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Vaitkevicius H, Vanagas V, Soliunas A, Svegzda A, Bliumas R, Stanikunas R, Kulikowski JJ. 2018. Fast cyclic stimulus flashing modulates perception of bi-stable figure. PeerJ 6:e6011
<https://doi.org/10.7717/peerj.6011>

Fast cyclic stimulus flashing modulates perception of bi-stable figure

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Many experiments have demonstrated that the rhythms in the brain influence an initial information processing. We investigated whether the alternation rate of the perception of a Necker cube depended on the degree of synchronization between two streams of spikes, one stemming from an external flashing image and the other from the action of an internal impulse stream. Knowing how a flickering stimulus with a given frequency and duration affects the alternation rate of bi-stable perception we could estimate properties of the internal signal. As the internal spike frequency is difficult to control, we varied the frequency of the flicker stimulus. Our results show that the duration of the dominant stimulus perception depends on the frequency or duration of the flashing stimuli. The values of the stimuli, at which the changes of the duration of the perceived image was maximal, we have called 'extremal'. While changing the flash duration, the extremal parameters repeated periodically at 4ms intervals. Increasing the duration of the extremal stimuli by less than 4 ms shortens the duration of the dominant stimulus perception. Hence we may conclude that it is not the stimulus duration but the accurate coincidence (timing) of the moments of switching on of external stimuli to match the internal stimuli which explains our experimental results.

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1 Abstract

2

3 Many experiments have demonstrated that the rhythms in the brain influence an initial
4 information processing. We investigated whether the alternation rate of the perception of
5 a Necker cube depended on the degree of synchronization between two streams of spikes,
6 one stemming from an external flashing image and the other from the action of an internal
7 impulse stream. Knowing how a flickering stimulus with a given frequency and duration
8 affects the alternation rate of bi-stable perception we could estimate properties of the
9 internal signal. As the internal spike frequency is difficult to control, we varied the
10 frequency of the flicker stimulus. Our results show that the duration of the dominant
11 stimulus perception depends on the frequency or duration of the flashing stimuli. The
12 values of the stimuli, at which the changes of the duration of the perceived image was

13 maximal, we have called ‘extremal’. While changing the flash duration, the extremal
14 parameters repeated periodically at 4ms intervals. Increasing the duration of the extremal
15 stimuli by less than 4 ms shortens the duration of the dominant stimulus perception.
16 Hence we may conclude that it is not the stimulus duration but the accurate coincidence
17 (timing) of the moments of switching on of external stimuli to match the internal stimuli
18 which explains our experimental results.

19

20 **Introduction**

21

22 Neurophysiological studies addressing the coding of visual information in the brain led to
23 the discovery of neurons which respond selectively to specific features of visual stimulus such as
24 size, colour, orientation, movement, characteristics of contour and spatial location: subsequently
25 called feature detectors (Lettvin et al., 1959; Hubel & Wiesel, 1959; Barlow, 1972; Barlow, et
26 al., 1967; DeValois, 1973; Bishop, 1996; Bishop & Pettigrew, 1986). It was believed that the
27 responses of these detectors lead to the identification of various features of stimuli essential for
28 recognition. However, the properties of these detectors were not sufficient to explain the
29 processes of stimuli perception and it became clear, that the spatial-temporal features (not spatial
30 features alone) of a stimulus are very important. In addition to the selection of basic features the
31 questions arise as to how these features are extracted from a background and analyzed and also
32 how more complex features are synthesized (“time –space” binding process King-Smith &
33 Kulikowski, 1975; Pomerantz, Sager & Stoeber, 1977; Parraga et al., 2005; Womelsdorf et al.,
34 2007; Lakatos et al., 2008).

35 It has been shown that the brain rhythms enhance responses of different detectors (Cardin
36 et al., 2009; Stanley et al., 2012), play a part in the formation of “more complex detectors”
37 (Kiper et al., 1996; Leonard et al., 1996), increase signal to noise ratio and, hence, help to
38 distinguish the signal from background noise (Kandil & Fahle, 2003; Roelfsema et al., 2004).
39 There is also evidence that these rhythmic processes can influence processes related to both
40 binocular and monocular rivalry or to bi-stable perception (Suzuki & Grabowecky, 2002; van Ee
41 et al., 2005; Alais & Blake, 2005) but the mechanisms of this influence are not yet understood.

42 Some researchers have indicated that high-frequency rhythms can control the input of
43 information in sensory systems (Gray & Singer, 1989; Cardin et al., 2009; Fründ et al., 2008;
44 Laczó et al., 2011; Stanley et al., 2012). It has also been shown that when the external rhythm of
45 a signal presentation coincided with the internal high-frequency rhythm, signal dispersion
46 decreased and its effectiveness increased (Montemurro et al., 2008; Fründ et al., 2008; Cardin et
47 al., 2009; Siegel et al., 2008; Vinck et al., 2010; Stanley et al., 2012). Thus, the factors
48 influencing the perception of bi-stable figures, are many (Blake & Lee, 2005; Lankheet, 2006).

49 Stanley et al. (2012) showed that the selectivity of cat LGN neurons, sensitive to the
50 direction of movement and orientation, increased with the occurrence of synchronous firing
51 (external and internal streams) at the inputs of neurons. These authors proposed that the
52 summation of excitation signals coming through different channels could not explain the
53 observed effect. In this case the number of events of precise timing of incoming spikes are
54 important but not the total cumulative effect. Moreover, it has been demonstrated that the greater
55 the phase shift in time between two sequences of spikes affecting inputs of a neuron, the less the
56 cumulative influence of these streams of impulses on the neuron activity. (Bi & Poo (2001);
57 Zhang et al., 1998; Song et al., 2000). This property could be used for both recognition and

58 memorizing of the time-space pattern characteristics of an impulse stream in neural nets
59 (Krunglevicius, 2015). It is proposed that for external pattern recognition it is important to know
60 when the time-space properties of an external impulses stream coincide with the properties of an
61 internal impulse stream. One research area where the properties of internal rhythms could be
62 investigated is perception of bi-stable images. It is important to know the properties of the
63 internal space-time pattern of the impulse stream when the alteration of ambiguous perception
64 occurs.

65 It is assumed that when input and internal impulses are synchronized, their impact on the
66 alteration of bi-stable perception increases. The question arises as to what are the temporary
67 properties of the internal impulse stream which cause the alteration of bi-stable perception. As
68 previously mentioned, the rhythmic processes can influence the processes related to both
69 binocular and monocular rivalry or to bi-stable perception (Suzuki & Grabowecky, 2002; van Ee
70 et al., 2005; Alais & Blake, 2005).

71 While varying the stimulus frequency, we recorded the alterations in perception of a
72 Necker cube and the duration of the perception of a dominant image. The aim was to test
73 whether the flash frequency and duration of stimuli influence perceptual alterations of bi-stable
74 images.

75

76

77 **Methods**

78 *Participants*

79 Eight subjects (7 males, 1 female) participated in the experiments. Three (32, 49 and 66
80 years old) had experience in psychophysical research. The other five (19, 20, 21, 22 and 22 years

81 old) were naive. Two experienced subjects participated in 20 sessions, one experienced and 1
82 naive subject participated in 10 sessions and the remaining four participated in only three
83 sessions. Results from the first session for one subject that participated in 20 sessions were
84 removed from the data analysis because they varied significantly and differed significantly from
85 the rest of his sessions. Subjects participated in one session per day, every day or with a less than
86 5-day interval. All subjects signed an informed consent approved by Vilnius Region Ethics
87 Committee of Biomedical Research.

88

89 ***Stimuli and apparatus***

90 Stimulus was the standard Necker cube, drawn in black lines on a white (85 cd/m² –
91 measured with PR680) background. The stimulus size was 1.7x1.7 degrees of visual angle. The
92 transparent slide with the Necker cube was mounted on the specially designed tachistoscope with
93 20 mm aperture. It had a chin or headrest, stabilizing the subject's head. White PC-controlled
94 LED illuminated the slide: a specially written program controlled an electric circuit to form LED
95 luminous flux and the data was transmitted to a PC through an LPT port. The stimulus was
96 switched on and off, i.e. flashed rhythmically at selected frequencies. The flash duration had an
97 accuracy of about 5 μs. Subjects watched the stimulus monocularly with the right eye and this
98 flashing image was seen for a fixed period. Subjects responded by pressing a key on a response
99 box connected to the LPT port of the PC.

100

101 ***Procedure***

102 The experiments were carried out in a dark and partly soundproofed room. Before each
103 session, the subject adapted to darkness for 10 min. The Necker cube was rhythmically turned on

104 and off within a block lasting 180 s. On and off periods were equal and the frequency (as
 105 duration) of presentation in one block was constant. Eighteen blocks, each with a different flash
 106 duration and with a 60 s pause in between the blocks, were randomly presented during each
 107 session. The minimal flash duration was 4 ms, the maximum 20 ms, i.e. flash duration varied in 1
 108 ms steps in the different blocks. The non-flashing Necker cube was presented in one block. The
 109 position of the Necker cube was called “up position” (abbreviated UP) if its front wall was
 110 perceived higher than the rear, and the alternative position was called “down position”
 111 (abbreviated DOWN). The task was to press and keep the key pressed when the position of the
 112 Necker cube DOWN was perceived and to release and keep the key released when the position
 113 of the Necker cube UP was perceived. Knowing the moments of perceptual changes it was
 114 possible to determine the duration of perception of each of the Necker cube positions. We named
 115 this duration of perception an absolute perception time (abbreviated PT).

116

117 ***Data analysis***

118 As the aim of this work was to check how the frequency and duration of stimulus affects
 119 the alternation of Necker cube perception, instead of PT we analyzed the changes of PT
 120 (abbreviated dPT), i.e. $\Delta\tau_{UP}(k,i) = \bar{\tau}_{UP}(i) - \tau_{UP}(k,i)$ and $\Delta\tau_{DOWN}(k,i) = \bar{\tau}_{DOWN}(i) - \tau_{DOWN}$
 121 (k,i) . Here i =the number of session, k = the block number ($k= 1, \dots, 18$), $\bar{\tau}_{UP}(i)$ and $\bar{\tau}_{DOWN}(i)$ is
 122 the mean dPT of UP and DOWN for all chosen blocks k over whole the i^{th} session, and $\tau_{UP}(k,i)$
 123 and $\tau_{DOWN}(k,i)$ is the mean dPT of UP and DOWN for block k of the i^{th} session. Next, we
 124 calculated the means of dPT for the k -th blocks over all n sessions separately for UP and DOWN,
 125 i.e. $\Delta\tau_{UP, DOWN}(k) = \sum_{i=1}^n \Delta\tau_{UP, DOWN}(k,i)/n$, and joint averaged UP and DOWN function: $\Delta\tau$

126 $(k) = M(\Delta\tau_{UP}(k) + \Delta\tau_{DOWN}(k))$. For the means of dPT ($\Delta\tau_{UP}(k,i)$ and $\Delta\tau_{DOWN}(k,i)$) we ran
 127 ANOVA and factor analysis.

128 Moreover, we determined the numbers of local extrema (maxima) of function $\Delta\tau(k,i)$ as a
 129 function of the duration frequency of the flashed stimulus. For that we firstly calculated the
 130 following function:

$$131 \quad \Delta\tau^1(k,i) = \begin{cases} 1, & \text{if } \Delta\tau(k-1,i) < \Delta\tau(k,i) > \Delta\tau(k+1,i) \\ 0, & \text{in other case} \end{cases},$$

132 i.e. function $\Delta\tau^1(k,i)$ will equal 1, if at point k a local maximum of function $\Delta\tau(k,i)$ is observed,
 133 otherwise it will equal 0. Next, we summed dependencies obtained over all sessions $\Delta\tau^1(k) =$
 134 $\sum_i \Delta\tau^1(k,i)$. The value of function $\Delta\tau^1(k)$ at point k is an integer number, and defines how many
 135 times a local maximum at point k (duration of displayed stimulus) was observed through all
 136 sessions. Furthermore, we calculated the mean value $M(\Delta\tau^1(k))$ of function $\Delta\tau^1(k)$. We also
 137 calculated how many maxima at point k of function $\Delta\tau^1(k)$ were above and below the value M .
 138 We assigned “1” for the all values that exceeded the value M , and “0” for the all values that were
 139 below the value M . Thus, we produced a sequence of 1’s and 0’s. The total number of 1’s is
 140 named “number of case A”, and the total number of 0’s is named “number of case B”. Thus, we
 141 had separate intervals at k -axis filled with 1’s and 0’s. The number of such intervals is called
 142 “number of runs”. We used “runs test for randomness” to check whether the distribution of 1’s
 143 and 0’s along the k -axis was random or non-random. In order to estimate how extreme points of
 144 function $\Delta\tau(k)$ were distributed over k -axis “runs test for randomness” was applied (Bradley,
 145 1968; SPSS)

146 The factor analysis (PCA) was separately run on each of four sets of data obtained for
147 *RB, AS, MK* and the five observers *Rm5* (aggregated data of *AV, IS, GS, MR* and *AS2*
148 observer).

149 As not all extracted factors may be significant (some may be related to random
150 changes/fluctuations), we need to identify non-random factors. One of the most commonly used
151 methods is the Kaiser's criterion (Fabrigar et al., 1999), which retains factors with eigenvalues
152 greater than 1. It is assumed that these factors characterize the assessed process reliably, although
153 it should be noted that, according to other researchers (Hayton & Allen, 2004), such a liberal
154 method of factor extraction does not guarantee that the selected factors will not be random. It is
155 therefore suggested to perform parallel factor analysis on a randomly formed data array with the
156 same data structure as the experimental data (Fabrigar et al., 1999; Hayton & Allen, 2004).
157 Random factors are extracted with parallel factor analysis. When eigenvalues of these random
158 factors are higher or approximately equal to eigenvalues extracted with PCA, the latter values
159 should be rejected as related to random influences. In order to identify non-random factor, we
160 also used parallel factor analysis. In our case the number of non-random factors was 6 to 7 and
161 they explained about 67 – 75% of the experimental data dispersion.

162

163

164

165 **Results**

166 The data revealed that the PT of the dominant image varied in timing from a few seconds
167 to ten seconds depending on the subject. For example, DOWN was perceived longer than UP by

168 subjects **RB** and **IS** (2.09 s vs 1.67 s and 3.65 s vs 2.57 s respectively), but UP was perceived
169 longer than DOWN by subjects **AS** and **AV** (8.4 vs 2.14 s and 4.07 s vs 3.04 s, respectively).

170 The results of ANOVA for a single factor (Table 1) reveal the factor of duration (the
171 duration of exposure was 18 values: 0 and 4–20 ms, where 0 = non-flickering condition) to be
172 significant for all subjects.

173 The statistical analysis (post hoc LSD test) of the experimental data confirmed that the
174 differences between the minimum and maximum values were statistically significant, and the
175 extreme points were recurrent (Table 1 and Fig. 1, 2 *a* and *b*).

176 In summary: the maxima and minima of function $\Delta\tau(k)$ differ from each other with
177 statistical significance (see Fig. 1 and 2 (*a*, *b*)). Furthermore, the preliminary statistical analysis
178 leads us to hypothesize that the influence of the stimulus duration could be periodic. In order to
179 check this hypothesis, we searched a periodic functions fitting for the approximation of
180 experimental function $\Delta\tau^1(k)$. In other words, we searched function:

$$181 \quad y(k) = a_0 + A \sin(\pi(k - \varphi_0)/w),$$

182 in regard to which square deviation of function $\Delta\tau^1(k)$ was minimal (see OriginPro 9.1 software
183 by OriginLab Corporation). Functions $y(k)$ are pictured by dotted lines in Fig. 1 and 2 *c*, *d*. Their
184 parameters (w) are presented in Table 2. According to the results of the approximation by the
185 sine function, the duration and frequency of the stimulus influences the changes of perceived
186 stimulus. This influence is repeated periodically with the changes to the frequency and duration
187 of the stimulus. The sine period is $T_{PT} = 2 \times w$, where w equals 3.8, 3.28, 3.42, and 2.98 ms for
188 subjects **AS**, **RB**, **MK** and **Rm5** respectively.

189 In a similar way the function $\Delta\tau^0(k)$ describes how the other extrema (minima) points of
190 function $\Delta\tau(k,i)$ are distributed along the k axis. Because the correlations between functions $\Delta\tau^l(k)$
191 and $\Delta\tau^0(k)$ were high and equal $-0.8 \div -0.9$, we analyzed only the functions $\Delta\tau^l(k)$.

192 It should be noted that although the $\Delta\tau(k)$ dependences established have a similar
193 periodicity for all subjects, the amplitudes of these functions at the extreme points vary
194 considerably for different subjects.

195 This could mean that the deviation of perception time (dPT) depends upon several
196 factors, rather than a single factor. That would be in agreement with other authors. For example,
197 it was demonstrated that the so called “stochastic resonance” in the presence of a hypothetical
198 neuronal noise and “periodic driving” (displaying stimulus) influence the alteration rate of the
199 perception of the dominant image (Kim, Grabowecky & Suzuki, 2006). Moreover, according to
200 Lankheet, (2006) the adaptation of detectors, and mutual backward lateral inhibition among
201 them, affects the alteration rate of the dominant image. Pearson & Brascamp, (2008); Knapen et
202 al., (2009) demonstrated that the properties of so called “perceptual memory” also have an
203 influence on the dominance of the perceived stimulus. Taking these findings into account a
204 factor analysis was run on the data ($\Delta\tau(k)$) (principal components analysis – PCA). As only each
205 of three subjects (**RB**, **AS** and **MK**) participated in a sufficient number of trials (20 trials), then
206 PCA was performed for these three subjects separately (Fabrigar et al., 1999). Moreover, PCA
207 was also run on aggregated data of five additional observers - **Rm5**

208 PCA identified up to six eigenvectors for each subject. These eigenvectors explain on
209 average 66.72 % -75% of the total data distribution. Parallel factor analysis (Fabrigar et al.,
210 1999; Hayton & Allen, 2004) was applied to identify non-random (significant) factors. As a
211 result, it can be argued that four or five factors are non-random. However, knowing the

212 significant factors it is difficult to identify the relationship of all extracted factors with the
213 processes responsible for the changes in perception of ambiguous figures. But some factor
214 loadings (F_3 or F_4) explicitly depend on stimulus duration. We need to examine in detail this
215 factor (F) loading, the value of those factor loadings versus duration of stimulus are shown in
216 Fig. 1 and 2 (*e, f*).

217 The curves (functions) shown are approximately periodic (Fig. 1, 2 (*a, b, c, d*)). The
218 standard peak analyzer procedure (OriginPro 9.1) was used to determine the maxima of
219 functions. The locations of peaks for the different functions varied slightly. The first (k_1), second
220 (k_2), third (k_3) and fourth (k_4) peaks are located along abscissa axis on intervals (5-7), (9-11), (13-
221 15) and (16-19) ms respectively. Differences in locations of the peaks for **RB**, **AS**, **MK** and **Rm5**
222 are approximately equal to 2 ms. However, the factor loadings have four – five peaks, which are
223 repeated at about the same value $\sim 3.5 - 4$ ms (see Fig. 1, 2 and Table 2). That means the
224 obtained functions are shifted in phase relative to each other and their periods differ slightly
225 (from 3.68 to 4ms).

226 It should be noted that for three observers (**RB**, **AL** and **MK**) the location of the peaks of
227 factor loadings approximately coincide with the peaks of dPT, ($\Delta\tau(k)$) and functions of
228 maximum number ($\Delta\tau^1(k)$) (Fig. 1(*e, f*), 2(*e, f*)). For these curves the first maxima are located at
229 about the same interval $\sim 7-8$ ms. The second, third and fourth peaks are at $10 \sim 11$ ms, $\sim 13-15$
230 ms and $\sim 17-19$ ms respectively. The averaged distance among the peaks of all three functions
231 for three observers (**RB**, **AS**, **MK**) are 3.93, 3.43 and 3.58 respectively. All of the functions for
232 **Rm5** data are also periodic, although their periods are slightly shorter. The averaged periods of
233 ($\Delta\tau(k)$), ($\Delta\tau^1(k)$) and F_3 equal 4, 2.98 and 3.68 ms respectively. Distances among minima are
234 also about 4 ms.

235 Some years ago we addressed the problem of how the duration and frequency of flashing
236 binocular competitive images affect the unstable perception in case of binocular rivalry. It was
237 shown that while the flash frequency was changing, the rate of perceptual alteration varied
238 periodically (Geissler et al., 2012; Vaitkevicius et al. 2013). In order to examine whether the
239 PCA results obtained in case of the perception of ambiguous figures and binocular rivalry are
240 similar, we compared these results. Fig. 3 graphically presents the factor loadings for
241 experimental data on binocular rivalry and on the data of the Necker cube perception.

242 Factor loadings obtained on the aggregated data for all observers who participated in
243 Necker cube and binocular rivalry experiments are approximated by the following functions:

$$244 \quad y_{Nc}(k) = 0.03 + 0.36 \sin \left[\frac{\pi(k + 0.02)}{2.34} \right] (F=5.24; p=0.02) \text{ and}$$

$$245 \quad y_{Br}(k) = -0.02 + 0.44 \sin \left[\frac{\pi(k + 0.19)}{2.27} \right] (F=6.67; p = 0.006) \text{ respectively.}$$

246 In both cases the periods of sine functions equal 4.68 and 4.54 ms. The periods of
247 experimental curves recently obtained equal 3.5 - 4 ms (see Fig. 1, 2 and Table 2), i.e.
248 differences are rather small.

249

250

251 Discussion

252 Analysis of the experimental results demonstrate that the duration and frequency of
253 flashing stimulus influence the perception time (PT) of a dominant image, extending or
254 shortening it. As our aim was to test whether the flash frequency and duration of stimuli
255 influence perceptual alterations of bi-stable images we analysed the changes of PT rather than
256 the absolute values. Similar analysis has been conducted by Fesi and Mendola (2014), who found

257 an inverse correlation between the alternation rate and the peak frequency of late evoked gamma
258 activity in the primary visual cortex (in regions V1 and V2) for bi-stable images. Analysis of the
259 data shows the influence of the stimulus frequency and durations on the alternation rate of
260 perception to be periodic. The extrema (maxima or minima) of all three functions ($\Delta\tau(k)$, $\Delta\tau^l(k)$
261 and loadings on F_3 factor) recur along the k -axis, not only periodically, but also located
262 approximately at the same places (see Fig. 1, 2 and Table 2). The stimuli, when the function $\tau(k)$
263 is maximal or minimal is referred to as extremal. Moreover, we see that the number of extrema
264 (maximum) versus duration of stimuli (or frequency of flashing) repeats periodically along the k
265 axis. Locations of maximum and minimum points, as well as distances between them along the k
266 axis are similar for all subjects.

267 Analysing maximum points of functions $\Delta\tau(k)$ and $\Delta\tau^l(k)$ along k -axis, we see that
268 maximum points repeat periodically at about 4 ms intervals. This is consistent with the results
269 described by Fesi & Mendola (2014) who showed that when the frequency of stimulus
270 presentation is synchronized with the gamma activity, the rate of perception change decreases.
271 According to the results obtained, when the duration of the extremal stimulus is increased by less
272 than 4 ms, the duration of the perception of the dominant image decreases, although the external
273 stimulus is longer and coincides in time with the internal action, the frequency of which keeps
274 constant. Lengthening the flashing period of extremal stimulus by 4 ms, resulted in the
275 probability of the extremal action of external stimulus recurring. On the basis of these results we
276 can state that the exact time (discrete time) of switching on of the stimulus (but not stimulus
277 duration) is important in order to reproduce the extremal action of the stimulus.

278 The same will be true if we analyse another distribution of extremal (minima) points
279 $\Delta\tau^0(k)$. The dependency $\Delta\tau^0(k)$ was calculated in the same way as the function $\Delta\tau^1(k)$. The
280 correlation between functions $\Delta\tau^1(k)$ and $\Delta\tau^0(k)$ was about $-0.8 \div -0.9$.

281 How could we explain, that the probability of change of perception versus the flicker
282 frequency (or duration) of stimulus is a periodic function?

283

284 ***Hypothetical mechanism of interaction between internal rhythm and sequence of external***
285 ***stimulus presentation***

286 Considering the influence of rhythmically flickering stimulus on the alternation rate of a
287 dominant image, it should be noted that the period of flicker is about $2 \times 4 \text{ ms} = 8 \text{ ms}$. In other
288 words, we assume that there is some internal rhythm, which specifies the discrete shortest time
289 moments, when the sensory system input is the most sensitive. If the frequency of the stimulus
290 presentation is a multiple of the frequency of this internal oscillator, then the efficiency of the
291 stimuli should recur and be maximum every 8 ms. Thus, according to these results, the frequency
292 of an internal oscillator should be approximately equal to $10^3 / (2 \times 4.0) = 125 \text{ c/s}$.

293 If a sequence of input stimuli coincides with a sequence of electrical activity of some
294 internal oscillator, the time span of a stimulus presentation completely overlaps the time span,
295 when the system is maximally susceptible. In this case, we can speak about synchronization of a
296 sequence of external stimulus with a rhythm generated by an internal generator. This agrees with
297 the experimental data of other authors (Vanagas et al., 1976; Geissler, 1987; Vanagas, 2001;
298 Hasenstaub et al., 2005; Geissler et al., 2012; Fesi & Mendola, 2014). Moreover, it has been
299 demonstrated that gamma frequency in the activity of thalamic cells boosts the selectivity of
300 “detectors” of orientation and direction of motion (Stanley et al., 2012) and that high frequency

301 activation of neurons in the barrel cortex of the mouse reduces the dispersion of the response to
302 olfactory stimulus (Huber et al., 2008).

303 The question is whether the efficiency of stimulus and its perceived brightness (strength)
304 may be related. It is well known that perceived brightness of flashing stimulus depends on the
305 flashing frequency and its duration (Talbot-Plateau law). In other words, the perceived brightness
306 depends on stimulus power (which in our case is constant). However, the law holds when the
307 frequency of flashing stimulus is higher than the critical flicker fusion (abbreviated CFF) (Hecht
308 & Wolf, 1932; Bartley, 1938), otherwise, the influence of rhythmic stimulus on perception is
309 more complex. For example, when the frequency of flashing stimulus increases, its perceived
310 brightness changes non-uniformly: it increases at the beginning and then decreases (“brightness
311 enhancement effect” Brücke-Bartley and Broca-Sulzer phenomena, Bartley, 1938, 1939).

312 Thus, when the frequency of stimulus presentation is lower than the CFF, the dependency
313 of brightness of perceived stimulus on frequency is complicated, and it is difficult to relate it
314 directly with the stimulus power. However, taking into account our data, it is difficult to explain
315 why the influence of stimulus varies periodically every 4 ms. Lengthening the optimal duration of
316 stimulus by 1, 2 and 3 ms, its efficiency initially reduces and recovers only after lengthening it by
317 4 ms. After this its efficiency reduces again, until it is lengthened again by another 4 ms etc. Thus,
318 duration of displaying stimulus alone does not determine the observed effect – the efficiency of
319 stimulus varies every 4 ms, i.e. it is also related to the moment of time when the stimulus is
320 switched on. Thus it can be related to the accurate coincidence in time of two streams (external
321 and internal) of neuron impulses (Huber et al., 2008; Stanley et al., 2012). That means the changes
322 of stimulus in time are important (at the moment of switching on stimulus its changes are

323 maximum), in other words we need to take into account the differentiation of stimulus with respect
324 to time.

325 The question is, whether such an information processing method, when the static signal is
326 differentiated with respect to time, can occur under natural conditions, when there is no flashing
327 signal in reality. Investigation of neural processes in the retina (Roska et al., 2006; Hsueh et al.,
328 2008) confirmed that the differentiation of signals with respect to time could be initiated at the
329 low level of the visual system. It is shown that ganglion cells receive excitation signals from
330 bipolar cells and inhibition delayed signals from amacrine cells. Due to this interaction, ganglion
331 cells get differentiated signals with respect to time. Moreover, it is well known that the eye is
332 constantly moving, hence the image of an object is shifted in time from one place to another on
333 the retina. Amplitudes of the small movements (or tremor) are about (20–40 arcsec) but
334 frequency can be high (80–250 Hz) (Carpenter, 1988; see also King-Smith 1978).

335 Due to these two processes at the output of separate ganglion cells, information about the
336 changes of image in the vicinity of its receptive field (RF) with respect to time and space can be
337 gathered. Thus, at the outputs of ganglion cells a high-frequency sequence of discrete signals can
338 be formed (Vaitkevičius et al., 1983).

339 There are experimental findings confirming that the micro movements of the eyes could
340 be involved in this low-level coding process of sensory information (differencing of signals with
341 respect to time and space) (Kulikowski, 1971; Leopold & Logothetis, 1998; Roska et al., 2006).

342 It is also important to note, that according to our data, the influence of the frequency of
343 stimulus flicker on the alternation rate of the dominant image perception is similar in both
344 conditions of a binocular rivalry and monocular perception of bi-stable images. Binocular rivalry
345 originates from the different images presented to the retinas of each eye: it is impossible for the

346 human to perceive two different stimuli at the same point in space. At any given moment of time
347 only one object (the dominant image) is perceived, and another object (the image on the retina of
348 the other eye) is not perceived – it is suppressed. The situation is different in the case of the
349 Necker cube: the image of a cube is displayed in the retina of one eye. In other words, two
350 different Necker cubes can create exactly the same perceived image. Since it is impossible to
351 perceive two different objects in the same time and point in space, the subject perceives only one
352 of two possible images (dominant image) at different moments in time, and any other possible
353 perceptual option is suppressed. The loadings on the factors (F3) as a function of stimulus
354 duration are similar both in the case of binocular rivalry and in the case of the Necker cube (see
355 Fig. 3). Comparing perception of ambiguous figures and binocular rivalry, O’Shea et al. (2009)
356 previously drew the same conclusion. Thus, we can assume that these factor loadings are the
357 result of similar processes involved both in monocular and binocular perception.

358

359 *Influence of other processes on perception*

360 The hypothesis about availability of discrete time moments optimal for the acceptance of
361 external stimulus can only partially explain the influence of the stimulus frequency and duration
362 on the alternation rate of bi-stable perception. The perception time of dominant images lasts for
363 seconds, and is many times longer than the duration of the period of effective synchronizing
364 rhythm. Consequently, the alternation rate of ambiguous images occurs after repeated
365 presentations of stimuli. How can this be explained? In addition to the hypothesis of adaptive
366 changes in activity of the dominant center corresponding to perception of a dominant stimulus, it
367 is necessary to note the following: there is evidence that the perception time of dominant image
368 (of bi-stable stimulus) increases when bi-stable stimulus is switched off for a few seconds and is

369 switched on again (Leopold et al., 2002; Leopold & Logothetis, 1999). As the duration of iconic
370 memory does not exceed 0.2–1 s (Sperling, 1967), the subject cannot see the stimulus at this
371 moment at all. It can be assumed that at least two processes must be distinguished in this case,
372 one related to the maintenance of the dominant image, another related to the influence on the
373 alteration of the perceived image. For perceptual alteration to occur, one should have an
374 alternative. However, after the stimulus is switched off the subject sees nothing (there is no
375 alternative stimulus in iconic memory) (Leopold & Logothetis, 1999). Due to inertia, only a trace
376 of the dominant image is maintained in the “top-down” streams but not in iconic memory. In this
377 case, the absence of stimulus on the input of the sensory system can extend the perception time
378 of the dominant image: as there is no information as to which alternative image is possible to see
379 (Leopold & Logothetis, 1999; Leopold et al., 2002; Lee et al., 2005; Pearson & Brascamp,
380 2008).

381 Thus, we can assume that in order to initiate the changes to a perceived image it is
382 necessary to have enough strong sensory stimuli, the time –space code of which would coincide
383 with the code of an alternative image.

384 We further conducted the simulation of interaction between the external and internal
385 streams of pulses. For the sake of simplicity, we assumed that the external and internal streams
386 of pulses can be described by sequences of rectified harmonic signals. Moreover, the external
387 and internal streams of pulses transferred to inputs of a neuron, the output of which was equal to
388 the product of two input stimuli (two rectified harmonic signals). Digital simulations
389 demonstrated that the beating of pulses of two streams originated at the output of this neuron.
390 When the frequency of the internal stimuli was a multiple of the frequency of the external
391 stimuli, the envelope of the beating can be described by a rectified single harmonic and the

392 maxima of the envelope along the k axis recurs periodically at intervals equal to the flash
393 duration of the external stimulus. Moreover, the value of all the maxima are equal. In other cases
394 the number of maxima of the envelope increase. They are distributed along the k axis non-
395 periodically and their amplitudes vary significantly. That is consistent with our experimental
396 results.

397 The maxima mean that the perception time of the dominant image increases and hence
398 the rate of the perceptual alteration decreases, i.e. the probability to perceive the suppressed
399 alternative image decreases. Thus, when the extremal sequence of stimuli are displayed, the
400 suppression of the alternative image increases maximally, i.e. the suppressive strength of the
401 external stimuli is maximal. According to (Stanley et al., 2012) it is not the duration of two
402 acting pulses but their accurate coincidence (timing) which determines the strength of the action
403 of these two stimuli (external and internal stimuli). If the frequency of the internal rhythm is
404 constant then, taking our data into account, this frequency should be approximately equal to 125
405 c/s.

406

407

408 **Conclusions**

409 Our paper addresses the problem of how the flickering image of a Necker cube influences
410 the alternation rate of the perception of an ambiguous figure. We measured the durations of the
411 perception of a dominant stimulus and calculated the changes in the duration of the dominant
412 stimulus perception versus the frequency and duration of a displayed Necker cube. These
413 changes in duration were longest at some values of the stimuli, which we called extremal.
414 Increasing these changes increases the duration of the dominant stimulus perception, i.e. the rate

415 of perceptual alternation decreases. While changing the duration and frequency of flash, the
416 extremal parameters recur periodically at approximately 8 ms intervals which suppose existence
417 of internal rhythm of 125c/s for bi-stable visual perception.

418

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Figure 1

The dPT function ($\Delta\tau(k)$) versus the flash duration (or block number) (a, b) for observers (*AS* and *RB*) respectively.

The abscissae - duration of flashing stimulus (ms), the ordinate - dPT value (s). The dashed line represents the dPT of non-flickering stimulus relative to the mean of perception time for all sessions of the given subject. The continuous curve with filled symbols - the curves dPT. Capital letters on the top of every picture mark different observers (number of all sessions, on which the data was collected, is in the brackets). The points labelled by asterisks mark points, where differences among neighbouring extrema of $\Delta\tau(k)$ were statistically significant. (**c, d**): The number of local maximum vs flash duration (function $\Delta\tau(k)$); (**e, f**): Factor loadings (F) vs the flash duration (ms) for observers **AS** and **RB** respectively. The solid lines present the functions pictured experimental dependences; the dashed lines are sinusoidal functions optimally approximated experimental dependences.

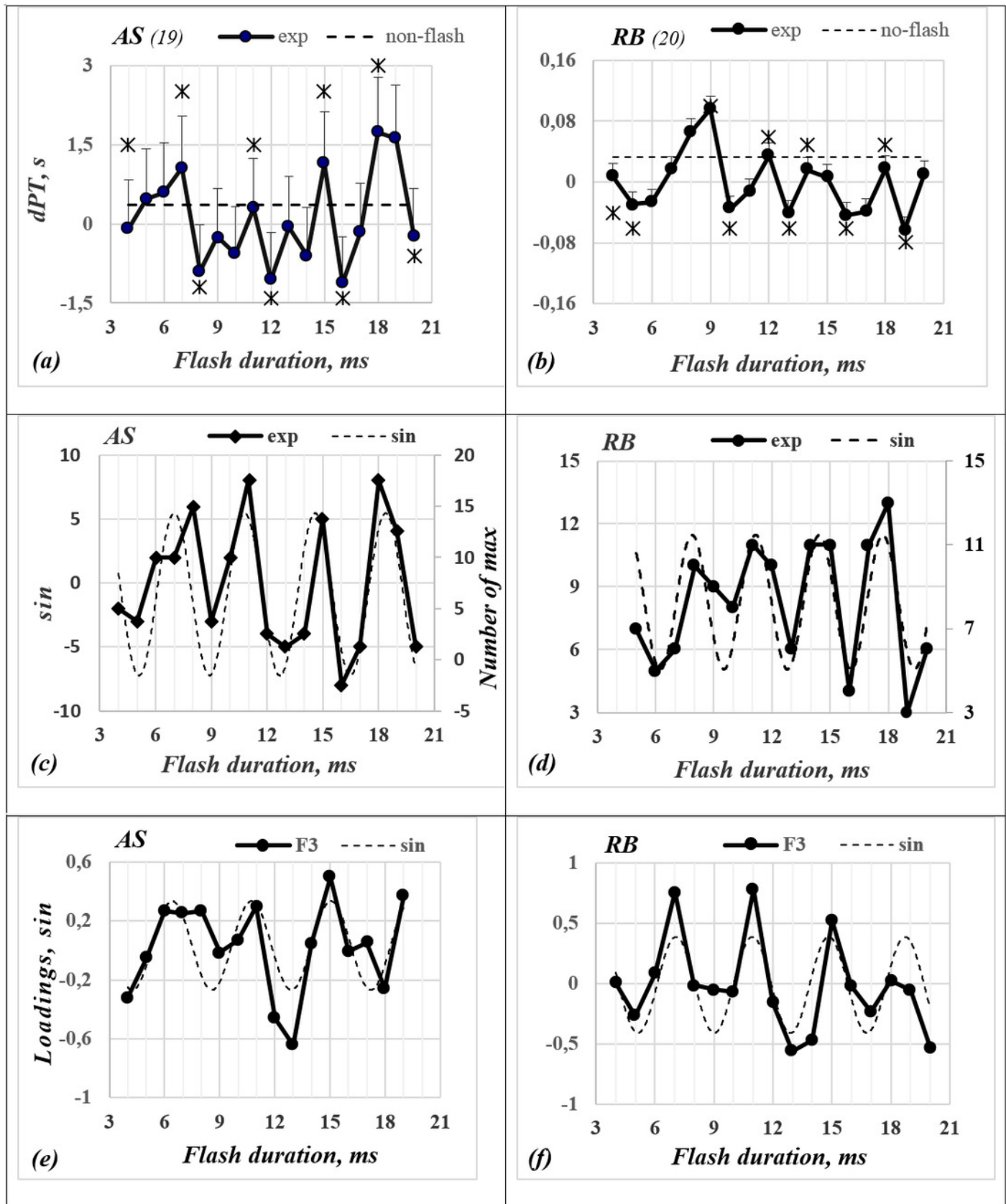


Figure 2

The analogous functions as in Figure 1 for *MK* and *Rm5* observers.

All the symbols are the same as in Figure 1.

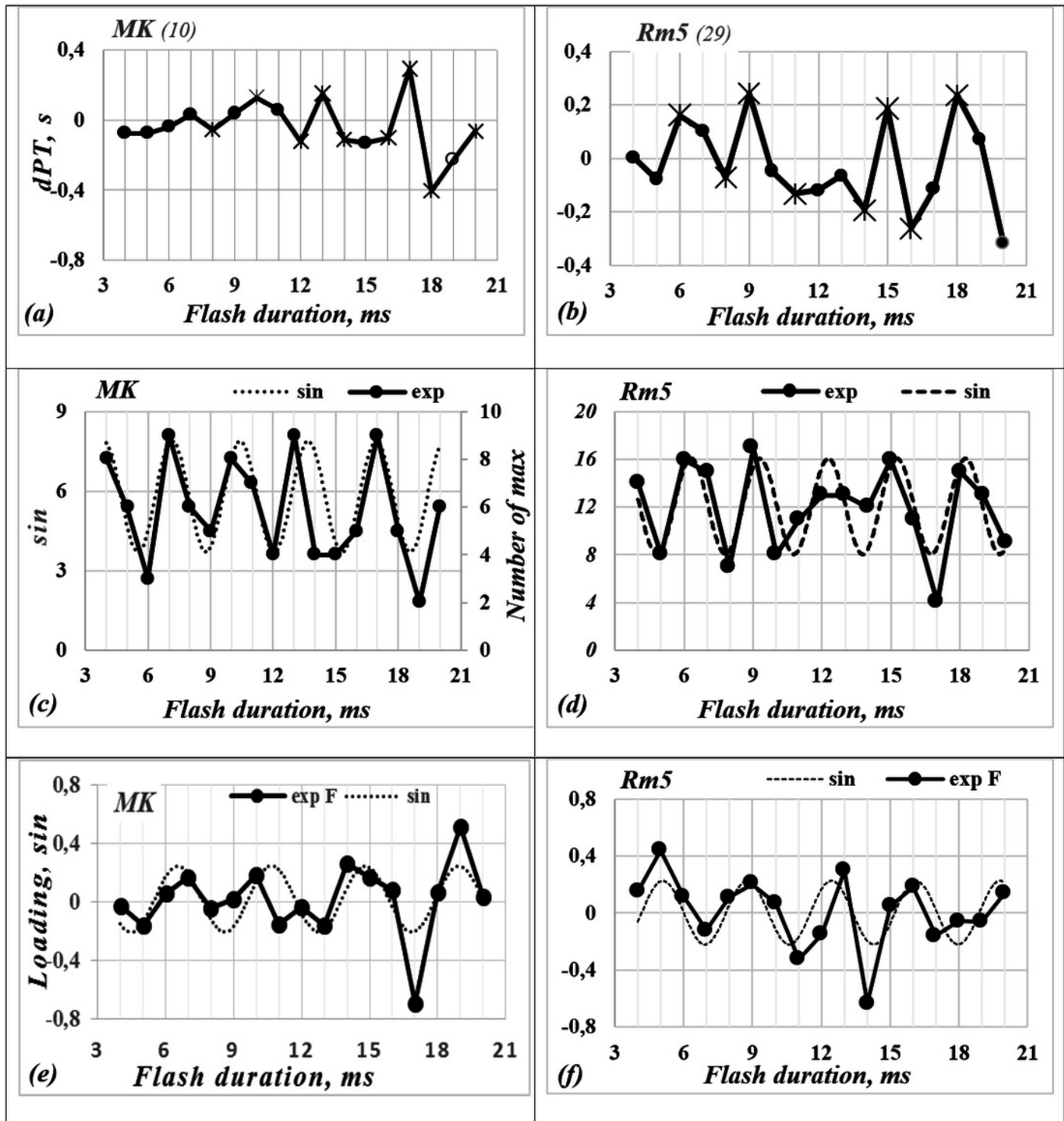


Figure 3

Factor (F3) loadings against duration of flashing stimulus.

(a) The continuous solid and dashed point-like curves are the factor loadings (F3) calculated for the Necker cube and binocular rivalry data of two different groups of observers respectively (Geissler et al., 2012; Vaitkevicius et al. 2013). **(b, c)** The solid line indicates factor loadings for Necker cube (**Nc**) and binocular rivalry (**BR**) respectively. The dashed lines show sine functions approximated experimental curves.

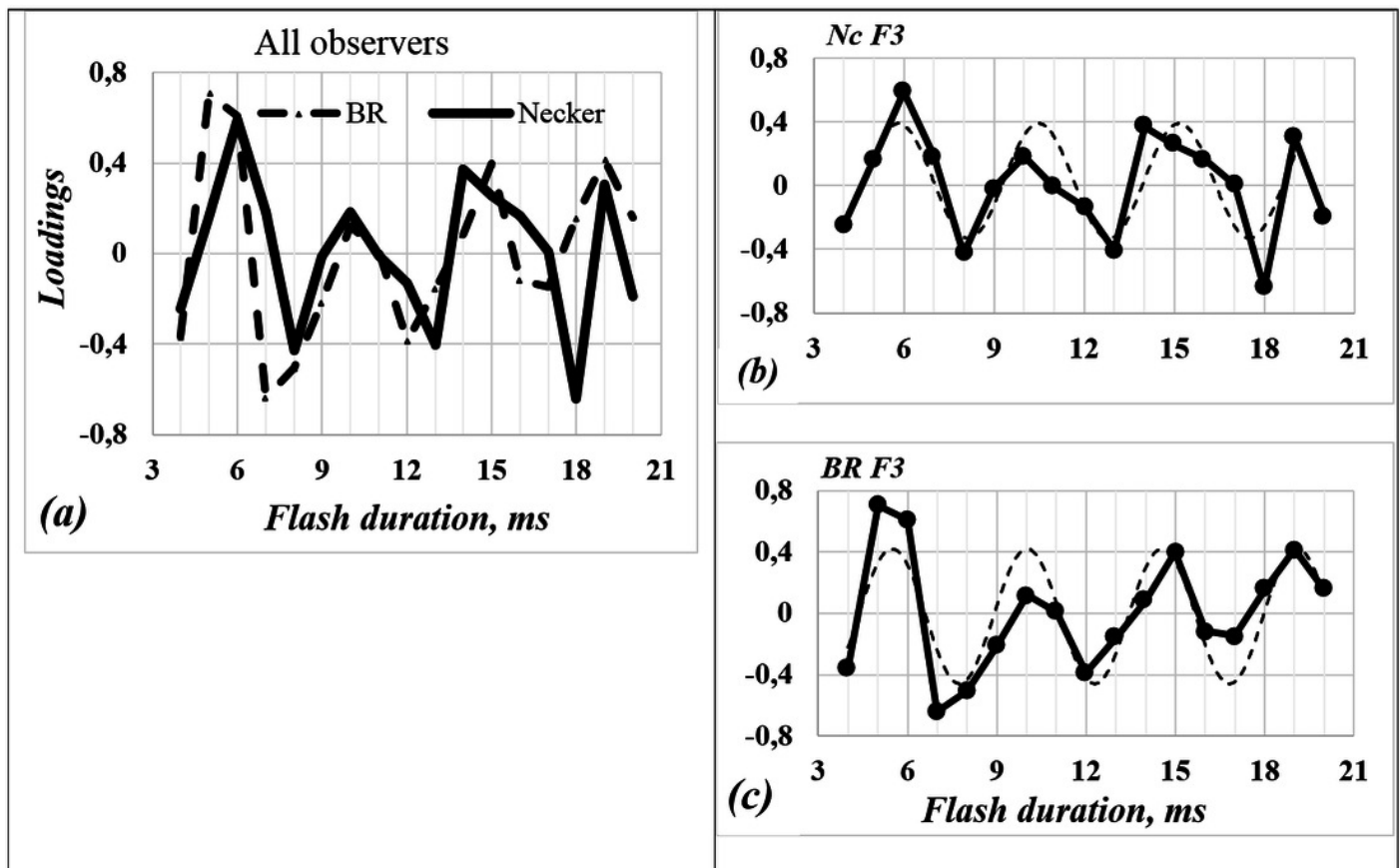


Table 1 (on next page)

ANOVA results for the factor of flash duration for separate subjects.

1

Subject	RB	AS	AV	AS2	IS	GS	MR	MK
	F(17, 32657) = 36.29; p < 0.0001	F(17, 5118) = 4.62; p < 0.0001	F(17, 8816) = 8.83; p < 0.0001	F(17, 9103) = 4.52, p < 0,0001	F(17, 2945) = 2.64; p < 0.0003	F(17, 6807) = 59.31; p < 0.0001	F(17, 4766) = 7.62; p < 0.0001	F(17, 2208) = 3,40, p < 0.0001

2

Table 2 (on next page)

The parameters of $y(k)$ functions.

Average	T_{PT}	k_4	k_3	k_2	k_1	Estimated	Subjects
3.93	Mean = 4	18-19	15	11	7	$\Delta\tau(k)$	AS
	3.80, ($w = 1.9$)	18	15	10-11	8	$\Delta\tau^1(k)$	
	~ 4 , ($w = 2$)	19	15	11	6-8	F	
3.43	Mean ≈ 3	18	14-15	12	8-9	$\Delta\tau(k)$	RB
	3.28, ($w = 1.64$)	19	14-15	11	8	$\Delta\tau^1(k)$	
	~ 4 , ($w = 2$)	18-19	15	11	7	F	
3.58	Mean = 3.33	17	13	10	7	$\Delta\tau(k)$	MK
	3.42, ($w = 1.71$)	17	13	10	7	$\Delta\tau^1(k)$	
	4 ($w = 2$)	19	14-15	10	7	F	
3.55	Mean = 4	18	15	9	6-7	$\Delta\tau(k)$	Rm5
	2.98, ($w = 1.49$)	18	15	9	6-7	$\Delta\tau^1(k)$	
	3.68, ($w = 1.84$)	16	13	9	5	F	

1 $\Delta\tau(k)$ – changes of perception time (PT) of dominant image;

2 $\Delta\tau^1(k)$ – number of maximum at point k along the abscissa.;

3 F factor loading.

4 k_1 , k_2 , k_3 and k_4 – the location of the first, second, third and fourth extrema peak (maxima) of

5 corresponding function along abscissa (k).

6

7

8