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1 The Implication of Specialized Neuronal Circuits Versus Neuronal Number for Concepts Concerning the Nature of Human Conscious Experience

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Sitting on top of the evolutionary process is the human brain. Its vast complexity, its capacity for complex problem solving, for inventiveness, for everything we know and appreciate about human cognition represents the finest achievement of the wondrous blind processes of selection that have gone on for millions of years. Many scientists have approached trying to gain clues to the understanding of the human brain's special mechanisms of action by studying other species. Fair game for this enterprise includes comparisons between bugs and beasts of all types and kinds. Everything from our genetic mechanisms to the capacity to sleep, to feel, to remember, to transmit retinal information to visual cortex and a myriad of other processes have all been enlightened by careful animal experimentation over the years. Some have even seen in these studies so many similarities in neural structures that proposals are commonly put forward that animals have perceptual and cognitive process much like our own—indeed, a consciousness much like our own. Such views are usually qualified by the assertion that whatever differences do exist in conscious processes between species can be easily explained by the greater size of the human brain. Somehow having more neural cells is thought to produce a greater computational capacity that in turn yields that special quality of human conscious experience.

In fact, it is well known that the human brain is inordinately large after being corrected for body weight. Allometric considerations find the human brain falling off the correlation line assessing body size and brain size. This gigantic biologic organ weighing between 1,100 and 1,300 grams sits magnificently on top of a small body, guiding its sensations, actions, and desire for reproduction. These elements of human activity are indeed quite similar to those seen in both near and distant evolutionary relatives sharing many common brain mechanisms. Even basic dimensions of mental life, such as memory, attention, and visual perception, seem to share mechanisms and brain structures in common, certainly with other primates. As a consequence, the extra cortex in humans is viewed as critical for the higher cognitive functions we enjoy.

Yet, there is this puzzle. We humans do not seem to need great quantities of our huge cerebral cortex in order to carry out our intellectual activities. A cardinal feature of split-brain research, for example, is that following disconnection of the human cerebral hemispheres, the verbal IQ of the left hemisphere remains largely intact (Nass & Gazzaniga, 1987). Indeed, the problem-solving capacity of the left hemisphere remains unchanged (LeDoux, Risse, Springer, Wilson, & Gazzaniga, 1977). Although there can be deficits in recall capacity (Phelps, Hirst, & Gazzaniga, 1992), by some performance measures the overall capacity to carry out problem solving seems unaffected. In other words, isolating essentially half of the cortex from the dominant left hemisphere causes no major change in intellectual function of the left hemisphere. This finding represents strong evidence that absolute cortical cell numbers have, at best, only a loose relation with human intelligence.

Related to the notion of special circuitry is the fact that disconnected right hemispheres are seriously impoverished in their ability to carry out a variety of computational tasks that the left would find easy to complete. In studies done some years ago in a small group of split-brain patients identified as having language capacities in each disconnected hemisphere, we carefully examined the problem-solving ability of the disconnected right and left hemispheres. Most commissurotomy patients do not have such abilities in their right hemisphere; correlated with that absence is an inability to carry out even the simplest perceptual and cognitive tasks. The small group we examined with language-capable right hemispheres were unable to make verbal inferences, solve spatial problems (Gazzaniga & Smylie, 1984), or generate indirect antonyms (Gazzaniga & Miller, 1989), to name a few of the tasks examined.

Although the right hemisphere remains superior for some activities such as the recognition of upright faces (Gazzaniga, 1989), some attentional skills (Mangun et al., 1992), and perhaps also emotional processes (Nass & Gazzaniga, 1987), it appears to be lacking in its overall cognitive capacity. In fact, it appears to be inferior to the mental capacities of a chimp.

The idea of the importance of specialized circuits is central to the field of human neuropsychology. Untold numbers of disease states have been reported that suggest there are specific disorders following focal lesions or long fiber-tract disconnections (Nass & Gazzaniga, 1987). Human brains seem to house a constellation of special-purpose networks that are given over to rather specific tasks. When that fact is considered in light of evolutionary processes, it is hard to imagine it could be any other way. Why would evolution leave to chance the building up of networks needed for each human to survive from scratch with each birth? Surely it is advantageous to be delivered into this world with as much original equipment as possible. Millions of years of evolution would allow for exactly this kind of thing; it seems more and more apparent that this is what has occurred (Gazzaniga, 1992).

This evolutionary perspective on brain organization and cognition suggests a number of important issues for cognitive neuroscientists (Gazzaniga, 1992). First, the implication is hard on everyday and classical ideas about learning, with the underlying assumption that any neural network can learn anything once inputs and outputs are specified. The evolutionary viewpoint would argue for not only the critical implications of the importance of specialized circuits but also the view that the human brain has a unique structural organization supporting these specialized circuits. I review data from my laboratory that is consistent with this view.

Second, the evolutionary view suggests that there should be some things humans are poor at learning. If humans have specialized circuits committed to performing particular traits, exposure to environmental stimuli to which they had not adapted might require cognitive processes they do not possess. There are many examples of such phenomena in the fields of language learning and perceptual psychology (Gazzaniga, 1992). For present purposes, these kind of data provide further evidence of the probability of identifiable capacities the human cognitive system possesses that other animals do not possess. Furthermore, because these data reflect the presence of specialized circuits, they should be found in one hemisphere or the other. There are many such examples; I relate observations from studies on the human capacity to make voluntary facial expressions (Gazzaniga & Smylie, 1990).

SPECIALIZED CIRCUITS FOR HUMAN CAPACITIES

Accepting the view that the human brain has special circuits for carrying out its various mental functions, one can consider the various levels of organization within the nervous system where this might appear. In what follows, the argument is made that the cerebral cortex is the custodian of new circuits critical for human cognitive processes. In this light, it is commonly observed that the overall plan of the mammalian brain seems quite similar among species. This is particularly true when comparing the primate and human brain. One of the reasons comparative studies are carried out is the belief that homologous brain structures may carry out common functions in the primate and human. Yet, there are important exceptions to this overall view. The human brain, quite simply, is different from the monkey brain. There are any number of similar structures carrying out different functions in the two species. Let me review work comparing two structures that we have studied directly and indirectly in our laboratory—the anterior commissure and the superior colliculus—and relate observations that emphasize the importance of studying the human brain per se.

The animal literature clearly shows that the anterior commissure transfers visual information. Although only the callosum was found to subserve interocular transfer in cats, the anterior commissure was found to be involved in visual transfer in chimpanzees (Black & Myers, 1964) and rhesus monkeys (Gazzaniga, 1966; Sullivan & Hamilton, 1973). Taken together, this kind of evidence provides strong reasons to believe the same might be true for humans.

Prior to the development of magnetic resonance (MR) imaging, we examined some patients who, by surgical description, had their anterior commissure intact and their callosum fully sectioned. Many of these patients transferred visual information. In an effort to account for this, we proposed that the remaining anterior commissure could vary in the kinds of information it could and could not transfer. We have now had the opportunity to scan many of those supposedly split-brain patients. In fact, the MR scans show the splenium had been spared in those cases where transfer of visual information was possible, thus explaining the transfer of information. In another series of patients, similar results were noted (Gates, Leppik, Yap, & Gumnit, 1984). Every time there is evidence of transfer of visual information that requires exact matching of stimulus features following supposedly full commissurotomy, there has been sparing of the splenium. This suggests that the anterior commissure, a structure that is clearly able to transfer visual information in the monkey and chimp, does not do so in the human.

The difference seen with fiber-tract systems is also apparent in more nuclear structures such as the superior colliculus. In this case, there is clear evidence from the monkey that this structure is crucially involved in the control of eye movements. Wurtz and colleagues (Mohler & Wurtz, 1977), for example, were able to demonstrate some years ago that primates with lesions of primary visual cortex were able to detect and direct their eyes in response to visual stimuli presented in the scotoma. They suggested that the superior colliculus, working either alone or in complementary fashion with visual cortex, could carry out these functions within the scotoma. Others have claimed that even higher order functions are possible following such occipital lesions (Pasik & Pasik, 1971; Weiskrantz, Cowey, & Passingham, 1977). Although similar claims have been made for the human (Weiskrantz, 1990), we have not succeeded in demonstrating residual function following lesions to primary visual cortex (Holtzman, 1984). More recently, we have been able to carry out microperimetry of patients with occipital lesions using an image stabilizer (Fendrich, Wessinger, & Gazzaniga, 1992; Wessinger, Fendrich, & Gazzaniga, 1991).

These studies have clearly shown that patients with so-called homonomous hemianopsia can have small islands of spared vision. In these islands, there is visual function. In most of the scotoma, however, there is no visual function, confirming the earlier work of Holtzman. In short, when visual function is possible there seems to be spared visual cortex. This observation was confirmed with MR brainprinting that revealed some intact primary visual cortex. Overall, it suggests that the spared superior colliculus in the human contributes in a different way to oculomotor functions.

The clear difference in function seen between monkey and human brains, combined with possible new anatomical correlates supporting these differences, suggests a cautious note when attempting to compare the function of similar brain structures across species. It suggests the arguments against such cross-species comparisons are as crucial today as they were when originally argued years ago.

With it established that the human brain has its own unique organization, it would be interesting to see how much of this organization might be due to genetic processes. For the past few years, we have been examining this issue by studying the brains of monozygotic twins. Our initial findings regarding the corpus callosum showed that this enormous fiber-tract system was more similar in area and shape in monozygotic twins than in unrelated twins (Oppenheim, Skerry, Tramo, & Gazzaniga, 1989). Using a new method of assessing the cortical surface areas of the human brain (Jouandet et al., 1989; Loftus, 1992), we have now studied the cortical surface of both male and female monozygotic twins (Green et al., 1991; Tramo, Loftus, Newton, & Gazzaniga, 1990; Tramo, Loftus, Thomas, Green, & Gazzaniga, in prep.). Such twins look alike, talk alike, behave similarly, think similarly, and so on. Are their brains alike? Normally there is great variation in the gross morphology of the brain. Although all brains have a similar overall plan, they vary tremendously in the details. Some brains have bigger frontal lobes than others. The pattern in the visual appearance of the cortex is called the gyral/sucal pattern. It varies, and that variation presumably reflects differences in underlying brain organization. Could it be that monozygotic twins had brains that were more similar than not? The fact that their overall cognitive skills are more alike would suggest a physical basis for their more similar cognition.

Until recently, no one has had information on this crucial point. Our laboratory has been working on quantifying MR images in a way that would allow one to examine various regions in each half brain and to assess their similarity in surface area. In this technique, MR imaging is used to form some 50 image slices of the brain, which are then reconstructed to make maps of the human cerebrum. With the maps made, it is easy to measure the cortical areas of the various major lobes of the brain, allowing us to estimate surface area from the three-dimensional reconstruction of the cortical surface itself. We have discovered that 15 regions in the left and 4 regions in the right hemispheres of females showed less variance in the twins as compared to unrelated controls. For male twins, there were fewer areas in the left and about the same number in the right hemisphere. Overall, we can conclude that twin brains are more alike than unrelated brains. These data also indicate that the development of left-hemisphere structures is under considerably more genetic control for women than for men.

THE CASE FOR UNIQUE HUMAN SYSTEM FUNCTIONING

If the human brain has unique organizational features and appears to have many of its major cortical surface areas specified by genetic mechanisms, then it might also seem likely that there would be capacities humans could engage in that other primates could not. The multitudinous new circuits in the much larger human cerebrum carry out activities other species simply do not possess. One such example of a human specialization is the capacity to make voluntary facial expressions. This is a very palpable trait of humans and easily accessible for study. It is not found in other primates including the chimpanzee (Premack, personal communication).

There is a variety of beliefs about how the brain is organized to perceive and produce facial expressions. In the perceptual domain, it appears that the right hemisphere has special processes devoted to the efficient detection of upright faces (Gazzaniga, 1989). Although the left hemisphere can also perceive and recognize faces and can reveal superior capacities when the faces are familiar, the right hemisphere appears specialized for unfamiliar facial stimuli (Gazzaniga & Smylie, 1983). Interestingly, this pattern of asymmetry for perceptual processes has also been shown for the rhesus monkey (Hamilton & Vermiere, 1988).

We recently examined the brain mechanisms involved in carrying out facial expressions in split-brain human patients. Disconnecting the two cerebral hemispheres allows the role the corpus callosum plays in controlling voluntary and involuntary expression to be assessed. It also allows examination of the ability of each hemisphere to initiate facial expressions. To understand the pattern of observed results, it is important to review the known neural mechanism active in controlling both voluntary and involuntary facial expressions.

The pattern of innervation for the upper half of the face is different from that of the lower half of the face, and the differences involve both central and peripheral systems. The neural mechanisms involved in voluntary facial postures are controlled by the cortical pyramidal system, whereas the control of spontaneous postures is managed by the extrapyramidal system. This diversity of innervation is reported to be responsible for the preservation of symmetrical spontaneous facial postures in the presence of unilateral damage to motor cortex. Patients with this lesion will evidence a contralateral facial droop that will resolve when smiling spontaneously. In this instance, although the pyramidal input to the facial nucleus is destroyed, the extrapyramidal input is not. It is also commonly reported that patients with extrapyramidal disease such as Parkinson's disease will display a masked face when at rest and then look more normal when smiling to command.

In our study, we examined the capacity of each cerebral hemisphere to initiate voluntary facial postures. Additional observations were made on spontaneous expressions. The results reveal marked differences in the capacities of each hemisphere to carry out commands, indicating that the corpus callosum plays a critical role in the normal production of voluntary symmetrical facial expressions. Examination of asymmetries in smiling to command revealed that when the command to smile was lateralized to the left hemisphere, the right side of the mouth dramatically commenced retraction as much as 180 milliseconds before the left side responded. When the command to "smile" was presented to the right hemisphere, none of the patients were able to carry out the response. In another series of tests on Cases JW and DR a lateralized drawing of a "happy face" or a "sad face" found the right hemisphere performing at chance. On trials in which an incorrect response had been made, say frowning to a happy face, JW was nonetheless able to draw out a picture of the happy face stimulus with his left hand. Additionally, no consistent asymmetries were noted on trials in which the left hemisphere responded correctly to the command to "frown." Although there were occasional indications that the lower right half face showed some earlier posturing, the overall bilateral response of the upper half face masked any consistent pattern.

In previous studies we have demonstrated that the right hemisphere is capable of producing involuntary or spontaneous responses such as smiling and laughing (Gazzaniga, 1970). In the present study spontaneous episodes were video recorded and analyzed with the optical disc method. No asymmetries in the facial response pattern were observed. It therefore appears that either hemisphere can generate spontaneous emotional events and that, because there are no apparent asymmetries in the facial response, different neural mechanisms are active for these expressions.

Most disconnected right hemispheres in split-brain patients are unable to carry out verbal commands (Gazzaniga, 1970). In the present study the right hemisphere failed not only when the command was printed out but also when the command was a graphic that depicted either a "happy" or "sad" face. Yet, many right hemispheres, including all three of the present cases, have the capacity to carry out some kinds of commands. It can respond to requests to move individual digits as well as make hand postures of all sorts (Gazzaniga, Boger, & Sperry, 1967; Volpe et al., 1982). It can control the upper facial muscles. Why, then, can it not respond to the command to smile or frown?

As already reviewed, mental operations ranging from making simple inferences to solving simple problems are all outside the cognitive range of the right hemisphere. These kinds of observations emphasize the superiority of the left hemisphere in interpreting events and its dominant role in organizing responses to those events. In the present context, high-level evaluative processes must be invoked to override a potentially spontaneous facial expression such as smiling. Such processes appear to be possible only in the left hemisphere; hence, that hemisphere appear to control voluntary expression. This sort of "voluntary" control appears different and involves more complex processes than those associated with making voluntary hand or foot postures in response to a cue. Therefore, where evaluations involve more psychological aspects of a person's expressions, the left hemisphere appears dominant. Specialized circuits carry out specialized functions.

SPECIALIZED CIRCUITS AND HUMAN CONSCIOUS EXPERIENCE

The human brain enables human conscious experience, and a working brain scientist always strives for insights into the nature of human conscious experience. Some might view the human with all of its domain-specific capacities, which have accumulated over millions of years of evolution, as a denigrated view of who we are and what we accomplish. The human brain's unique organization – its unique capacities for problem solving, for language, for making voluntary facial expressions, for deception, and for belief formation – empower a viewpoint of specific systems in the brain for enablement of these capacities. They can be lost through specific brain

damage or can be isolated by disconnection procedures. The capacities must reflect the actions of specific circuitry within the human brain.

Still, many other scientists believe the sensations we experience as human conscious agents are the product of the vast computational power our huge cerebral cortex must allow – with each person starting from scratch and building up his or her own story over a lifetime. This mix of ideas generates a difficult-to-state and fairly vague view that human conscious experience is a "thing" that emerges from the human being's information-processing capacity. This view finds solace in the idea that neural networks can be trained to do almost anything and that, given the right circumstance, good cognition will follow.

My own view is that there is another way of looking at these issues. An idea that builds on the realization that human consciousness, at its core, is a feeling – a feeling about special capacities humans possess.

The modern human brain is a bundle of special-purpose systems allowing people to communicate, evaluate facial expressions, make inferences, interpret feelings, moods, and behaviors, and all the rest. Studying patients with brain damage reveals how specific these capacities can be. One capacity can go without the other. Each of these activities is managed by neurons in ways that find scientists fundamentally ignorant. Millions of neurons are churning away to produce these human talents. Yet, to define that as consciousness is somehow missing the point. Consciousness is a feeling about these specific capacities that are managed by specialized circuits. My guess is that we are looking in the wrong wood pile for the answer to the problem of human consciousness.

There are some obvious aspects of human consciousness that we always lose sight of. First, one does not learn to be conscious! When the brain starts to function, up it comes, just like steam out of a turbine. There is no getting rid of it. The feeling of consciousness is not unlike other seemingly unfathomable feelings like the feeling to survive. It is there. Oddly, philosophers and biologists have not tortured themselves about understanding such feelings. Yet, it is surely no simpler to understand and know the mechanisms about those feelings than to understand human consciousness itself.

Second, the feeling of being conscious never changes in life. Let me illustrate this with an anecdote. A few years ago, my 76-year-old father, a physician of enormous intelligence and savvy, sat in his easy chair contemplating something or another doing so after years of strokes that were slowly consuming his cerebral cortex. Mercifully, the strokes did not impair his language and thought processes. He knew of my profession and the kinds of issues that interested me. I asked him how he felt, to which he replied, quite simply, "Mike, I feel 12. I always have and I always will." For him, his consciousness was the same. The computational skills were vanishing just like they are for all aging brains, but the feeling of being conscious never seems to go.

To put some neural hardware on this idea, modern brain science knows that subcortical structures are heavily involved in the management of feeling—of felt states. These systems change very little with aging. They stay more insulate from the ravages of the cell death accompanying aging, and it is these same brain areas that generate the feelings associated with the specialized perceptual and cognitive capacities humans have accumulated over millions of years. Consciousness is a feeling—a feeling about domain-specific capacities that have accumulated over millions of years of evolution.

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