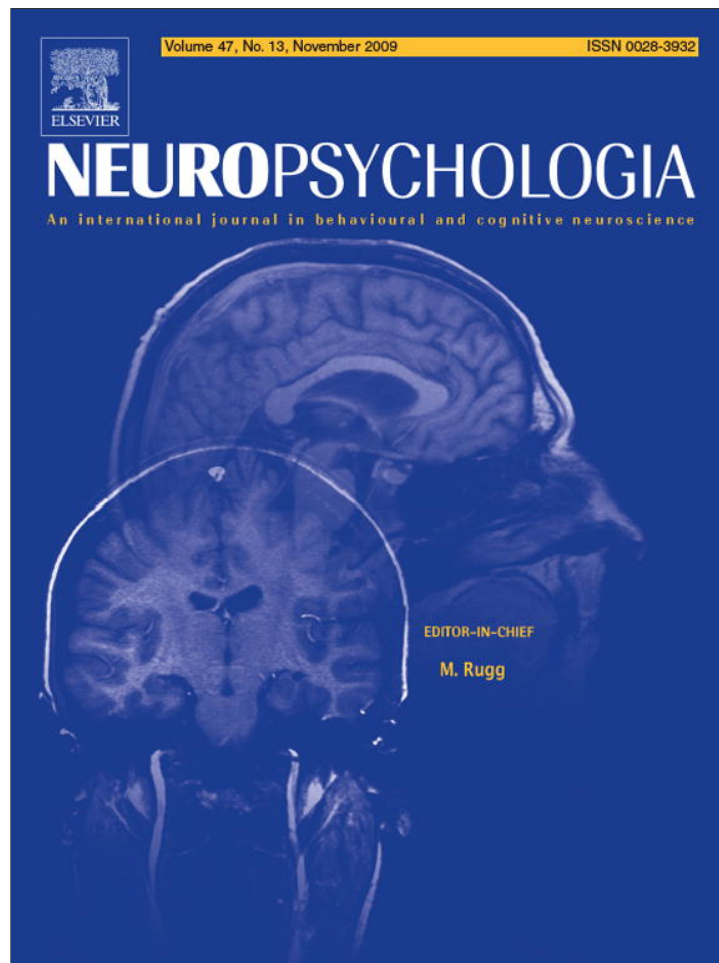


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

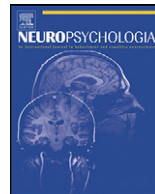
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Note

Evidence of midline retinal nasotemporal overlap in healthy humans: A model for foveal sparing in hemianopia?

C.A. Marzi*, F. Mancini, I. Sperandio, S. Savazzi

Department of Neurological & Visual Sciences, University of Verona and National Institute of Neuroscience, Italy

ARTICLE INFO

Article history:

Received 19 February 2009
 Received in revised form 13 May 2009
 Accepted 14 May 2009
 Available online 22 May 2009

Keywords:

Macular sparing
 Poffenberger paradigm
 Hemiretinal differences

ABSTRACT

The existence of midline retinal nasotemporal overlap in humans is controversial. Here we used the Poffenberger paradigm and monocular vision to assess the existence of a midline retinal area projecting to both hemispheres and of a possible differential contribution of the two hemiretinae. When brief visual stimuli were presented at 1° eccentricity they were responded to equally quickly with either hand while at 6° the hand on the same side as the stimulated hemifield was consistently faster than the contralateral hand. This pattern of results is consistent with a nasotemporal overlap at 1° and a complete lateralization at 6°. Both hemiretinae contribute to the overlap area which can be considered as responsible for foveal sparing in hemianopic patients.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Neuroanatomical studies in non-human primates and other mammals have demonstrated the existence of a strip of central retina that sends its projection to both hemispheres (Stone, Leicester, & Sherman, 1973), the so-called nasotemporal overlap. A similar midline overlap area is difficult to demonstrate histologically in humans and most of the available evidence concerns the phenomenon of macular sparing in hemianopic patients. In some of these patients the boundary between the hemianopic and the normal side of the visual field does not coincide exactly with the vertical meridian and the foveal macula is not split in half, with the portion that should be blind still functioning. This phenomenon, however, is controversial (see Leff, 2004) in that it is not present in all patients and when present shows different degrees of sparing, see Reinhard and Trauzettel-Klosinski (2003). Neuroanatomical studies in non-human primates who underwent a unilateral optic tract section and consequent retrograde degeneration of retinal ganglion cells provided evidence that the strip of overlap between degenerated and spared cells is about 1° wide and is roughly parallel to the vertical meridian (Stone et al., 1973; Stone & Fukuda, 1974) with the extreme upper and lower portions wider (5°) than the central portion (0.6°), see Fukuda, Sawai, Watanabe, Wakakuwa, and Morigiwa (1989). More recently, a similar strip of overlap has been shown by using a scanning laser ophthalmoscope

in 20 patients with homonymous hemianopia without macular sparing (Reinhard & Trauzettel-Klosinski, 2003; see also Trauzettel-Klosinski & Reinhard, 1998). In practically all eyes the seeing area extended from the vertical meridian into the blind hemifield and formed a vertical strip often with a concave spared area within the foveal half of the blind hemifield. It is interesting to point out that none of the patients showed a more extended foveal sparing. These results confirm the monkey anatomical data; however, a somewhat different result has been obtained by Leventhal, Ault, and Vitek (1988), with horseradish peroxidase injection in the monkey lateral geniculate nucleus (LGN). They found a 2–3° region of nasal hemiretina close to the foveal pit containing bilaterally projecting cells. This would account for foveal splitting in the temporal retina and foveal sparing in the nasal retina and a pattern fitting these data has been observed in hemianopic patients with foveal splitting in the eye ipsilateral to the lesion and foveal sparing in the contralateral eye. In contrast, Gray, Galetta, Siegal, and Schatz (1997) using functional magnetic resonance imaging (fMRI) found no evidence of a bilateral representation of the fovea in hemianopic patients and Bischoff, Lang, and Huber (1995) with a scanning laser ophthalmoscope, provided evidence that macular sparing was related to fixation shifts thus representing a perimetric artefact. By the same token, there is evidence from neuromagnetic (Portin, Salenius, Salmelin, & Hari, 1998; Portin, Vanni, Virsu, & Hari, 1999) and fMRI studies (Sereno et al., 1995) of activation restricted to one visual cortex even with stimuli presented very close to the vertical meridian in the contralateral hemifield. These data in humans are in keeping with those obtained previously with functional methods in the monkey by Tootel, Switkes, Silverman, and Hamilton (1988). However, one might argue for all these studies that small stimuli very close to the vertical meridian might indeed activate both

* Corresponding author at: Department of Neurological & Visual Sciences, University of Verona, 8, Strada Le Grazie, 37134 Verona, Italy. Tel.: +39 045 8027143; fax: +39 045 8027279.

E-mail address: carloalberto.marzi@univr.it (C.A. Marzi).

hemispheres but as the nasotemporal overlap is small, only a tiny proportion of axons project to the wrong hemisphere and their contribution might be invisible to fMRI. Also no macular sparing was found by Sugishita, Hemmi, Sakuma, Beppu, and Shiokawa (1993) who tested hemianopsics by means of fundus perimetry combined with fundus image analysis so as to measure the distance from the foveal centre of the stimulus projected on the retina. Their conclusion was that macular sparing, if it exists, must be less than 0.4° wide. A similar conclusion was reached by applying the same procedure to callosum-split patients (Sugishita, Hamilton, Sakuma, & Hemmi, 1994).

Another source of data on nasotemporal overlap comes from behavioural studies in healthy individuals by using paradigms that make it possible to assess interhemispheric transfer (IT) time or hemispheric interactions and asymmetries (see for reviews Marzi, Bisiacchi, & Nicoletti, 1991; Lavidor & Walsh, 2004). Lines and Milner (1983) presented brief light flashes to various points of the visual field along the horizontal meridian and asked participants to press a key as quickly as possible with either the hand ipsilateral or contralateral to the stimulated hemifield following stimulus onset. While the ipsilateral hemifield-hand combinations can be processed within one hemisphere, the contralateral combinations require an IT. This is the rationale of the so-called Poffenberger paradigm originally described by Poffenberger in 1916 (see Marzi, 1999). Typically, crossed responses are slower than uncrossed responses and the crossed–uncrossed difference (CUD = 3–5 ms) is taken as a measure of IT time (see for reviews Marzi et al., 1991; Zaidel & Iacoboni, 2003). Lines and Milner (1983) found a reliable CUD even at 1/2° from the fovea and this argues for a macular splitting with a very small or non-existent nasotemporal overlap. A similar result was obtained by Lines (1984) on a patient with callosal agenesis. Harvey (1978) used a choice reaction time paradigm with visual stimuli at increasing distance from the fixation point and found a large CUD (25 ms) even with stimuli presented at eccentricity of 0.25° and 0.5°. However, the use of a choice reaction time and the huge CUD found raise the possibility of spatial compatibility effects that might have contaminated the assessment of the CUD, hence of the existence of a nasotemporal overlap, a problem that is absent with a simple RT paradigm where spatial compatibility effects do not play a significant role in the CUD (Anzola, Bertoloni, Buchtel, & Rizzolatti, 1977; Berlucchi, Crea, Di Stefano, & Tassinari, 1977). An even more complex behavioural paradigm, also providing no evidence of nasotemporal overlap, has been used by Haun (1978) with vocal RT to letters and a recognition memory task. Furthermore, somewhat discrepant results have been reported by Fendrich and Gazzaniga (1989) who tested split-brain patients in tasks of interhemispheric stimulus comparison. They asked a commissurotomy patient to compare target figures presented 1° or less from the retinal midline with figures presented 2.5° from the midline in the same or opposite visual field. In the latter condition, accuracy was at chance while this was not the case for within field comparisons. This evidence of macular splitting was partly at odds with a subsequent study (Fendrich, Wessinger, & Gazzaniga, 1996) in which another commissurotomy patient was asked to compare gratings of different orientation in the two hemifields. With brief stimulus presentations and eccentricity of 2°, accuracy was at chance while with longer stimulus duration and 1° eccentricity performance was above chance. These results suggest the existence of a narrow zone of nasotemporal overlap at the vertical meridian.

In the light of these discrepant results, in the present study we decided to use a large number of participants to test for the existence of a naso-temporal overlap in healthy humans and in case of a positive answer to find out which of the two hemiretinae was responsible. By using monocular viewing we compared the CUD for visual stimuli presented at 1°, that is in an area of presumed nasotemporal overlap with that for stimuli at 6°, that is, in an

area with a likely minimal or no nasotemporal overlap. It is well established that RT increases from central to peripheral stimulus presentations and therefore in the present study we manipulated the size and intensity of the stimuli to try and equalize overall speed of responses for the two eccentricities of stimulus presentation taking into account the cortical magnification factor (see Anstis, 1996; Cowey & Rolls, 1974).

2. Methods

2.1. Participants

Twenty right-handed (12 females) naive students took part in the experiment. Their age ranged between 19 and 34 years (mean 24.9) and they had normal or corrected-to-normal visual acuity. All gave informed consent and the experiment was carried out in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Apparatus, stimuli and procedure

The participant was seated in front of a computer monitor (Sony Trinitron Multiscan E530) with the eyes at 57 cm from the centre of the screen in a dimly lit room. Stimuli were presented monocularly by occluding one eye with an eye-patch following an alternation order balanced across subjects. Each eye was tested in each subject. Participants were asked to maintain the gaze on the fixation point at the centre of the screen and to respond to the onset of the stimuli as quickly as possible by pressing the space-bar of the computer key-board with the index-finger of either the right or the left hand according to a pre-established sequence. Two kinds of visual stimuli were presented with an exposure duration of 80 ms either to the left or to the right of the fixation point along the horizontal meridian: a 0.5° circle centred at an eccentricity of 1° with a luminance of 8.16 cd/m² and a 3° circle centred at an eccentricity of 6° with a luminance of 1.36 cd/m². The background luminance was 0.001 cd/m². The stimulus size at the two eccentricities was scaled to take into account the cortical magnification factor (see Anstis, 1996; Perry & Cowey, 1985). Stimulus intensity was controlled in order to obtain the same total amount of luminance as a function of the stimulus area. The combinations of responding hand and side of stimulation were counterbalanced across subjects: For alternating hands, half of the participants followed an ABBA sequence while the other half followed a BAAB sequence while side of stimulation followed a randomized order. An acoustic warning stimulus (200 ms duration) prompted the participants to maintain fixation steady. The interval between the acoustic warning stimulus and visual stimulus onset was randomized within the temporal window of 400–700 ms. Catch trials (48) in which after the warning signal the target stimuli were not presented were introduced to discourage the participants from responding to the tone rather than to the target stimulus. There were 60 trials (30 for each eye in every participant) for each of the four visual field/hand combinations, with an overall number of 240 presentations for each participant. The range of accepted RTs was 140–650 ms. Rejected trials were a minuscule minority. They were not entered into the analyses; in addition, a few outliers were detected by means of the Grubbs' test, extreme studentized deviate method (Grubbs, 1969) and discarded. Also, the proportion of omission errors was negligible. Eye movements were controlled by means of an infrared camera placed in front of the participants all of whom were able to keep a very stable fixation. Participants were adapted to the room ambient light for a few minutes prior to testing.

3. Results

RTs in the various crossing conditions are shown in Fig. 1.

A preliminary ANOVA showed no reliable differences of eye, hand and visual hemifield. The crucial analysis for the present purposes was carried out with a three-ways ANOVA with hemiretina (Nasal, Temporal), crossing condition (uncrossed, crossed), eccentricity (1°, 6°) as main factors. The factor hemiretina did not reach significance [$F(1,19)=3.512, p=0.076$]; however, there was a tendency for faster RT in the nasal hemiretina (305.8 ms) with respect to the temporal hemiretina (307.7 ms). Also eccentricity did not reach significance [$F(1,19)=4.230, p=0.054$] but there was a trend toward a RT advantage for 6° (304.8 ms) with respect to 1° eccentricity (308.7 ms).

Importantly, the only significant main factor was crossing condition [$F(1,19)=18.131, p<0.001$] with the uncrossed condition (304.7 ms) yielding faster RT than the crossed condition (308.7 ms). Notably, the CUD of 4.0 ms is perfectly within the range (3–5 ms) of the normal CUD documented by numerous studies (see Marzi

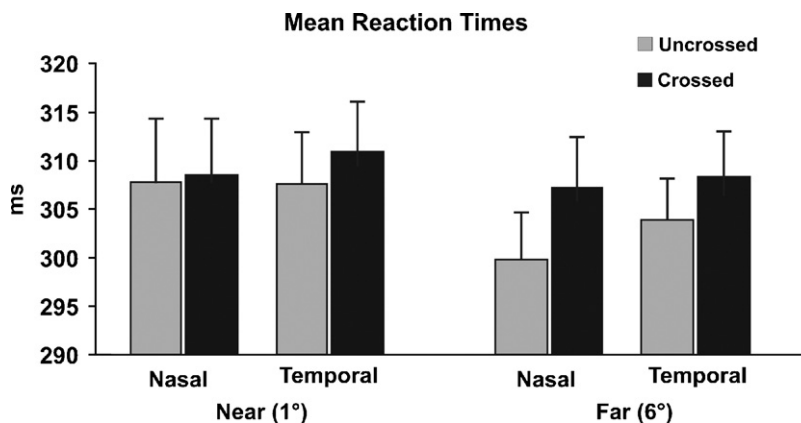


Fig. 1. Mean (with standard error) reaction time as a function of crossing condition, hemiretina and eccentricity of stimulus presentation.

et al., 1991, for a meta-analysis). The lack of reliable hemiretinal differences is not surprising with stimuli presented relatively close to the fovea as in the present study. It has been shown that the nasal hemiretina advantage in RT is small or non-existent close to the fovea and increases progressively with eccentricity along the horizontal meridian (Chelazzi et al., 1988). This is in keeping with the observed (non-significant) trend favouring the nasal hemiretina found in the present experiment. Finally, the lack of a reliable effect of eccentricity is related to our adjustment of stimulus size and brightness to equate visibility at the two different positions. In fact, our adjustment procedure yielded a paradoxical non-significant advantage for the more peripheral eccentricity.

As to first-order interactions, hemiretina by crossing condition [$F(1,19) = 0.004$, $p = 0.952$] was far from significance and the same was true for hemiretina by eccentricity [$F(1,19) = 0.395$, $p = 0.537$].

Only crossing condition by eccentricity was significant [$F(1,19) = 5.285$, $p < 0.05$]. Post hoc T -tests with Bonferroni correction showed that the only significant comparison [$T(19) = 4.244$, $p < 0.001$] was between uncrossed (301.8 ms) and crossed conditions (307.7 ms) at 6°. This interaction is important because it shows that there is no stimulus lateralization at 1°, and this is compatible with a midline nasotemporal overlap, while there is a lateralization effect at 6° showing that at this distance from the fovea there is no longer an overlap zone.

Furthermore, the second-order interaction hemiretina by crossing condition by eccentricity was also significant [$F(1,19) = 4.553$, $p < 0.05$]. Bonferroni corrected T -tests showed that the difference between uncrossed (299.7 ms) and crossed (307.2 ms) conditions was significant [$T(19) = 2.924$, $p < 0.01$] only for the nasal hemiretina at 6°. Fig. 2 shows the CUD scores as a function of hemiretina and eccentricity. By inspection of the figure one can notice a clear tendency for the CUD to increase from 1° to 6° in the nasal hemiretina while this is not the case for the temporal hemiretina.

4. Discussion

The aim of the present study was to assess with a simple behavioural technique the presence of a retinal midline nasotemporal overlap in healthy individuals. To do that we tested participants monocularly with the Poffenberger paradigm with stimuli presented to the nasal or temporal hemiretina either within the presumed overlap area or well beyond it. Thus, at variance with previous studies, our paradigm enabled us to determine not only the possible existence of an overlap zone but also to assess whether there was an asymmetrical contribution of the two hemiretinae. Another novel feature of our experiment was that the stimuli presented at the two eccentricities were matched in size according to

the cortical magnification factor and were also matched in overall luminance. As a consequence, RT rather than being faster at more central eccentricities did not show reliable differences between central and more peripheral stimulus presentations with a slight non-significant advantage for 6° over 1° (see Fig. 1). The important result was that for 1° presentations there was no reliable CUD while at 6° the CUD was statistically reliable. The extent of midline violation of the crossing rule was about the same for the two hemiretinae with a tendency for a smaller CUD, hence for a wider overlap, for the nasal hemiretina and this would be in accordance with neuroanatomical data in monkeys and in hemianopic human patients showing an asymmetry of the overlap zone presumably restricted to 1° in the nasal retina side. As to the more general controversy on the existence of an overlap zone, our results are in broad agreement with those of Fendrich and Gazzaniga (1989) and Fendrich et al. (1996) who found a small area of overlap within the first 1–2° from the foveal midline. In contrast, they are at odds with previous behavioural studies on healthy humans which did not find an overlap area at the midline. Among those studies the only employing a simple RT task was Lines and Milner's (1983) who used a Poffenberger paradigm with stimuli presented at various eccentricities along the horizontal meridian and found a CUD even at the smallest eccentricity. However, in that study participants were tested binocularly and therefore it could not be assessed whether the CUD was similar for the two hemiretinae. Harvey (1978) used a choice RT and, as mentioned in the Introduction, did not control for spatial compatibility a condition which plays a prominent role in choice, as opposed to simple RT. This might have contributed to

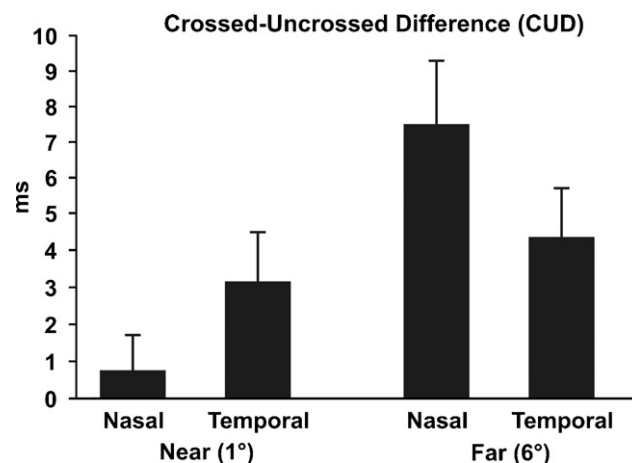


Fig. 2. Mean (with standard error) crossed-uncrossed difference (CUD) in reaction time as a function of hemiretina and eccentricity of stimulus presentation.

obscure an overlap zone. Haun (1978) studied hemispheric asymmetries with stimuli presented very close to the fixation point and found a hemifield difference in vocal RT for letters with a right field advantage for extreme right handers and a left field superiority for extreme left handers. This is a complex task with a possible contribution of letter scanning patterns and the hemifield asymmetries found have not been replicated (Tassinari, Morelli, & Berlucchi, 1983). On the whole, therefore, the above studies cannot be compared with the present experiment which employed a simple RT paradigm.

In sum, our study provides evidence of a retinal nasotemporal overlap in the human visual system and this is in keeping with a wealth of anatomical and neurological data. This conclusion is at odds with a recent review by Lavidor and Walsh (2004) reporting a series of laterality neuropsychological studies mainly employing alphabetical material or face stimuli whose results can be better explained by the split fovea rather than by the bilateral projection theory of retinal decussation. One should consider, however, that more recent studies by Jordan and colleagues (Jordan, Paterson, & Stachurski, 2009; Jordan et al., in press) could not confirm Lavidor and Walsh (2004) reported evidence of a split fovea. We believe that the problem of the existence of a retinal nasotemporal overlap may be more parsimoniously dealt with by means of a simple task the performance in which can be more directly related to the anatomical and ophthalmological evidence. Our study relies on a simple paradigm consisting in the speeded response to light onset which presumably mainly taps the activity of visual areas outside the primary visual cortex or even of subcortical areas such as the superior colliculus (SC). Thus, in principle, while neuropsychological tasks tapping cortical cognitive functions might reveal a split fovea, simple visual responses mainly subserved by subcortical centres might show a nasotemporal overlap. Brain imaging studies have provided evidence of a complete lateralization of visually induced activation in the visual cortex. By the same token, functional mapping of the SC recently carried out by Schneider and Kastner (2005) found that stimulation of one hemifield produced strictly contralateral activation. However, one should consider that the visual stimuli used (rotating rings) are not particularly suitable for revealing a naso-temporal overlap. It would be interesting to study fMRI activation in the SC with lateralized single stimuli similar to those employed in the behavioural paradigms.

What could be the possible function of nasotemporal overlap and the small reaction time difference? One possibility is that there are conditions of stereoscopic vision where convergent disparity produces images on the temporal side of each fovea which are initially restricted to separate hemispheres. In this case nasotemporal overlap makes it possible to send projections to the same hemisphere and this could be important with respect to the timing of inputs to cortical disparity detectors. The same argument applies to small divergent disparity near the fovea, except that it is now the two nasal hemiretinae that are involved.

From a more general view point we think that the existence of a functional dissociation between the pattern of lateralization of ganglion cells projecting to the geniculostriate versus colliculus–extrastriate system in humans is a reasonable possibility that awaits further research. The presence of a bilateral projection from the fovea might be useful for ensuring a rapid bihemispheric response to unstructured visual stimulation mainly subserved by the colliculus–extrastriate system. In contrast, cognitively more demanding stimuli might profit from a sharp unihemispheric activation (see Lavidor & Walsh, 2004, but see Jordan et al., 2009, in press) as that typical of the geniculostriate system. In this respect part of the contrasting results about the presence of foveal sparing or splitting in patients with hemianopia may depend on the task used for testing the residual visual functions.

Acknowledgment

Part of this research has been made possible by a grant from CARIVERONA, Verona, Italy.

References

- Anstis, S. (1996). Adaptation to peripheral flicker. *Vision Research*, 36, 3479–3485.
- Anzola, G. P., Bertoloni, G., Buchtel, H. A., & Rizzolatti, G. (1977). Spatial compatibility and anatomical factors in simple and choice reaction time. *Neuropsychologia*, 15, 295–302.
- Berlucchi, G., Crea, F., Di Stefano, M., & Tassinari, G. (1977). Influence of spatial stimulus-response compatibility on reaction time of ipsilateral and contralateral hand to lateralized light stimuli. *Journal of Experimental Psychology: Human Perception & Performance*, 3, 505–517.
- Bischoff, P., Lang, J., & Huber, A. (1995). Macular sparing as a perimetric artifact. *American Journal of Ophthalmology*, 119, 72–80.
- Chelazzi, L., Marzi, C. A., Panozzo, G., Pasqualini, N., Tassinari, G., & Tomazzoli, L. (1988). Hemiretinal differences in speed of light detection in esotropic amblyopes. *Vision Research*, 28, 95–104.
- Cowey, A., & Rolls, E. T. (1974). Human cortical magnification factor and its relation with visual acuity. *Experimental Brain Research*, 21, 447–454.
- Fendrich, R., & Gazzaniga, M. S. (1989). Evidence of foveal splitting in a commissurotomy patient. *Neuropsychologia*, 27, 273–281.
- Fendrich, R., Wessinger, C. M., & Gazzaniga, M. S. (1996). Nasotemporal overlap at the retinal vertical meridian: Investigations with a callosotomy patient. *Neuropsychologia*, 34, 637–646.
- Fukuda, Y., Sawai, H., Watanabe, M., Wakakuwa, K., & Morigiwa, K. (1989). Nasotemporal overlap of crossed an uncrossed retinal ganglion cell projections in the Japanese monkey (*Macaca fuscata*). *Journal of Neuroscience*, 9, 2353–2373.
- Gray, L. G., Galetta, S. L., Siegal, T., & Schatz, N. J. (1997). The central visual field in homonymous hemianopia. Evidence for unilateral foveal representation. *Archives of Neurology*, 54, 312–317.
- Grubbs, F. (1969). Procedures for detecting outlying observations in samples. *Technometrics*, 11, 1–21.
- Harvey, L. O., Jr. (1978). Single representation of the visual midline in humans. *Neuropsychologia*, 16, 601–610.
- Haun, F. (1978). Functional dissociation of the hemispheres using foveal visual input. *Neuropsychologia*, 16, 725–733.
- Jordan, T. R., Paterson, K. B., Kurtev, S., & Mengyun, X. (in press). Re-evaluating split-fovea processing in word recognition: Effects of word length during monocular viewing. *Cortex*.
- Jordan, T. M., Paterson, K. B., & Stachurski, M. (2009). Re-evaluating split-fovea processing in word recognition: Effects of word length. *Cortex*, 45, 495–505.
- Lavidor, M., & Walsh, V. (2004). The nature of foveal representation. *Nature Reviews Neuroscience*, 5, 729–735.
- Leff, A. (2004). A historical review of the representation of the visual field in primary visual cortex with special reference to the neural mechanisms underlying macular sparing. *Brain and Language*, 88, 268–278.
- Leventhal, A. G., Ault, S. J., & Vitek, D. J. (1988). The nasotemporal division in primate retina: The neural bases of macular sparing and splitting. *Science*, 240, 66–67.
- Lines, C. R. (1984). Nasotemporal overlap investigated in a case of agenesis of the corpus callosum. *Neuropsychologia*, 22, 85–90.
- Lines, C. R., & Milner, A. D. (1983). Nasotemporal overlap in the human retina investigated by means of simple reaction time to lateralized light flash. *Experimental Brain Research*, 50, 166–172.
- Marzi, C. A. (1999). The Poffenberger paradigm: A first, simple, behavioural tool to study interhemispheric transmission in humans. *Brain Research Bulletin*, 50, 421–422.
- Marzi, C. A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*, 29, 1163–1177.
- Perry, V. H., & Cowey, A. (1985). The ganglion cell and cone distributions in the monkey's retina: Implications for central magnification factors. *Vision Research*, 25, 795–810.
- Portin, K., Salenius, S., Salmelin, R., & Hari, R. (1998). Activation of the human occipital and parietal cortex by pattern and luminance stimuli: Neuromagnetic measurements. *Cerebral Cortex*, 8, 253–260.
- Portin, K., Vanni, S., Virsu, V., & Hari, R. (1999). Stronger occipital cortical activation to lower than upper visual field stimuli. Neuromagnetic recordings. *Experimental Brain Research*, 124, 287–294.
- Reinhard, J., & Trauzettel-Klosinski, S. (2003). Nasotemporal overlap of retinal ganglion cells in humans: A functional study. *Investigative Ophthalmology and Visual Science*, 44, 1568–1572.
- Schneider, K. A., & Kastner, S. (2005). Visual responses of the human superior colliculus: A high-resolution functional magnetic resonance imaging study. *Journal of Neurophysiology*, 94, 2491–2503.
- Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., et al. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, 268, 889–893.
- Stone, J., & Fukuda, Y. (1974). The naso-temporal division of the cat's retina re-examined in terms of Y-, X- and W-cells. *Journal of Comparative Neurology*, 155, 377–394.

- Stone, J., Leicester, J., & Sherman, S. M. (1973). The naso-temporal division of the monkey's retina. *Journal of Comparative Neurology*, *150*, 333–348.
- Sugishita, M., Hamilton, C. R., Sakuma, I., & Hemmi, I. (1994). Hemispheric representation of the central retina of commissurotomy subjects. *Neuropsychologia*, *32*, 399–415.
- Sugishita, M., Hemmi, I., Sakuma, I., Beppu, H., & Shiokawa, Y. (1993). The problem of macular sparing after unilateral occipital lesions. *Journal of Neurology*, *241*, 1–9.
- Tassinari, G., Morelli, M., & Berlucchi, G. (1983). Interhemispheric transmission of information in manual and verbal reaction-time tasks. *Human Neurobiology*, *2*, 77–85.
- Tootell, R. B. H., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. *Journal of Neuroscience*, *8*, 1531–1568.
- Traubitzel-Klosinski, S., & Reinhard, J. (1998). The vertical field border in hemianopia and its significance for fixation and reading. *Investigative Ophthalmology and Visual Science*, *39*, 2177–2186.
- Zaidel, E., & Iacoboni, M. (2003). Introduction: Poffenberger's simple reaction time paradigm for measuring interhemispheric transfer time. In E. Zaidel, & M. Iacoboni (Eds.), *The parallel brain. The cognitive neuroscience of the corpus callosum* (pp. 1–7). Cambridge, MA: MIT Press.