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### **Electronic Letters to:**

Visual Neurophysiology:

Givago S. Souza, Bruno D. Gomes, Cézar A. Saito, Manoel da Silva Filho, and Luiz Carlos L. Silveira

Spatial Luminance Contrast Sensitivity Measured with Transient VEP: Comparison with Psychophysics and Evidence of Multiple Mechanisms Invest. Ophthalmol. Vis. Sci. 2007; 48: 3396-3404 [Abstract] [Full text] [PDF]

# Electronic letters published:

Multiple Mechanisms in the VEP Hans Strasburger, Ian J. Murray (23 July 2009)

Author Response: Multiple Mechanisms in the VEP Luiz Silveira (23 July 2009)

## Multiple Mechanisms in the VEP

Hans Strasburger, Professor University of München, U. Göttingen, Ian J. Murray

Send letter to journal: <u>Re: Multiple</u> <u>Mechanisms in the</u> <u>VEP</u>

Email Hans Strasburger, et al. We decidedly agree with the conclusion of Souza et al.<sup>1</sup> about the operation of two separate mechanisms in the VEP. We came in fact to a very similar conclusion in a paper in 1993 in *Clinical Vision Sciences*<sup>2</sup> (available from our Web <u>site</u>). We there ascribed the non-linear, dichotomous characteristics of the VEP to putative sustained and transient mechanisms. The most likely underlying neural substrate for these mechanisms are the parvo (sustained) and magno (transient) streams as Souza et al. indicate. Of course currently, it is thought that the magno pathway is composed of some neurons with transient and others with more sustained characteristics. Magno neurons have high contrast gain and this is seen in the VEP data.

In our paper<sup>2</sup> the evidence is from a factor analysis of the variance in the VEP amplitude versus spatial-frequency data. Two thirds of the total variance was explained by just two orthogonal factors, one specialized for low (up to 3 cpd) and the other for high spatial frequencies. The two mechanisms were shown to have different phase characteristics, so their signals partially cancel at intermediate spatial frequencies, giving rise to a "notch" in the amplitude data.

The nonlinearity in the contrast response that Souza et al. found – which implies a non-linear system behavior – has also been described earlier by Bain and Kulikowski<sup>3</sup> and Murray and Kulikowski.<sup>4</sup> They also considered the high-contrast limb to reflect the transient (M), and low-contrast limb the sustained (P) mechanism and proposed separate linear regression functions. At that time of course the physiological parvo/mango had not been established. Souza's data reinforce the original ideas and at the same time provide a more contemporary interpretation of how VEPs vary with luminance contrast.

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23 July 2009



Hans Strasburger<sup>1</sup> and Ian Murray<sup>2</sup>

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2. Strasburger H, Murray IJ, Remky A. Sustained and transient mechanisms in the steady-state visual evoked potential. Onset presentation compared to pattern reversal. *Clin Vision Sci.* 1993;8:211-234.

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### Author Response: Multiple Mechanisms in the VEP 23 July 2009

Luiz Silveira

We decidedly agree with Strasburger and Murray's comments about the Send letter to presence of two separate mechanisms in the human visual evoked journal: potential (VEP). A considerable amount of information has been collected Re: Author Response: Multiple in the last fifty years about the morphology and physiology of the Mechanisms in the neurons located along the M and P pathways.<sup>1</sup> This includes some key VEP aspects of the M and P cell physiology: M cell responses are Email Luiz Silveira predominantly phasic (transient) while P cell responses are predominantly tonic (sustained)<sup>2</sup>; M cells are very sensitive to low-contrast achromatic stimuli while P cells only respond to high contrast achromatic stimuli but are very sensitive to red-green stimulation  $^{3-5}$ ; M cell activity seems to be the physiological substrate of many psychophysical phenomena underlying achromatic vision such as the heterochromatic flicker photometry.<sup>6</sup> Our results obtained by stimulating human observers with phasereversal, black-and-white sinusoidal gratings, and by recording transient visual evoked potentials (VEPs) from the scalp are suggestive that for spatial frequencies between 2 and 10 cycles / degree there are at least two visual pathways involved in achromatic contrast processing. At low stimulus contrasts, a very contrast sensitivity mechanism such as the M (magnocellular) pathway, and at high stimulus contrasts one or more mechanisms with low contrast sensitivity such as the P (parvocellular) pathway dominate the transient VEP (Fig. 1).<sup>7</sup> At lower spatial frequencies, 0.4-0.8 cycles / degree, the mechanism very sensitive to contrast predominates at low contrasts and then saturates at high contrasts.<sup>7</sup> Our results are in the same line of evidence as the previous work of Bain and Kulikowsky,<sup>8</sup> Nakayama and Mackeben,<sup>9</sup> Parker et al.,<sup>10</sup> Murray and Kulikowski,<sup>11</sup> and the results published in Strasburger et al.<sup>12</sup> These authors made use of a range of spatial frequencies and contrasts, as well

as temporal frequencies that elicited either transient or steady-state

VEPs. The work of Strasburger and colleagues differ from the previous work and from the work that we have published two years ago in several ways. Strasburger and colleagues were particularly interested in a region of reduced VEP amplitude observed at intermediate spatial frequencies, and they used phase-reversal and onset / offset steady state VEPs combined with principal component analysis of the VEP amplitude to map this notch in the mean amplitude versus spatial frequency function. Strasburger and colleagues and the authors of those previous works interpreted the VEP double-slope function that showed up in a range of stimulus configuration as due to evoked activity of a pattern (low contrast, high spatial frequency) or a movement (high contrast, low spatial frequency) detection mechanism. In the seventies and early eighties, visual science literature was strongly dominated by extensive research performed in the domestic cat, a nocturnal, red-green color blind mammal. Cat vision heavily depends of the alpha and beta visual pathways, both of them very sensitive to chromatic contrast. In fact, cat beta cells have a contrast sensitivity that in absolute terms is similar to the contrast sensitivity of primate M cells, while cat alpha cells are much more sensitive to contrast.<sup>13</sup> Thus, for many years and in many ways

human psychophysics had to rely upon a vast amount of information collected about the cat visual streams of information. Presently, as pointed out in Strasburger and Murray's letter, we are in a privileged situation, contemplating the realm of human visual psychophysics from the solid point of view derived from extensive work on primate M and P pathways performed in the last two decades.

More recently, we extended our observations comparing the contrast sensitivity of different components of transient pattern-reversal and transient onset/offset VEPs (Souza GS, et al. *IOVS* 2008;49:ARVO E-Abstract 3313), the contrast sensitivity of transient versus steady state VEPs<sup>14</sup> as well as VEPs elicited by chromatic gratings presented in a variety of ways (Barboni MT, et al. *IOVS* 2008;49:ARVO E-Abstract 3315).<sup>14-16</sup> Our results are consistent with the presence of at least two VEP components, exhibiting features associated with the activity of the M and P pathways.

Parallel processing such what occurs in vision seems to be the rule in sensory and motor systems and across species. Primate vision combine the information provided by the M and P pathways (as well as by other pathways that have collectively been labeled as K or koniocellular pathways) to solve the requirements for perception, motor planning, and motor control including refined information about target location, time of occurrence of an event, and spatial and temporal frequency

discrimination in different degrees for each task.<sup>17</sup> Each subcortical pathway conveys to the visual cortex information with different degrees of precision in each dimension, and there the information is combined and sent to the different cortical streams as requested to build visual representations for perception and action, each representation being the

optimum trade-off in the information space for each task.<sup>17,18</sup>

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**Figure 1.** Transient VEP P100 amplitude as a function of contrast. Circles and bars represent means and standard deviations from six subjects. At low spatial frequencies (0.4 cycles / degree, top panel), VEP amplitude initially raises from very low contrast levels and then saturates in high contrasts. At intermediate spatial frequencies (2 cycles / degree, middle panel), a double-slope function can be used to describe the amplitude response across contrast (filled and empty circles; note the small notch at intermediate contrasts). At high spatial frequency, notwithstanding the presence of the two mechanisms, VEP amplitude versus contrast gradually becomes dominated by the mechanism with low contrast sensitivity. Data points were plotted against linear contrast instead of log contrast as in Souza et al. Figure 5<sup>7</sup> to reveal additional subtleties of the VEP amplitude versus contrast behavior.

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