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CONTRAST GAIN OF MAGNO-CELLS REVEALED IN NEW METHOD OF MEASURING CONTRAST SENSITIVITY AND REACTION TIME

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Abstract

Measuring the speed of responses to low contrast stimuli may provide better insights into functional capabilities, anatomical and physiological dichotomy of the retino- cortical pathways.Two new computer tests are developed to measure response times as the contrast of the stimulus is varied. Firstly, large numbers (1-8) 4-cm high appears on the screen in sequentially reducing contrast. The subject quickly touches the numbers in order and time is recorded. Secondly, a large (4-cm) solid square appears in one of four quadrants on the display screen. As soon as the subject touches a square, it disappears and a new square appears. There are 6 sweeps of the contrast range that can give two presentations at up to 24 contrast levels. The test provides measures of threshold CS and responds times as a function of contrast. In 8 normal subjects, we performed the number-search test and the detection test for both blinking and jumping squares. The result shows that the reaction time increases with increasing contrast sensitivity. Our graph is biphasic in nature, revealing the activity of two mechanisms with different reaction times: transient/sustained, magno/parvo. The first phase with asymptote reaction time revealed activity of parvocells (sustained cells) which dominates at low contrast sensitivity and the steep second phase, revealed contrast gain and the activity of magnocells (transient) at supra threshold contrast. This simple test may be similar to the pedestal paradigm.

Keywords: Contrast sensitivity, contrast gain, transient/sustained, Magno/parvocells

INTRODUCTION

The biphasic nature of the contrast sensitivity versus reaction time function, was first suggested in [1}, who interpreted this as revealing the activity of transient mechanism at high contrast and sustained mechanism at low contrast. This biphasic function was later re-interpreted in terms of P and M pathways[2]. Analysis of our results of a new computer- based contrast sensitivity and reaction time test, also revealed a biphasic function which we used to asses the functions of parvo and magno cells and to demonstrate the contrast gain control in magno cells and its absence in parvo cells.

Two distinct channels, different in their temporal and spatial frequencies had been suggested on the ground of psychophysical experiment in the human visual system: one that gives transient responses to the onset and offset of flashed stimuli operating at low and moderate spatial frequencies and two, channels that give sustained responses for the whole duration of the stimulus operating at moderate and high spatial frequencies[3-14].This characteristic has electrophysiological parallels differentiating transient from sustained cells as shown by transient channels having a shorter response latency to photic and electric stimulation of the optic nerve [15,16], and that their fibers have a higher conduction speed, than do sustained channels [17-19].

These latency differences as measured by simple reaction time may reflect either a shorter latency and faster conduction speed or a shorter conduction route or both found in transient channels as opposed to sustained ones[10]. Transient channels are known to project from retina directly to superior colliculus and indirectly via the lateral geniculate nucleus to the visual cortex[17]. Thus a faster mean reaction time to low spatial frequency gratings possibly reflects, either a shorter and more direct transient channel conduction route from the retina to the superior colliculus, a faster transient channel to the visual cortex and /or superior colliculus or both of these factors.

Harwerth and Levi[1][1] and later Felipe et al [20] showed that the decrease in reaction time as contrast increases is characterised by a discontinuity at a contrast level around 0.1, which they considered to be the result of sustained and transient channels operating at different contrast ranges. Convincing evidence exist that there is a discontinuity in RT-contrast functions and that the different branches reflect transient- and sustained-like activity [21].

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RTs are likely, influenced by the anatomical and physiological characteristics of the retino-cortical pathway. Two main classes of retinal ganglion cells project to the lateral geniculate nucleus (LGN) in higher primates. These cell types are named after the laminae of the LGN to which they project; M cells project to the Magnocellular laminae and P cells to the Parvocellular laminae [22,23]. These pathways remain segregated as far as the input layers of striate cortex, where there said to be a considerable overlap between them[24,25].

M and P neurons in neurophysiological experiments have been differentiated according to their processing of luminance contrast, M neurons have high luminance contrast sensitivity and exhibit high contrast gain (i.e. they respond vigorously to small changes in contrast), while P neurons have low contrast gain but show a high degree of temporal and spatial linearity [26-34].

It was finally shown that the different regions of the reaction times vs. contrast function represent the activities of mechanisms having different contrast gain[2,35].

Contrast gain

Contrast gain has been described as the rapidity of response amplitude increase with increase in stimulus contrast or the increase in response per unit change in contrast, and it is measured directly as the initial slope of cell contrast-response function in neurophysiology and can be used to differentiate the MC and PC cells [26,30](its unit is logCS/msec).

High degree of temporal linearity has been observed in Parvo cells [37] this is due to their lack of contrast gain control mechanism [34,38]. Features of contrast gain control include rapid response saturation as a function of contrast accompanied by an advance of response phase. Magno cells show contrast gain control mechanism [38]. In [1] the flat part of the biphasic curve was said to correspond to faster RTs and the operation of transient mechanism. This was re-interpreted by [2,22,35]as been mediated by the P pathway.

AIM OF THIS STUDY

This study determines contrast thresholds and provide measures of speed of response to low contrast supra-threshold stimuli. The result was used for a possible psychophysical explanation of the dichotomy in the retino-cortical pathway (i.e. sustained/transient, parvo/magno, contrast gain/response gain.

METHODOLOGY

Subjects

Four normal subjects (GAB, RED, RTW and DT) participated in this study. They were all staff of school of Optometry University of California,(UC) Berkeley, except GAB who was a visiting scholar. They all signed the informed consent form. The UC Berkeley Committee for the Protection of Human Subjects approved the experimental protocol. The experiment was done after the patient have completed routine eye examination. Subsequently, (twelve years later) six normal subjects took part in a similar study at the Department of Optometry, University of Benin, Benin City.

Material

Equipment and procedures of this study have been described in details in a previous paper [39]. All visual tasks were performed while the subject views a touch screen monitor (which has a timing advantage) with 40cm diagonal screen. Calibration of luminance and signal strength was done using a spectra spot meter. Contrast was first expressed as the Michaelson ratio and was later converted to Weber ratio for easy comparison of result with Pelli – Robson Pelli-Robson contrast sensitivity chart.

The stimuli were generated by a computer program Proto Genie (Pasadena) Inc using Java (Sun Microsystems). The background luminance was set at 88.5cd/m^2, which corresponds to a signal value of 200 (Red=200, Green=200 and Blue=200) while the foreground color was chosen to create specific contrast for the different tasks.

There are three different tasks performed at a specific sequence for each observer, firstly is one number test (search test) and secondly, two objects detection test (blinking and jumping in selectable modes).

The search test is made up of six screens, each with a number sequence (1-8) as object. The contrast reducing progressively from 1 (0 log unit) to 8 (2.1 log unit), in 0.3log unit steps for the first screen. 1 (.1 log unit) to 8 (2.2 log unit) for the second screen and 1(.2 log unit) to 8 (2.3 log unit) for the third screen. These three screens are repeated twice. The numbers are in randomly assigned positions and the exposure time is limited to 20 secs, with maximum trial time of 2.04min for the number test.

The object detection test has selectable modes of either blinking or jumping. The object is a large square of 30mm, which subtends an angle of 3.5^0 at 50cm. There are two runs (blinking and jumping). Each has 3 trials of 8 screens, with the contrast of the object decreasing in 0.3 log unit steps from 0 log unit to 2.1 log unit sequence in the first trial, 0.1 to 2.2 in the second and 0.2 to 2.3 log unit sequence in the third trial. Exposure time for each screen was 6 secsand a pause of 0.5 secs.

PROCEDURE

Prior to performing this test the subject's biodata were collected. These included, age, visual acuity values, Bailey Border CS test and occasionally, Pelli-Robson CS test values. The subject's task wasto locate the position of the object on the monitor screen by touching the screen (which is sensible to touch). For each touch, the computer automatically recorded the response time, contrast difference, gun strength values of the red, blue, and yellow guns, print size, the screen number, and whether the location was an accurate hit or miss. Each subject performed a total of six search tasks (i.e. six number screens), six blinking sequences and six jumping sequences.

RESULTS

The average reaction time versus contrast graph for 4 normal subjects (GAB, DT, RED and RTW) are represented in Figure 1 and the average V.A, CSB and age are 20/20, 1.9, 42.25yrs. (These basic and demographic values should come before the test result values). The number test is represented by the black dot and line, the Blink test by the blue triangle while the Jump test is represented by the red square. It is a typical sample of what the graph pattern is like in this study. Reaction time data were plotted against log contrast sensitivity in all the cases at a fixed spatial frequency of 3.5cycles/degree. It is evident that the reaction time increases with increase contrast sensitivity. Threshold logCS was on the average 2.3 (Michaelson contrast) at a response time of 4msec.The graph typically shows two phases. The first phase is flat and the second phase is an upward swing which starts on the average at about logCS of 1.6 and is more pronounced at logCS 1.8. The first phase represents steady speed or the asymptote period and the last phase represents a slow down at reduced contrast or change in speed or the period of contrast gain. Another characteristics of the entire graph are, that the black graph (number) has a lot of noise and is generally faster (about 0.5secs) than the blink and jump result. Also, on the average the threshold contrast is higher for the blink and jump result when compared to the number. Each point is the average of two readings. The graph agrees with the biphasic nature of the reaction time versus contrast sensitivity curve as described by [1], but like [2], we also disagree with which part of the graph represents transient or sustained channels.

The result also agrees with previous findings that is, reaction time increases with increasing contrast sensitivity and levels off at the middle phase which represents the asymptote (RT_0) of the equation given by previous author [35].

$$RT = RT_0 + k \log CS \quad (1)$$

Where RT is reaction time, RT_0 is the asymptote (absolute) RT, k is the steepness of the curve (representing the contrast gain) and CS is contrast sensitivity.

Our result also obeys one example of cognitive science several psychophysical laws which is Piéron's Law, it states that mean response times (MRT) decrease as a power law with increasing stimulus intensity [40]

$$MRT = \alpha I^{-\beta} + \gamma \quad (2)$$

α and β are scaling parameters that determine the slope of the function and γ is an intercept [41]. Originally, Piéron's Law was formulated as an effect of stimulus intensity [42]. However over the last century, the law has been reported in many different domains, including brightness detection[42], taste detection of dissolved substances [43], odor detection [44], and the go/no-go task [45]. In recent years, Piéron's Law has been found to hold in two- alternative forced choice (2AFC) tasks as well [46-48].

Equation (2) can be re written as

$$RT = RT_O + \beta I^{\alpha} \quad (3)$$

Where RT_O is the asymptotic RT, β is a free parameter I is the intensity of the stimulus and α is the exponent of the function [49,50]. An equation similar to (1) (2) and (3) derived by[51] with the exponent being equal to -1:

$$RT = RT_O + kC^{-1} \quad (4)$$

The Pierons law is identical to the Naka-Rushton equation which is used to describe contrast-response functions of neurons in the visual pathway [29,32], If the reciprocal of RT in (1) is given as a function of contrast (C):

$$RT^{-1} = 1 / (RT_O^{-1} + k.\log CS) - (RT_O^{-1} . \log CS) / (\log CS + k . RT_O^{-1}) \quad (5)$$

Reaction times can be linked to response amplitudes and gain characteristics of P and M cells. The slope of the Naka-Rushton function (contrast gain) is used to describe contrast gain. The slope of the Naka-Rushton function (5) at 0% is used to describe sensitivity of cells. Its slope at contrast sensitivity of logCS is;

$$(RT^{-1} .\log CS) = \log CS / (RT_O^{-1} .\log CS + k) – RT_O^{-1} . \log CS^2 /(k . RT_O^{-1}. \log CS)$$

$$(RT^{-1} .\log CS) = \log CS / (RT_O^{-1} .\log CS + k) – RT_O^{-1} .\log CS /(k . RT_O^{-1})$$

The slope at 0 logCS is:

$$RT^{-1} = RT_O^{-1} / k . RT_O^{-1} = k^{-1} \quad (6)$$

Equation (6) shows direct relationship between reaction time and sensitivity of the cells or gain, the higher the reaction time the higher the gain and the lower the reaction time the lower the gain or the sensitivity of the cell.

Thus, if sensitivity equals gain, we then have a low sensitivity (lower reaction time) in P- dominated channels at high contrast and a high sensitivity (higher reaction time) in M-dominated channels at low contrast.

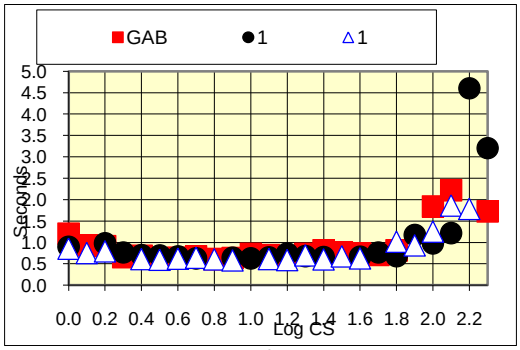

Fig 1: The average contrast gain for the M-cells is 7 secs/logCS while the contrast gain for P cells is 0.088secs/logCS.

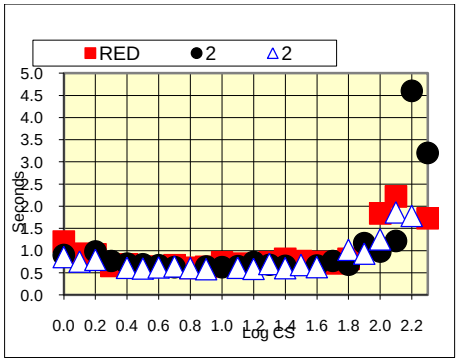

Fig. 2

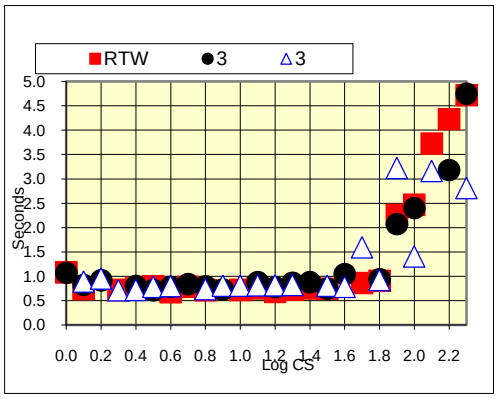

Fig 3

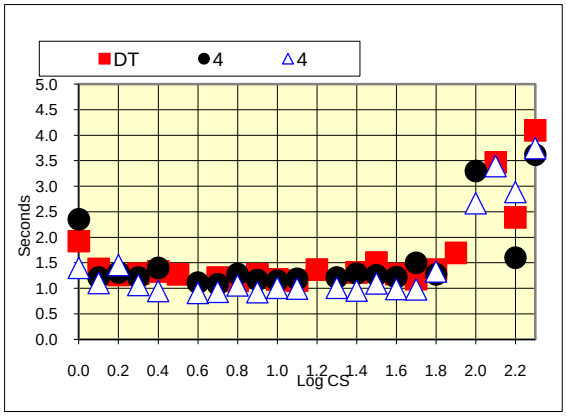

Fig 4

Fig 1-4: represents the graph for each of the 4 normal subjects (GAB, DT, RED and RTW), the individual V.A, CSB and age are on the top panel of each graph. The number test is represented by the dot and line, the Blink test by the triangle while the Jump test is represented by the square. In fig 2contrast gain for M cell was 9.8 while that of P cell was 0.0625. In fig 3contrast gain for M cell was 4.75 and that of P cell was 0.066.Fig 4 shows the contrast gain for M cells to be 4.5 and that of P cell to be0.0625.

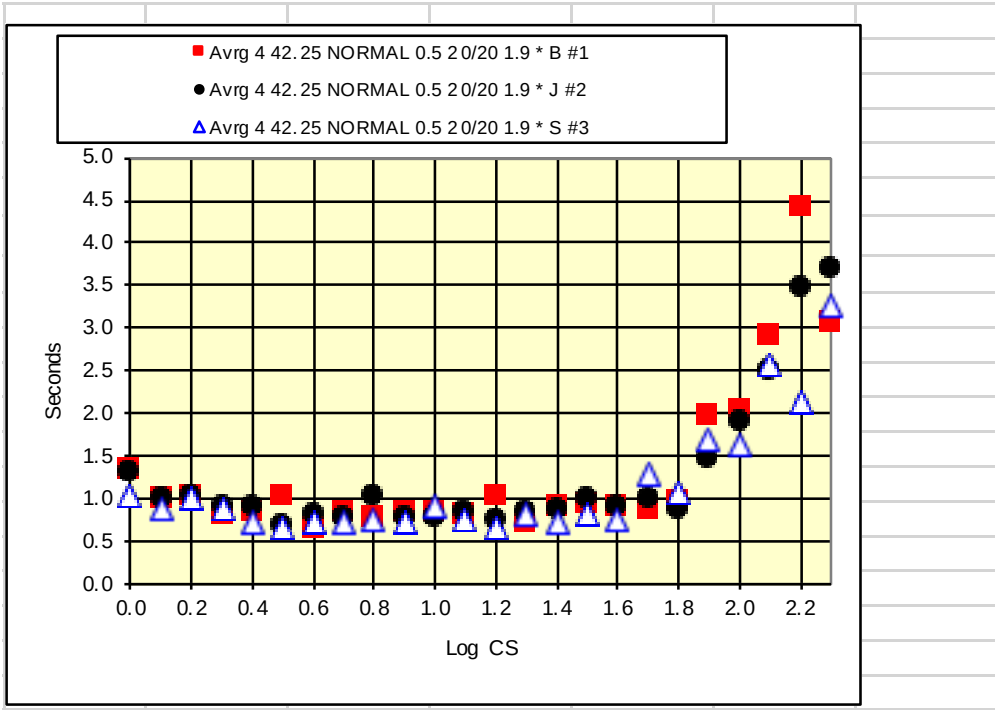

Fig 5: represents the average graph for 4 normal subjects (GAB, DT, RED and RTW), the average V.A, CSB and age are 20/20, 1.9, 42.25yrs. The number test is represented by the dot, the Blink test by the triangle while the Jump test is represented by the square. The average contrast gain for the M-cells is 5 secs/CS while the contrast gain for P cells is 0.0625secs/CS.

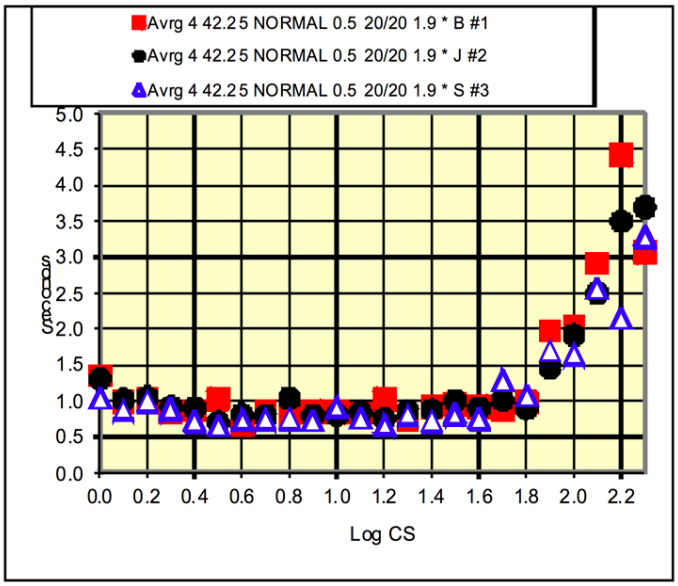

Fig 6 represents the average graph for 4 normal subjects, in Nigeria. The average contrast gain for the M-cells is 7 secs/CS while the contrast gain for P cells is 0.125secs/CS.

The first phase (from 0.0 to 1.5logCS) represents the action P-dominated channels, low (fast) reaction time, low gain, low sensitivity at high contrast, it is also the asymptote period. The second phase (1.6 to 2.3 logCS), then represents the action of M-dominated channels at high (slow) reaction time, high gain, high sensitivity at low contrast. The break point, (i.e. the point of change from transient to sustained activity) was reported by Harweth and Levi[11] to be at contrast levels below about 5-10%, in the normal subject, here the break point is 3.2% (1.5logCS).

DISCUSSION

Murray and Plainis [35] positprevious authors [1,20]misinterpreted their data. In their view it is not feasible that transient mechanisms account for the fast RTs at high contrasts and sustained mechanisms for the slow RTs at low contrasts. On the contrary, low contrast gratings must be detected exclusively by M-cells. Obtaining fast RTs simply shows that the mechanism mediating the response has high sensitivity to the testing conditions. This position of Murray and Plainis[35]clearly explains our graph that the second phase which shows an increase in reaction time with increase in contrast sensitivity (slope of the graph k), after the asymptote period is the period of contrast gain of Magno cells.

Contrast gain is regulated by the state of light adaptation. Contrast gain has been linked to reaction times as a function of stimulus contrast [32,52]. For the parvo cell (PC) pathway, the contrast gain for achromatic stimulation is less than 1; values of 0.15–0.50 are typical. For the MC pathway, the contrast gain for achromatic stimulation is greater than 1; values of 5–8 are typical.Contrast sensitivity is proportional to constrast gain [29].

Although RT data and physiologically based contrast gain are derived from different experimental conditions, the qualitative comparison made in our result hints at the neurophysiological basis of simple RTs.

The explanation given for Contrast gain control is the extra-classical receptive field (ECRF) which modifies the response of the classical receptive field (CRF) by the simultaneous presentation of stimuli that are incapable of evoking a response themselves [26,52,53].They show that the ECRF is strong in MC cells and mostly absent in PC cells of the macaque retina; contrast gain controls are already known to be strong in MC cells and, if present at all, are far weaker in PC cells [29,33,54].

The link between the ECRF and the contrast-gain control of cat retinal ganglion cells is suggested in the work of Shapley and Victor [55-57],who further show that in Y cells the contrast gain control occurs before the generation of the frequency-doubled response to contrast reversal.

There are two types of attention, exogenous and endogenous. Exogenous attention is involuntary, stimulus-driven, and has a transient effect, which peaks at about 100 ms and decays shortly thereafter. Endogenous attention is voluntary, conceptually driven (e.g., according to instructions), and has a sustained effect, which takes about 300 ms to be deployed and can last up to seconds [58-60]. Hermann et al [58] model, predicts that attention increases response gain when the stimulus is large and the attention field small (endogenous), and increases contrast gain when the stimulus is small and the attention field large (exogenous).

Endogenous attention is similar to CRF, and exogenous attention is similar to ECRF.

Supposed meaning of sustained reaction time is that the reaction time is sustained for a long change in contrast while transient reaction time depicts that the reaction time keeps changing as the contrast is altered or changed.
Sinz and Bethge [61] showed that the temporal properties of the contrast gain control mechanism can have a critical effect on the redundancies that originate from the spatial contrast correlations in natural images.

CONCLUSION

In verbal communication, Ian Bailey was of the opinion that the test is able to determine the speed of response at super threshold and he evokes a natural image of the speed of response of a driver to a pedestrian in a grey dress trying to cross a tarred road when it is raining. The test seems not only to be able to achieve this but estimate what is going on at the retinocortical pathway at the same time.The first phase with asymptote reaction time revealed activity of parvo cells (sustained cells) which dominates at low contrast sensitivity and the steep second phase, revealed contrast gain and the activity of magno cells (transient) at supra threshold contrast. We therefore suggest that this test might be able to reveal lesions in the retinocortical pathway as it affects the parvo and magno cells in form of deviations from the normal graphs. This simple test may be similar to the pedestal paradigm.

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