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Visual interhemispheric communication and callosal connections of the occipital lobes

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ABSTRACT

Callosal connections of the occipital lobes, coursing in the splenium of the corpus callosum, have long been thought to be crucial for interactions between the cerebral hemispheres in vision in both experimental animals and humans. Yet the callosal connections of the temporal and parietal lobes appear to have more important roles than those of the occipital callosal connections in at least some high-order interhemispheric visual functions. The partial intermixing and overlap of temporal, parietal and occipital callosal connections within the splenium has made it difficult to attribute the effects of splenial pathological lesions or experimental sections to splenial components specifically related to select cortical areas. The present review describes some current contributions from the modern techniques for the tracking of commissural fibers within the living human brain to the tentative assignation of specific visual functions to specific callosal tracts, either occipital or extraoccipital.

1. Introduction

The general plan of the mammalian visual system provides for a projection of each half of the visual field onto the contralateral cerebral hemisphere. Visual inputs thus channeled into one cerebral hemisphere can normally be compared, contrasted and integrated with those of the other hemisphere for enabling unitary visual perceptions and shared visual memories. Control of the two sides of the body in voluntary visually guided movements similarly entails an orderly visuomotor coordination between the two hemispheres. Many other visual performances requiring an interaction between the hemispheres comprise the interhemispheric transfer of learned visual discriminations, the perceptual constancy of static or moving visual objects across long-range horizontal retinal translations, the ability to judge whether stimuli in the two half fields are the same or different, the fusion into continuous percepts of alphabetic material, faces and objects straddling the fovea, the naming of objects and symbols projected to the non-speaking hemisphere, and so forth.

The first convincing demonstration that the corpus callosum, alone or together with other commissures, is essential for most such forms of interhemispheric interaction and communication was provided by the experiments of Myers (1956) and Sperry (1961) in callosotomized cats and monkeys with visual inputs restricted to one hemisphere. The results were then extended and qualified with regard to the human brain by Sperry et al. (1969) in epileptic patients submitted to section of the forebrain commissures for treatment of drug refractory epilepsy (see Glickstein and Berlucchi, 2008).

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The two occipital lobes are regarded as the visual part of the brain par excellence, even though they may take up nonvisual functions in cases of congenital or acquired peripheral blindness (e.g., Merabet and Pascual-Leone, 2010; Renier et al., 2010; Watkins et al., 2012), and even though vision also depends on other cortical areas in extraoccipital brain regions, particularly in the temporal and parietal lobes (e.g., Rajimehr and Tootell, 2008; Wandell and Winawer, 2011). In what follows I do not intend to present a systematic review of neuroanatomic and behavioral evidence on the participation of the occipital lobes to interhemispheric interactions. Instead I focus on a few recent studies which have advanced and under certain respects changed our understanding of such participation. New data have come from modern techniques applied to the living human brain, including the tracking of commissural fiber tracts with functional magnetic resonance (fMRI) and diffusion tensor imaging (DTI), as well as the cortical imaging and retinotopic mapping with fMRI and high density electrical and magnetic recording. Aspects of the subject which are not considered here have been dealt with in recent reviews on visual interhemispheric transfer (e.g., Schulte and Müller-Oehring, 2010).

2. The occipital lobes

According to Brodmann (1909) each occipital lobe includes the three cytoarchitectonic areas 17 (area striata), 18 (area occipitalis) and 19 (area praeoccipitalis). Areas 17 and 18 correspond to two retinotopically organized representations of the contralateral visual field called V1 and V2. Area 19 contains a similar complete retinotopic contralateral representation called V3, plus (involving perhaps neighboring regions of the parietal and temporal lobes) 10 or more additional areas identified by their correspondence with distinct but less complete or less organized visual field representations (Rajimehr and Tootell, 2008; Wandell and Winawer, 2011). In primates, including humans, area 17 (or V1 or area striata) is the only cortical recipient of visual inputs from the thalamic relay of the optic pathway, the lateral geniculate complex. Information is then transmitted from V1 directly or indirectly to all the other occipital cortical areas, collectively called extrastriate areas. Visual areas are connected with one another according to multiple serial and parallel patterns within hierarchical organizations in which feedforward connections are usually matched by feedback connections. Distinct neuronal populations in V1 and V2 respond selectively to primary attributes of the visual input such as lightness, simple contour orientation or wavelength or direction of motion, while higher order extrastriate areas specialize in the perception of complex visual stimuli such as objects, faces, bodies, alphabetical material and various kinds of motion perception (Rajimehr and Tootell, 2008; Wandell and Winawer, 2011).

For the present purposes it is necessary to start from the already mentioned notion that visual information from the right and left halves of the visual field is initially projected only to the contralateral occipital lobe. This is because of the orderly division in the optic chiasm of the crossed fibers from the nasal hemiretinae and the uncrossed fibers from the temporal hemiretinae, including the splitting of the foveal projections at the midline. It is still debated whether this splitting is absolutely precise or there is a foveal region that projects to both hemispheres (e.g., Brysbaert et al., 2012), but if such region exists visual field analyses in split-brain (Sugishita et al., 1994) and hemianopic patients (Reinhard and Trauzettel-Klosinski, 2003) suggest that it is probably limited to less than a degree on the horizontal meridian. Callosal connections are by far the most important, though not the only pathway through which visual cortical areas in the occipital, temporal and parietal lobes of each hemisphere can receive visual information from the ipsilateral half of the visual field. The callosal connectivity of an occipital area can in principle be gleaned from the degree and extent of ipsilateral field represented in it (Tootell et al., 1998). In cats (Berlucchi and Antonini, 1990) and monkeys (Van Essen et al., 1982) all or most occipital areas may contain an at least partial ipsilateral field representation limited to the vertical meridian region. The old erroneous belief that human area V1 is totally acallosal was due to the fact that callosal connections are restricted to the vertical meridian representation at the border between V1 and V2, so that most of V1 is free of callosal connections (see Glickstein and Berlucchi, 2008). Both the post-mortem tracing of degenerating callosal axons in brain with circumscribed occipital lesions, and DTI tractography in vivo have definitely confirmed the existence in a postero-inferior section of the splenium of callosal projections from and to V1 (Dougherty et al., 2005a; and 2005b; Saenz and Fine, 2010; Putnam et al., 2010), although the sensitivity of the latter method is presently insufficient to specify the origin and termination of callosal fibers within V1. That the ipsilateral field coverage increases from the limited vertical meridian representation between V1 and V2 to higher order areas is suggested by retinotopic mapping with fMRI. As shown in Fig. 1, the percentage of responses to ipsilateral field stimulations grows from about 5% in V1 and V2 to more than 20% in ventral and lateral occipital areas (Henriksson et al., 2012). Analyses by fMRI of the distribution of population receptive fields in V1, V3 ventral and temporal-occipital cortex indicates that receptive field centers are restricted to the contralateral visual field, so that the coverage of the ipsilateral visual field is mostly due to the size of the receptive field portions lying across the vertical meridian from the receptive field centers (Amano et al., 2009). Where receptive fields are very large, as in part of the temporo-occipital cortex, the coverage of the ipsilateral visual field can be quite extensive (Fig. 2). Increasingly loose retinotopy, large receptive fields and broad ipsilateral field representation are found in extraoccipital visual areas, suggesting a transition from a predominantly local visual space processing in occipital areas to a predominantly global visual space processing in parietal and temporal cortices (Jack et al., 2007).

3. Neuronal mechanisms and pathways for visual interhemispheric transfer

As originally shown in split-chiasm cats (Berlucchi and Rizzolatti, 1968; Berlucchi and Antonini, 1990), visual cortical receptive fields straddling the midline can be built up through the convergence onto the same neuron of an