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Research Report

ERP evidence for the split fovea theory

Clara D. Martin[a,b,c,*], *Guillaume Thierry*[b,d], *Jean-François Démonet*[c], *Mark Roberts*[b], *Tatjana Nazir*[a]

[a]*Laboratoire Langage Cerveau et Cognition, Institut des Sciences Cognitives, CNRS, 67 bd Pinel, 69675 Bron Cedex, France*
[b]*School of Psychology, University of Wales, Bangor, UK*
[c]*INSERM U825, Hôpital de Purpan, F-31059, Toulouse Cedex, France*
[d]*ESRC Centre for Research on Bilingualism in Theory and Practice, University of Wales, Bangor, UK*

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ABSTRACT

According to the 'bilateral representation theory', a complete copy of the words presented foveally is received simultaneously in the left and right visual cortices. However, a growing body of observations, which has led to the 'split fovea theory', proposes a functional split of the foveal area between the two hemispheres. In the present study we tested these two accounts using an adapted version of the Reicher–Wheeler paradigm. Ten control participants and ten participants with developmental dyslexia undergoing electroencephalographic recordings were asked to identify one of five letters in a string. The target letter was systematically presented at fixation but the horizontal positioning of the letter string was varied such that the stimulus fluctuated in both the visual hemifields over the experiment. ERP results showed that letter strings encompassing the foveal field were not sent to both cerebral hemispheres simultaneously when fixation coincided with extreme letter positions (i.e., first or last). Indeed, the P1 peak was delayed in this case, which was interpreted as the result of a transfer of visual information from the contralateral hemisphere via the splenium of the corpus callosum. Consistent with the 'split fovea theory', this result suggests that a minimal amount of graphic input is necessary to induce a P1 event. The interhemispheric transfer time (IHTT) deducted from peak-to-peak P1 latency delays ranged from 26 to 42 ms. As previously observed, the IHTT was significantly faster for right-to-left than left-to-right transfer in the control group. IHTT was marginally shorter in control participants as compared to participants with developmental dyslexia, and the faster transfer to the left hemisphere seen in the former was not found in the latter.

1. Introduction

The division of the brain in two halves creates a challenge for explaining how foveally presented words are perceived (Brysbaert, 2004). According to a classic theoretical stand, two complete copies of a foveally presented visual stimulus are sent in parallel to the left and the right hemisphere (Leventhal et al., 1988; Stone et al., 1973; Trauzettel-Klosinski and Reinhard, 1998). This "bilateral representation" theory assumes that left and right visual fields (LVF and RVF) overlap along the vertical meridian and that a copy of visual information presented foveally is sent to the primary visual cortex of each of the hemispheres. Both hemispheres then process the same information without the need for interhemispheric transfer.

* *Corresponding author.* L2C2, Institut des Sciences Cognitives, CNRS, 6 bd Pinel 69675 Bron Cedex, France. Fax: +33 4 37 91 12 10.
E-mail address: clmartin@isc.cnrs.fr (C.D. Martin).

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Support for this theory comes from the fact that patients with hemianopia sometimes show sparing of central vision (see Trauzettel-Klosinski and Reinhard, 1998), and that horseradish peroxidase injections in the dorsal lateral geniculate nucleus show incomplete crossing of the nasal fibers in the optic chiasm (Leventhal et al., 1988; Stone et al., 1973). However, other authors have questioned this hypothesis because supporting behavioral evidence is frail (e.g., Brysbaert, 1994a, b, 2004; Corballis and Trudel, 1993; Fendrich et al., 1996; Lavidor and Ellis, 2003; Lavidor et al., 2004; Celesia et al., 1993; Chiang et al., 2004; Ellis et al., 2005; Gray et al., 1997; Sugishita et al., 1994; Symonds and Mackenzie, 1957; Tootell et al., 1988). Corballis and Trudel (1993), for instance, failed to find evidence for foveal word recognition in a split-brain patient, although his performance was good for parafoveal word presentation in both LVF and RVF. Fendrich et al. (1996), who also tested split-brain patients, suggested that each hemisphere may have a weak representation of the contralateral hemi-retina, which does not allow fast recognition of small letters. Finally, Lavidor and Walsh (2003) showed that unilateral repetitive transcranial magnetic stimulation (rTMS) significantly impairs lexical decision latencies to centrally presented words. This observation clearly supports the notion that representation of foveally displayed words must be split between the cerebral hemispheres (the so-called split fovea theory) because foveal representation of the non-stimulated hemisphere could otherwise serve recognition (see Shillcock et al., 2000).

The question on the representation of foveally displayed words in the two hemispheres of the brain leads naturally to the study of interhemispheric transfer of information. Based on studies of epileptic patients who have undergone callosotomy, it is established that visual information is transferred from one visual cortex to its contralateral homologue via the splenium of the corpus callosum (e.g., Censori et al., 1989). The time needed for this transfer of information is referred to as interhemispheric transfer time (IHTT). IHTT in humans was first estimated from reaction times in behavioral studies (Brizzolara et al., 1994; Davidson et al., 1990; Poffenberger, 1912; see Bashore, 1981 for a review). In the last two decades, however, event-related potentials (ERPs) have improved the precision of IHTT evaluation based on latency measures of the P1 component, a positive going ERP wave peaking about 100 ms after visual stimulus onset believed to reflect feature extraction in visual areas (Tarkiainen et al., 2002). The P1 is generally slightly delayed and smaller in amplitude over the hemisphere ipsilateral to the visual field in which the stimulus is presented (Bayard et al., 2004). The difference in peak latencies between the P1s recorded over ipsilateral and contralateral regions of the scalp vis-à-vis the stimulated visual field is believed to reflect callosal transfer time (see Saron and Davidson, 1989 for a review). IHTT has been estimated to be about 10–15 ms (Brown et al., 1998; Saron and Davidson, 1989), with a slower left-to-right than right-to-left transfer in right-handed subjects (Ipata et al., 1997; Saron and Davidson, 1989).

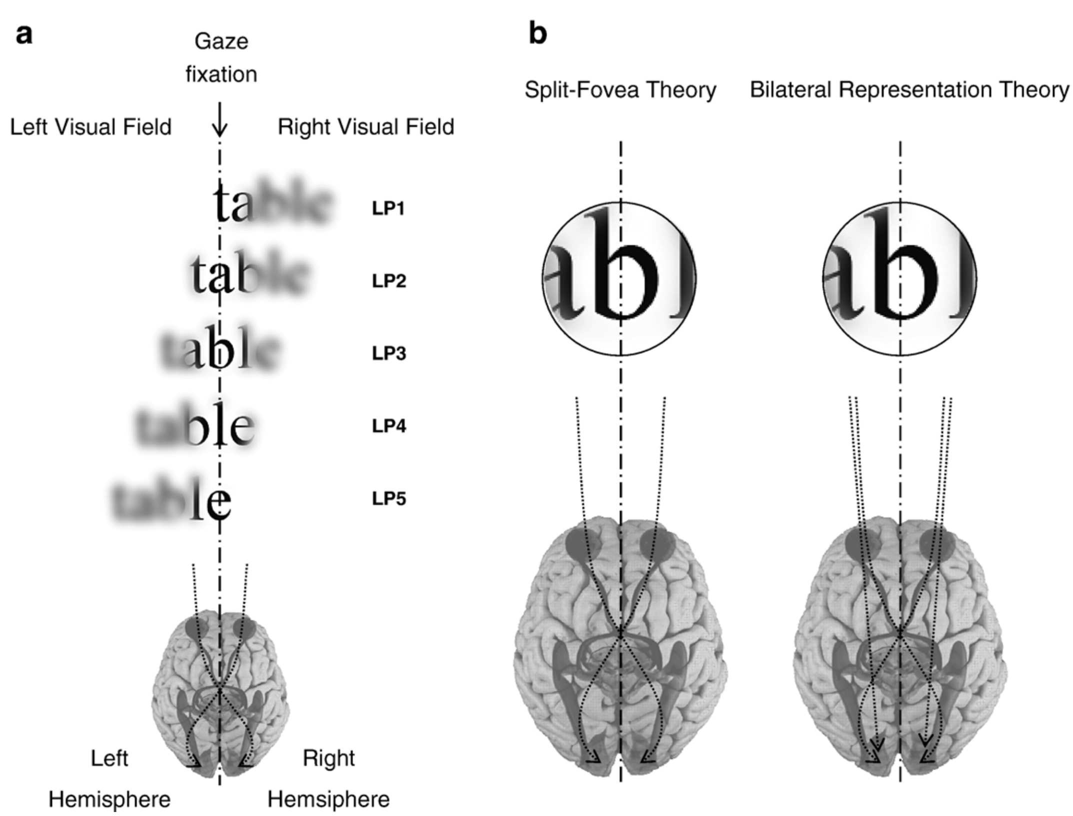

Fig. 1 – Stimulus display and predictions from the two competing theories. (a) Position of the stimulus vis-à-vis fixation in the different experimental conditions. The target letter was always centered at fixation and coincided with the first, second, third, fourth or fifth letter of the letter string (LP = letter position). (b) Predictions from the split fovea theory and the bilateral representation theory regarding the projection of foveally displayed information.