BRIEF REPORTS

Reaction times reveal the contribution of the different receptor components in luminance perception

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Piéron (1914, 1920, 1952) demonstrated that simple reaction time decays as a hyperbolic function of luminance. Similarities between cell latencies and reaction time (RT) to luminance suggest that this relationship may be determined by retinal processes. If the exponent of the Piéron function is specific to a given sensory modality, as assumed by some authors (e.g., Bonnet, 1992a, 1992b; Norwich, 1987), it should reflect receptor activities. Consequently, functions with different exponents should fit data for different luminance ranges. In a contrast-discrimination experiment, we investigated this question with a large range of luminance levels in a two-alternative spatial forced-choice task. The results of the experiment show that three functions with different exponents fit RT to the three luminance ranges (scotopic, mesopic, and photopic). The exponent decreases with increasing luminance. The findings indicate that the exponent and the asymptotic latency of the RT function reflect receptor activities of the visual system.

Classically, data obtained in experiments relating reaction time (RT) to intensity are fitted to a single power function. Simple reaction time (SRT) decreases when the intensity of a given stimulus increases (see, e.g., Cattell, 1886; Exner, 1868; Piéron, 1914, 1920, 1952; Wundt, 1886). The original equation for this function was introduced by Piéron (1914, 1920, 1952):

$$(SRT - t_0) = \beta I^{-\alpha},$$

where SRT is simple reaction time, t_0 is the asymptotic RT reached at the highest stimulus intensities, β is a free parameter, I is the intensity of the stimulus, and α is the exponent of the function.

Some authors have provided evidence that choice reaction time (CRT) also decreases when the luminance of the stimulus increases (e.g., Lappin & Dish, 1972; Pachella & Fisher, 1969; Posner, 1986). Moreover, Pins and Bonnet (1996) have shown that the Piéron function adequately describes the relationship between CRT and luminance and that the exponent of the function does not change with the complexity of the psychophysical task. In particular, it does not seem to matter whether the task is an SRT or a CRT task. Piéron functions would differ only by the constant t_0 and the parameter β .

Similarities between measures of cell latency and measures of RT to luminance have been reported. On the basis of a comparison of RT, alpha blocking latency, and the latency of b-wave of the electroretinogram, Bernhard (1940) concluded that all three measures followed a similar function, differing only by an additive constant. Monnier (1949) reached the same conclusion by studying retinal time, retinocortical time, alpha blocking time, and motor RT. Later, using computer-averaging techniques to extract cortical potentials evoked by brief flashes from electroencephalographic (EEG) recordings, Vaughan and colleagues (Vaughan, 1966; Vaughan, Costa, & Gildden, 1966; Vaughan & Hull, 1965) demonstrated that the latency of various components of the evoked response can be described by the Piéron function with an exponent similar to the values for RT. More recently, Donner (1989) and Djupsund, Fyhrquist, Hariyama, and Donner (1996) showed that latency functions of ganglion cells in the frog visual system were highly similar to that obtained in human psychophysics. In both cases, the decrease of latency with intensity is fitted by power functions, and the exponents are very similar. All these studies provide arguments for linking psychophysical data to receptor activities, suggesting that the relation between luminance and RT may be determined by retinal processes.

On theoretical (Norwich, 1987; Norwich, Seburn, & Axelrad, 1989) and empirical (Bonnet, 1992a, 1992b; Ward & Davidson, 1997) grounds, it can be assumed that the parameter α of the Piéron function is specific for a given sensory modality and presumably for each receptor type. Moreover, some authors (Baird, 1970; Baird &

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Noma, 1978; Link, 1992; Teghtsoonian, 1971) suggested that the exponent of the Stevens function would be related to discriminability, or, in other terms, to the Weber ratio. Similarly, Bonnet (1997) and Ward and Davidson (1997) suggested that the exponent of the Piéron function is also related to contrast discrimination. The psychophysical methods would, therefore, reflect a unique sensory function for stimulus discrimination. RT would then depend on the discriminability of luminance from its background. As a consequence, it is likely that the parameter α of the Piéron function reflects the discrimination capacity of early visual processes, namely at the receptor level.

Moreover, it can be assumed that discriminability (Weber ratios) varies with the luminance levels, but not exactly in the same way for the scotopic and photopic ranges (see, e.g., Graham, 1965; Hecht, 1934; Hecht, Peskin, & Patt, 1938; Hood & Finkelstein, 1986). A similar conclusion holds for luminance adaptation (Haig, 1941; Hecht & Shlaer, 1938; Hood & Finkelstein, 1986). Hood and Finkelstein described the brightness discrimination function as having two branches corresponding to the two types of receptors. They added that discrimination of luminances is better in the cone activity region. If the exponent reflects the discriminative capacity of the receptors, the relationship between intensity and RT would not be the same in the different luminance regions (scotopic, mesopic, and photopic). Since the visual system is a dual system (rods/cones), different functions are expected to describe RT data for the different luminance ranges. Specifically, a difference in the exponents is to be expected.

Some authors (Doma & Hallett, 1988, 1989; Mansfield, 1973) have argued previously in that direction. Mansfield (1973) first fitted a single function to all his SRT data for a series of different intensities and found, like Piéron (1914, 1920, 1952), an exponent of -0.3 . He then looked for more specific effects. The author mentioned that below a certain intensity level, the borders of the luminance stimulus (flash) appeared indistinct, and, for monochromatic stimuli, appeared colorless. Using this criterion, Mansfield partitioned his data into two parts, corresponding to "scotopic" and "photopic" components. Observing a disconnection between these two, he fitted two functions to his data. The asymptotic latency (t_0) for the scotopic component was found to be longer than the one for the photopic component, but the exponents were said to be the same. However, the number of levels used in the scotopic range was not explicitly mentioned in the paper. In fact, the experimental conditions used by Mansfield may have not really explored the scotopic region.

Doma and Hallett (1988, 1989) reached conclusions similar to Mansfield's. In a study of saccadic eye movement latencies to stimuli of different wavelengths, they fitted two different functions for the pure scotopic and the pure photopic components and found that in some cases mesopic RT followed the scotopic function (their blue-green data). In other cases, they assumed an interaction of rod and cone mechanisms in the mesopic re-

gion where RT defined a transition between the two other functions (their yellow data).

In fact, there are two possibilities concerning the mesopic region: (1) Assuming that the rod and the cone systems are functionally independent, mesopic RT could follow either the photopic or the scotopic function. If, for example, mesopic RT follows the scotopic function (see, e.g., Doma & Hallett, 1988, 1989), latencies to mesopic luminances would be determined predominantly by the rod input. On the other hand, one may assume that the response depends on the faster process. It would then be expected that mesopic RT obeys the photopic function. Bujas, Szabo, Mayer, Ajdukovic, and Vodanovic (1989) found receptor independence in taste experiments. Two different taste stimuli gave two mean RTs, a shorter and a longer one. When the two tastes were mixed, RT to the mixture corresponded to the taste stimulus yielding the shorter RT. In this case, only two functions, with different exponents, would be expected. (2) Assuming that, as suggested by retinal physiology, the rod and the cone systems are interactive, mesopic RT would reflect the combined response of both rod and cone mechanisms and would describe a transition between the functions for photopic and scotopic luminances (Doma & Hallett, 1988, 1989). In the latter case, three RT functions with different exponents and asymptotic times would be expected. In the low mesopic range, the contribution of rods would be greater than that of cones that are at threshold, whereas in the high mesopic range, the contribution of the cones would be predominant.

Although previous authors (Doma & Hallett, 1988, 1989; Mansfield, 1973) accepted at least two different processes, their analysis of the data did not reveal differences in the exponents of the different functions. Doma and Hallett fitted scotopic data with an exponent $\alpha = -1$ and took a function with the same exponent for photopic data. However, they never tried to fit a function to mesopic data. If the exponent of the Piéron function reflects the discriminative capacity of the different receptors, different exponents should describe RT data for the *three* luminance regions. The previously reported absence of an effect on this parameter of the function may have resulted from the use of a restricted luminance range, with rather few scotopic and mesopic values.

The question concerning where to put the limits of the scotopic-mesopic and of the mesopic-photopic regions is, though critical here, open to debate. In the present experiment, we started from an *a priori* determination of these limits between the three luminance regions (see, e.g., Buser & Imbert, 1987; Graham, 1965). We used at least five levels in each of the three luminance regions to test the hypothesis that different exponents describe RT data for these different regions.

The experiment was run with white stimuli on a black background. Luminances ranged from supposed scotopic to photopic levels. Five luminance levels were chosen in each of the three regions, with a geometrical progression

of about 1.6. The three regions of luminance for the stimuli were first determined by classical luminance values found in the literature (e.g., Buser & Imbert, 1987; Graham, 1965). According to these authors, the scotopic region ranges from the absolute threshold to about 0.3 cd/m^2 , the mesopic region from 0.3 to 3 cd/m^2 , and higher luminance levels belong to the photopic region. This choice may be somewhat arbitrary given that other authors (e.g., Davson, 1962; Hood & Finkelstein, 1986) have reported different limits, particularly between scotopic and mesopic regions. For that reason, several fittings were run in the present experiment in order to find the most likely solution. The stimuli were presented with a constant eccentricity, allowing us to test the different luminance levels. A "weak eccentricity" was chosen (1.25°) in order to present stimuli beyond the fovea in a region where the rod and cone densities are about equal.

METHOD

Subjects

Four trained subjects took part in the experiment. One of them was D.P. All subjects had normal or corrected-to-normal vision.

Procedure

The stimuli were presented binocularly on a high-resolution black-and-white video monitor (Addonics, MON-7D5). They were generated through a personal computer (Hewlett-Packard VECTRA QS20 80386) using a special graphics "adaptator" (VGA trident) providing a display of 800×600 pixels (VGA Hi) at a 60-Hz frame rate (noninterlaced). Careful calibration of each RGB combination was carried out with a

Pritchard photomultiplier and cross-checked with another device standardized to a CS 100 Minolta photometer.

The stimulus was a luminous rectangle ($30' \times 7.5'$ of arc) shown on a dark background (0.02 cd/m^2) in a dark room. This stimulus has been used previously in some of the experiments of Pins and Bonnet (1996).

The subject was placed at a viewing distance of 70 cm. The head position was stabilized by means of a chinrest. He/she looked at a central fixation dot ($1.5'$ of arc diameter, 10 cd/m^2), and on each trial, the luminous rectangle appeared with its center located at 1.25° to the left or right of the fixation point. Within a given session, the two spatial locations (left/right) were randomly presented from trial to trial. Since Pins and Bonnet (1996) have shown that the Piéron function fits CRT as well as SRT, we chose to use a CRT task in which the subject had to decide whether the stimulus appeared to the left (left key) or to the right (right key) of the fixation point (a two-alternative spatial forced-choice task).

The luminance levels ranged from just above threshold to photopic levels. In fact, the analysis of some SRT data using luminance levels from the threshold region (Chocholle, 1940, in audition; Piéron, 1914, in vision) showed that the exponent of the Piéron function rose greatly in this region. This happened because uncertainty about the presence of the stimulus added to the effect of intensity per se: In this region, there is an effect of luminance on both RT and the percentage of correct responses. The different intensities were presented in different experimental blocks of trials (pure blocks) in order to avoid adaptation effects due to changes of luminance from trial to trial. Since the classical expected intensity function is a hyperbolic curve, these levels of luminance followed an approximately geometrical series. Each of the 15 luminance levels ($0.16, 0.18, 0.20, 0.22, 0.25, 0.28, 0.45, 0.81, 1.41, 3.08, 5.54, 10.01, 17.94, 32.30$, and 58.18 cd/m^2) was presented in pure blocks (using only one luminance level) of 100 trials. Preliminary experiments showed that no systematic difference was observed between pure and mixed (i.e., different luminance levels are mixed in the same experimental block) blocks when subjects were trained. Each pure block was repeated five times. In one experimental session, five blocks of trials, each with different luminance levels, were presented. The lumi-

Figure 1. Mean reaction time (RT) over the total range of luminances. The small squares represent the standard deviations. RT decreases with increasing luminance. The Piéron function was fitted for all the luminance levels (adjustment of a single function).

nance level used in each block was varied irregularly, but low intensities never followed immediately after the highest one. There were 15 experimental sessions. Thus, 500 RTs were recorded for each luminance level and for each subject. The median of the RTs was calculated for each session, and these medians were averaged over the repetitions.

Presentation time was about 83 msec (five frames). This presentation duration is beyond the limit generally reported for temporal summation of Bloch's law (see, e.g., Graham, 1965; Mansfield, 1973; Ueno, 1977). RT measurements were rounded to the closest millisecond as indicated by the external clock driven by the computer. The appearance of the target was preceded by an auditory warning signal (1000 Hz, 500 msec). Five preparatory periods (500, 750, 1,000, 1,250, and 1,500 msec) were used and presented randomly according to an exponential distribution in order to minimize anticipatory responses. At the beginning of each session, the subject was dark adapted, and pauses were made between blocks of different luminances.

RESULTS

The percentage of correct responses ranged from 96% to 99%. Such a low rate of errors is generally observed in well-trained subjects. It is likely to reflect an optimization of the speed-accuracy tradeoff function. RT was considered independently from the response type (correct vs. error), since the analysis of the correct responses

led to exactly the same conclusions (the median of errors RT was 293 msec). The mean difference between the median RTs according to the localization (left/right) of the stimulus was about 17 msec. For further analysis, the results were averaged over this factor, which had no significant effect [$F(1,3) = 5.05$, n.s.].

Adjustment of a Single Function

As shown in Figure 1, CRTs decreased with increasing luminance of the stimuli. The mean RT difference between the two extreme levels of luminance was 124 msec. A within-subjects analysis of variance (ANOVA) confirmed that the intensity effect was significant [$F(14,42) = 78.37$, $p < .001$].

In a first step, the Piéron function was fitted to the mean data for all the luminance levels. Two different fitting procedures were compared. First, an iterative procedure based on a least squares method of the log-transformed data was used. For successive values of t_0 , the parameters α and β were estimated (see Mansfield, 1973). The procedure stopped when the best correlation was obtained. The second procedure given by the program SigmaPlot

Figure 2. The three curves show the Piéron function fitted to the a priori ranges of the data ($N = 15$, $\sum d^2 = 46.40$). In order to improve the visibility of the data in the low range, the luminance level axis is presented in logarithms. Luminance levels ranging from 0.16 to 0.25 cd/m^2 correspond to the low range (black filled circles) above the threshold region. They are coded by the rods. Those ranging from 5.84 to 58.18 cd/m^2 correspond to the high range (open circles) and are coded by the cones. Those ranging from 0.28 to 3.08 cd/m^2 correspond to the middle range (gray circles) and are coded by the two types of receptors. The points on the graph represent the mean reaction times (RTs) of the medians. The exponents and the asymptotic latencies of the adjusted functions decrease with increasing luminance.

ran directly on the untransformed data. Since the results of the two procedures were very close, only the results of the second procedure are given here. In order to choose between different solutions, the squared deviations between the observed RT and the fitted results were summed ($\sum d^2$) and used as the criteria of the goodness of the fits. Of course, the comparisons are valid only if the number of observations (N) is the same.

The global function fitted on the entire luminance set was as follows (see Figure 1):

$$TR - 250.06 = 25.52 I^{-0.78} \quad (\sum d^2 = 341.22).$$

A similar trend was observed for each subject individually, with the following exponents: D.P., -0.71 ; A.C., -0.62 ; T.P., -1.33 , and B.D., -0.77 .

Adjustment of Several Functions

If the goodness of the fit of a single Piéron function is perfect, the same estimate of the parameters should be obtained whatever the range of the data used to estimate them. This is not the case, as we have observed in different analyses.

We first studied the goodness of the fit when three functions were fitted to the three a priori ranges of the data. The equations are as follows (Figure 2):

$$\text{Low range: } TR - 318.47 = 0.003 I^{-5.40}$$

$$\text{Middle range: } TR - 245.32 = 34.51 I^{-0.54}$$

$$\text{High range: } TR - 199.09 = 68.12 I^{-0.09}$$

The total $\sum d^2 = 46.40$ ($N = 15$). Hence, it can be concluded that this three-function solution is much better than the single global function. A similar trend was observed for each subject.

A within-subjects ANOVA confirmed that the intensity effects were significant for each luminance range [low range, $F(4,12) = 26.29, p < .001$; middle range, $F(4,12) = 23.52, p < .001$; high range, $F(4,12) = 3.56, p < .039$]. This result shows that there is a specific effect of intensity on CRT within each luminance region.

Moreover, the exponents decreased with increasing luminance range. A within-subjects ANOVA, computed on exponents, confirmed that this effect was significant [$F(2,6) = 10.71, p < .011$]. These results suggest that the amplitude of the intensity effect on RT changes with the intensity region. This effect is the smallest in the high range (but remains significant), the largest in the low range, and of intermediate amplitude in the middle region. Moreover, the parameter t_0 decreases at the same time.

We also studied two other solutions, namely a two-function solution and a three-function solution, both with free limits. For the two-function solution, the two sets of parameters were estimated in changing the limit between the low and the high range with a minimum of five

Figure 3. The two curves show the best fit with a two-function solution ($N = 15$, $\sum d^2 = 69.58$). The luminance-level axis is presented in logarithms. Luminance levels ranging from 0.16 to 0.28 cd/m^2 correspond to the low range (black filled circles). Those ranging from 0.445 to 58.18 cd/m^2 correspond to the high range (open circles). The points on the graph represent the mean reaction times (RTs) of the individual medians.

Figure 4. The three curves show the best fit with a three-function solution ($N = 15$, $\sum d^2 = 42.25$). The luminance-level axis is presented in logarithms. Luminance levels ranging from 0.16 to 0.25 cd/m^2 correspond to the low range (black filled circles) above the threshold region. They are coded by the rods. Those ranging from 3.08 to 58.18 cd/m^2 correspond to the high range (open circles) and are coded by the cones. Those ranging from 0.28 to 1.41 cd/m^2 correspond to the middle range (gray filled circles) and are coded by the two types of receptors. The points on the graph represent the mean reaction times (RTs) of the medians.

luminance levels in each range. Thus, we compared 5 levels in the low range with 10 levels in the high range (6/9, 7/8, etc.). Each time the global $\sum d^2$ was calculated with $N = 15$. The best fit (Figure 3) was obtained with six luminance levels in the low range and nine in the high range ($\sum d^2 = 69.58$). The equations are as follows:

$$\text{Low range: } TR - 309.21 = 0.050 I^{-3.80}$$

$$\text{High range: } TR - 244.43 = 35.50 I^{-0.56}$$

Thus the three-function solution afforded a better fit. A similar trend was observed for each subject.

In order to try to improve the three-function solution, we varied the limits between the low, middle, and high ranges and compared the global $\sum d^2$ in each case. From every combination we have used, never with fewer than four luminance levels in one of the ranges, the best fit we have obtained ($\sum d^2 = 42.25$) was with the five lowest levels in the low range, the four next in the middle range, and the six next in the high range. The equations are as follows (Figure 4):

$$\text{Low range: } TR - 318.47 = 0.003 I^{-5.40}$$

$$\text{Middle range: } TR - 182.42 = 97.12 I^{-0.24}$$

$$\text{High range: } TR - 242.41 = 38.91 I^{-0.50}$$

DISCUSSION

The present data confirm that CRT decreases with increasing luminance, as shown previously by Pins and Bonnet (1996). The classical Piéron function provides a reasonably good fit for the total range of intensity levels used here. A two-function solution improves the goodness of fit; however, the best fits were obtained with the three-function solution, which presumably corresponds to the three luminance regions (scotopic, mesopic, and photopic).

As the three-function solution shows, the effect of intensity on RT reflected by a difference in exponents is not the same within each of the different luminance regions. It turns out that the best of the three-function solutions traced the same limit between scotopic and mesopic as our a priori choice, extending the photopic region over the middle range by only one experimental step.

Our observations partly confirm Mansfield's (1973) and Doma and Hallett's (1988, 1989) findings, suggesting that latency functions reveal different receptor activities of the visual system. In our data, however, the exponents of the two functions obtained for photopic and scotopic components were different. We have tried to fit a Piéron function to the two extreme ranges (scotopic and photopic), with an exponent of -1 ($\sum d^2 = 130.69$, $N = 11$) and compared the goodness of fit with our

three-function solution ($\sum d^2 = 40.5$, $N = 11$). In the two cases, the functions were fitted for the same luminance steps (five in the scotopic and six in the photopic). In this respect, our results do not agree with Doma and Hallett's (1988, 1989) conclusion that the exponent for scotopic and photopic functions is the same.

The value of the exponent of the global function found by Mansfield (1973; $\alpha = -0.3$) is consistent with the assumption that the range of luminances in his experiment did not contain many values in the scotopic range, if any.

We considered two possibilities for the variation of RT in the mesopic region: (1) independence of the activities of the two types of receptors (rods/cones) and (2) interaction between them. Our results are more compatible with the second suggestion. In fact, as indicated by the different exponents obtained in the three luminance regions, not just two, but three functions relate luminance to RT, implying that mesopic luminance levels depend on the two receptor systems (rods and cones). The closer we get to the presumed limit of the photopic region, the stronger the influence of the cones. Such a result is compatible with studies of Ikeda and Urakubo (1969) and Benimoff, Schneider, and Hood (1982), which showed, in brightness-matching and magnitude-estimation tasks, that the visual system combines rod and cone signals at and above threshold. The presumed interaction of rod and cone mechanisms in the mesopic region finds expression here in the function fitted to the middle range of luminance levels. The exact values of its limits necessarily remain uncertain. As noted in the introduction, in the lowest range of the mesopic region, the cones, being near their own threshold, cannot be very influential. Complementarily, in the highest range of the mesopic region, the rods are saturated and may not contribute much to the response. Thus it is clear that the true limits of the mesopic region should be a little larger than estimated on the basis of RT. The estimated limits are, however, similar from subject to subject within the precision given by the choice of our luminance steps.

The data are furthermore compatible with the assumption that three functions fit RT over a large range of luminance levels. The difference in the exponents suggests that RT distinguishes psychophysically the photopic, mesopic, and scotopic regions. The asymptotic RT (t_0) varies in parallel with the exponent and it can thus be assumed that the three functions reflect activities at the physiological level. Consequently, RT measures disentangle the relative contributions of the different receptor systems coding different luminance regions. Additionally, our results also provide some evidence in favor of a close relationship between RT and contrast discrimination, since a higher exponent was obtained in the luminance region in which discrimination is known to be poorer (scotopic) and a lower exponent in the luminance region in which discrimination is known to be better (photopic).

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