Reciprocal organization of the cerebral hemispheres

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The cerebral hemispheres are anatomically and neurophysiologically asymmetrical. The evolutionary basis for these differences remains uncertain. There are, however, highly consistent differences between the hemispheres, evident in reptiles, birds, and mammals, as well as in humans, in the nature of the attention each applies to the environment. This permits the simultaneous application of precisely focused, but narrow, attention, needed for grasping food or prey, with broad, open, and uncommitted attention, needed to watch out for predators and to interpret the intentions of conspecifics. These different modes of attention can account for a very wide range of repeated observations relating to hemisphere specialization, and suggest that hemisphere differences lie not in discrete functional domains as such, but distinct modes of functioning within any one domain. These modes of attention are mutually incompatible, and their application depends on inhibitory transmission in the corpus callosum. There is also an asymmetry of interaction between the hemispheres at the phenomenological level.

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The fact that the brain, an organ which exists precisely to make connections, has a deeply divided structure has remained largely unexplained and even unexamined. Nevertheless, speculation on the nature of the difference between the two cerebral hemispheres goes back more than two millennia: Greek physicians in the third century BC held that the right hemisphere was specialized for perception, and the left hemisphere for understanding.[1] In more recent times, Wigan in 1844 deduced from a series of clinical cases that we 'must have two minds with two brains,' a redundancy which he thought protected against injury to one or other hemisphere, but with mental illness being the cost to the individual when they were in conflict.[2] In the later 19th, and particularly in the 20th, century following the first callosotomy procedures of Sperry and Bogen, there arose a plethora of theories about the different functions the two hemispheres might perform, which broadly distinguished a verbal, rational, analytic left hemisphere from a visuospatially orientated, emotional, and holistic right hemisphere, though the evolutionary origin and basis of their anatomical and functional separation remained obscure.[3] Subsequent research has in any case revealed that each hemisphere contributes to language, visuospatial skills, reason, and emotion, indeed to virtually every cerebral function, suggesting that the bihemispheric structure of the brain is an anomaly. At the same time, the persistence in popular

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culture of outdated characterizations of hemisphere difference has meant that the topic has somewhat fallen into disrepute.

Yet many important authors in the field (eg, Hellige,[4] Ramachandran,[5] Crow,[6] Cutting[7,8]) accept that there is something manifestly important here that requires explanation. Hellige, while emphasizing that 'in the intact brain, it is rarely the case that one hemisphere can perform a task normally whereas the other hemisphere is completely unable to perform the task at all,' notes that 'the range of tasks showing hemispheric asymmetry is quite broad' and that 'thus far, it has not been possible to identify any single information-processing dichotomy that could account for anything close to this entire range of hemispheric asymmetries... Whatever links there might be between the various hemispheric asymmetries, they would seem to be determined in some other way or according to some other principle.'[4] What might that principle be?

Brain asymmetries exist at many levels of description

The fact that hemispheric asymmetries exist at every level of description suggests that the interhemispheric distribution of neuropsychological functions is unlikely to be random. Such asymmetries exist at the gross anatomical level in the size, weight, and conformation of either hemisphere as a whole,[9,10] but as well as differing in the size and shape of a number of defined brain areas,[11] the hemispheres differ in the number of neurones,[12] neuronal size,[13] and the extent of dendritic branching within areas.[14,15] The ratio of white to gray matter also differs, being higher in the right hemisphere.[16,17] Neurochemically the hemispheres differ in their sensitivity to hormones[18] and to pharmacological agents,[19] and there are significant differences in the ratio of dopaminergic to noradrenergic neurotransmission.[20,21]

Functional independence of the hemispheres increases with evolution

Furthermore, the corpus callosum appears to be primarily involved in maintaining functional independence of the hemispheres. Though it contains an estimated 300 to 800 million fibers connecting topologically similar areas in either hemisphere, only 2% of cortical neurons are connected via the corpus callosum.[22,23] What is more, a large number of these connections are functionally inhibitory.[24,25] Significant populations of cells projecting to the corpus callosum are GABA-ergic, and although the majority are glutamatergic, the excitatory fibers often terminate on interneurons whose function is inhibitory.[26,27] Stimulation of neurons in one hemisphere commonly results in an initial brief excitatory response, followed by a prolonged and often widespread inhibition in the contralateral hemisphere.[28,29] Clearly the corpus callosum does also have excitatory functions, and both are necessary for normal human functioning,[24,30] but the primary function of the corpus callosum may in fact be to allow reciprocal hemispheric inhibition.[31-33] Separation of hemispheric function appears to accelerate with evolution, since interhemispheric connections decrease relative both to brain size,[22] and to the degree of brain asymmetry.[34] In the ultimate case of *H. sapiens*, the twin hemispheres have been characterized as two autonomous systems.[35]

Attentional asymmetry in birds and animals

Functional brain asymmetries exist also in birds and animals. Lateralization of function is widespread in vertebrates,[36] and appears to have evolutionary advantages. For example, Braun writes that 'the vast database of animal research [and] human neuropsychiatric research … both clearly establish numerous important and spectacular specializations of the right hemisphere,' as well as of the left.[37]

It is argued here that these apparent specializations relate to differences in the mode of attention. Animals and birds experience competing needs. This can be seen at one level in terms of the types of attention they are required to bring to bear on the world. There is a need to focus attention narrowly and with precision, as a bird, for example, needs to focus on a grain of corn in order to distinguish it from the pieces of grit on which it lies. At the same time there is a need for open attention, as wide as possible, to guard against a possible predator. Chicks achieve this by prioritizing local information with the right eye (left hemisphere), and global information with the left eye (right hemisphere). Chicks that are properly lateralized are more able to use these two types of attention effectively than are those in which, experimentally, lateralization has not been permitted to develop (by depriving them of light exposure on day 19 of incubation).[38] For many species of birds and animals there are biases at the population level towards watching out for predators with the left eye.[38-46] Equally fixating an object, especially prey or food, is preferentially carried out using the right eye and foot.[47]

Individual animals with more strongly lateralized brains are better able, because of hemisphere specialization, to forage and remain aware of predators,[48] and are more efficient,[49] with shorter reaction times.[50] But advantages accrue not only to the individual: being a more lateralized species at the population level carries advantages in social cohesion.[51-53] The right hemisphere appears to be deeply involved in social functioning, not just in primates, where it is specialized in the expression of social feelings, but in lower animals and birds as well.[38,39,54-56] Toads, for example, attend to their prey with the left hemisphere, but interact with their fellow toads using the right hemisphere,[57] and while black-winged stilts peck more, and more successfully, at prey using the right eye, males are more likely to direct courtship displays to females that are seen with their left eye.[55] In most animal species, intense emotional responses are related to the right hemisphere and inhibited by the left.[61] Some of the same neuroendocrine hemisphere differences that characterize the human brain are already present in the brains of rats[58,59]: this may be related to the fact that in rats, as in humans, the right hemisphere is the main locus of early social experience.[60]

Lateralization brings evolutionary advantages, particularly in carrying out dual-attention tasks.[41] In general terms, the left hemisphere yields narrow, focused attention, mainly for the purpose of getting and feeding. The right hemisphere yields a broad, vigilant attention, the purpose of which appears to be awareness of signals from the surroundings, especially of other creatures, who are potential predators or potential mates, foes, or friends; and it is involved in bonding in social animals. Individual human brains, like animal brains, that are less lateralized (as defined by handedness) than the norm appear to show global deficits. In humans this applies across all forms of reasoning, verbal and nonverbal.[62] In a word, asymmetry pays.[63]

Attentional asymmetry in humans

This relationship between mode of attention and lateralization in animals also pertains in humans. It is conventional to distinguish five types of attention: vigilance, sustained attention, and alertness, forming the *intensity* axis, and focused attention and divided attention, forming the *selectivity* axis of attention.[64] The different types of attention can be demonstrated to be distinct and independent of one another, and subserved by a number of different brain structures distributed extensively over the prefrontal, anterior cingulate, and posterior parietal areas of both hemispheric cortices. Within either hemisphere, and between hemispheres, the system of control processes is complex. However, some broad consistent differences in hemisphere specialization are striking.

Vigilance and sustained attention are grossly impaired in subjects with right-hemisphere lesions,[65-67] especially right frontal lesions,[68] and by contrast, are preserved in left-hemisphere lesions.[69] Right-hemisphere lesions also lead to perceptuomotor slowing, a sign of diminished alertness, associated with lapses of attention,[70-76] though in one study slowing was associated with lesions in the left dorsolateral prefrontal cortex.[77] Studies in both normal subjects[78,79] and split-brain subjects[80] corroborate the role of the right hemisphere in the "intensity" aspects of attention, confirmed by neuroimaging.[81,82]

The other main axis of attention is *selectivity* (focused and divided attention). Although selective attention may be bilateral,[83] deficits in focused attention are more severe with left-hemisphere injury,[76,85] typically in the left caudate,[77] or left anterior cingulate.[84] Normal subjects show a left-hemisphere preference for choice reactions,[86,87] and imaging suggests focused attention is associated with activity in the left orbitofrontal cortex and basal ganglia.[88] By contrast, lesions in the right inferior parietal lobule cause the most serious impairment of global attention.[89]

As regards divided attention, the evidence is less conclusive. While some studies suggest that both left and right hemispheres are involved,[77] there appears to be a clear primary role for the right hemisphere, especially the right dorsolateral prefrontal cortex.[88,90]

In summary, there is evidence of left-hemisphere dominance for local, narrowly focussed attention and right-hemisphere dominance for broad, sustained, global, and flexible attention.[65,66,91-95] The scope of the right hemisphere's world is broad.[96-97] Subjects with a right-hemisphere lesion start with the pieces and put them together to get the overall picture, whereas those with a left-hemisphere lesion prefer a global approach.[98-102] Right-hemisphere damaged subjects seem unable to adjust the breadth of the "spotlight" of their attention and suffer 'an excessive and more or less permanent narrowing of their attentional window.'[103]

The attentional difference between the hemispheres has many consequences for the phenomenological world which each construes, potentially accounting for a range of apparent functional specializations of either hemisphere. These specializations, which the author has described in detail and discussed at length elsewhere,[104] offer perceptual advantages that are reciprocally related, and are summarized in the following section.

Some consequences for hemispheric specialization

The above distinction in attention could be seen as offering the reciprocal possibilities of breadth and flexibility in apprehending the unpredictable and (as yet) unknown, versus the focus and precision required to grasp and use what is familiar and has already been prioritized as of interest.

The new versus the known

The right hemisphere alone attends to the peripheral field of vision from which new experience tends to come; only the right hemisphere can direct attention to what comes to us from the edges of our awareness, regardless of side.[105,106] Anything newly entering our experiential world instantly triggers release of noradrenaline, mainly in the right hemisphere.[96,107] Novel experience induces changes in the right hippocampus, but not the left.[108] Phenomenologically it is the right hemisphere that is attuned to the apprehension of anything new.[38,107,109-118] This difference is pervasive across domains. Not just new experience, but the learning of new information or new skills also engages right-hemisphere attention more than left,[119,120] even if the information is verbal in nature.[121,122] However, once the skills have become familiar through practice, they shift to being the concern of the left hemisphere,[107] even for skills such as playing a musical instrument.[123]

The left hemisphere prioritizes the expected, and its process is predictive.[124,125] This makes it more efficient in routine situations, but less efficient wherever the initial assumptions have to be revised,[126,127] or when there is a need to distinguish old information from new material that may be consistent with it.[128] Because the left hemisphere is drawn by its expectations, the right hemisphere outperforms the left whenever prediction is difficult because the situation is new to the subject.[129] The link between the right hemisphere and what is new or emotionally engaging exists not just in humans, but already in higher mammals: for example, horses perceive new and possibly emotionally arousing stimuli with the left eye.[130]

Possibility versus predictability

The right hemisphere is more capable of a frame shift;[131-133] the right frontal lobe is especially important for flexibility of thought, with damage in that area leading to perseveration.[134-136] In problem solving, the right hemisphere presents an array of possible solutions, which remain "live" while alternatives are explored;[137,138] the left hemisphere takes the single solution that seems best to fit what it already knows and latches onto it.[21,139] Ramachandran's studies of anosognosia reveal a tendency for the left hemisphere to deny discrepancies that do not fit its already generated schema of things, a strategy that works well in familiar situations in which there are time-costs to exploring unnecessary possibilities. The right hemisphere, by contrast, is actively watching for discrepancies, more like a devil's advocate.[140] Both approaches are needed, but are mutually contradictory.

These differences operate across all realms and apply equally to the verbal as to the visuospatial. For example, the left hemisphere operates focally, suppressing verbal meanings that are not currently relevant, whereas the right hemisphere recruits wider semantic associations,[141-145] and the right posterior superior temporal sulcus may be selectively involved in verbal creativity.[146] In the "close" situation, by contrast, the left hemisphere actively suppresses the right, to exclude associations which are semantically only distantly related.[147,148]

Integration versus division

In general the left hemisphere is more closely interconnected within itself, and within regions of itself, than the right hemisphere.[14,17] By contrast, the right hemisphere has a greater degree of myelination, facilitating swift transfer of information between the cortex and centers below the cortex,[17] and greater connectivity in general.[149] Functionally, its superior integration is evidenced by EEG measures[150] and by the more diffuse but overlapping somatosensory projections and auditory inputs in the right hemisphere.[151]

At the experiential level it is also better able to integrate perceptual processes, particularly bringing together different kinds of information from different senses.[109,154,155] By contrast, the left hemisphere may be 'inadequate for the more rapid complex syntheses achieved by the [right] hemisphere.'[156]

As mentioned, new stimuli lead to release of noradrenalin in the right hemisphere. Its neurons are relatively resistant to fatigue, so that exploratory attention is held open across a greater expanse of both space and time.[21] The range of the right hemisphere is further increased by the fact that it has a longer working memory, and so is able both to access more information and hold it together at any one time for longer.[157] It is capable of bearing more information in mind and doing so over longer periods, with greater specificity (which also means less susceptibility to degradation over time by memory).[128,157-159] This broader field of attention, open to whatever may be, and coupled with greater integration over time and space, is what makes possible the recognition of broad or complex patterns, the perception of the "thing as a whole," seeing the wood for the trees.[160-163] In short, the left hemisphere takes a local short-term view, where the right hemisphere sees the bigger picture.

The whole versus the part

The link between the right hemisphere and holistic or *Gestalt* perception is one of the most reliable and durable of the generalizations about hemisphere differences, which follows from the differences in the nature of attention.[95,164-168] The right hemisphere sees the whole, before whatever it is gets broken up into parts in our attempt to know it, and its holistic processing is not based on summation of parts. The right hemisphere, with its greater integrative power, is constantly searching for patterns in things, and its understanding is based on complex pattern recognition.[164-169] On the other hand, the left hemisphere sees part-objects.[118,170-172]

Subjects with unilateral brain damage show complementary deficits in drawing skills, depending on whether it is right or left hemisphere function that is compromised. The productions of those with right-hemisphere damage, relying on their left hemisphere, lose overall coherence and integrity, and become so distorted they are barely recognizable: there is no grasp of the *Gestalt*. The drawings of those with left-hemisphere damage, by contrast, relying on their right hemisphere, exhibit relative poverty of detail, because the accent is on the shape of the whole.[173,174]

Context versus abstraction

For the same reason that the right hemisphere sees things as a whole, it also sees each thing in its context, as standing in a qualifying relationship with all that surrounds it, rather than taking it as a single isolated entity.[129,175-176] Whatever is not explicit or literal, that requires contextual understanding, depends on the right frontal lobe for its meaning to be conveyed or received.[176] The right hemisphere understands from indirect contextual clues, not only from explicit statement, whereas the left hemisphere will identify by concepts rather than from the experiential context (eg, identifies that it must be winter because it is "January," not by looking at the trees).[177,178]

This difference is particularly important when it comes to language. Whereas the left hemisphere has more sophisticated syntax and a greater semantic range, the right hemisphere takes whatever is said within its entire context.[179] It is specialized in pragmatics, the art of contextual understanding of meaning, and in using metaphor.[180,181] The right temporal region appears to be essential for the integration of two seemingly unrelated concepts into a meaningful metaphoric expression.[182] All conceptual thought is ultimately metaphorical in nature.[183] The left hemisphere, because its thinking is decontextualized, tends towards a relatively inflexible following of the internal logic of the situation, even if this is in contravention of everything experience tells us.[184]

Individuals versus categories

At the same time it is the right hemisphere that stores details to distinguish specific instances.[185] The right hemisphere presents individual, unique instances of things and individual, familiar, objects, where the left hemisphere represents categories of things, and generic, nonspecific objects.[118,186-187] In keeping with this, the right hemisphere uses unique referents, where the left hemisphere uses non-unique referents.[118,119,188-190] It is with the right hemisphere that we distinguish individuals of all kinds, places as well as faces.[191] In fact it is precisely its capacity for holistic processing that enables the right hemisphere to recognize individuals, since individuals are *Gestalt*, indivisible, wholes.[159,186,192] In keeping with the principle that it is not *what* is done, but *how* it is done, that distinguishes the two hemispheres, one cannot say that one hemisphere deals with single items ("units'"), and the other with "aggregates." Both deal with "units" and both deal with "aggregates." Thus, the right sees individual entities (its kind of units) in all their uniqueness, and it sees them as belonging in a contextual whole (its kind of aggregate), from which they are not divided. By contrast the left sees parts (its kind of units), which go to make up a something which it recognizes by the category to which it belongs (its kind of aggregate). However, the relationship between the smaller unit and the broader aggregate in either case is profoundly different: as is the mode of attention to the world with which it is associated.

Where the left hemisphere is more concerned with abstract categories and types, the right hemisphere is more concerned with the uniqueness and individuality of each entity.[189,193,194] The right hemisphere's role as what Ramachandran has described as the"anomaly detector" might in fact be seen rather as an aspect of its preference for things as they actually exist (which are never entirely static or congruent—always changing, never the same) over abstract representation, in which things become fixed and equivalent, types rather than individuals.

Where the left hemisphere utilizes abstract categories, the right hemisphere organizes experience according to specific exemplars.[195-198] The left hemisphere takes an invariant or abstracted view in its representation of objects, where the right hemisphere uses stored "real world" views in order to group experience.[195,199-200]

The living versus the nonliving

The left hemisphere has more capacity for the abstract or impersonal, whereas, in keeping with its more contextualized view, the right hemisphere is less prone to abstraction, and prioritizes the personal.[201,202]

The left hemisphere is better at appreciating analytic or mechanical structures, whereas the right hemisphere is better adapted to an appreciation of wholes, such as living entities, that have not been put together from parts. The right hemisphere is more concerned with living individuals than manmade objects.[203] The left hemisphere alone codes for nonliving things,[204-207] while both hemispheres code for living things.[206-208] However, at least one study has found a clean divide between the hemispheres, the left coding for the nonliving, and the right for the living, regardless of the task.[209] The body image as a whole is a right-hemisphere entity, whereas body parts are the province of the left hemisphere.[210]

The left hemisphere codes for tools and machines.[118,204-206,208,209] Right-hemisphere damage leaves the ability to use simple tools unaltered, whereas left-hemisphere damage renders the sufferer incapable of using a hammer and nail, or a key and a padlock. However, right-hemisphere damage particularly impairs naturalistic actions involving a sequence of steps, for example making a cup of coffee or wrapping a present.[211-212]

Corballis writes that 'there is a case for supposing that the left side represents the fruits of human invention, including language, manufacture, and a partwise way of representing objects.'[213] He draws attention to the affinity of the left hemisphere for everything it has itself made. The right temporal region, by contrast, appears to have areas not only specific for living things, but additionally for all that is specifically human.[214-216] Such judgments of "humanness" are separate from the right hemisphere's superior ability to recognize faces.[217]

The need to reconcile irreconcilables

The narrow focus of attention of the left hemisphere predisposes it to adopt a part-wise representation of reality, which promotes the transformation of a continuous process into a series of static points. This may underlie the different contributions made by each hemisphere to the appreciation of music and the sense of time, as well as to spatial depth.[104]

The broader scope of attention of the right hemisphere, which sees the individual in relation to others—in animals and birds, to predator or conspecific—leads to its prominent role in social understanding in humans, including in "theory of mind," and the expression of, and receptivity towards, social emotions. Decety and Chaminade note that 'self-awareness, empathy, identification with others, and more generally inter-subjective processes, are largely dependent upon … right hemisphere resources.'[218] These issues, which also have implications for the moral sense and the sense of the self, are complex and are explored at length elsewhere.[104]

Overall, there is the requirement, on the one hand, for a highly focused form of attention, directed towards an object that is already known, and which must be resolved precisely if it is to be grasped or used. This includes food or prey, but also anything that is to be used or manipulated. This is mediated by the left hemisphere, and crows already exhibit a strong right eye bias for tool manufacture, even where using the right eye makes the task more difficult.[219,220] In man the left hemisphere is also the controller of the grasping right hand, and of the denotative and explicit (rather than connotative or implicit) aspects of language whereby we make meaning precise, or as we say "grasp" it (cf French *com-prendre*, German *be-greifen*). On the other hand, this narrowly focused kind of attention is disruptive of continuity and context, and there is a need for an attention of broader scope, mediated by the right hemisphere, that is not distinct, precise, and manipulative, but reciprocal, more tolerant of uncertainty and ambiguity, and intersubjective in nature.

The difference can be seen at its simplest in processing visual imagery. Blurred or indistinct images are easily processed by the right hemisphere, but not by the left, even where the nature of the task would suggest that it should be more problematic for the right hemisphere.[221]

One of the most consistent early findings in hemisphere specialization was that whenever an image is either only fleetingly presented, or presented in a degraded form, so that only partial information is available, a right-hemisphere superiority emerges.[221-223] Sergent was able to demonstrate that this is the case even when the material is verbal, and its converse, namely that when images are presented for longer than usual, thus increasing their certainty and familiarity, a left-hemisphere superiority emerges, even in face recognition.[224] According to Sergent, letters of the alphabet 'represent a finite set of stimuli that are sharply focused, familiar and overlearned,' whereas visual images 'represent a potentially infinite set of shapes of large visual angle size, with different levels of structure of unequal importance and salience that are most often unfamiliar to subjects.' Here a common thread unites, on the one hand, the left hemisphere's affinity for what it itself has made (here language), familiarity, certainty and finitude, and, on the other, the right hemisphere's affinity for all that is new, unknown, uncertain, and unbounded.[93]

The nature of interhemispheric relations

Given the difference in concerns, how are the relationships between the two hemispheres managed in practice?

The experience of callosotomy is instructive. Behavioral disturbances following callosotomy take the form not, as might have been expected, of loss of function, but, on the contrary, of failures of functional inhibition. In this respect, split-brain subjects are like patients who have suffered a stroke or other neurological injury affecting the corpus callosum: there is a problem of compromised interhemispheric inhibition.[225-226]

The inhibitory nature of the corpus callosum is adaptive and creative, rather than restrictive, and the ability to maintain separation while communicating information is essential. Banich notes that:

> the major finding to come out of our laboratory since the mid-1980s is that interhemispheric interaction is much more than just a mechanism by which one hemisphere "photocopies" experiences and feelings for its partner. Interhemispheric interaction has important emergent functions—functions that cannot be derived from the simple sum of its parts … the nature of processing when both hemispheres are involved cannot be predicted from the parts.[23]

One of the many misconceptions of the popular culture surrounding hemisphere difference is that creativity is a function of the right hemisphere alone. Certainly there is plenty of evidence that the right hemisphere is important for creativity,[227] which, given its ability to make more and wider-ranging connections, and to think more flexibly, is hardly surprising.[228] But this is only part of the story. Both hemispheres are importantly involved. Creativity depends on the union of things that are also maintained separately—the precise function of the corpus callosum, both to separate and connect. Division of the corpus callosum does in fact impair creativity in individuals.[229]

Asymmetry of interhemispheric inhibition

Interhemispheric competition is differently regulated in different individuals. For certain tasks, one or other hemisphere generally tends to predominate, its particular cognitive and perceptual style as a whole being more suited to the task in question, but interindividual differences exist, with characteristic and consistent biases associated with differing degrees of arousal and activation in either hemisphere. This phenomenon is known as "hemispheric utilization bias" or "characteristic perceptual asymmetry." [230-233]

Through examining these perceptual asymmetries, the relationship between the hemispheres can be seen to be itself asymmetrical. For example, in experiments where a task is carried out requiring attention to the nonfavored visual field (the field contralateral to the nonfavored hemisphere), while irrelevant, distracting information is presented to the favored visual field, those subjects with a characteristic left-hemisphere bias found that the already strong tendency for the left hemisphere to prioritize the right visual field, and downplay the left visual field, was enhanced. This meant that the irrelevant information in the right field interfered with the task going on in the left field (controlled by the right hemisphere). But for those with a characteristic right-hemisphere bias, when conditions were reversed, no such competitive effects were seen: irrelevant information in the right hemisphere's favored left field did not interfere with the subject's ability to attend to the matter in hand going on, now, in the right field (the field favored by the left hemisphere).[234] This confirms a more even distribution of "concern" in the right hemisphere than in the left, consonant with the well-known phenomenon of hemineglect following right-hemisphere insult, but going further. Having a "utilization bias" in favor of the left hemisphere intensifies this effect, whereas having a similar bias in favor of the right hemisphere does not.

Furthermore, in the majority of normal subjects transfer of information from left hemisphere to right hemisphere takes place more slowly than transfer from right to left,[235-237] even where the task is by nature better suited to the right hemisphere.[238] Interhemispheric competition is also revealed by response to injury. In 1890, Brown-Séquard found he was able to reverse a paralysis caused by a lesion in one hemisphere of a frog by inflicting a similar lesion at the same point in the contralateral hemisphere.[239] In accordance with this, if, following a brain injury, the contralateral hemisphere is disabled temporarily by transcranial magnetic stimulation, an improvement in function in the damaged hemisphere results.[240,241] Similarly, a subsequent insult to the contralateral hemisphere yields an improvement in function in the originally damaged hemisphere.[242] But such interhemispheric competition appears again to be asymmetrical, with the suppressive effect of the left hemisphere on the right being greater than that of the right on the left.[240,243] Moreover, in chicks there is an asymmetry in favor of the right hemisphere, but when the commissures develop in adult birds, this permits the left hemisphere to have an inhibitory effect on the right hemisphere to a greater extent than the right hemisphere has on the left; severing of the commissures re-establishes the primary asymmetry.[4,244]

Finally there may be costs as well as benefits to mutual inhibition, as callosotomy subjects reveal. Though they have handicaps, they can carry out some tasks more swiftly than normal subjects.[245] For example, tasks involving focused attention usually engage primarily the left hemisphere. But in split-brain patients, the left hemisphere cannot so effectively inhibit the right, so that both are able to bring focused attention to bear (the right hemisphere can also yield focused attention), and both contribute, with the result that the task is carried out in half the time.

Conclusion

One possible explanation of the asymmetry and differential development of the cerebral hemispheres lies in the need to apply simultaneously mutually incompatible modes of attention to the world. This difference in attention can account for a wide range of so-called hemisphere specializations, and is facilitated by a corpus callosum which is able to balance facilitatory against inhibitory transmission. There is also an asymmetry in the way in which the two hemispheres mutually inhibit one another's contribution to the phenomenological world which favors the left hemisphere. ❑

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Organización recíproca de los hemisferios cerebrales

Los hemisferios cerebrales son anatómica y neurofisiológicamente asimétricos. Las bases evolutivas para estas diferencias aun no están determinadas. Sin embargo, hay diferencias altamente consistentes entre los hemisferios, que son evidentes en reptiles, pájaros y mamíferos, así como también en humanos, como ocurre con la atención que cada uno aplica al ambiente. Esto permite la aplicación simultánea de una atención focalizada con precisión, pero limitada, que es necesaria para conseguir alimento o atrapar una víctima, con una atención amplia, sin límites y no definida necesaria para protegerse de los predadores e interpretar las intenciones de los congéneres. Estas diferentes formas de atención pueden dar cuenta de un rango muy amplio de observaciones repetidas que se relacionan con la especialización hemisférica, y sugieren que las diferencias hemisféricas no están localizadas en áreas funcionales distintas, sino que corresponden a diferentes formas de funcionamiento dentro de una misma área. Estas formas de atención son mutuamente incompatibles y su aplicación depende de la transmisión inhibitoria en el cuerpo calloso. A nivel fenomenológico también hay una asimetría de la interacción entre los hemisferios.

Organisation réciproque des hémisphères cérébraux

Les hémisphères cérébraux sont anatomiquement et neurophysiologiquement asymétriques. L'origine de ces différences au cours de l'évolution reste mal connue. Les hémisphères cérébraux présentent des différences constantes, chez les reptiles, les oiseaux et les mammifères comme chez les humains, dans la nature de l'attention que chacun porte à l'environnement. Ceci permet la mise en place simultanée d'une attention ciblée avec précision, mais étroite, nécessaire à la capture de nourriture ou d'une proie et d'une attention plus large, ouverte et non dirigée nécessaire à la surveillance de prédateurs et à l'interprétation des intentions des congénères. Ces différents modes d'attention sont responsables d'un très large éventail d'observations répétées concernant la spécialisation hémisphérique, et suggèrent que les différences entre les hémisphères résident dans des modes distincts de fonctionnement quel que soit le domaine et non dans des domaines fonctionnels indépendants. Ces modes d'attention sont mutuellement incompatibles et leur application dépend d'une transmission inhibitrice dans le corps calleux. Il existe également une asymétrie d'interaction entre les hémisphères au niveau phénoménologique.

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