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Hemispheric specialization and regulation of motor behavior on a perspective of cognitive neuroscience

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Updated by topics

SUMMARY

Introduction
Our understanding of functional brain organization is due to advances in neuroimaging technologies and to an intensive clinical research. Recently, cognitive science (cognitive neuroscience), combined with advances in technology, have changed our understanding of brain-behavior relationship. This symbiotic relationship has allowed a better characterization of the lesion site in patients with brain disorders and patterns of activation in healthy subjects.

Objective
In this article we discuss the contribution of the left hemisphere and right hemisphere involvement in the regulation of motor behavior; this will allow us to better understand the lateralization of motor functions.

Development
The results support the view of left-hemisphere dominance for language and motor control, and right hemisphere dominance for spatial functions and attention. Specialized areas are probably pre-determined and certain functions are lateralized to one or other hemisphere due to the efficient organization and information processing in the brain.

Conclusion
In the studies reviewed, specific functions for each hemisphere were observed, suggesting the existence of a complex organization that recruits several areas of the Nervous System for adequate performance of a task.

Key Words: Motor behavior, functional specialization, functional integration, sensorimotor integration, cognitive neuroscience.

RESUMEN

Introducción
Nuestra comprensión de la organización funcional del cerebro se debe a los avances en las técnicas de neuroimagen y a una intensa investigación clínica. Recientemente, la ciencia cognitiva (neurociencia cognitiva) en combinación con los avances tecnológicos han cambiado nuestra comprensión sobre la relación cerebro-conducta. Esta relación simbiótica ha permitido una mejor caracterización del sitio de la lesión en pacientes con trastornos cerebrales y de los patrones de activación en sujetos sanos.

Objetivo
En el presente artículo se discute la contribución del hemisferio izquierdo y la participación del hemisferio derecho en la regulación de la conducta motora; esto nos permitirá comprender mejor la lateralización de las funciones motoras.

Desarrollo
Los resultados apoyan la visión de un predominio del hemisferio izquierdo para el lenguaje y el control motor, y un predominio del hemisferio derecho para las funciones espaciales y la atención. Las áreas especializadas son probablemente predeterminadas y ciertas funciones están lateralizadas a uno u otro hemisferio, esto debido a la eficiente organización y procesamiento de la información en el cerebro.

Conclusión
En los estudios revisados, se observaron funciones específicas para cada hemisferio, lo que sugiere la existencia de una compleja organización que recluta a varias áreas del Sistema Nervioso para el adecuado desempeño de una tarea.

Palabras clave: Conducta motora, especialización funcional, integración funcional, integración sensitivomotora, neurociencia cognitiva.

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INTRODUCTION

Progress in the understanding of functional brain organization is due to advances in neuroimaging technologies and to an intensive clinical research. Recently, cognitive science —specifically cognitive neuroscience— combined with numerous advances, has made a great impact on our understanding of brain-behavior relationships. This symbiotic relationship between neuropsychology and neuroscience continues and has been achieved by developing the neuroimaging methods. This has allowed a better characterization of the lesion site in patients with brain disorders and patterns of activation in healthy subjects. This symbiosis is especially attractive when combined with cognitive paradigms, with the most advanced neuroimaging methods, in order to address issues related to cognition and its relation to neuroanatomical aspects.[1]

Its complexity makes the brain looks like a large open system integrating many different and complex systems. Modern neuroimaging techniques allow us to observe live brain function in real time during the performance of cognitive or behavioral tasks. This leads to a more current and integrated view of the brain, where multiple areas, either simple or complex, are activated at the same time.[2] Based on this cutting-edge vision, researchers have struggled to support the principles governing cortical involvement from the perspective of functionality.[3-6] Thus, two basic principles have been proposed: functional specialization, which refers to the idea that certain regions of the brain play specialized roles; and functional integration, which implies that specific tasks require extensive interactions among specialized brain regions.[7]

Traditionally, cognitive neuroscience depends on animal studies information and on research in patients with focal brain lesions in order to determine the role of specific areas. The first research method has the disadvantage of generalizing results due to the different types of species used in the studies and also to the fact that many higher order cognitive functions are inherent in every human being. The second research method has the problem that the lesion is not usually focal, and what is being investigated is the rest of the brain function after a long-term reorganization with a lack of contribution of the injured area.[1] Regarding studies of cortical lesions, the localizationist doctrine effectively contributed on the aspects of functional differentiation of the cerebral hemispheres. Since Paul Broca and Carl Wernicke's studies it was observed that language areas are altered with the existence of a specific lesion in the left hemisphere. Accordingly, John Hughlings Jackson led the discussion through his experiments for a possible dominance of the right hemisphere due to its importance in visuospatial functions.[8] By contrast, Liepmann noted a significant interhemispheric asymmetry in relation to motor skills, with the argument that the left hemisphere plays a predominant role in motion control, rectifying that this hemisphere contains "motion formulas" aimed at both sides of the body.[9]

Based on these discussions, now neurology has been focused on the specialized functions of the left hemisphere that are essential for language and motor skills. Studies show that this lateralization is well established for right-handed individuals[10-12] and that this could be programmed during development[13,14] after the onset of the perceptual-motor specializations that are essential in the initial period of pregnancy.[15-17] However, this issue still generates discussions.[18,19] A possible hypothesis is that functional connections between cortical areas of the hand and tongue[20,21] may have been essential for the evolution of hand gestures language rather than vocal words,[22] a fact that is supported by the use of gestures that usually come with the expression of speech.[23] In this context, some studies have found that Broca's area is associated with different motor functions and not only with language but also with planning, recognition and imitation of gestures[24-26] as well as the syntactic operations necessary for the hierarchical representation of the sequential behavior.[27,28]

The aim of this article is to discuss the contributions of the left hemisphere in the regulation of motor behavior and participation of the right hemisphere in such process to better understand their involvement in the lateralization of motor functions. Therefore, it is proposed that the lateralization of motor functions is a versatile process in which the functional involvement of both hemispheres is not fixed but flexible, and guided by several fundamental factors.

CONTRIBUTIONS OF THE LEFT AND RIGHT HEMISPHERES IN THE REGULATION OF THE COGNITIVE ASPECTS OF MOTOR BEHAVIOR

Experts in neurology and neuropsychology typically focus their attention on contralesional motor deficits but ipsilesional deficits are also present and are considered to be associated with the cognitive demands of movements (e.g., planning, development and selection of motor programs). These deficiencies have functional implications, especially in patients with aftereffects of cerebrovascular accident (CVA) who use their ipsilesional limbs to compensate the hemiplegia. Previous studies have highlighted the importance of the left hemisphere compared to the right one to control the ipsilesional movement, for example, by the limb of a patient with apraxia[29] and sequence of movements.[30,31] Some tasks are more controlled by the right hemisphere or need both hemispheres;[32] but the point of discussion is the role of the left hemisphere in complex movements, since it is dominant in controlling many actions, such as language.

Hemispheric specialization is closely linked to hemispheric dominance and brain functions. The predominance of the left hemisphere for motor skills has been attributed to anatomical and functional asymmetries of the primary motor cortex (M1) and downstream pathways[33,34] as the secondary motor and association areas.[35] The hand contralateral map in right-handed subjects provides strong evidence of an asymmetry in the area M1,[36-39] which is probably related to the changes experienced in early development. This fact was observed in the performance of tasks made with the dominant hand and non-dominant hand in right-handed subjects, which results in a greater spatial dispersion in the motor areas of the left hemisphere than in the right-hand areas.[40] Functional magnetic resonance imaging (fMRI)[41] and transcranial magnetic stimulation (TMS)[42] studies have shown the above aspects.

The asymmetry of motor and association areas reflects a secondary application of certain functions of specialized brain regions. This was observed in studies with patients who suffered lesions in the left hemisphere. Individuals showed a decrease in the performance of skillful actions with both hands. The right hemisphere lesions cause restricted deficits to the contralateral hand.[43-45] Haaland et al.[36] showed, in healthy people, a greater involvement of the premotor areas and of left parietal hemisphere compared to the right hemisphere in areas of high command related to the complexity of the task. According to these findings, several hypotheses have been offered as a basis for this asymmetric functional model of the left hemisphere such as the behavior of sequential actions, the organization and selection of movements,[46,47] bimanual coordination,[48,49] perception and interpretation of actions,[50] and moreover, the movements in sequence[51] that strengthen the role of the left hemisphere in speech and writing.[52,53]

But the real role of the right hemisphere in the regulation of motor behavior is still not well defined. The evidence is aimed at a small representation on the area M1 of the right hemisphere compared to the left one in right-handed people, related to a decrease of the skill of the non-dominant hand.[54]

In association areas, the specialized functions related to planning are not well developed,[55] probably due to the strong demand for "clues" to select a specific external representation that involves the motor processing of the new exploration of situations.[56]

The issue of processing the exploration of new situations is consistent with the theory that the left hemisphere acts on aspects of movement in open circuit (based on well-established motor programs), while the right hemisphere is crucial to all aspects of movement in closed circuit (depending on the sensory feedback).[38] However, Haaland et al.[37] study provides no evidence that this dichotomy is related to hemispheric asymmetry. On the other hand, it has been proposed that the left hemisphere controls the trajectory of the limb, while the right hemisphere regulates the position and posture of the limb used in the task.[57] This premise is consistent with studies made in patients who showed a different behavior in cases of lesions to the left and right hemispheres, in the beginning and at the end of the movement with the addressed target.[58]

Therefore, so far the more likely is that the left-hemisphere specialization is limited by the specifications of the dynamic tasks' feedback, while the right-hemisphere specialization includes sensory mechanisms that control the final positioning of the limb.[59]

However, some authors state that the right hemisphere is in charge of functions such as spatial memory, learning and orientation,[57] which suggests that its prevalence is due to the storage of global features, while the left-hemisphere specialization is made by the specific processing features.[60] Thus, the specialization of the right hemisphere in spatial functions may be due to the involvement of spatial attention control in left and right fields of vision[61] or to a supervision function that is evident especially in conflict situations[62] among the intention of the movement, proprioception and visual feedback.[63]

THE INTERACTION BETWEEN THE FACTORS RELATED TO THE TASK AND THE EXECUTOR

Understanding the function of the Central Nervous System (CNS) regarding the regulation of movement is essential in several areas of research. Considering the foregoing, we will discuss that participation of each cerebral hemisphere in motion controlling depends mainly on aspects related to the task and the executor. Therefore, we should point out the type and complexity of the movement, the skill level of the executor, whether the CNS is damaged or not, and the focus of attention of the executor, as these factors influence how hemispheres behave in the regulation of movement.

Factors Related to the Task

The process related to the type of movement has an important role in the regulation mechanisms of motor behavior. In particular, sequential representations and their characteristics are associated with the left hemisphere, regardless of the hand used for the task.[36]

Thus, the left hemisphere may be involved specifically in the planning of sequential acts resulting in the response selection, preparation and/or recovery.[36,64] In order to achieve specific goals with a purpose, it is proposed that each hemisphere contributes differently in the specific control of trajectory and final position.[59,65] This distinction is due to the contribution of the left hemisphere in the planning of the dynamics of the limbs, while the right one is essential to specify the final position of the grasping movements through the sensory regulation. The contribution of each hemisphere is also modulated by the complexity of the movement. While a simple movement, like bending a finger, is organized by a local neuronal network. The more complex actions, such as demands related to a sequence of finger movements, require the distributed participation of neural networks, often bilaterally.[36,64] In this sense, the recruitment of both hemispheres seems to be affected by the increased attention or the executive control parameters, or by the use of operations that specialize in each hemisphere. Therefore, it is common knowledge that the pathways between hemispheres take into account the coupling or decoupling of relevant information.[66] Actually, this input occurs between both hemispheres, as shown in the learning transfer studies that investigate the transmission of information when a specific task is performed with one hand only, since, generally, the performance advantages are found both in the trained and untrained hand.[67]

Factors Related to the Executor

The process related to the executor has great importance in the regulation of motor behavior. According to these principles, the experiment of Goldberg et al.[68] proposed that the right-hemisphere processing is driven by the external environment, while the left-hemisphere processing is guided by internal representations.[37,69] This is consistent with the observations made in studies where patients with lesions in the right parietal cortex showed spatial neglect. They have seen a severe change of scanning movements to the right side, which was attenuated when movements were directed toward a target.[70] It is suggested that both types of action require different information input or support processes with a characteristic contribution of both hemispheres. These functional differences between hemispheres support a shift from right to left regarding the hemispheric importance, such as the development of skills. In fact, this development is often associated with a partial transition in the generation of external-to-internal movement control. This fact occurs, for example, when learning a difficult bimanual task,[6] where eventually a reduced activation in the right hemisphere takes place, while activation of the left hemisphere becomes more imminent. Since the reduced activation in the right hemisphere is associated with a lower demand for the spatial characteristics of motion tracking, the increase of participation and representation is consolidated.[67,70]

The CNS has operational changes due to certain neural patterns. An example of this occurs after a lesion, particularly in cortical areas associated with the bilateral control of a given function as the pre-motor cortex that can take on more responsibilities in the motor processing, in addition to its crucial role in the functional recovery.[58,71]

This implies that both hemispheres are equipped with functional abilities that they can perform under specific conditions and also this supports the idea that the participation of certain neural networks for the regulation of motor behavior is flexible, although there is evidence that the motor deficit differs as whether lesions are in the left or right hemisphere.[72] This issue requires a more detailed assessment of what "to one side" and "the extent of the lesion" mean, as well as the task and the laterality limitations.

Finally, attention may modulate the involvement of both hemispheres.[73] In particular, changes in spatial attention between global and local levels of representation rely on processes related to the left and right hemispheres, respectively. Furthermore, these changes also depend on the relevant demands and not on the voluntary movement, as the attention aimed at motion improves the selection of representations. These findings show that the demands of the executor's tasks and characteristics are factors that influence on the regulation of motor behavior and, therefore, may promote hemispheric asymmetries and inter-hemispheric interactions. Such facts show that a dynamic balance between the existing restrictions induces to certain operation modes.[6] For example, one can quote the general orientation that is particularly relevant for new and unexplored actions most associated with the right hemisphere. On the other hand, it bears mentioning the treatments related to the representations that occur due to an action planning-based experience, most of the treatments in connection with the left hemisphere. These findings support the functional contribution that both hemispheres are flexible. Such flexibility causes an adapted and specialized motor behavior. Therefore, observation of motor tasks —i.e. the sequential movements of the fingers— is widely used in various types of experiments allowing to obtain results in favor of separate processes (mainly in the left hemisphere).[1,6]

Sensorimotor integration and information processing

The sensorimotor integration may be defined as a process whereby the sensory stimuli are converted into motor commands, sensory information is integrated by the CNS and is used for executing motor programs.[56] In this case, the CNS processes information from multiple sensory channels and adapts to the environment that allows the execution of specific tasks and of movements with focused objectives.[74,75] Thus, performing a movement involves integration among the different senses, especially sight, hearing, somesthesia, etc. In recent decades there have been several experiments in order to clarify the brain processes and areas involved in the integration of sensory information and execution of the motor gesture. Werhahn et al.[76] found, through the use of TMS, that when the upper contralateral limb of subjects was anesthetized, the ipsilateral muscles had an increase in the motor evoked potentials (MEPs). Moreover, it was observed that there was a reduction in the excitability of the contralateral hemisphere motor cortex of the anesthetized limb against the excitability of the motor cortex of the hemisphere related to the unanesthetized limb.

According to these principles, if certain functions are lateralized to both hemispheres, the efficient processing of information is essential to the representation of such functions. Many of these interactions occur through the corpus callosum considering pre-motor information transfer related to care, feedback and errors.[77] This interhemispheric communication involves both functional inhibition and facilitation. Although these inhibitory interactions are essential in the preparation of unilateral movements, they are responsible for neutralizing the production of mirrored movements,[49,78] i.e., involuntary movements of the contralateral hand, which conducts voluntary actions. From the lateralization of motor behavior point of view, there is evidence of many inhibitory circuits between the motor cortex of the left and right hemisphere in right-handed subjects.[79] Such functional distinction could contribute to hemispheric differences in the regulation of motor behavior, probably from childhood, during certain processes that assume an asymmetric inhibitory behavior.[80]

Facilitating the transfer of information between the hemispheres is essential when their processing is necessary for a satisfactory performance in the task. In the context of the regulation of motor behavior, the corpus callosum and its information exchange mechanism have been viewed with special interest in the coordination of bimanual tasks.[81]

As demonstrated so far, the level of interhemispheric communication is related to the complexity of the task[3,6] and is necessary for the learning of new motor patterns.[3,5,6]

Thus, the interactions of the corpus callosum provide a link to the specification of high level motor parameters (such as the speed with which the limb involved in the movement acts) or the selection of a response[82,83] and, probably constitute a physiological basis neural[84] for sharing information that is evident when participating in bimanual tasks with different patterns movimiento.[85] In summary, this adaptive motor behavior depends on inhibitory processes that can help you explore the benefits associated with the transformation of specialization hemispheric processes that enable and facilitate the integration of information in both hemispheres. This implies that the allocation of motor behavior processing resources is a dynamic process by which the segregation and integration of these functions occur in a flexible manner.

However, our question is: How the brain organizes information from different specialized regions, since each can process information in different ways? To better understand this, it is important to consider how the processing of information is coordinated interhemispherically. A possible mechanism of interactions among large-scale regions is the temporary creation of dynamic connections based on the timing of neural activity.[86-88] Thus, the coherence function is regarded as relevant by several electrophysiological studies such as electroencephalography, magnetoencephalography and local field potentials.[89-91] Particularly, coherence is a means for capturing neuronal communication through various sectors of the cerebral cortex encoding different information that may be related to different frequency bands. For example, the beta frequency band (~ 14-30 Hz) is related to the synchronized activity observed in sensorimotor areas.[92]

Thus, the dynamic organization of neuronal activity in the frequency domain may provide a means of data processing given the task demands such as the close relationship between changes in corticocortical coherence and behavioral outcomes, which supports this point of view.[93] Based on these principles, the study of Andrew et al.[94] found that the initial increase in coherence may be a reflection of changes in interhemispheric communication that are specifically related to bimanual learning and these can be transmitted through the corpus callosum. These results may help explaining some neurophysiological data of clinical observation in patients with lesions of the corpus callosum that may show the deficit outcome in the acquisition of new bimanual tasks, but not necessarily in the performance of bimanual activities previously learned.

This dynamic organization also suggests that the activity of various harmonized brain areas represents a basic mode of communication with different frequencies that is based on the formation of neural networks, which translates the transformation output in a more efficient behavior. As to the evidence presented in the previous topics, it is suggested that with the development of skills, motor representations, such as those established for the left hemisphere, can support more effectively the information processing within distinct brain regions. An example is that, during the acquisition of a new bimanual task, it has been shown that an initial profile of associations between corticocortical areas is gradually adjusted as the routine becomes a stable and optimized-behavior performance[5,93,94] until ultimately results in a functional pattern that is mostly orchestrated by the left hemisphere during the performance of learned bimanual tasks.[3,5,6]

IS THE LATERALIZATION OF MOTOR FUNCTIONS REALLY A DYNAMIC PROCESS?

The functional involvement of both the left and right hemisphere in the regulation of motor behavior seems not fixed, but rather a dynamic process. Within this context, this section addresses a new perspective on the dynamics of this process, also arguing that the lateralization of motor function is characterized by different communication channels and intra-and interhemispheric dynamics. Accordingly, neuroimaging and clinical studies with patients help identifying critical neuronal areas and systems for cognitive processes in particular.[95] However, studies in patients with brain lesion are limited by the inability to control the location of the lesion, the size and the trend to be focused on the importance of a single space instead of a number of areas that may be critical and may form a neural circuitry that controls a complex function.

In this regard, an important and interesting question is whether two or more areas can control different cognitive mechanisms that contribute to the execution of a complex task. In short, if a lesion in the region or in regions A and B causes deficits in a task A′, then the area or areas A and B must be activated when a healthy individual performs task A′, as a lesion in the region or regions A and B causes deficits in task A′, but not in task B′, then the area A or A and B should be the activated areas when a healthy person performs task A′, but not when performing task B′. This was observed in the study of Haaland et al.[37] when they investigated motion sequences in healthy subjects. By means of functional magnetic resonance imaging (fMRI), the it was verified that left frontal and parietal regions are activated when healthy subjects perform the complex motion sequence, but not with the simple movements. Moreover, it was observed that complex sequences are organized, causing great activation in the inferior parietal region, while the identification or selection of the effector mechanism appropriate for the sequence produces activation in the superior parietal region.[32]

Therefore, studies show that the hemispheric asymmetries and optimal balance between the hemispheres could be useful in understanding the pathologies and diseases like autism and schizophrenia, in which modulations can be partly seen as a hemispheric specialization atypical or incompatible to the integration among dysfunctional neural systems; for example, the dysfunction of neurons in the mirror circuit.[96] The regulation of inter-hemispheric information is possibly executed and operated on several levels. The first level (short term) is influenced, for example, by factors such as attention and context. The second level (medium term) is affected by factors such as learning and functional recovery. Finally, the third level (long term) is formed by the development, aging, high level of skills and chronic disease. Therefore, this view is opposed to the traditional point of view that lateralization of motor functions is considered as a static process.

CONCLUSION

The findings described in the bibliography show a great interest in studying the phenomenon of regulation of motor behavior, particularly with regard to the lateralization of motor functions.[97] Traditionally, researchers have been investigating the dominance of the left hemisphere in language and motion control, while a domain of the right hemisphere has been investigated regarding space and attention representations. Although the specialized areas are probably predetermined, (SIC) through a combination of interactions that a behavior is coherently achieved.[98] In this sense, a strong pattern of connections in parallel to a greater reliance on the left-hemisphere representations provides the basis for a more refined motor repertoire, and specialization of the right hemisphere also appears to contribute to a skilled behavior.

Moreover, it is through an active interaction of the information processing —especially by the corpus callosum— that the transfer of information takes place in processes such as sensorimotor integration, decision making and motor preparation.[99] As seen in the above issues, this process does not occur in a fixed manner, but through dynamics driven by different characteristics of the task and the executor, thus forming the motor behavior. Thus, the pattern of hemispheric asymmetry that is the basis of the organization of motor activity is a multifaceted and more complex pattern than a simple dichotomy of functions. So, through neuroimaging studies, several data were observed in patients with brain lesions associating the deficits observed in the performance of tasks with brain lesions (i.e. the hemisphere), which shows that it is not possible to interrupt selectively the specific cognitivemotor functions, causing important discussions of how the brain represents and regulates motor behavior.

Within this context, an important issue to explore is how each hemisphere contributes to the characteristics of the task and the executor, which allows the opportunity to observe and better understand the nature of the interhemispheric process. These opinions are not only crucial for theories of motion control, but also for advanced rehabilitation interventions in an attempt to restore the motor behavior of patients suffering from CNS lesions.

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