



Review

Interactions between brain structure and behavior: The corpus callosum and bimanual coordination

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ARTICLE INFO

Article history:

Received 18 October 2013

Received in revised form 30 January 2014

Accepted 13 March 2014

Keywords:

Corpus callosum

Partitioning schemes

Bimanual coordination

Mediating factors (age, pathology, training)

Split-brain patients

Diffusion tensor imaging

Coordination constraints

ABSTRACT

Bimanual coordination skills are required for countless everyday activities, such as typing, preparing food, and driving. The corpus callosum (CC) is the major collection of white matter bundles connecting both hemispheres that enables the coordination between the two sides of the body. Principal evidence for this brain–behavior relationship in humans was first provided by research on callosotomy patients, showing that sectioning (parts of) the CC affected interactions between both hands directly. Later, new noninvasive in vivo imaging techniques, such as diffusion tensor imaging, have energized the study of the link between microstructural properties of the CC and bimanual performance in normal volunteers. Here we discuss the principal factors (such as age, pathology and training) that mediate the relationship between specific bimanual functions and distinct anatomical CC subdivisions. More specifically, the question is whether different bimanual task characteristics can be mapped onto functionally distinct CC subregions. We review the current status of this mapping endeavor, and propose future perspectives to inspire research on this unique link between brain structure and behavior.

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1. General introduction

The corpus callosum (CC) is the largest white matter structure consisting of approximately 250 million fibers and connecting mainly homotopic, but also heterotopic brain areas of both hemispheres (Jarbo et al., 2012). It is a fascinating part of the brain because of its role in a variety of everyday behaviors, its large variability across individuals and the ambiguity regarding its structure and function. For example, there is (albeit inconclusive) evidence that the size and shape of the CC covary with age (e.g., Junle et al., 2008), gender and handedness (for review see Bishop and Wahlsten, 1997; Luders et al., 2014; Shin et al., 2005; Westerhausen et al., 2004, 2003; Witelson, 1989; Witelson and Goldsmith, 1991). Furthermore, the countless ways of subdividing the CC in separate structures and the uncertainty about their functional meaning, make the CC a very interesting white matter pathway to explore in more detail.

The present review focuses on the specific role of the CC in bimanual coordination. In daily life, we produce bimanual movements with a tremendous variety in how both hands interact with each other. Principal evidence for the importance of the CC in these movements has been provided by seminal studies on split-brain (or callosotomized) patients (Eliassen et al., 2000; Franz et al., 1996, 2000; Kennerley et al., 2002; Preilowski, 1972). In particular, sectioning the anterior part of the CC, to overcome spreading of epileptic activity, has been shown to result in slower and less accurate bimanual performance (Preilowski, 1972). This inspired early thinking that especially the anterior part of the CC was important for bimanual coordination.

Whereas studies on split-brain patients have greatly expanded our insights into the role of the CC in the control of bimanual movement, the advent of noninvasive brain imaging and brain stimulation technologies, has enabled scientists to explore the link between bimanual coordination and the CC in *healthy populations* with much higher resolution. Furthermore, noninvasive brain stimulation techniques, such as transcranial magnetic stimulation (TMS), have increased our basic understanding of interhemispheric interaction effects, and of the balance between inhibitory and excitatory functioning of the CC (see Section 3). Evidence for the major importance of this interhemispheric balance has been provided in stroke (Takeuchi et al., 2005) and aging (Fling and Seidler, 2012) research. In addition, brain structural imaging techniques, and particularly Diffusion Magnetic Resonance Imaging (such as diffusion tensor imaging; DTI), have paved the way for the provision of metrics to characterize the microstructural organization of the CC, by measuring the directionality of water diffusion (Basser et al., 1994; Basser and Pierpaoli, 1996; Beaulieu, 2002; Jones and Leemans, 2011; Le Bihan et al., 2001; Tournier et al., 2011). This has enabled neuroscientists unsurpassed capabilities to reveal associations between brain structure and behavior in general and between CC substructures and bimanual coordination in particular (e.g., Bonzano et al., 2008; Johansen-Berg et al., 2007; Muetzel et al., 2008; Sullivan et al., 2001).

In the present review, we will first discuss evidence for the specific association between the CC and bimanual coordination in the context of age-related and training- and pathology-induced changes in CC structure. The underlying assumption here is that, if the CC is important for bimanual coordination, the structural status of the CC will have direct implications for the quality of bimanual coordination performance. Moreover, the CC is not a single entity or unitary structure, but rather exhibits diversity in structure and function, and also regarding its differential development throughout life (see Appendix A). The complex architecture of the CC with its subdivisions (see Section 2), in association with the specific type of information and/or sensory modality conveyed, can help determine the associations between CC substructures and the different functional expressions of bimanual coordination (e.g., Gooijers et al., 2013). Accordingly, the degree to which specific bimanual task characteristics can be mapped onto structurally distinct CC subregions is a recurrent major theme in the present review.

2. Subdivision schemes of the corpus callosum

As briefly mentioned above, the CC is not a single entity but is composed of several subdivisions showing highly differentiated functions. Accordingly, exploring associations between the CC and bimanual coordination will benefit from detailed knowledge about this multimodal architecture, as will be discussed in Sections 3 and 4. To achieve this aim, we will first provide an overview of the available CC subdivision schemes, with segmentations based on either classical anatomy, geometry, histology, or in vivo anatomy.

2.1. Anatomical subdivision

The best known anatomical CC subdivision is simply based on the shape of the CC. The ventral, anterior tip is known as the rostrum. Dorsal to the rostrum, a curve can be observed which is termed the genu. The large middle portion is the body/truncus and the small part connecting the body and the splenium (posterior end), is the isthmus (see Fig. 1B) (see Catani and de Schotten, 2012). However, the rostrum and genu are often united, as well as the body and the isthmus, resulting in only 3 segments (genu, body and splenium). Another anatomical subdivision scheme is based on the association between the distribution of Wallerian degeneration in the CC and the anatomical locations of focal gray matter lesions (see Fig. 1C) (Delacoste et al., 1985).

2.2. Geometrical subdivision

The eighties and nineties were characterized by the emergence of geometrical segmentations of the CC. The best known example is the one proposed by Witelson (1989). She divided the CC in 7 segments along the anterior–posterior direction in the mid-sagittal section (see Fig. 1D). The anterior one third comprises fibers from the prefrontal, premotor and supplementary motor cortex. These

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