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Sensitivity to stimulus onset and offset in the S-cone pathway

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Abstract

Previous work [Vassilev, A., Mihaylova, M., Racheva, K., Zlatkova, M., & Anderson, R. S. (2003). Spatial summation of S-cone ON and OFF signals: Effects of retinal eccentricity. *Vision Research*, *43*, 2875–2884; Vassilev, A., Zlatkova, M., Krumov, A., & Schaumberger, M. (2000). Spatial summation of blue-on yellow light increments and decrements in human vision. *Vision Research*, *40*, 989–1000] has shown that spatial summation of brief S-cone selective stimuli depends on their polarity, increments or decrements, suggesting involvement of S-ON and OFF pathways, respectively. This assumption was tested in two experiments using a modified two-color threshold method of Stiles to selectively stimulate the S-cones. In the first experiment we measured detection threshold for small 100 ms S-cone selective increments and decrements presented within three types of temporal window, rectangular, ramp onset/rapid offset and rapid onset/ramp offset. The ramp-onset threshold was higher than the ramp-offset threshold regardless of stimulus sign. In the second experiment we measured reaction time (RT) with near-threshold stimuli spatially coincident with the background to avoid spatial contrast. RT distribution for S-cone selective 500 ms increments and decrements was unimodal and followed stimulus onset. An increase of stimulus duration to 1000 and 2000 ms resulted in the appearance of responses following stimulus offset. The results suggest that, for *brief* S-cone selective increments or decrements, the human visual system is more sensitive to stimulus onset than to stimulus offset. Only for longer stimuli is the offset important, probably due to slow adaptation at a postreceptoral level.

Keywords: S-cones; ON/OFF pathways; Reaction time; Color vision

1. Introduction

The primate retina contains three types of cones subserving daylight vision with sensitivity maxima in different regions of the visible spectrum: short wavelength sensitive (S-cones), middle wavelength sensitive (M-cones) and long wavelength sensitive (L-cones). The signals originating from the M- and L-cones are segregated at the bipolar cell level into ON and OFF retino-geniculo-cortical pathways driven by luminance increase or decrease (Kuffler, 1953; reviewed by Fiorentini, Baumgartner, Magnussen, Schiller, & Thomas, 1990; Wässle & Boycott, 1991). Segregation of the S-cone signals into ON and OFF pathways is less well understood and is still a matter of debate (reviewed, e.g. by Calkins, 2001; Lee, 1996; Martin, 1998; Vassilev, Mihaylova, Racheva, Zlatkova, & Anderson, 2003; for recent controversial viewpoints see Lee, Telkes, & Grünert, 2005). The majority of morphological, physiological and psychophysical data favors the existence of separate S-ON and S-OFF pathways. According to most electrophysiological findings, S-OFF cells are encountered much more rarely than S-ON cells in primate retina and LGN (e.g. De Monasterio, 1979; Derrington, Krauskopf, & Lennie, 1984; and recently Smajda, Buzas, FitzGibbon, & Martin, 2006). This relationship seems to change radically at the cortical level. Callaway (2005) reported a "surprisingly large number of LGN-afferents in superficial layers of the primary visual cortex with blue-OFF inputs". De Valois, Cottaris, Elfar, Mahon, and Wilson (2000) found that the S-OFF input to simple cells in the macaque striate cortex is as common as the S-ON input.

The asymmetrical representation of S-cone ON and OFF pathways (at subcortical level, at least) should be reflected

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in the spatial characteristics of S-cone vision. In previous works, we measured Ricco's area of complete spatial summation (Vassilev, Zlatkova, Krumov, & Schaumberger, 2000; Vassilev et al., 2003). The two-color threshold method of Stiles (Wyszecki & Stiles, 1982) was modified by initially adding blue light to a bright yellow background in order to subsequently present blue-light increments and decrements. While of similar size for both stimuli in the central retina (up to 5–10 deg eccentricity), beyond this Ricco's area increased much faster for decrements and was 2–4 times larger than Ricco's area for increments at 20 deg from fovea. The estimated average number of S-cones, covered by Ricco's area at 20 deg along the temporal meridian was about 45 for increments and about 100 for decrements. The difference could not be attributed to optical factors and was assumed to be due to a difference in the spatial properties of the S-cone ON and OFF pathways.

Selective stimulation of the ON or OFF pathways is not an easy task due to possible increases or decreases in the background activity of each that could convey information about stimulus onset and offset (Bowen, 1997). Different approaches have been used in preceding works such as combining adapting and test stimuli with ramped onset or offset (e.g. De Marko, Smith, & Pokorny, 1994; Krauskopf, 1980; Krauskopf, Williams, & Heeley, 1982; Shinomori, Spillmann, & Werner, 1999), masking of stimulus onset or offset (Schwartz, 1996) and pharmacological blocking of the ON pathways in the monkey (Smith, Harwerth, Crawford, & Duncan, 1989). Vassilev et al. (2000, 2003) have assumed that detection of brief S-cone increments is mediated by ON pathways and detection of brief S-cone decrements is mediated by OFF pathways but this assumption has not been verified. The stimulus was a 100 ms rectangular pulse meaning that, regardless of stimulus sign, it included both a luminance increment and decrement. In the case of increments, luminance increase took place at stimulus onset and luminance decrease took place 100 ms later at stimulus offset. The reverse was true for decrements. Thus the relevance of their data to the ON/OFF dichotomy of the S-cone pathway might only be valid if, under their experimental conditions, the visual system was more sensitive to stimulus onset than to its offset.

Two types of experiments were performed to test this assumption. In the first experiment we measured detection threshold for blue-on-yellow test stimuli presented within different temporal windows: (1) rectangular window, (2) ramp onset/rapid offset or (3) ramp offset/rapid onset (see Fig. 1). If the onset contributes more than the offset to detection of rectangular pulses, stimuli with ramp onset should have higher threshold than stimuli with ramp offset.

In the second experiment, we used the reaction time paradigm of Tolhurst (1975) with near-threshold long-lasting stimuli to provide an independent second comparison of sensitivity to stimulus onset and offset. Tolhurst presented gratings of different spatial frequency and found that reaction time distribution (RTD) was bimodal at low spatial frequency with responses associated with stimulus onset

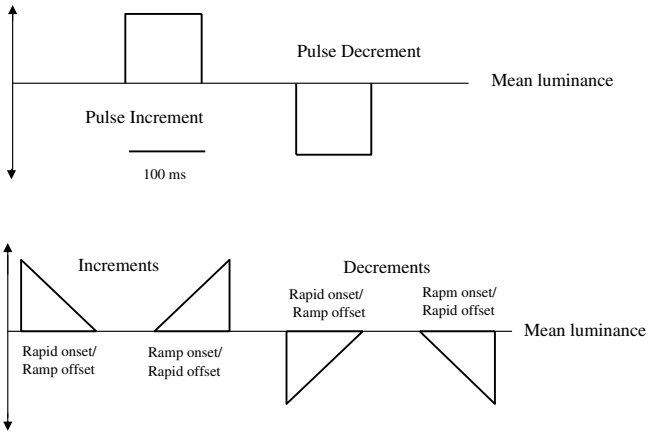

Fig. 1. Schematic of the test stimuli with different temporal windows, presented in Experiment 1. Duration for all stimuli was 100 ms.

or offset and unimodal at high spatial frequency with RTD rising quickly after stimulus onset and decaying exponentially. His inference was that low spatial frequencies are processed by a transient mechanism while high spatial frequencies are processed by a sustained mechanism. The same paradigm was used by Schwartz and Loop (1982) as well as by Schwartz (1992) to compare the temporal properties of the chromatic and achromatic systems. Stimulus duration in their studies was 1000 ms and detectability was about 80%. Luminance modulation (white-on-white or red-on-red) resulted in bimodal RTD similar to RTD at low spatial frequency. Colored stimuli were presented on a white background following King-Smith and Carden (1976) who have shown that some wavelengths, when presented on a white background, are detected by their color under near-threshold conditions. Colored stimuli gave rise to unimodal RTD rising quickly after stimulus onset and decaying exponentially like RTD at high spatial frequency. Schwartz and Loop (1982) reported also that extension of stimulus duration to 2000 ms did not result in a lengthening of the RT histogram as expected for a fully sustained mechanism. They concluded that color detection was mediated by a mechanism with a longer response window than the luminance onset detection but was not truly sustained and thus named it "quasi-sustained".

An important feature of the results obtained by Schwartz and Loop (1982) and Schwartz (1992) is the lack of responses associated with the offset of colored stimuli. Their findings support the assumption (not explicitly stated by them) that, under some conditions, the offset of colored stimuli does not contribute to their detection. The lack of responses to stimulus offset in these experiments suggests that the paradigm can be applied to compare the sensitivities of the S-cone system to the stimulus onset and offset. Some of their experimental conditions have probably favoured S-cone selective stimulation yet the inference about the lack of stimulus-offset contribution to its detection cannot readily be applied to our previous experiments (Vassilev et al., 2000, 2003). We compared responses to S-cone increments and decrements while Schwartz's experi-

ments involved increments only. The difference in the behavior for S-cone increments and decrements found by us concerns the retinal periphery and Schwartz presented the stimuli in the central retina. Central and peripheral retina are known to differ markedly in their temporal properties. Being concerned with color vision in general, Schwartz did not specify the spectrum of his white background and no inferences about the adaptational state and relative sensitivity of each cone type and rods to the stimuli are possible. Recent studies have found large differences between RTs to rod-selective increments and decrements (Cao, Zele, & Pokorny, 2007). Rod intrusion might have affected RTD in Schwartz's experiments. All the above indicate the necessity of obtaining RTDs with S-cone increments and decrements under the conditions of our previous experiments.

2. Methods (General)

In both experiments, the two-color threshold method of Stiles was used to selectively stimulate the S-cones (Wyszecki & Stiles, 1982). The apparatus has been previously described (Vassilev et al., 2000). The source of blue light was a monitor (17-in. EIZO T562-T), controlled by a Visual Stimulus Generator (VSG 2/3, Cambridge Research Systems). The refresh rate was 100 Hz. The monitor screen was partially masked and its angular size was 29 deg horizontally and 21 deg vertically at a viewing distance of 57 cm. A slide projector back-illuminated a milk plexiglass to provide the bright yellow component. Both sources were superimposed at the eye by a neutral semitransparent mirror. The beam of the slide projector was passed through a yellow glass filter (PITMO–OC12 with transmission maximum at 600 nm, half-height at 560 and 700 nm and virtually no transmission below 530 nm). The spectrum of the light sources is illustrated in Vassilev et al. (2000). Spectra and luminance were measured at the eye position.

The experiments were performed in a dark room. Viewing was with the right eye through the natural pupil. Its diameter was about 4 mm at the background intensities employed in most experiments. Observers adapted for 10 min in darkness and then to the background for 2 min. The background consisted of intense yellow light (360 cd/m^2) to which some blue light (1.4 cd/m^2) was added. Previous experiments of ours have shown that the threshold/background intensity curve reached a plateau above 220 cd/m^2 thus becoming independent of the background level (Vassilev et al., 2000). The background intensity of 360 cd/m^2 (about 4500 photopic trolands for a pupil diameter of 4 mm) was assumed high enough to isolate the S-cone mechanism at the detection threshold. The test stimulus was a luminance increase or decrease over a variable area of the blue component. Stimulus spatial and temporal parameters were different in the two experiments reported here and are specified in the relevant sections (Experiments 1 and 2).

Three observers took part in Experiments 1 and 2 (KR, MSM and ZS) and a forth observer (IH) took part in Experiment 2. Observers were 27, 31, 53 and 27 years old, respectively. The first three served also in our previous experiments (Vassilev et al., 2003). Observers color vision was tested by Rabkin's color plates (Eighth Edition, Moscow, 1985), and Album Tritan de Ph. Lantony (Lineau Ophtalmologie, Paris, 1985). No test revealed color perception abnormalities in any observer. Informed consent was obtained from each of them before testing. KR, MSM and IH needed no optical correction, ZS required a +1D spherical-lens correction.

3. Experiment 1: Effect of stimulus temporal window on the detection threshold

3.1. Methods

The stimuli consisted of luminance increments or decrements over a circular area 1–1.4 deg in diameter depending on the observer's sensitivity. For both stimulus types, three types of temporal window were used (Fig. 1): rectangular (rapid onset and offset), ramp onset/rapid offset and rapid onset/ramp offset. The stimuli were presented at 15 deg from the fixation mark along the temporal horizontal meridian. Stimulus duration was 100 ms.

The observer triggered the stimuli by pressing a button. The psychophysical procedure was a two-interval forced choice method combined with a staircase procedure (three correct-one incorrect variant). Two other buttons were used to report the interval during which the stimulus was seen. Step size was 0.05 log units. The staircases for increments and decrements were randomly interleaved. The procedure continued until each staircase accumulated six reversals around a steady level. The threshold was measured as $\log \Delta I/I$ in percent, where ΔI is the threshold luminance modulation and I is the luminance of the blue background component. The threshold value was the geometric mean of the last six reversals. A daily session lasted about 40 min and included 2–3 staircases with each stimulus type. The data presented below are the geometric means of 7–10 staircases.

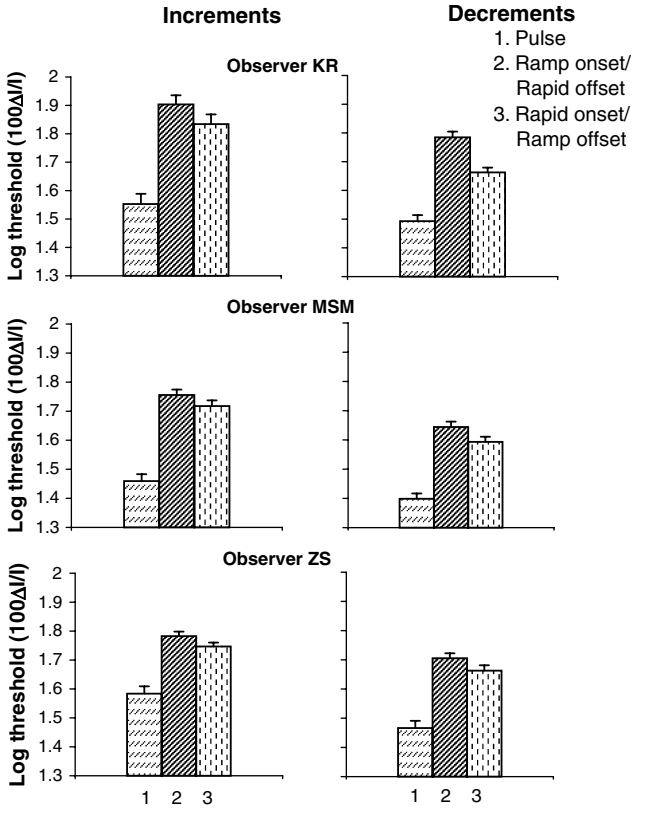

Fig. 2. Log threshold for detecting pulsed and ramped blue-on-yellow stimuli. Left—increments, right—decrements. Left column in each group—pulse stimuli, middle column—ramped onset, right column—ramped offset. Vertical bars—95% confidence interval. Data for all ovservers.

3.2. Results

The results are presented in Fig. 2. Each pair of graphs shows the results obtained with one observer. The left graph is for increments and the right graph is for decrements. Each graph consists of three columns. The left column is for rapid onset–offset (rectangular pulses), the middle is for ramp onset/rapid offset and the right is for rapid onset/ramp offset. Vertical bars represent the 95% confidence interval. The threshold was lowest with rectangular temporal window as expected in view of the highest stimulus energy in this case. It is obvious from Fig. 1 that the rectangular window allowed twice as powerful a stimulus to be presented in comparison with the ramp windows. The threshold for rectangular pulses was lower by 0.2–0.3 log units in comparison with the stimuli presented within a ramp temporal window. The mean difference across observers and stimulus conditions was 0.24 log units. It was significantly lower ($p < 0.005$) than the expected 0.3 log units difference according to Bloch's law of complete energy integration. The deviation is probably related to incomplete temporal summation at the stimulus duration of 100 ms (see Section 3 for an estimate of critical duration). The main finding, seen from Fig. 2, is that in comparison with the rectangular pulses the absence of a rapid onset increased the threshold more than the absence of rapid offset.

The onset–offset difference was small but consistent across the observers. Two-factor with replication ANOVA (Statistica, 1984–2000, Stat Soft, Inc) was used to separately test each observer's data for the effects of the following factors: (1) ramp temporal waveform type, i. e. the ramp position at stimulus onset or offset; (2) stimulus polarity, increment or decrement. The effect of each factor was significant (Table 1) but no interaction among the factors was found. The significance of the temporal window was not imposed by the pulse stimuli (those data were not included in the analysis) and is somewhat surprising in view of the small effect of the ramp position. The results suggest that the visual system is more sensitive to the onset than to the offset of rectangular stimuli irrespective of stimulus sign, increment or decrement. An additional finding was the effect of stimulus polarity on the detection threshold. In all but one of nine cases (MSM, rectangular pulse) the threshold was lower for decrements than for increments.

Table 1
Two-factor with replication ANOVA (Experiment 1)

	df	MS effect	*df*	MS error	*F*	*p*-level
Observer KR						
Ramp position	1	0.076	32	0.004	19.590	0.0001
Stimulus polarity	1	0.179	32	0.004	46.291	0.0000
Position × polarity	1	0.009	32	0.004	2.302	0.1390
Observer MSM						
Ramp position	1	0.029	65	0.006	4.907	0.0303
Stimulus polarity	1	0.149	65	0.006	25.379	0.0000
Position × polarity	1	0.000	65	0.006	0.064	0.8010
Observer ZS						
Ramp position	1	0.023	52	0.004	5.948	0.0182
Stimulus polarity	1	0.095	52	0.004	25.015	0.0000
Position × polarity	1	0.003	52	0.004	0.749	0.3908

The relatively small ramp effect might be due to the short stimulus duration (100 ms) and therefore short ramp interval. This duration was selected in order to be the same as in the experiments of Vassilev et al. (2000, 2003) and to avoid eye movement artifacts. We looked, therefore for an additional comparison of the sensitivity to stimulus onset and offset.

4. Experiment 2: Reaction time distribution with near-threshold S-cone increments and decrements

4.1. Methods

The apparatus used in Experiment 1 also generated the stimuli and background in Experiment 2. A response box of our own design was connected to the computer to trigger the trials and measure reaction time (RT). It incorporated a timer and a processor. Stimulus control was within the Windows environment and our program blocked any other parallel processing during a trial. The timer was triggered immediately at stimulus onset and stopped on the press of a second key on the response box Interruption of the electrical chain by pressing on the key, i.e. the start of response, stopped the timer.

Long stimulus durations are needed in order to separate reactions to stimulus onset from reactions to stimulus offset. Stimulus duration of 500 ms was selected in pilot experiments. While the duration of 500 ms was found long enough to separate onset from offset reaction times, stimuli of 1000 and 2000 ms were also presented in order to verify whether or not the response to near-threshold stimuli is related to stimulus transients (Tolhurst, 1975).

The retinal image of a long-lasting stimulus of small size would move over the retina due to fluctuations in eye position and lens accommodation thus creating temporal transients. Such transients should be avoided in view of our aim to study the efficiency of stimulus onset and offset. Our solution to the problem was the following. Both stimulus and background were large and spatially coincident. They subtended 29 deg horizontally and 21 deg vertically at the eye, i.e. they covered the entire monitor screen. No fixation mark was used since it would also give rise to spatial contrast during stimulus presentation. The observers were merely asked to look at the middle of the field. Since RT was measured with near-threshold stimuli, we assumed that the boundaries between the stimulation field and its dark surround were too distant and changed their color too little to affect RT.

The test stimulus was a luminance increment or decrement of the blue background component. The observer started each trial by pressing a button. This was followed immediately by a warning click. Stimulus onset was ran-

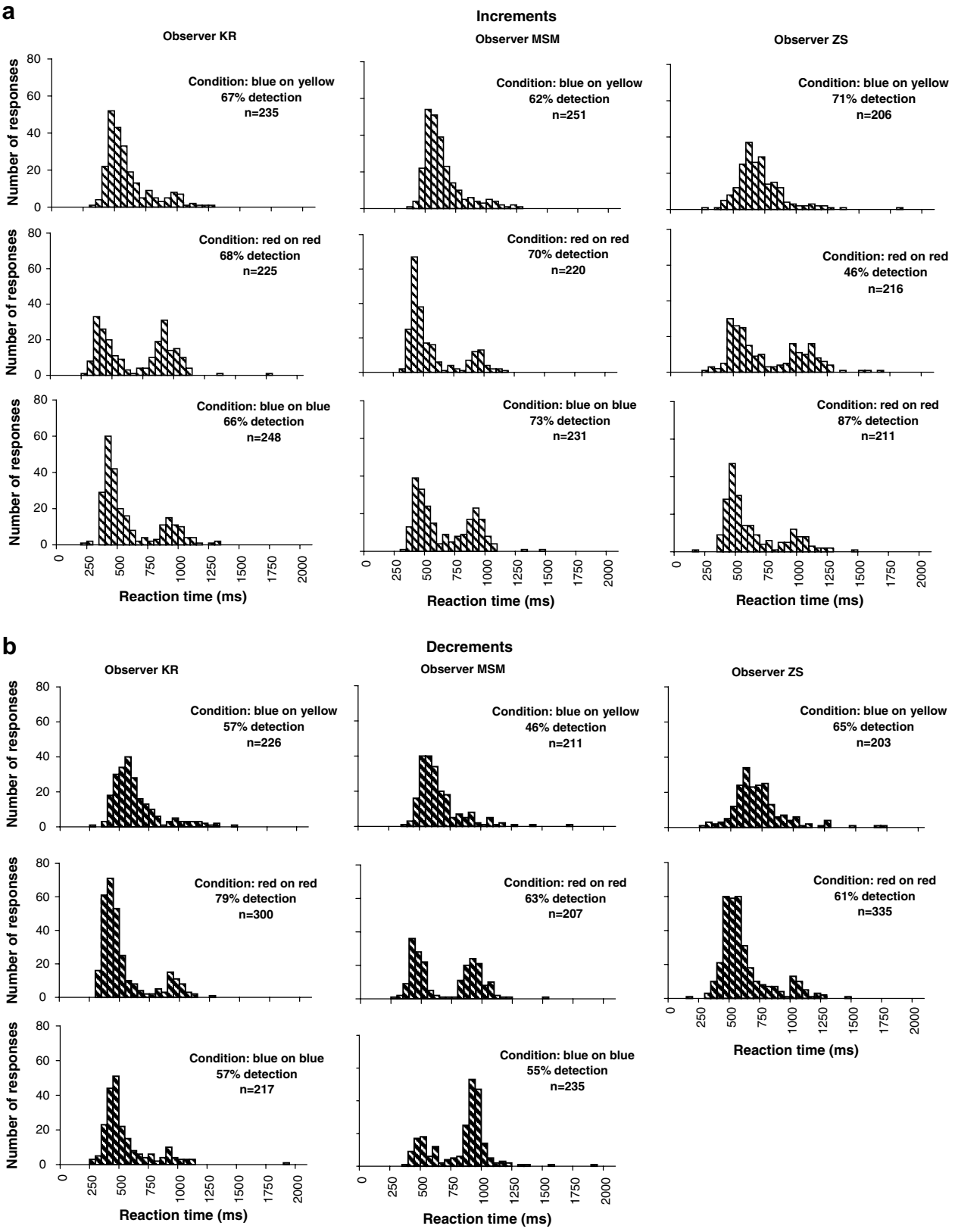

Fig. 3. (a) RTDs with blue-on yellow, red-on-red and blue-on-blue increments. Stimulus duration 500 ms. RTDs with the highest and at the same time closest percentage of misses were compared. Data for all observers. (b) RTDs with blue-on yellow, red-on-red and blue-on-blue decrements. Stimulus duration 500 ms. RTDs with the highest and at the same time closest percentage of misses were compared. Data for all observers.

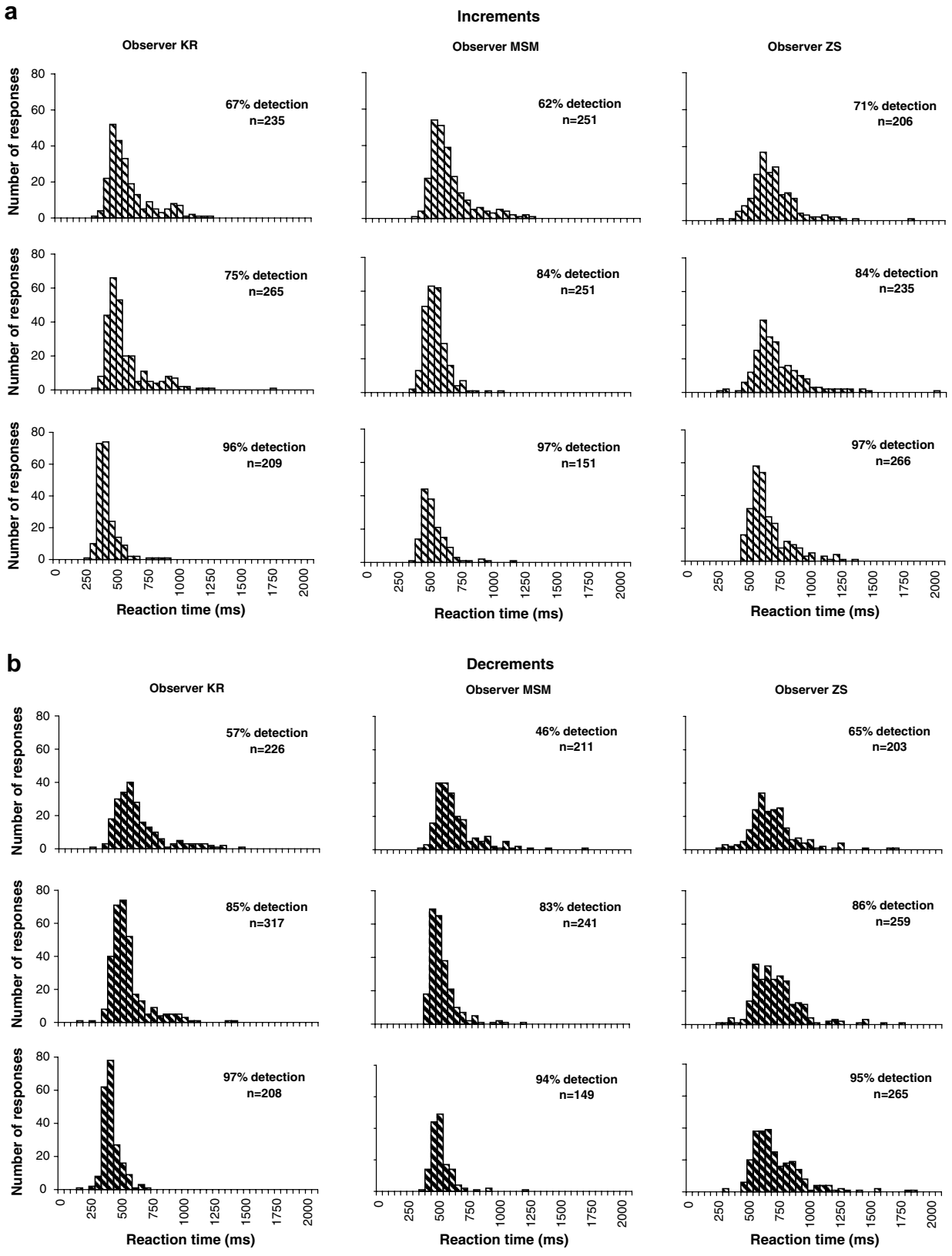

Fig. 4. (a) Comparison of RTDs with near-threshold blue-on-yellow increments at different detection levels. Data for all observers. (b) Comparison of RTDs with near-threshold blue-on-yellow decrements at different detection levels. Data for all observers.

domized within the 800–1200 ms range following the warning signal according to a negative exponential function. Check trials with a probability of 0.2 were randomly mixed with trials containing a stimulus. Their presence

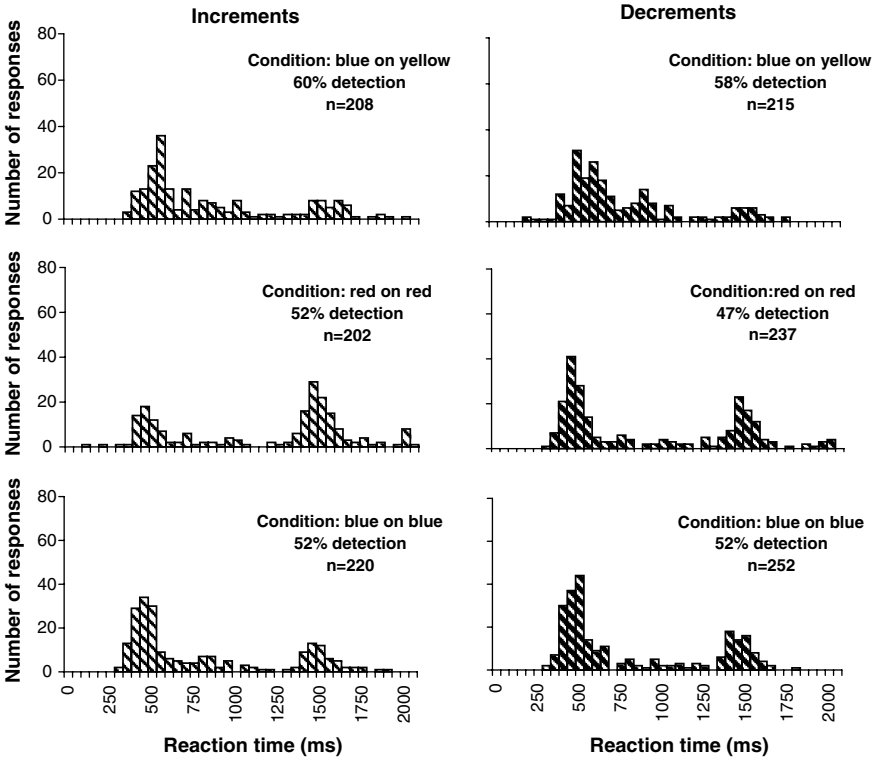

Fig. 5. RTDs with 1000 ms blue-on-yellow, red-on-red and blue-on-blue stimuli. Observer KR.

maintained the uncertainty about stimulus occurrence until the end of the warning interval.

Control experiments with blue-on-blue and red-on-red stimuli were run in separate daily sessions. The background was blue (1.4 cd/m^2) or red (6 cd/m^2) light in these cases. The only difference between the blue-on-blue and blue-on-yellow experiment was the absence/presence of the yellow background component.

The same three observers took part in Experiment 2 at the stimulus duration of 500 ms. They were instructed to press a button on the response box as soon as possible on detecting that something changed in the stimulation field. Their detection threshold was first measured and RT was recorded at several near-threshold levels. This allowed us to collect RT data within the 50–100% frequency range of stimulus detection and compare RT distributions at different levels of signal detectability. One of the observers (KR, an author) and a new naïve observer (IH) took part in the RT measurements at the stimulus duration of 1000 or 2000 ms.

A daily session consisted of 6 blocks (5 with observer MSM) and each block consisted of 60 trials. Increments and decrements were randomly interleaved within a block. Each daily session lasted about 1 h and included 1–3 min of rest between the blocks and 10 min rest after the third block. The sessions were repeated until the accumulation of at least 200 RTs with two exceptions (149 and 151 RTs, Fig. 5, Observer MSM). Observer ZS could not participate in the blue-on-blue controls.

4.2. Results

The false alarms were less than 5%. RT distributions (RTDs) are shown in Figs. 3–6. The column width is 50 ms. RT grouping at this interval was found suitable to visualize response locking to stimulus onset and offset. Fig. 3a represents the RT distribution for the three types of increments, blue-on-yellow, blue-on-blue and red-on-red and stimulus duration of 500 ms. Fig. 3b illustrates the results for decrements. The RTDs for red-on-red and blue-on-blue (the middle and lower rows in Fig. 3) were clearly bimodal with a peak separation of about 500 ms. The first peak followed stimulus onset by 300–400 ms and the second peak followed stimulus offset by approximately the same delay. As seen in the upper row in Fig. 3a and b, the frequency of responses to blue-on-yellow stimuli rose to a peak and then decayed without forming a second peak.

RTD depends on stimulus detectability. As stimulus contrast increases, the frequency of responses to stimulus onset increases thus diminishing the chance of responses to stimulus offset. It was, therefore, important to ensure that the difference in RTDs among the three types of stimuli was not due to the selected stimulus contrast and, thus due to detection rate. Fig 4 represents RT distributions for blue-on-yellow stimuli from the lowest to the highest detection levels. Data for all three observers are presented. No distribution exhibited clusters of responses to both stimulus onset and offset that were typical with red-on-red and blue-on-blue stimuli.

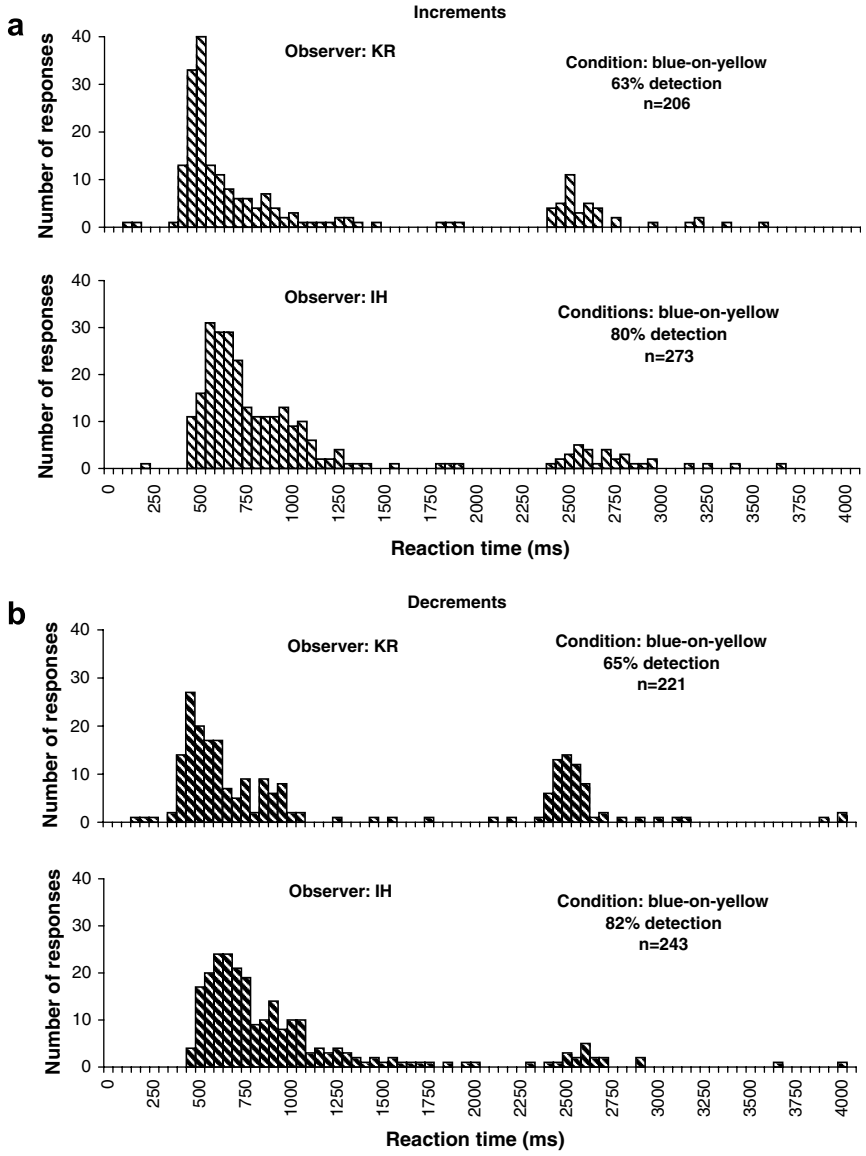

Fig. 6. (a) RTDs with 2000 ms blue-on-yellow increments. Observers KR and IH. (b) RTDs with 2000 ms blue-on-yellow decrements. Observers KR and IH.

Locking the peak in the RTDs to stimulus onset and offset can be made explicit by varying stimulus duration. Fig. 5 shows RT distributions obtained with stimuli lasting 1000 ms. The graphs for red-on-red and blue-on-blue stimuli are bimodal again with the peaks separated by approximately 1000 ms thus supporting the assumption that most responses to these stimuli are triggered by stimulus onset and offset. RTDs obtained with blue-on-yellow stimuli that lasted for 2000 ms are presented in Fig. 6. The increased stimulus duration changes the distribution of responses to the blue-on-yellow stimuli converting it from unimodal to bimodal. The second peak followed the first one by a time interval similar to stimulus duration, 1000 or 2000 ms, as should be for responses related to stimulus offset. It was usually lower than the second peak for red-on-red and blue-on-blue stimuli. Increasing stimulus duration from 1000 to 2000 ms increased the amplitude of the second peak (Observer KR, Figs. 5 and 6).

Of particular interest (see Section 3) is the effect of stimulus duration on the distribution of responses grouped around the first mode. The distributions at the shortest and longest durations (500 and 2000 ms) are compared in Fig. 7. Note that RTDs are presented in a way different from the preceding figures. Histograms would have overlapped and are substituted by curves. Furthermore, each point in the graphs represents the frequency of responses within a given time interval as the percentage of all responses shorter than 2000 ms instead of the number of responses in the preceding figures. This way of data comparison eliminates the effect of difference in the total number of responses recorded in the separate stimulus conditions. It also eliminates the effect of responses related to stimulus offset that were seen at stimulus duration of 2000 ms only. RTDs obtained at similar levels of

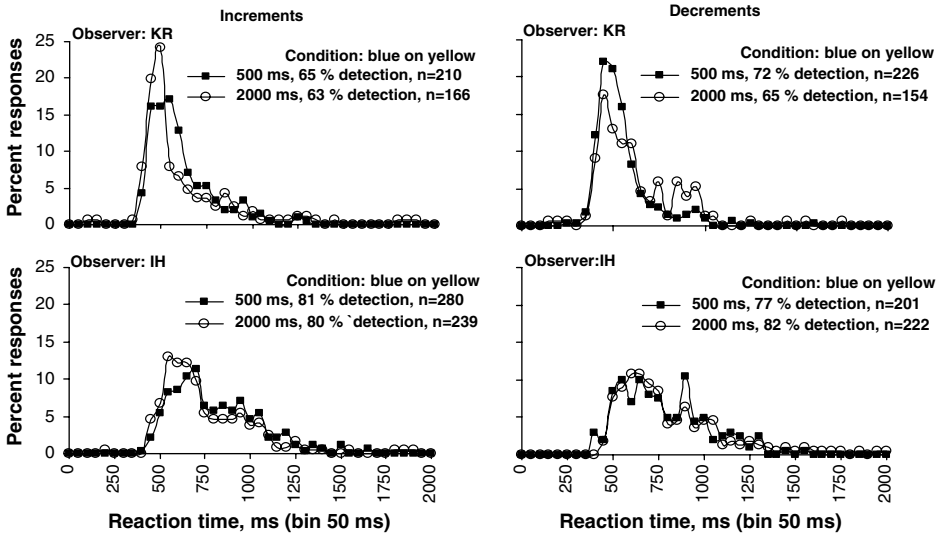

Fig. 7. RTDs locked to the onset of stimuli lasting for 500 or 2000 ms. The distributions are presented by curves rather than histograms in order to reduce crowding.

detectability are compared. The RTDs were asymmetric with a shallower right descending branch that often formed a plateau. These characteristics were common for both stimulus durations. The curves at 500 and 2000 ms overlap each other to an extent suggesting that stimulus duration did not affect the distribution of responses that follow stimulus onset.

5. Discussion

The results of the present experiments can be summarized in the following way. The threshold of S-cone selective (blue-on-yellow) stimuli presented within a ramp temporal waveform depended on the ramp position. The threshold of stimuli with ramp onset was higher than the threshold of stimuli with ramp offset regardless of stimulus sign, increment or decrement (Fig. 2). Reaction-time distribution (RTD) for brief, 500 ms rectangular S-cone increments and decrements was unimodal and indicated that reaction time was mainly locked to stimulus onset. At longer stimulus duration, 1000 ms and particularly 2000 ms, a number of responses formed a second peak locked to stimulus offset (Figs. 5 and 6). Stimulus duration did not affect the distribution of responses grouped around the onset peak (Fig. 7). These results show that the human visual system is more sensitive to the onset than to the offset of brief S-cone selective stimuli regardless of stimulus polarity, increment or decrement. An additional finding was a higher increment threshold than the decrement threshold. Several topics related to these results are discussed below.

5.1. Sensitivity to the onset and offset of S-cone selective stimuli

The difference between the detection thresholds for stimuli with ramp onset or offset was small (Fig. 2). A possible reason for the small effect is that a temporal window of 100 ms was not long enough to reveal to their full extent the significance of stimulus onset or offset for detection by a slow system like a color pathway and particularly the S-cone pathway. Swanson, Ueno, Smith, and Pokorny (1987) have shown that the impulse response function (IRF) for chromatic stimuli is unimodal and of longer time constant than IRF for luminance stimuli. Shinomori and Werner (2003) have found that the IRF for the S-cone system has a much longer time constant than the luminous IRF. Consistent with these data is the longer duration of complete temporal summation of S-cone selective stimuli than of luminance stimuli (Murzac, Vassilev, & Zlatkova, 2003). Since the experimental conditions in the last study were identical to the present one, it is important to note that the estimated time interval of complete summation was of the order of 70 ms at the retinal position tested in the present experiments. These data may explain why detection of the 100 ms ramped waveform was largely, but not wholly, independent of the position of the transient (onset or offset). (Remember that no longer stimulus durations were used in order to avoid generation of temporal transients by eye movements.) Therefore, we consider the difference between the ramp-onset and ramp-offset thresholds as a qualitative rather than quantitative evaluation of sensitivity to stimulus onset and offset. Indeed, the results of Experiment 2 suggest much lower sensitivity to the offset than to the onset of short-lasting S-cone selective stimuli.

The results of Experiment 2 are consistent with those of Schwartz and Loop (1982) and Schwartz (1992) who compared RTDs in response to near-threshold chromatic and achromatic increments. In their experiments, the RTDs of achromatic stimuli were bimodal and RTDs of chromatic stimuli were unimodal. Furthermore, the RT mode of chromatic stimuli was delayed in comparison with that of achromatic stimuli. The same features can be seen in

our Figs. 3–5. Three of our findings, relevant to the discussion about the relationship between sensitivities to stimulus onset and offset as well as to the type of response, transient or sustained, are to be noted: First, RTs to S-cone selective stimuli were collected over a wide range of stimulus detectability. This ensured that the unimodal RTD with our brief S-cone selective stimuli was not a result of a high percentage of responses triggered before stimulus offset. Second, the interval between the two modes in the bimodal RTDs matched stimulus duration (Figs. 3, 5 and 6). This finding supports the assumption that most responses were triggered by stimulus onset and offset including the responses to long lasting S-cone selective stimuli. Third, the first mode in a RTD with S-cone selective stimuli was sometimes followed by a plateau (e.g. Figs. 6a, b and 7, Observer IH). Such RTDs might result from responses of a sustained mechanism sensitive to stimulus presence rather than stimulus transients. If that were the case, an increase of stimulus duration would have increased the variance of responses that follow stimulus onset. The comparison between RTDs at 500 and 2000 ms did not confirm this prediction. As seen in Fig. 7, the distributions were similar to each other. On the other hand, RTD with S-cone selective stimuli tended to be wider than RTD with luminance stimuli locked to stimulus onset. All these properties can be explained by the larger time constant of the S-cone impulse response function (Shinomori & Werner, 2003) resulting in a "response window" (Schwartz & Loop, 1982) longer than that of the luminance system yet of finite length. Such a relationship can be modeled by a process described by Watson (1986, pp. 6–10). It calculates the difference of two linear low-pass filters, the subtractor being scaled by a transience factor between 0 and 1. The degree of transience determines the sensitivity to stimulus transients. The model cannot, however, explain the asymmetry in sensitivity to stimulus onset and offset. Additional data that support the existence of asymmetry and its possible mechanism are presented below.

The inference about lower efficiency of the offset than the onset of brief S-cone selective stimuli is supported by introspection. The second peak in the luminance RTDs of Observer MSM was sometimes higher than the first peak (e.g., Fig. 3b, blue-on-blue stimulus). In a discussion on completion of the experiments, MSM explained that, if uncertain about stimulus appearance, she waited for its disappearance to decide that a stimulus had been presented and respond. She was, however, unable to apply the same strategy to blue-on-yellow stimuli, a finding indicating low efficiency of blue-on-yellow offset.

Further support for our inference comes from recordings of human visually evoked cortical potential (VECP). Jankov (1988) recorded VECP in 14 trichromats applying Stiles two-color method of selective stimulation of the S- and L-cones. He used a 10 deg test light of 700 ms duration, superimposed on a 15 deg steady adaptation field. VECP components elicited by violet (451 nm) light on yellow (547 nm) background were compared with VECP elicited by red (630 nm) light on blue–green (490 nm) background. In contrast to the red light, where VECPs of large amplitude were seen both at onset and offset of the stimulus, off-components to violet light were recorded only occasionally (with 2 of his 14 subjects) and were always of small amplitude. Spectral sensitivity measurements indicated that rods did not mediate the response to violet light. Furthermore, Jankov reports an unpublished observation by Klingaman of 1983 that the sensations evoked by the red and green mechanism have a "brisk" onset and offset while the sensation evoked by the blue mechanism is "sluggish" in its onset and particularly slow in its offset. This observation calls for comparison of sensitivity to onset and offset of stimuli that selectively stimulate the red and green mechanisms. We were unable to perform this due to technical limitations.

5.2. The mechanism of low sensitivity to the offset of brief S-cone selective stimuli

The difference in sensitivity to stimulus onset and offset in the present experiments might be due to the temporal dynamics of adaptation. The inter-stimulus interval in our experiments was about 5–7 s while the stimulus lasted for 0.5, 1 or 2 s. Thus, there was more time for adaptation to the background than to the stimulus. Whether or not this time relationship results in higher sensitivity to stimulus onset than offset depends on the speed of adaptation. Psychophysical data suggest a fast phase, less than 100 ms, of recovery in sensitivity after luminance perturbation followed by a slow adaptation process (e.g. Crawford, 1947; Hayhoe, Benimoff, & Hood, 1987). Adaptation after chromaticity perturbation is slower and is assumed to reflect receptoral and postreceptoral mechanisms (Hughes & DeMarco, 2003; Jameson, Hurvich, & Varner, 1979; Mollon & Polden, 1979), including gradual recovery from polarization in the blue–yellow (Pugh & Mollon, 1979) or red–green (Reeves, 1982a,b; Stromeyer, Cole, & Kronauer, 1985) opponent channels. The time constant of recovery of sensitivity for the short-wavelength mechanism after extinction of a long-wavelength field can exceed 30 s (Augenstein & Pugh, 1977; Pugh & Mollon, 1979). Yeh, Lee, and Kremers (1996) studied the time course of adaptation of macaque retinal ganglion cells belonging to either the magnocellular (M) or parvocellular (P) pathway following changes in the retinal illuminance or chromaticity. Adaptation of both M and P cells after a change in illuminance was relatively rapid and largely complete within 100 ms. Adaptation of P cells after a change in chromaticity was much slower and took from several seconds to several tens of seconds depending on whether the maintained activity was enhanced or depressed. Interestingly, adaptation of M cells after a change in chromaticity was also slower than after a change in luminance. Unfortunately, Yeh et al. (1996) did not record from cells with S-cone input. However, according to Reid and Shapley (2002) the response of the S-ON and S-OFF geniculate cells is

the most sustained and the response of the neurons in the magnocellular layers is the most transient. If the type of response correlates with the time course of adaptation, as is probably the case, one should expect the adaptation of cells conveying S-cone signals to be the slowest.

When small and short-lasting S-cone stimuli are presented at the retinal periphery, the threshold for decrements is higher than the threshold for increments (Vassilev et al., 2000, 2003). The "slow-adaptation hypothesis" of relative insensitivity to the offset of S-cone selective stimuli predicts that increasing stimulus duration would decrease the difference in threshold for increments and decrements. The prediction was tested in the 70–500 ms range with blue-on-yellow stimuli presented at 20 deg from fovea along the temporal meridian. Indeed, the difference between increment and decrement thresholds diminished with stimulus duration (Racheva & Vassilev, 2004). The hypothesis is also supported by the appearance of responses clustered after stimulus offset when stimulus duration is increased (Figs. 5 and 6).

5.3. Sensitivity to increments and decrements and its relationship with the ON/OFF dichotomy

The finding of lower decrement than increment threshold (Experiment 1: Fig. 2 and Table 1) is consistent with other studies (reviewed by Bowen, Pokorny, & Smith, 1989; Watson, 1986) reporting lower cone decrement threshold than increment threshold. This difference is of theoretical interest because of its incompatibility with a simple linear model of temporal sensitivity (Watson, 1986). In the case of S-cone vision at the retinal periphery, the relationship between S-cone increments and decrements depends on stimulus size. The decrement threshold is higher with small stimuli and equal to the increment threshold or lower than it when stimulus size is large (Vassilev et al., 2000, Figs. 4 and 5; Vassilev et al., 2003, Fig. 5). The stimuli used in the present experiment were of the size that yielded lower decrement threshold at the location tested. The effect of stimulus size is not new. In experiments with luminance increments and decrements Patel and Jones (1968) have found lower decrement than increment threshold, the difference being reduced by the increase of stimulus size and duration as well as by the increase of background intensity. The size effect strongly suggests that signals generated by increments and decrements are not transmitted within a single neuronal pathway. The most natural explanation of the size effect is that different neural pathways collect positive (ON) and negative (OFF) signals. The terms ON and OFF are used here (as is the common practice) to indicate increase or decrease of light intensity. We assume that, due to the asymmetry of sensitivity to the onset and offset of brief S-cone rectangular pulses, S-cone increments and decrements of threshold intensity trigger preferentially ON or OFF channels, respectively despite of the presence of both ON and OFF components in each pulse. Thus, both psychophysical and physiological data allow for the following explanation of our data. Sensitivity to the offset of brief S-cone selective stimuli is low due to slowness of adaptation of the short-wavelength system to the new color created by adding the test stimulus to the background. The slow course of adaptation is probably related to the long time constant of the so-called restoring force (Pugh & Mollon, 1979) that takes place at a postreceptoral opponent site to adjust the neutral point of the blue–yellow channel. Most experiments on color adaptation have been performed under intense background perturbation. In the experiments by Hughes and DeMarco (2003) a 2-s flash that had an approximate 18% S-cone contrast elevated the threshold of an S-cone selective test probe that lasted for more than 1 s. Insofar as our test stimuli were of threshold intensity, we assume that even minimal changes in background color trigger this mechanism, an assumption deserving further investigation.

Recent morphological data (Calkins & Sterling, 2007) show that S-cone signals are conveyed to ganglion cells subserving the luminance ON and OFF pathways. These findings evoke the question of why the reaction time distribution of S-cone selective stimuli is so different from the distribution in the control experiments with luminance signals. One possible reason is the relative small contribution of S-cones to the luminance channel due to their low density. Another possible reason is that, under the conditions of our experiment, the luminance channel was strongly stimulated by the intense yellow background and luminance modulation by the test stimuli was subthreshold. Indeed, luminance modulation was less than 0.3 percent and the test stimulus was perceived as color change rather than as luminance change.

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