strategies already at an early age (14), in particular when they learn to speak (14, 62). The evolution of language in humans is widely believed to be one of the primary catalysts of human collaboration (14, 62, 63) and combined with potential development of brain networks related to internal processing such as the default mode network—a central brain network involved in mental self-projection (64) and social cognition (65) (*SI Appendix*)—may have allowed our species to exchange information, make plans (63), share intentions, and otherwise develop ways for advanced social understanding (66, 67) and coordinated behavior in larger groups (68). Adaptations to brain circuitry and functional brain systems supporting complex language functions, theory of mind and, internal processing may thus have been of particular importance for human evolution (69, 70).

A human investment in language and default mode systems may not necessarily be discordant with a specialization for working memory. The human brain has expanded an estimated 3 to 4 times over the last 6 to 7 My (71) and absolute expansion of the neocortex is widely believed to have been one of the major catalysts for the development of a broad range of advanced cognitive functions in the genus *Homo* (72, 73), including working memory skills and executive functioning (74). An interesting open question is whether chimpanzees have potentially derived advanced working memory and spatial attention skills, accompanied by investments in underlying brain systems, or whether humans have the

same specialization, albeit overshadowed by larger investments in, for example, language and default mode systems. Alternatively, humans may have (relatively) decreased investment in certain patterns of connectivity, with human evolution involving a reconfiguration of connectivity across distinct distributed networks. In the latter case, the relative prominent position of spatial working memory systems in the chimpanzee brain may reflect an ancestral condition, rather than a derived trait. Our cross-species comparison involved only humans and chimpanzees, and is thus limited with respect to providing more insight into this question. A more elaborate comparison, involving comparisons to other great apes and in particular bonobos [with which chimpanzees share a more recent common ancestor around 1–2.5 Mya (19)] would be of great interest. Some theoretical insights may however be provided by cognitive trade-off hypotheses which predict that physical constraints and general limitations to brain resources may have played an important role in shaping brain systems and a species' specific behavioral and cognitive repertoire (75–80). The brain is considered an expensive tissue (81–83) and spatial and metabolic constraints of cognitive networks force a compromise between controlling "costs" and allowing the emergence of expensive but adaptive topological patterns and functions (77, 84). Such constraints have led to evolutionary adaptations in fundamental properties of axonal organization to maintain long-range brain synchronization and communication in larger brains (85). They may also highlight the possibility of differential expansion of neural projection systems (77, 86). Besides the language system, studies have suggested the default mode network to be particularly developed in humans (56, 87, 88) and high investments of connectivity in these networks may have come at the (relative) expense of other anatomical and functional brain systems.

Methodological aspects of our study have to be considered. An important point is the assessment and comparison of the cognitive scores across chimpanzees and humans. A direct comparison of cognitive scores across species remains difficult and has known limitations (57, 89). In addition, in the first part of our study we explored overlap in cognitive brain systems underlying general cognitive abilities across humans and chimpanzees, and in the second part we examined possible divergence in particular systems (e.g., language, working memory) between the two species. While related, concepts such as general intelligence and specific cognitive functions such as language and working memory are not identical, with a relationship between these concepts being complex and a topic of ongoing investigations in the field (90, 91).

Second, in assessing overlap in systems related to cognitive variation in the two species, we focused our comparative analysis on aspects of nonverbal and nonsocial cognition, examining the neurobiological systems associated with skills such as problem solving and spatial reasoning (*Materials and Methods*). Studying aspects of social cognition would be of equal value (see for example refs. 92–96), but our study design had clear limitations in this respect. Individual data on cognitive tasks related to social cognition were found to be less comparable between the chimpanzee and human populations. Attempts of mapping brain circuits related to social cognition scores in the human group on the basis of the NIHTB-CB tasks did not display significant predictive power between the discovery and replication human datasets (see *SI Appendix*). This lack of consolidation of the circuitry related to social cognition in the human population to begin with, made the next step of exploring individual variation in similar circuits in the chimpanzee population highly exploratory and in our opinion unjustified. An alternative exploratory analysis examining brain connectivity in an a priori "social cognition" map derived from the literature (97–99) (*SI Appendix*, Fig. S4) showed more prominent connectivity in the human brain compared to chimpanzees (*SI Appendix*). As mentioned, a further point of consideration is that the performed cross-species comparison involved a comparison between chimpanzees and humans. While strong efforts are being made to scan and reconstruct connectome maps from (postmortem) samples of a wider range of mammalian species (100), including monkeys and great apes (101), combined MRI and cognitive data from nonhuman primate subjects are very limited. We used the extensive NCBR database as one of the largest resources of neuroimaging and cognitive measures of chimpanzee and great-ape data available.

Third, we used the NeuroSynth database to derive brain maps of brain function and cognition, a validated automated framework based on text-mining, meta-analysis and machine-learning on fMRI data of over 14,000 functional human MRI studies (44). However, it is important to consider that the derived functional brain maps are based on meta-analysis of the included studies in the database. Some terms are better represented in the database than others (e.g., more studies are available, some terms are more often used then others), resulting in not all of the brain maps being derived with the same level of statistical power (102). In addition, these mappings are based on human fMRI studies and similar functional mappings in chimpanzees (and/or other great ape species) are not available. To what extent brain functions map to similar areas and networks in the human and chimpanzee brain remains an open question; our study assumes a certain level of overlap (103, 104).

Fourth, our comparative connectivity analysis is based on the comparison of anatomical connectivity derived from diffusion MRI data. Diffusion MRI allows for measurements of brain connectivity in vivo, making it a suitable method for the examination and comparison of brain connectivity in the human and chimpanzee brain, but diffusion MRI is also known to have clear limitations in terms of accuracy and efficacy of the reconstruction of white matter bundles (see *SI Appendix* for sensitivity analyses). The observed correlations between connectivity and cognitive performance in humans ($r = 0.09$ to 0.26 across the test and validation sets) suggest that the variance of standardized test performance explained by individual differences in diffusion MRI-based connectivity is indeed limited ($R^2 = 3$ to 7%), but consistently present across different scanners and acquisition protocols.

Materials and Methods

Subjects and Data Acquisition.

Human MRI and cognitive data. Human MRI and cognitive data ($n = 1,111$ subjects, 605 female, 28.9 ± 3.6 y) were included from the HCP database (37, 38) (S1200 release). HCP data included high-resolution T1 and DWI data and an extensive battery of cognitive tests as part of the NIH Toolbox Cognition Battery (NIHTB-CB) (105). A composite cognition score was computed per subject as the average over the age-adjusted scores of the performance on the following tasks: Dimensional Card Sorting Task (providing insight into executive functioning), Pattern Completion Processing Speed (processing speed), Picture Sequence Memory (episodic memory), and the List Sorting task (working memory) of this test battery [Supplementary Methods; a full description and validation of the tasks of the NIHTB-CB is presented here (106) (105)]. These subitems were selected to capture aspects of spatial reasoning and problem solving (in contrast to "social cognition"), tasks that were most comparable to tasks assessing "physical cognition" in the chimpanzees as measured in the PCTB (see below). The derived composite cognitive score was representative of the NIHTB-CB Cognition Fluid Composite ($r = 0.96$, $P < 0.001$; validation of our main analysis with this composite score revealed similar results) and NIHTB-CB Cognition Total Composite score capturing aspects of both nonverbal and verbal cognition ($r = 0.81$, $P < 0.0001$). HCP subjects passing MRI QC ($n = 1,052$) were split into a discovery set ($n = 480$ subjects, Q3 release) and a test set ($n = 572$, Q4 release) with no sample overlap

between the two sets. Additional data of, respectively, the Amsterdam Open MRI Collection (AOMIC) (107), the MACC study (108) and connectivity summary statistics of (109, 110) were used as validation datasets (Supplementary Methods).

Chimpanzee MRI and cognitive data. Out of a total dataset of 52 chimpanzees as part of the National Chimpanzee Brain Resource (NCBR, https://www.chimpanzeebrain.org) combined T1, DWI and cognitive data were available for 45 adult chimpanzees (*Pan troglodytes*, 22.8 ± 10.4 y, 28 female). Chimpanzees were housed at Yerkes National Primate Research Center (YNPRC) in Atlanta, Georgia. Procedures were carried out in accordance with protocols approved by the YNPRC and the Emory University Institutional Animal Care and Use Committee (IACUC, approval #:YER-2001206). All data were obtained prior to the 2015 implementation of U.S. Fish and Wildlife Service and NIH regulations governing research with chimpanzees and all chimpanzee scans were completed by the end of 2012; no new data were acquired for this study. MRI was acquired on Siemens 3T Trio Tim Scanners and included the acquisition of a structural T1 scan and diffusion MRI scans (see Supplementary Methods for details). Cognitive scores were assessed using the *primate cognition test battery* (PCTB), including a detailed test with subitems measuring multiple aspects of cognitive functioning, originally developed by Hermann et al. (92) and updated by Hopkins et al. (16). The PCTB includes a large test battery organized in two major cognitive domains, providing subitem scores for the different aspects of primate cognition, categorized and referred to, respectively, "physical" and "social" cognitive capacity (see also ref. 16). In this study, we focused on "physical cognition", measuring aspects of causality, spatial cognition, and quantity discrimination (see *SI Appendix* for a detailed description of the tasks included, detailed descriptions of each of the tasks are also presented in ref. 16), of which also human-comparable tests were available. While a comparative analysis on aspects of social cognitive scores would be of equally high interest (see for example refs. 95 and 96), a comparison of data on social tasks across the chimpanzee and human population was found to be more difficult; measures of social cognition between chimpanzee NCBR and human HCP data were measured across varying modalities, and to be less statistically powerful, limiting a direct comparative analysis (see also discussion). A composite summary score was calculated as the mean of the following physical cognition subitems: *a.* spatial memory, *b.* object permanence, *c.* rotation, *d.* transposition, *e.* quantity, *f.* causality (noise), *g.* causality (visual), *h.* tool use, and *i.* tool properties (see *SI Appendix* for details; a full description on each of the specific tasks is listed in ref. 43).

Human–chimpanzee comparative dataset. We further included a comparative dataset of human and chimpanzee subjects that were age-matched, acquired on the same type of MRI scanner (Supplementary Methods), and acquired using highly similar protocols to improve direct comparisons of human and chimpanzee neuroimaging data (8)–this dataset was used for the human–chimpanzee comparison of relative connectivity strength of a-priori and NeuroSynth-derived brain maps of language and working memory, see below.

Image Processing and Connectome Construction. For all of the datasets (i.e., all human and chimpanzee) the T1 image was processed using FreeSurfer (111), which involved tissue segmentation (see Supplementary Methods for details). DWI images were preprocessed using FSL (112), including correction for eddy-current, motion, and susceptibility distortions (Supplementary Methods). Connectome reconstruction was performed by means of deterministic fiber tracking (113) (see Supplementary Methods for details). Fractional anisotropy (FA) was taken as the metric of connectivity strength, interpreted as a metric of pathway microstructural organization. FA connectivity matrices were resampled to a Gaussian distribution ($M = 0.5$, $SD = 0.10$) for the examination of relative differences between subjects, allowing intersubject and cross-species comparison ruling-out effects of global differences in FA between individual datasets and protocols (27).

Human Brain Connectivity and Involvement in Cognitive Brain Function.

Human CWAS. We adopted a connectome-wide association study (CWAS) approach for this analysis–an approach conceptually highly similar to genome-wide association studies in the field of genetics (see Supplementary Methods for a more detailed description). HCP discovery dataset was used to map the contribution of each connection to individual variation in cognitive performance. The association between connectivity strength and the HCP-derived cognitive score was computed using linear regression.

PCS. Resulting unstandardized coefficients of the linear regression were stored in a connectivity–cognition matrix. Predictive power of these summary statistics was quantified using the HCP test set, defining a PCS for each subject in the test set based on the computed summary statistics matrix. PCS is inspired by the computation of polygenic risk scores in the field of genetics (114) (see also Supplementary Methods), taking the top ~29% connections with the highest regression coefficients (corresponding to the top 5% of all possible connections in the connectivity matrix) and multiplying the suprathreshold values of the summary statistics matrix with the normalized FA connectivity matrix and then taking the mean over all nonzero values. PCS-predicted cognitive scores were correlated with the true empirical cognitive scores of the individual subjects. Two external replication datasets were used for validation (Supplementary Methods).

Human–chimpanzee PCS. The PCS approach was similarly applied to the chimpanzee data (see *SI Appendix* for details). Normalized FA connectivity strength of each connection in the chimpanzee connectome was multiplied by the human CWAS-based regression coefficient of the corresponding connection in humans, resulting in a predicted involvement in cognitive performance for that particular connection in the chimpanzee subject. PCS-predicted cognitive scores were again correlated to the empirical cognitive scores of the chimpanzees.

Brain maps. Connectivity between regions of a priori and data-driven functional brain systems was examined. Two types of analyses were performed. First, brain maps for "language" and "working memory" were derived based on a priori mappings of well-defined brain areas involved in these cognitive functions based on literature (e.g., language: left hemispheric BA 44/45, 36/22/21/37; working memory: SPL/IPS, BA6,46, see *SI Appendix* for details). We also examined connectivity between brain areas related to sensory processing and brain areas associated with social cognition (*SI Appendix*). Brain maps were alternatively derived for a wide range of brain functions from the NeuroSynth database, a rich database of meta-analysis data of over 14,000 human functional MRI studies (44) describing a broad range of behavioral and cognitive brain functions (see *SI Appendix*, Methods).

Data, Materials, and Software Availability. The used human data are part from the open-source HCP and available from https://humanconnectome.org. The used chimpanzee data are part of National Chimpanzee Brain Resource and available at (https://www.chimpanzeebrain.org). Brain mapping data were taken from the NeuroSynth database and available at https://neurosynth.org. Connectivity data used as validation dataset 1 and 3 (MACC) are available at the Dutch DANS repository (https://doi.org/10.17026/dans-xwt-z3fg) adhering to EU regulations. A subset of dataset 1 was collected under informed consent that provides restrictions to including collected individual data to a public resource under Dutch regulations. These data are available on reasonable request to the authors. Connectivity data from the AOMIC used in this study as validation dataset 2 is available at https://openneuro.org.

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Author affiliations: [a]Department of Complex Traits Genetics, Center for Neurogenomics and Cognitive Research, Vrije Universiteit Amsterdam, Amsterdam Neuroscience, Amsterdam 1081 HV, the Netherlands; [b]Department of Child Psychiatry, Amsterdam University Medical Center, Vrije Universiteit Amsterdam, Amsterdam Neuroscience, Amsterdam 1081 HV, the Netherlands; [c]Department of Sleep and Cognition, Netherlands Institute for Neuroscience, An institute of the Royal Netherlands Academy of Arts and Sciences, Amsterdam 1105 BA, the Netherlands; [d]Department of Psychiatry, Brain Center University Medical Center Utrecht, Utrecht University, Utrecht 3584 CX, the Netherlands; [e]Department of Child and Adolescent Psychiatry, Erasmus Medical Center, Rotterdam 3015 CE, the Netherlands; [f]Department of Psychiatry, University Medical Center Groningen, University of Groningen, Groningen 9700 RB, the Netherlands; [g]Institute for Translational Psychiatry, University of Münster, Münster 48149, Germany; [h]Department

of Psychiatry, Psychosomatic Medicine and Psychotherapy, University Hospital Frankfurt, Goethe University, Frankfurt 60438, Germany; [l]Emory National Primate Research Center, Emory University, Atlanta, GA 30329; [j]Department of Pathology and Laboratory Medicine, Emory University School of Medicine, Atlanta, GA 30307; [k]Department of Comparative Medicine, Michael E. Keeling Center for Comparative Medicine and Research, University of Texas MD Anderson Cancer Center, Bastrop, TX 77030; [l]Center for Translational Social Neuroscience, Emory University, Atlanta, GA 30329; [m]Department of Anthropology, Emory University, Atlanta, GA 30322; [n]Silvio O. Conte Center for Oxytocin and Social Cognition, Emory University, Atlanta, GA 30322; and [o]Department of Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA 30322

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