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Journal
Proceedings of the National Academy of Sciences of the United States of America, 110(supplement_2)

ISSN
0027-8424

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Publication Date
2013-06-18

DOI
10.1073/pnas.1307207110

In the light of evolution VII: The human mental machinery

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In his Notebook C, Darwin gave us one of his first insights into human nature. There, referring to the human being, Darwin wrote: "He is Mammalian—his origin has not been indefinite—he is not a deity, his end under present form will come, (or how dreadfully we are deceived) then he is no exception.—he possesses some of the same general instincts, & moral feelings as animals.—they on the other hand cannot reason—but Man has reasoning powers in excess. Instead of definite instincts—this is a replacement in mental machinery—so analogous to what we see in bodily, that it does not stagger me." (1)

As Darwin noted, our mental machinery makes us different. For instance, it allows us to ask about ourselves, about what a human is. It enables us to question what we are and the ways in which we reached our current nature. One thing we have discovered is that humans possess certain unique mental traits. Self-reflection, as well as ethic and aesthetic values, is among them, constituting an essential part of what we call the human condition. The human mental machinery led our species to have self-awareness but, at the same time, a sense of justice, willing to punish unfair actions even if the consequences of such outrages harm our own interests. Also, we appreciate searching for novelties, listening to music, viewing beautiful pictures, or living in well-designed houses.

However, why is this so? What is the meaning of our tendency, among other particularities, to defend and share values, to evaluate the rectitude of our actions and the beauty of our surroundings? The human mental machinery obviously refers to the brain, so the answer to the preceding questions must come from neural considerations. What brain mechanisms correlate with the human capacity to maintain inner speech, or to carry out judgments of value? To what extent are they different from other primates' comparable behaviors?

This collection of colloquium papers aims to survey what has been learned about the human "mental machinery" since Darwin's insights. The colloquium brought together leading scientists who have worked on brain and mental traits. Their 16 contributions focus the objective of better understanding human brain processes, their evolution, and their eventual shared mechanisms with other animals. The articles are grouped into three primary sections: current study of the mind/brain relationships; the primate evolutionary continuity; and the human difference: from ethics to aesthetics.

Current Study of the Mind/Brain Relationships

John Searle (2) opens the proceedings with a philosophical introduction to the still elusive question of consciousness. To discuss the eventual scientific approach to a Theory of Mind (ToM), the author analyzes the relationships between subjective feelings, like mental issues, and objective (i.e., scientific) approaches to them. Distinguishing between ontologic and epistemic approaches to the subjectivity/objectivity issue, Searle holds that mental issues, such as consciousness, can be scientifically reached, concluding in this way: "I think the future of this entire discussion we have been having [in the colloquium] lies in a better understanding of the brain." Indeed, this is the objective that initially led to the organization of this Sackler colloquium.

ToM is also the approach chosen by Robert Seyfarth and Dorothy Cheney (3) in the next contribution. As the authors state, a subconscious, reflexive appreciation of others' intentions, emotions, and perspectives lies at the roots of human ToM. The adaptive advantages of an attribution of thoughts and intentions to predict others' behavior mainly consist of helping to form strong, permanent social bonds. Empirical study of monkeys' relationships shows these bonds. Following this point, Seyfarth and Cheney give data on different kinds of social challenges among female baboons that are better solved by means of affiliative behavior.

Even if ToM is a good hypothesis to link close social relationships to mental constructs and reproductive success, an eventual border might separate human consciousness from nonhuman primates' more "instinctive" behaviors. George Mashour and Michael Alkire (4) focus on this eventual difference. On the grounds of a comparative review of neurobiology, psychology, and anesthesiology, the authors hold that the basic neurophysiologic mechanisms supporting consciousness in humans are found at the earliest points of vertebrate brain evolution. Mashour and Alkire propose to study this evolution by means of models coming from the recovery of consciousness after general anesthesia in animals.

Primate Evolutionary Continuity

Shared neurologic mechanisms are the main argument in favor of continuity between nonhuman and human primates' minds. Several contributors to this Sackler colloquium have studied these common mechanisms in the field of memory and its brain counterparts. Robert Clark and Larry Squire (5) offer a history of the scientific debate provoked by Owen's proposal (6) of a lack of evolutionary continuity between human and

This paper serves as an introduction to this PNAS supplement, which resulted from the Arthur M. Sackler Colloquium of the National Academy of Sciences, "In the Light of Evolution VII: The Human Mental Machinery," held January 10–12, 2013 at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. It is the seventh in a series of colloquia under the general title "In the Light of Evolution" (ILE; see Box 1). The complete program and audio files of most presentations are available on the NAS Web site at www.nasonline.org/evolution_vii. Papers from the first six colloquia in the "In the Light of Evolution" series titled "Adaptation and Complex Design," "Biodiversity and Extinction," "Two Centuries of Darwin," "The Human Condition," "Cooperation and Conflict," and "Brain and Behavior" were published in earlier volumes of PNAS.

Author contributions: C.J.C.-C., R.G.L., J.C.A., and F.J.A. wrote the paper.

The authors declare no conflict of interest.

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Box 1. In the light of evolution. In 1973, Theodosius Dobzhansky (21) penned a short commentary entitled "Nothing in biology makes sense except in the light of evolution." Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences have often been neglected, misunderstood, or purposefully misrepresented. Biodiversity—the genetic variety of life—is an exuberant product of the evolutionary past, a vast human-supportive resource (aesthetic, intellectual, and material) of the present, and a rich legacy to cherish and preserve for the future. Two urgent challenges, as well as opportunities, for 21st-century science are to gain deeper insights into the evolutionary processes that foster biotic diversity and to translate that understanding into workable solutions for the regional and global crises that biodiversity currently faces. A grasp of evolutionary principles and processes is important in other societal arenas as well, such as education, medicine, sociology, and other applied fields including agriculture, pharmacology, and biotechnology. The ramifications of evolutionary thought also extend into learned realms traditionally reserved for philosophy and religion. The central goal of the "In the Light of Evolution" (ILE) series is to promote the evolutionary sciences through state-of-the-art colloquia—in the series of Arthur M. Sackler colloquia sponsored by the National Academy of Sciences—and their published proceedings. Each installment explores evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the ILE series aims to interpret phenomena in various areas of biology through the lens of evolution, address some of the most intellectually engaging as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

other primates on the grounds of several brain traits, hippocampus minor (HM) among them (7). Because HM was proposed to have a strong role in the organization of memory, the possibility of using animal models appeared, thus supporting evolutionary continuity for the neuroanatomy of human memory. Clark and Squire examine such cross-species similarities in the field of the multiple-memory systems paradigm, offering challenges to the animal model when concurrent discrimination tasks are considered in both humans and monkeys.

Two articles focus on the evolution of memory. Peter Carruthers (8) points out that, despite being fundamental to learning, speech, reading comprehension, prospection, and planning, as well as to reflective serial conscious reasoning, working memory (WM) has been scarcely investigated from an across-species perspective. On the grounds of current research, Carruthers holds that WM is a homologous trait shared by humans and nonhuman primates although our species is unique in aspects like inner speech. Also, humans may be unique in making frequent task-independent use of their WM abilities. However, in the absence of direct comparative studies, claims on the WM continuity or discontinuity remain somewhat speculative.

Timothy Allen and Norbert Fortin (9) offer a complementary analysis of the large body of research on the evolution of episodic memory (EM). The authors propose that proto-EM systems link avian and human phylogenies, supporting the homologous character of traits, such as hippocampal-parahippocampal-prefrontal pathways that would be shared from a common neural ancestry, as opposed to the alternative possibility of evolutionary convergence. Despite this shared capacity, Allen and Fortin discuss eventual divergences, such as with regard to human language, self-consciousness, empathy, and ToM, holding that these constitute species-specific attributes associated with the expansion in human brains of prefrontal areas.

Differences in social behavior between species rely in part on the neuromodulatory regulation of neural circuits. Steve Chang et al. (10) offer clues on how biological specializations for social function transform ancestral mechanisms by means of duplication, repurpose, or differential regulation at multiple levels of organization, from neurons and circuits to hormones and genes. Social behavior shapes the structure and function of these mechanisms in a feedback way. Therefore, the authors hold that a neuroethological approach to the study of human and nonhuman primate social behavior might clarify the phylogeny of interactions between social behavior and neuromodulatory regulation.

The counterpart of phylogeny is ontogenetic development. Comparisons between human and macaque neocortical development show differences that might relate the relatively prolonged neuronal maturation in humans to the enhancement of social learning and transmission of cultural practices, including language. However, few data exist on the ontogenetic neural development of the apes that are more closely related to humans. By means of an experimental analysis, Serena Bianchi et al. (11) show for the first time how *Pan paniscus* synaptogenesis matches the human case, with a peak of synapse density during the juvenile period (2–5 y of age). Also, chimpanzees and humans share a late development of dendrites of prefrontal pyramidal neurons, compared with sensorimotor areas, offering a common potential for enhanced developmental plasticity. The authors hold that their findings suggest that several key features of human brain ontogeny emerged before the divergence of the chimpanzee and human lineages.

Human Difference: From Ethics to Aesthetics

As stated above, our species and other primates share different memory systems. However, James McGaugh (12) argues in his contribution that, although forgetting is the common fate of most of our experiences, mechanisms exist that somehow permit us to create lasting memories of our more important experiences. The author explores such mechanisms. Several neurobiological systems link this selective capacity to emotional arousal, giving clues about how humans and other animals reach memory-enhancement episodes by means of an activation of brain regions such as the amygdala. The fact that some subjects are able to keep highly superior autobiographical memory raises the question of how this capacity might be associated to genetic and brain particularities.

Self-awareness and the capacity to evaluate others' acts and their consequences are among the main components of altruistic behavior. Three articles in these proceedings deal with different aspects of altruism and its more extreme related behaviors. Barbara Oakley (13) examines the mechanistic bases of biased altruism, in which attempts to promote the welfare of others results in unanticipated harm. She defends the need for quantitative models of altruistic behavior along a spectrum ranging from strong benefit to extreme harm. These models might help to scientifically distinguish between beneficial and harmful egoistic behavior, as well as clarify the relationships among egoism, altruism, and pathological altruism.

Sarah Brosnan (14) begins her contribution with a question: What leads us to care about justice? She proposes a comparative approach to clarify why justice, which is a highly important component of our values, is so difficult to achieve. By means of experiments on primates' answers to perceived inequities in social interactions, Brosnan concludes that humans are not alone in responding negatively to differential treatment. Although nonhuman primates do not show a sense of justice in the same sense that humans do, understanding their responses may help to anticipate, prevent, and perhaps solve problems arising from the human perception of inequity.

Beyond direct perception of equality/inequality in social relationships, altruism and, more generally, human cooperation can be related to indirect reciprocity based on reputation. Because social reputation is directly observed, but widely spread by communication, indirect reciprocity can reach highly sophisticated patterns. Erez Yoeli et al. (15) offer experimental results on large-scale (a total of 2,413 participants) cooperation between small groups under laboratory conditions. Because the subjects were California residents of 15 homeowners associations that voluntarily participated in an energy-saving program, the experiment matched real world conditions of cooperation. Yoeli et al.'s results provide evidence that observable participation in favor of public goods promotes cooperative behavior. The authors hold that reputational concerns were the driving force to reach such a high level of indirect cooperation, suggesting easy and practical ways to improve future public policy initiatives.

Robert Zatorre and Valorie Salimpoor (16) review empirical evidence for the neural substrates of several aspects of musical perception. First, the authors identify the auditory cortical circuits that are responsible for encoding and storage of tonal patterns. Then, they study the functional role of brain areas, such as the nucleus accumbens, codifying the reward value of music. The authors suggest that the cortical system, highly evolved, decodes tonal or rhythmic relationships present in music, thereby generating expectations about upcoming events based on the subjects' former events. In turn, the striatal dopaminergic system would add the emotional arousal associated with these predictions.

Experimental approaches to visual issues constitute the next contribution to the colloquium. Leanne Chukoskie et al. (17) study how subjects search a novel scene for a target whose location was stochastically drawn on each trial from a fixed prior distribution. Participants rapidly learn where to search, looking near previously rewarded locations and avoiding previously unrewarded sites. A reinforcement-learning model, similar to that used previously to examine both foraging animal behavior and neuronal firing of dopaminergic cells, can describe the resulting search performance. In addition, this search performance approaches the theoretical optimum on this task. Thus, the authors offer a framework for considering how prior experience guides saccade choice during natural vision.

A complementary phenomenon provides the focus for Oshin Vartanian et al. (18), who provide for the first time clues on how variation in contour impacts aesthetic judgments and approach decisions about the places in which we live and work, thereby influencing how we feel and act. Subjects are more likely to judge spaces as beautiful if they are curvilinear rather than rectilinear. Curvilinear spaces activate the medial orbitofrontal cortex, a region strongly implicated in reward, which is particularly activated among architects compared with nonarchitects when assessing the aesthetic value of buildings. In contrast, contour has no impact on approach decisions. Contemplating curvilinear spaces activates the precentral gyrus—a region engaged in motor imagery and the planning of voluntary motor movement. Although curvilinear spaces did not result in a greater likelihood of deciding to enter such areas, they might facilitate the production of visual and motor imagery consistent with movement planning in that context. The authors conclude that their research sheds light on a fundamental question—why is it that we have come to prefer the places that we do?

Finally, by analyzing the dynamics of brain functional connectivity, Camilo Cela-Conde et al. (19) offer the first identification of brain networks engaged within distinct time frames during the appreciation of beauty. A fast aesthetic perception of the beautiful/not-beautiful condition of each visual stimulus appears within 250–750 ms whereas further aesthetic appreciation processes are subsequently performed in the 1,000- to 1,500-ms range. The delayed processes activate a brain network matching the default mode network, present during subjects' resting state.

Concluding Note

The explicit objective of this colloquium—improving our knowledge of the content of Darwin's mental machinery—constitutes an endless task. However, the colloquium papers offer fresh perspectives coming from interdisciplinary approaches that open new research fields and constitute the state-of-the-art in some important aspects of the mind/brain relationships. An intriguing contradiction seems sketched from the contributions to the colloquium. On the one hand, continuity exists between the mental machinery of humans and nonhumans primates. On the other hand, humans manifest conspicuous evolutionarily derived, i.e., exclusive, mental/neural traits. Darwin himself solved this apparent paradox. In chapters III, IV, and V of *The Descent of Man* (20), Darwin holds that human moral and mental faculties differ from those of animals, but not in a fundamental way. Coming back again to the Notebook C annotation (1): "[Man] possesses some of the same general instincts, & moral feelings as animals [. . .] but Man has reasoning powers in excess [. . .] this is a replacement in mental machinery."

ACKNOWLEDGMENTS. The organizers and founding editors of the "In the Light of Evolution" series (J.C.A. and F.J.A.) are the academic grandson and son, respectively, of Theodosius Dobzhansky, to whose fond memory this series is dedicated. May Dobzhansky's words and insights continue to inspire rational scientific inquiry into nature's marvelous operations.

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