Available online at www.sciencedirect.com
SCIENCE DIRECT
International Journal of Psychophysiology 57 (2005) 187 – 194
INTERNATIONAL JOURNAL OF PSYCHOPHYSIOLOGY
www.elsevier.com/locate/ijpsycho

The human Retinal Functional Unit

Robert Galambos[a,*], Gábor Juhász[b], Magor Lorincz[b], Nora Szilágyi[b]

[a]University of California, San Diego, 9500 Gilman Dr., La Jolla, CA 92093, USA
[b]Hungarian Academy of Sciences, Neurobiology Research Group at Eötvös, Loránd University, Pázmány Péter stny. 1/C, 1117, Budapest, Hungary

Received 23 November 2004; accepted 28 January 2005
Available online 17 May 2005

Abstract

It has long been known that readers of this page will move their eyes from one fixation to the next two to four times per second. It follows from this fact that each fixation triggers a unique optic nerve volley lasting up to 300 ms that contains all the information the retina processes between fixations. Here we give such volleys a name (Retinal Functional Unit, RFU) and use human subjects and interstimulus interval (ISI) experiments to define some of their properties. We report that RFUs can be dissected into an initial fraction that reaches the cortex and a later fraction that may not, depending on the ISI between successive stimuli. During the dissection process the perceptions of the stimuli change in an orderly way, such that successive thresholds of "twoness", color, and duration are reached as a function of increasing ISI. We conclude that volleys from the tens or hundreds of thousands of active axons contained in every RFU exit the retina in a precisely determined temporal order, and add this conclusion to three others for which we have already published the supporting data. 1) The mammalian retina normally takes about 300 ms to process a visual stimulus. 2) The ca. 300 ms end product, an RFU, contains in neuronal form all the photochemical information acquired during one fixation. 3) These information-rich volleys reach the cortex with little or no change thanks to monosynaptic transfer in the thalamus.

Keywords: Ganglion cell; Interstimulus interval; Visual perception

1. Introduction

The following introduction is intended to set the stage for the human experiments this paper reports. It briefly summarizes previous results obtained from the Wistar rat, our model of the mammalian visual system (Galambos et al., 2000, 2001; Galambos and Juhasz, 2001; Szabo-Salfay et al., 2001). Two small LEDs glued to the rat's skull deliver red stimuli on command (continuous, intermittent, or both) as the animal sleeps or moves about in darkness within a small box. Three implanted electrodes sample the electrical responses the stimuli generate at the corneal surface, in the optic chiasm, and on the visual cortex.

Unlike the conventional microelectrode experiment, which has more limited goals, our three-electrode array enables a systems analysis using the field potentials generated at the morphological beginning, middle and end of an active visual system. The neuronal information acquired at the retinal level is described and then reexamined twice for modifications as it moves to and through the lateral geniculate nucleus to reach its cortical destination. Fig. 1 presents typical results generated by a rat in slow wave sleep when stimulated by 0.5 ms red flashes. As we will see, these rat results supply valuable information for understanding human visual behavioral responses.

The most important finding illustrated in Fig. 1 is this: retinal ganglion cell volleys measured at the optic chiasm electrode are normally triphasic in form and about 300 ms in duration. Called histograms in our rat publications, we rename them Retinal Functional Units (RFU) for the human experiments here. Rat RFUs change systematically but always retain their ca 300 ms triphasic waveshape during light adaptation, stimulus luminance change (Galambos et al., 2000), and as much as a five log unit variation in

* Corresponding author. 8826 La Jolla Scenic Dr, La Jolla, CA 92037, USA. Tel.: +1 858 453 0151.
E-mail address: rgalambos@ucsd.edu (R. Galambos).

0167-8760/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.ijpsycho.2005.01.013

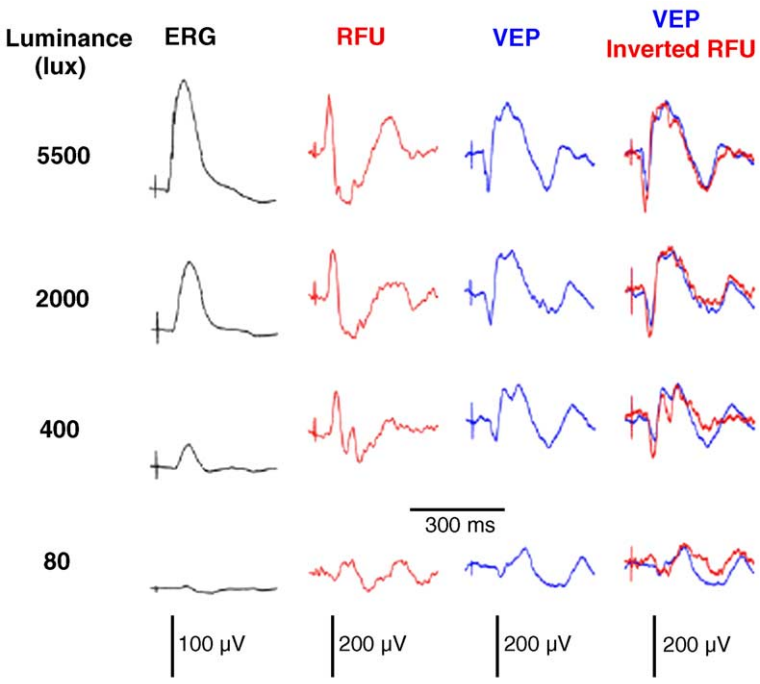

Fig. 1. Simultaneous recording at cornea, chiasm and visual cortex of the responses to 0.5 ms red LED flashes delivered to a rat in slow wave sleep. The corneal trace (ERG) shows the electroretinogram b-wave, which varies widely as the luminance varies over about three log units. The chiasm trace (RFU) shows the ganglion cell volley en route to the lateral geniculate nucleus (LGN) synapse; we have given the name Retinal Functional Unit (RFU) to this compact 300 ms volley, which we have found to be the obligatory output of the rat retina. The cortical trace (VEP=Visual Evoked Potential) shows the RFU after its transfer at LGN. On the right the chiasm trace has been electronically inverted and superimposed on the cortical trace; the degree to which the two traces differ estimates what the LGN transfer has added or subtracted from the RFU. The similarity indicates that the temporal sequence in which activated ganglion cell axons left the retina is delivered almost exactly to the cortical neurons for further processing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stimulus duration (Galambos and Juhasz, 2001). RFU amplitudes are significantly larger when the animal is in slow wave sleep (compared to waking and REM; see Galambos et al., 2001), and, as Fig. 1 shows, the RFU waveshapes turn up inverted at the visual cortex electrode, which strongly suggests the lateral geniculate nucleus transfers its input monosynaptically to the cortex under our recording situations (Galambos et al., 2000, 2001; Galambos and Juhasz, 2001). These and other facts collected in our three publications suggest our systems approach may have identified in this rat RFU an important link in the chain of physiological events responsible for that animal's visual perceptual experiences.

If the output of the human retina resembles that of the rat, it should be true that any stimulus pair, S1 and S2, will evoke RFU1 and RFU2, each of which will last about 300 ms. This being so, all the information RFU1 carries about S1 will reach the brain only when the S1–S2 interstimulus interval (ISI) is 300 ms or longer. At ISIs less than 300 ms, the onset of RFU2 will fall upon and interrupt RFU1, dividing the information it contains about S1 into a first part that reaches the brain and a second part that does not. If the information RFU1 carries away from the retina is in fact arranged in such an orderly way, the perceptions viewers have of S1 should change systematically as more and more of RFU1 reaches the cortex, where the final steps in creating visual experiences take place. The possibility that RFU1 has such an orderly, information-rich internal structure leads directly to the following four hypotheses the human experiments in this report will test.

First, a subject viewing two brief light flashes as the interval between them increases from zero may fail at first to see S1 because the fraction of RFU1 that reaches the cortex contains too little information about S1. Second, as the ISI lengthens beyond where S1 is first seen, the viewer should describe S1 increasingly more accurately because more and more of the information RFU1 contains about S1 is reaching the cortex. Third, as the ISI increases, S1 should always appear to be shorter in duration than S2, but at about 300 ms and beyond they should be called equal.

Because human optic nerves contain about a million ganglion cell axons, each 300 ms RFU volley probably includes hundreds of thousands of active fibers. Do these nerve impulses leave the retina in an orderly or random manner? Our fourth hypothesis–that their departure is precisely ordered within the RFU–will be disconfirmed if, as the ISI increases, the subject group fails to report similar perceptual changes at similar ISIs.

What follows are seven experiments divided into two groups. In all of them subjects report what they see when 1 ms red and green flashes, S1 and S2, are presented in rapid succession in an ISI paradigm. Group I includes the four

experiments that directly test our hypotheses—that the normal retinal output is a 300 ms volley; that it reaches cortex intact; that each volley represents the orderly sequential activation of a large fraction of the total ganglion cell population; and that the ISI procedure dissects such volleys into fractions that correlate positively with changes in the visual perceptual experience.

Group II adds controls and more experiments that supplement and support the data acquired in Group I. Overall, the results confirm our four hypotheses and fully support our main claim that the obligatory output of the human retina to every adequate stimulus is the ca. 300 ms volley we call an RFU.

2. Methods

The seven experiments that follow all share most of the features described for Experiment 1; additional details appear where relevant.

2.1. The stimulus

A protective goggle of the type workers use was modified by drilling a hole in each of its plastic lenses to accommodate a two-color LED (red, green; Bright LED Co.) glued into it with its lens surface pointed toward the eye. Because head shapes differ, the LED surfaces (diameter 5 mm) are finally located 20–30 mm in front of the pupils when the goggle is worn; at this distance the red and green pulses appear to be large, out of focus, and in the same place. The output of both the red (650 nm) and green (557 nm) elements is 350 mcd/mm2 (as measured with a Lunasix luxmeter) at the 20 mA saturation current. A digital stimulator delivered 1 ms square pulses at 20 mA to each color element and controlled the interval between them.

2.2. Subjects

A total of 15 subjects was tested; of these 12 (9 female; age range 21–35) participated in Experiment 1. All were university students or employees with no previous experience as subjects in visual experiments. Recording procedures complied with the Hungarian Ethical Committee Guidelines for Conducting Human Research, which agrees with the European Community Ethical Rules for Human Research.

2.3. Procedure for Experiment 1

Subjects were light adapted for at least 10 min while seated facing a white wall in a room lighted by overhead fluorescent tubes; the ambient level was 2800 lx in the region of the subject's eyes. Wearing the goggles and using the right eye, subjects first correctly identified the red and green flashes. The experiment was then explained to them in general terms and they were told they would answer the following questions:

1. Did you see one flash or two?
2. What color was it (when they reported one), or what were their colors (when they reported two)?
3. (when they reported two flashes) Which one lasted longer, the first or the second?

During data acquisition a pencil tap on the table was the signal to look at the LED and withhold blinks because a flash was about to appear. The experimenter then pressed a button to present the pair of 1 ms colored flashes. Subjects' verbal answers were entered manually into a protocol book as a function of ISI between the flashes; their final answers define the twoness, color, and duration thresholds in ms.

As noted, Experiment 1 tested the right eye of 12 subjects. The first three subjects were tested once. The next eight were tested once on each of five different days. One subject reported seeing separate red and green flashes at all ISIs through her right eye, which her ophthalmologist has since said requires a −6 diopter correction. When tested through her left eye her responses were like those of the other subjects. We have no explanation for this anomaly. She was tested early in the series and has not yet been available for retesting. None of her data are included in the averages.

Pilot studies established ISI ranges of interest near 50, 100, and 300 ms. During experimental sessions thresholds were acquired in order beginning with ISIs near 50 ms. An up and down method of limits procedure was used in which ISI changed in progressively smaller steps; when near threshold, 1 ms steps were used. The three threshold estimates, which take about 20 min to acquire, are called here one test. The data tabulation sheets yielded the individual twoness, color, and duration threshold numbers. We calculated the descriptive statistics (mean and standard deviation, S.D.) and used ANOVA followed by the Newman–Keuls post hoc test (Statistica for Windows) for the data.

3. Results

3.1. Group I

3.1.1. Experiment 1. Monocular (right eye) red/green presentation

Eleven subjects quickly learned to perform the test and together produced a total of 43 estimates of the twoness, color, and duration thresholds. The results, which are shown as bar graphs in Fig. 2 and as a mean and standard deviation (S.D.) list in Table 1, can be summarized as follows:

1. A 1 ms red pulse followed by a 1 ms green pulse is seen as a single flash, orange or yellowish green in color, until the ISI reaches about 65 ms. This well-known threshold

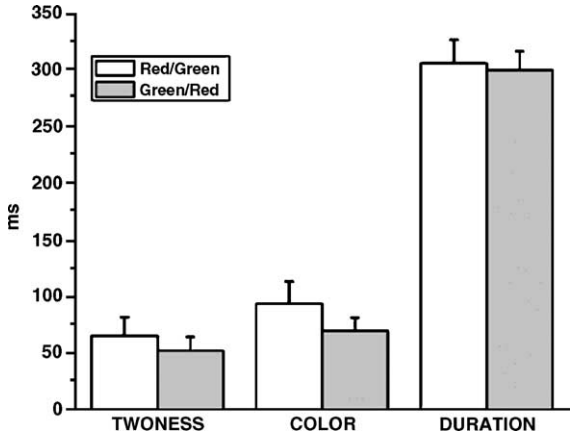

Fig. 2. Twoness, Color and Duration thresholds for red/green and green/red which subjects report the flash pair is (a) first perceived as two (the Twoness threshold), (b) first correctly seen as red followed by green or green followed by red (the Color thresholds), and (c) finally perceived as equal in duration (the Duration threshold).

phenomenon—the ISI at which a stimulus pair seen as one is first seen as two—will for convenience be called the twoness threshold here.

2. Subjects reported all flashes to be either orange ($n=8$) or yellowish green ($n=3$) at and beyond the twoness threshold up to an ISI of about 93 ms; at 93 ms and thereafter the first pulse was always called red, the second green. The ISI at which the colors are first correctly identified will be called the color threshold.
3. At ISIs less than about 300 ms and longer than about 60 ms, all viewers said the second flash appeared to be longer in duration than the first. At about 300 ms they all reported the two appeared to have the same duration. This ISI defines the duration threshold.

The data collected in Experiment 1 are fully analyzed in the Discussion.

3.1.2. Experiment 2. Monocular (right eye) green/red presentation

Experiment 2 is the green/red version of Experiment 1. Six subjects participated; all had also served in Experiment 1. Their averaged twoness, color, and duration thresholds are shown in Fig. 2 adjacent to the corresponding red/green results; Table 1 reports the statistical results. Apparently the order in which the colored stimuli are presented is a relatively unimportant variable.

Table 1
Mean and standard deviation (S.D.) values of Twoness, Color and Duration thresholds for all color combinations

Color sequence	Threshold	Mean ± S.D.
Red/green	Twoness	64.7 ± 16.7
	Color	92.8 ± 19.6
	Duration	305.6 ± 20.7
Green/red	Twoness	51.5 ± 12.4
	Color	68.9 ± 11.9
	Duration	299.8 ± 16.2
Red/red	Twoness	60.0 ± 23.1
	Duration	279.7 ± 12.0
Green/green	Twoness	54.9 ± 27.3
	Duration	303.0 ± 17.7

3.1.3. Experiment 3. Monocular (right eye) red/red and green/green presentations

Six subjects participated; two had not been tested previously. Their averaged twoness and duration thresholds resemble those yielded in the red/green and green/red presentations. The data are listed in Table 1 and plotted in Fig. 3.

3.1.4. Experiment 4. Eye closed control

In our previous studies with rats (Galambos et al., 2000, 2001; Galambos and Juhasz, 2001; Szabo-Salfay et al., 2001) the retina was illuminated from behind by LEDs glued to the skull. We undertook to simulate that unusual stimulus path in these human studies by delivering the stimuli through the closed eyelid. One experienced subject with eyes closed (monocular right-eye red/red presentation) reported, in three trials, mean twoness and duration thresholds of 57 and 299 ms (compared to his eye-open norms of 42 and 292 ms, respectively). A flash viewed through a closed lid will enter primarily through the sclera (the eyeball rolls upward when the eye closes) and illuminate the retina diffusely. The data indicate the retina creates similar RFUs out of both the more or less full-field scleral illumination and the limited 10–20° visual angle illumination produced by the goggle LED; at the minimum, the conclusion from Experiment 4 is that focused images and visual angle considerations are not critical for understanding our experimental results.

3.2. Group II

3.2.1. Experiment 5. Binocular red/green presentation

Because identical red/green LEDs are installed in both goggle lenses, it is possible to stimulate the eyes with

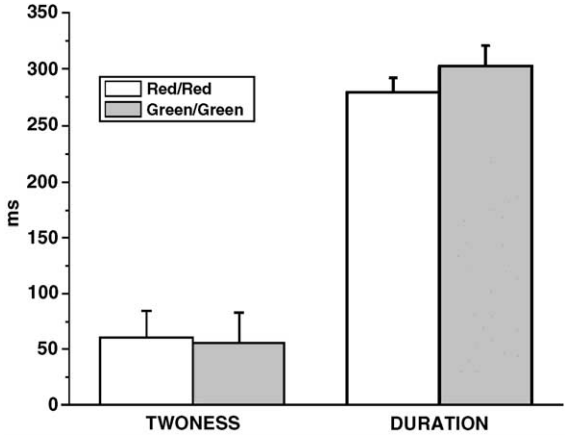

Fig. 3. The Twoness and Duration thresholds reported by subjects when the sequence is green followed by green and red followed by red.

either color and in any desired order. Two subjects, both participants in Experiments 1 and 2, received a 1 ms red flash in one eye and a 1 ms green flash in the other eye. Both reported seeing simultaneous flashes, one red, the other green when the ISI was zero. As the ISI increased they both saw the green flash (S2) move away from the red one in time. Finally, they always said no when asked whether one flash appeared to be longer in duration than the other.

The complete absence of interaction in the perceptions of S1 and S2 during this binocular ISI presentation is strong evidence that the retina, not some central region, is where the stimulus pair interacts during monocular presentations. The left and right RFUs created during such binocular presentations deliver their unique endoretinal analyses to the visual cortex for further processing, where no interaction takes place, according to the subjects' reports.

3.2.2. Experiment 6. Eyes closed; binocular red/red presentation

Uncontrolled variables in Experiment 5 include the possibility the two stimuli subtend different visual angles, and/or are not fused binocularly. Experiment 6 is a control for these variables: both eyes were closed and both stimuli were red. In this situation both retinas will be widely and diffusely illuminated. Two subjects reported seeing two red flashes at all ISIs (10–300 ms), both seemingly the same in duration. In short, and as in Experiment 5, there is no twoness threshold and no duration threshold when both eyes are closed and one receives S1 while the other receives S2. In theory, RFU1 and RFU2 deliver similar amounts of feature-free, wide-field information to the visual cortex in Experiment 6; presumably, the main if not the only difference between the two RFUs is time of arrival. Interestingly, even though both left and right visual cortex receive similar information-impoverished inputs from the two eyes, the retinal origin of each RFU is still perfectly preserved and there is no evidence of interaction at a central level.

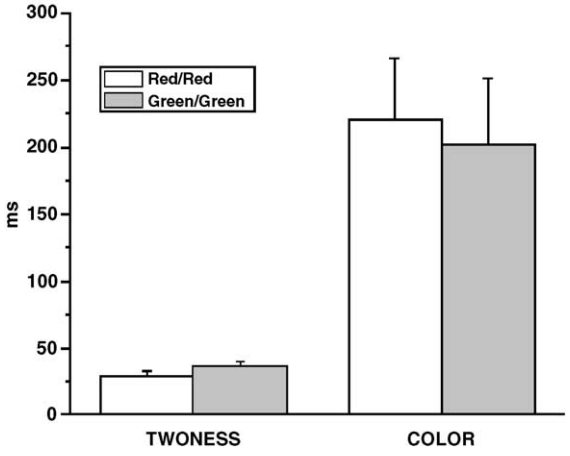

Fig. 4. Twoness and color thresholds for a red–green colorblind subject.

Table 2
Twoness, color, and duration judgments for one colorblind subject

	Red/green mean±S.D.	Green/red mean±S.D.	Green/green mean±S.D.	Red/red mean±S.D.
Twoness	28.7±4.0	36.5±3.1	24.7±5.6	23.1±3.2
Color	220.8±45.9	201.6±49.9		
Duration	All duration judgments unreliable			

$n=5$ for each condition.

3.2.3. Experiment 7. Testing a red–green colorblind subject

A red–green colorblind student was tested five times in each of the monocular red/green, green/red, red/red, and green/green versions of the test. Fig. 4 and Table 2 show the results. His twoness thresholds are both lower (23 and 36 ms) and consistently less variable (S.D. 3–5 ms) than those of any other subject in the study; by this test his eye distinguishes one from two stimuli at a shorter ISI and more reliably than most normal eyes. He also unquestionably detects a difference between red and green pulses, but with difficulty and at unusually long ISIs (220.8±45.9 in the red/green version and 201.6±49.9 in the green/red). As for his answers to the question which lasted longer, his answers were so varied we concluded he was probably merely guessing.

The main purpose of this experiment was to find out whether the responses given by a subject with a known retinal abnormality differ from our norms. The affirmative answer appears, in addition, to have uncovered new information about one variety of color blindness, which suggests that a systematic study of it and the many other types of color disturbance using our ISI procedure might also yield interesting new results.

4. Discussion

4.1. The fate of the four hypotheses presented in the Introduction

1. When the interval between two brief light flashes is progressively increased from zero, normal viewers do in fact fail to report S1 and S2 as separate events until that interval reaches 50–60 ms, which is about 20–25% of the duration of a typical 300 ms RFU. The interval at which a pair of stimuli is first seen as two was measured to be 44 ms more than a century ago (Schafer, 1900); we give it the name twoness threshold here.
2. At the ISI where S1 is first reported as a separate event in the red/green and green/red versions of the experiment, its color is incorrect, and this "error" disappears abruptly when about 35% of RFU1 (ISI about 90 ms) is permitted to reach the cortex. This phenomenon, named the color threshold here, has not been reported previously, so far as we are aware.
3. Subjects do say S1 is shorter in duration than S2 until the interval between them reaches about 300 ms, which is

also the 100% duration of a typical RFU. The ca. 300 ms ISI at which S1 and S2 appear, for the first time, to have the same duration is named the *duration threshold* here; the phenomenon has not been reported previously, so far as we are aware.

4. Two results indicate that the ganglion cell volleys making up an RFU do leave the retina in a precisely ordered way. First, normal subjects have no difficulty identifying the twoness, color, and duration thresholds, and second, the post-stimulus latency they assign to each of these is highly reliable statistically within and across subjects (Table 1).

4.2. General conclusions about the mammalian visual system derived from our experimental results

In the 23 Group I experiments, 13 subjects agreed that the first flash is shorter in duration than the second one until the interval between them reaches about 300 ms. Furthermore, we have always found about 300 ms to be the duration of the entire ganglion cell volley rats send into the optic nerve following light pulse stimulation (Galambos et al., 2000, 2001;Galambos and Juhasz, 2001; Szabo-Salfay et al., 2001). We infer from these findings that the rat, human, and perhaps every mammalian retina requires only about 300 ms to process all the information collected during one fixation, and consider the name Retinal Functional Unit (RFU) to be appropriate to use for these compact ca. 300 ms ganglion cell volleys retinas normally dispatch to the brain.

The Group I experiments also show it is possible to fractionate these human RFUs into a part that reaches the brain for further processing and a part that is lost when a second stimulus follows at a short ISI; furthermore, as the fraction that gets there increases in duration, the perceptual experience grows progressively in richness, detail, and accuracy. This simple dissection process has identified three RFU landmarks–the twoness, the color, and the duration thresholds–which we examine one by one in what follows.

4.2.1. The percept threshold concept

Identifying the time that passes between receiving and perceiving a stimulus is an old problem, and its solution for vision already has at least two names. In 1923 Froelich's term was "Empfindungszeit" (sensation time; see Froelich, 1923). Efron used "processing period" 30 years ago (Efron, 1967, 1970) and gave 60–70 ms as the reasonable value based on estimates the seven investigators he cited had reached with indirect methods (the numbers varied between 60 and 90 ms). These and other investigators have searched for a single "processing time"; by contrast, our Group I experiments have identified three of these, not just one. We will call them percept thresholds, each of which has a unique percept latency.

The event percept threshold is defined as the shortest ISI at which a pair of visual stimuli perceived as one is first perceived as two. When Exner found 44 ms to be the "smallest possible interval between two stimuli to produce two sensations" more than a century ago (Schafer, 1900, p. 614), he also found the event percept threshold of his first stimulus has a latency of 44 ms. In 1972 Boynton published a scholarly examination of what we call the twoness threshold problem listing 72 references (Boynton, 1972), and in that same year Peck and Lindsley reported, for cats, the event percept threshold for the first stimulus of their pair varied between 76 and 90 ms (Peck and Lindsley, 1972). Our situation is unusual in that S1 and S2 are complementary colors which our subjects with normal eyes call orange or yellowish green at all ISIs between zero and about 92 ms. Even so, these subjects saw the pair as one flash at ISIs below 50–65 ms (see Table 1 for details) and as two flashes at longer ISIs. In other words, the event percept threshold of all the S1s in Table 1 was reached when the initial 20–25% of RFU1 arrived at the cortex.

4.2.1.1. Backward masking. When S1 and S2 are the same (e.g., Exner's two electric sparks, or a pair of 1 ms red light pulses) and only one is perceived, it cannot be known which event it is, but when they are different (e.g., a circle and a square), it will always be S2 that is seen (for examples see Breitmeyer, 1984; Ramachandran and Cobb, 1995). ISI experiments in which S2 is perceived and S1 is not have been called either backward masking or metacontrast experiments for about 50 years, and generations of psychologists have been challenged to explain the puzzling counterintuitive fact that S2 is perceived before S1. Currently, a large literature seems agreed that a much discussed but still unexplained process at the cortical level "masks" S1 "backwards" (see Breitmeyer, 1984 for a review).

Our description and definition of the human event percept threshold suggests a completely different answer. S1 is not "masked at the cortical level"; S1 is unseen because 75–80% of the information in its RFU has been prevented from reaching the cortex.

What happens in ISI experiments is that the onset of RFU2 divides RFU1 into two fractions at the point where it overlaps RFU1; the twoness threshold (or its synonym, the event percept threshold) is reached when the initial fraction exceeds 20–25% of RFU1 in ms. In the experiments summarized in Table 1 all event percept thresholds range between 50 and 65 ms, but event percept thresholds can vary more widely than this. Thus for human viewers they ranged between about 20 and 80 ms depending on stimulus duration, type, and luminance as well as the ambient level, the dark interval between the pairs, and the subject's instructions (see Kietzman and Sutton, 1968 for these examples).

4.2.1.2. The pre-percept interval. Note that as the ISI increases from zero and the twoness threshold is approached, the fractionated RFU1 has been delivering increasing amounts of information about S1 to the cortex.

Because S1 is not yet reported to be a perceived event, the information about it is below the level of conscious perception, or, by dictionary definition, subliminal. We suggest *pre-percept interval* as a useful name for such very important subliminal periods. In the psychological literature certain types of priming experiments provide well-known examples of subliminal stimuli that clearly influence the perception of subsequently presented stimuli. As our interpretation of the ISI experiments implies, the ability of the priming stimulus (which is the initial fraction of RFU1) to exert this influence will improve as its duration increases until it finally becomes long enough to be perceived, which, according to Greenwald, typically takes place at around 60–70 ms in such experiments (Greenwald, 1992). Given these facts, priming experiments would appear to be simple examples of fractionated RFU1 experiments in which the subliminal information delivered to the cortex in the pre-percept interval is experimentally identified, quantified, and evaluated.

Two generalizations will summarize this brief discussion of backward masking and priming experiments. First, no stimulus will be perceived as a visual event until a critical initial fraction of the information in its RFU reaches the cortex, and second, as that critical fraction is approached in the pre-percept interval, increasing amounts of information about the stimulus (S1) will reach the cortex and be stored.

4.2.1.3. The color percept threshold. As already stated, when our subjects received red and green pulse pairs they sometimes reported seeing flashes colored orange or yellowish-green. This appears at first glance not to be a new fact about the human visual system because over a hundred years ago Helmholtz knew that, when mixed, the complementary red and green wavelengths are perceived as orange or yellowish. However, he probably did not know that the pair does not have to be presented simultaneously; our viewers saw orange flashes when the green 1 ms pulse was separated by as much as 92 ms from the 1 ms red one. Evidently a retinal perturbation created by a 1 ms red pulse (S1) is stored in some form in the retina throughout the 92 ms during which its interaction with the moving S2 (the 1 ms green pulse) always yields the "orange" sensation. We are unaware of any existing retinal model that deals with these facts. It is also unclear what new retinal process becomes engaged when the subjects suddenly report, at ISIs near and beyond 90 ms, that the red flash is red and the green one green.

A satisfactory description of these retinal processes that result in different color perceptions (first "orange", then "red and green") out of 1 ms red/green pairs will first identify an early subsystem (ISI less than 90 ms) during which the retinal circuits store and "mix" cone responses (to obtain "orange"), followed by a retinal subsystem (at about 90 ms and beyond) that mediates what cortex must receive if it is to produce the "correct" perceptions (red and green) for the two now widely separated 1 ms stimulus pair.

Meanwhile, throughout the ISIs during which RFU1 reaches and moves beyond the twoness and color perception thresholds, S1 and S2 continue to be judged different in duration, with S2, as always, the longer.

4.2.1.4. The duration percept threshold. Our literature search has also failed to find an experiment in which subjects compare two 1 ms flashes for duration and report S2 to be longer than S1 until the ISI is about 300 ms. These duration decisions, which finally identify the percept threshold of duration, prompt the question whether the normal RFU delivers a terminal cue of some sort that signals the cortex all of its information has been downloaded. In any event, the finding seems to reinforce our two major claims (Galambos and Juhasz, 2001): first, all stimulus-initiated retinal volleys last about 300 ms, and second, RFU transfer through the lateral geniculate synapse is monosynaptic because simple (non-"cognitive") rat and human cortical responses are also about 300 ms in duration.

4.2.1.5. Processing details. What happens to the RFU1 fraction attenuated in duration by an overlapping RFU2 after it leaves the eyeball? Our rat experiments make the following sequence highly probable. Each RFU, whether abbreviated or not, reaches the contralateral lateral geniculate, which transfers it monosynaptically to the cortex (Galambos and Juhasz, 2001). Depending on how much S1 information the cortex receives, it will process its RFU input into one or more of the percepts–twoness, color, duration–as well as any others for which percept thresholds remain to be defined. In humans, central processing is not limited, of course, to that 300 ms; cognitive processing to yield the P300, N400, and other waveshapes extracted from the brain waves can add up to hundreds of additional ms (Rugg and Coles, 1995). Given the available evidence, a different but equally satisfactory databased physiological explanation for the percept threshold phenomena we report will be difficult to devise.

5. Conclusions

1. The current popular view of the mammalian visual perceptual mechanism (e.g., Livingstone and Hubel, 1988), which is based mainly on microelectrode evidence collected at all levels from the retinal depths to the cortical surface, generally neglects the functional implications of the optic nerve volleys that leave the retina during such acts as reading (e.g., Martinez-Conde et al., 2000). Our findings begin to supply this analysis with the description of the RFU. Its presently known features, properties and contributions can be recapitulated briefly in the following way.
2. Normal human retinas generate and present to the brain an endless series of ca. 300 ms ganglion cell volleys (RFUs). RFUs are no longer mere theory or hypothesis;

their existence is supported directly by the evidence developed in both the human experiments reported in this paper and by our rat data in the publications already cited. Indirect evidence also comes from the fact people everywhere transfer information visually, at a 2–4 Hz rate, from what they see on a printed page to a memory of what has just been read. The probability is remotely small that someone will ever demonstrate that the normal retina of a behaving rat, cat, or primate is not producing RFUs.

3. This view of retinal processing is heuristic; it has already prompted informative new experiments and supplied databased interpretations for old perceptual conundrums. A few examples can be noted. We chose the ISI procedure when we realized the first of two 300 ms RFUs will be overlapped by the second whenever the ISI is less than 300 ms, and predicted from this inferred fact that the perception of S1 will vary in systematic ways with ISI. As we have seen, ISI experiments do indeed control how much of the information in RFU1 reaches the cortex, and the number and types of perceptions viewers experience do indeed increase in proportion to how much of RFU1 is permitted to get there. Hence the experiments affirm the hypotheses stated in our Introduction: manipulation of the S1–S2 interval profoundly influences perception of S1. The ISI technique has also revealed the new fact that the retina processes 1 ms red/green photon streams in different ways before and after RFU1 reaches the color percept threshold, a result that raises interesting questions like the following. If 1 ms blue and yellow photon streams are similarly separated in an ISI experiment, would they appear to be white up to and beyond a twoness threshold and then, like our red/green pair, reach a color threshold when the ISI nears 100 ms?

As for those old conundrums, the awkward but durable idea S2 “masks” S1 “backward” at the cortical level is likely to yield to the evidence established by our experiments: a stimulus event will not be reported as perceived unless and until a threshold amount of the information in its RFU reaches the cortex. Among several recent demonstrations of this rule, the MEG study of Liu et al. (2002) shows subjects correctly distinguish an automobile from a face after 90 ms exposures (about 30% of their RFUs, we presume) but require exposures of 170 ms (about 56%) in order to name faces correctly.

Finally, emboldened by the new data, correlations, and conclusions just listed, we predict suitable experiments will identify many more percept thresholds in the RFU 50–300 ms range. After all, every bit of information the cortex uses to produce a visual perceptual experience was first encoded in the ca. 300 ms RFUs the retinas created out of momentary photoreceptor versions of the visible environment.

Acknowledgements

We thank the subjects for participating and S.A. Hillyard and M. Loop for critical advice on the interpretation of the data. NSZ and GJ were supported by grants OTKA TS044711 and MEDICHEM 8_11.

References

Boynton, R.M., 1972. Discrimination of homogeneous double pulses of light. In: Jameson, D., Hurvich, L.M. (Eds.), Visual Psychophysics. Springer, Berlin, Germany, pp. 202–232.

Breitmeyer, B.G., 1984. Visual Masking: An Integrative Approach. Clarendon, Oxford, UK.

Efron, R., 1967. The duration of the present. Annals of the New York Academy of Sciences 138, 713–729.

Efron, R., 1970. The minimum duration of a perception. Neuropsychologia 8, 57–63.

Froelich, F.W., 1923. Über die Messung der Empfindungszeit. Zeitschrift für Sinnesphysiologie 54, 58–78.

Galambos, R., Juhasz, G., 2001. How patterns of bleached rods and cones become visual perceptual experiences: a proposal. Proceedings of the National Academy of Sciences of the United States of America 98, 11702–11707.

Galambos, R., Szabo-Salfay, O., Barabas, P., Palhalmi, J., Szilagyi, N., Juhasz, G., 2000. Temporal distribution of the ganglion cell volleys in the normal rat optic nerve. Proceedings of the National Academy of Sciences of the United States of America 97, 13454–13459.

Galambos, R., Szabo-Salfay, O., Szatmari, E., Szilagyi, N., Juhasz, G., 2001. Sleep modifies retinal ganglion cell responses in the normal rat. Proceedings of the National Academy of Sciences of the United States of America 98, 2083–2088.

Greenwald, A.G., 1992. New look 3. Unconscious cognition reclaimed. American Psychologist 47, 766–779.

Kietzman, M.L., Sutton, S., 1968. The interpretation of two-pulse measures of temporal resolution in vision. Vision Research 8, 287–302.

Liu, J., Harris, A., Kanwisher, N., 2002. Stages of processing in face perception: an MEG study. Nature Neuroscience 5, 910–916.

Livingstone, M., Hubel, H., 1988. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science 240 (4853), 740–749.

Martinez-Conde, S., Macknik, S.L., et al., 2000. Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. Nature Neuroscience 3 (3), 251–258.

Peck, C.K., Lindsley, D.B., 1972. Average evoked potential correlates of two-flash perceptual discrimination in cats. Vision Research 12, 641–652.

Ramachandran, V.S., Cobb, S., 1995. Visual attention modulates metacontrast masking. Nature 373, 66–68.

Rugg, M.D., Coles, M.G.H., 1995. Electrophysiology of Mind. Oxford University Press, New York.

Schafer, E.A., 1900. The cerebral cortex. In: Schafer, E.A. (Ed.), Textbook of Physiology. Young J. Pentland, New York, pp. 592–615.

Szabo-Salfay, O., Palhalmi, J., Szatmari, E., Barabas, P., Szilagyi, N., Juhasz, G., 2001. The electroretinogram and visual evoked potential of freely moving rats. Brain Research Bulletin 56, 7–14.