REAL-TIME GATING OF CYCLIC BRAIN ACTIVITY: EVIDENCE FROM MODULATIONS OF BINOCULAR RIVALRY INDUCED BY RAPID STIMULUS INTERRUPTIONS†

H.-G. Geissler1*, V. Vanagas2, A. Svegzda2, R. Blumus2, R. Stanikunas2, H. Vaitkevicius2**

1University of Leipzig; 2University of Vilnius

* hans-g.geissler@rz.uni-leipzig.de ** Henrikas.Vaitkevicius@ff.vu.lt

Abstract

According to widespread opinion, perceptual-cognitive information processing is founded on systems of mutually tuned neural oscillations flexibly adapting to environmental constraints and task demands. From directly observable phenomena ubiquitous in the brain, this view seems to be well-supported. However, it ignores important prerequisites of stability, selectivity and protection against disturbances. Regular timing patterns surfacing in resonant states of the brain suggest that they are accomplished by delay-based gating mechanisms whose action in support of precise temporal coordination hardly ever comes directly into sight. Exploring the effects of rapid stimulus interruptions (25 to 125 Hz) on binocular rivalry, we demonstrate – for the first time for such a large range – fine-grained cyclic modulations that are evenly spaced in time rather than frequency. Our results support the view that recurrent chains of neural delays play a leading role in the selective amplification of preferred cycles. This agrees with range constraints specified by the time-quantum approach, TQM.

The claim that the bodily basis of perception and consciousness resides in cyclic carrier processes within the nervous system dates back to the very beginnings of psychophysics (Fechner, 1860). What was a speculative idea in those days has led after the discovery of periodic fluctuations in potentials recordable from the scalp (Berger, 1929) to a rich literature on correlative relationships. It is only during the last few decades that various testable hypotheses on the causal roles of synchronous oscillatory activity in information processing have become the focus of extensive physiological research. Among others, the idea has received prominence that binding of segregated pieces of sensory information into unique percepts is achieved through synchronous oscillations of populations of neurons (Eckhorn et al., 1988; Gray et al., 1989); cycles of fast oscillations in the Gamma and Beta ranges were proposed to result from segmentation of longer cycles in the Alpha or Theta bands (Lisman & Idiart, 1995; cf. Sompolinsky & Tsodyks, 1994, for an analogue on the neuron level); more recently, a mechanism for recoding amplitude information into phase positions within the gamma cycle was suggested (Fries et al., 2007, for a brief review). Also, great efforts have been undertaken to disentangle the complex functional interrelationships of activity in different frequency bands in early stages of cognition. A salient example is the inhibition-timing hypothesis (Klimesch et al., 2007; Klimesch, 2011) claiming that ongoing alpha activity and early evoked visual (P1) potentials form an integrated functional system selectively channeling initial memory access.

As part of those developments, there arose and took root two closely related, but more unspecific suggestions that because of their universal character cannot be tackled on the same, primarily inductive basis. One is the supposition that frequency and phase of neural oscillations, or compounds of them, may generally play the roles of fundamental parameters for transient coding and processing of information throughout the brain as a whole. The other
assumption is more of a background idea, namely the widely shared, though unproven, belief that all forms of functionally engaged oscillations of cooperative and competitive neuronal mass activity can ultimately be captured as facets of the behavior of non-linear oscillators.

Hopes that these fairly undifferentiated claims could before long be made exact within readily available system-theoretic frameworks and thereby converted into testable predictions have so far not come true. In this paper, we adopt a deductive alternative capitalizing upon psychophysical evidence. As we will show, law-like invariance properties inferred from fine-grained perceptual-cognitive response patterns bear directly on the phase-frequency issue. Yet, while suggesting a beautiful simple compatibility of phase-frequency coding in absolute terms, the same principles simultaneously challenge plain oscillator intuitions. Specifically, the observed regularities point to a less easily detectable second type of cyclically operating real-time mechanisms that tend to suppress detrimental oscillatory driving and generate states of fine-tuned transient quantization vital for stability and sustained multi-leveled process organization. In the second part of this paper we will for the first time report evidence in support of this view from a critical test in an experiment in binocular rivalry, the alternation of perceived images occurring when the eyes are presented with incompatible visual patterns (see Blake, 2005, for an introduction).

Because of integer-ratio relationships between adjacent components, the spectrum-like discrete patterns from which the key invariance properties can be extracted will here be referred to as “quantal structures”. As a compact basis of accumulated evidence, we relate to the so-called Time Quantum-Model, TQM – not a model in the customary sense, but a condensed, continuously updated interpretation of laws and numerical invariants inferred from a larger collection of quantal structures (see Geissler, 1987, 1992, for early versions).

As a prerequisite for treatment of the issues at hand, a brief recapitulation of essentials of TQM appears imperative.

**Basic hypotheses and TQM core structure**

To start with the general rationale of the enterprise: Unlike common inductive strategies that translate empirically established relationships into directly testable hypotheses or into models from which directly testable hypotheses are derived, the TQM approach translates the invariant properties it sets out from into currently not directly testable general hypotheses that are treated as axioms and are not required to form a complete system or model. TQM itself consists in a revisable integrated interpretation of these hypotheses in terms of underlying cyclic processes. On a trial basis, this core structure is implemented for the phenomena under investigation in order to derive testable predictions. Thus the essence of TQM lies exclusively in the predictive power of the implementations of the hypotheses adopted, which allow deductions that are subject to empirical corroboration or falsification.

Among the three most basic hypotheses entering into TQM there are two that root in regularities that quantal time structures not only share with non-quantized time dependencies, but also with psychophysical ratio-scaling data that are obtained for non-temporal continua of the character of intensities (Teghtsoonian, 1971). Most fundamental is the observation that quantal time structures in terms of the proportions between the largest and smallest values across limited ranges do not exceed upper bounds of 20 to maximally 30. In the renowned “multiplication table” of Latour (1967), for example, the lowest value is located somewhat above 9 ms and the highest (concluded) one at 220 ms, which yields a ratio close to 24. For TQM, estimates of the obtainable maximum have led to Range Hypothesis (H1), maintaining that internal representations of time form ranges such that the ratio of the largest to the smallest possible value within a given range is a constant $M \leq 30$. Note that this figure agrees fairly closely with the constant established by Teghtsoonian for judged magnitudes (Teghtsoonian, 1971; see also Teghtsoonian & Teghtsoonian, 1997).
The second basic regularity relates to an empirical law ubiquitous in psychophysics: Weber’s Law, which was generalized for time as “Scalar Timing” (Gibbon, 1977). The corresponding TQM hypothesis for internal representations was first stated in Geissler (1985). Its quantitative specification, first derived by Teghtsoonian (1971) in terms of judged magnitudes, amounts to the Dispersion-Progression Hypothesis (H2) saying that along a full quantal range the Weber fraction has a constant value $C \equiv 1/30$ (Ekman’s Constant”).

H1 and H2, if stated in terms of judged magnitudes, do not straightly transfer to physical values with possible equivalents in physiological observations. But their time-related versions do. Yet, due to the relational nature of H1 and H2, absolute measures of time are still lacking. The key hypothesis through which TQM fills this gap derives from a third inherent regularity of quantal structures, namely spacing of components approximately on a uniform lattice of possible values. This expresses itself in Greatest Common Denominators that according to H1 increase in linear progression with range size, starting from a smallest absolute value corresponding to the shortest range observed. A landmark on the way to the disclosure of this intriguing regularity is represented in work on visual pattern recognition by Vanagas, Balkelite, Bartusjavicus, & Kirvelis (1976; cf. also Vanagas, 1994, 2001). In this study, due to an unusually minute gradation of stimulus presentation times, small processing steps of, on average, about 9 milliseconds could for the first time be made visible in the percentage-correct functions. Critical intervals of that duration or small integer multiples of it have later repeatedly been also found in RT-based analyses (e.g. Puffe, 1990; Bredenkamp, 1993; Petzold & Edeler, 1995). The seemingly universal role of an even shorter unit of half that size, i.e. of $\sim 4.5$ ms (in the following, $Q_0$) became apparent from a reanalysis of larger samples of quantal structures from different paradigms by Geissler (1987). Beyond its demonstration as Largest Common Denominator, most convincing evidence of its real existence so far comes from analyses of small fluctuations under near-identical conditions (cf. Geissler et al., 1999; Kompass, 2004). As a quantitative postulate about internal representations, the modular property described was stated as Time-Quantum Hypothesis (H3): Possible periods are integer multiples $N$ of modular units $Q_q$ (H3a), which in turn are integer multiples $q$ of an elementary smallest unit $Q_0$ (H3b).

For illustration of how the hypotheses relate to TQM, consider Figure 1. In the wave scheme at the top, the modular quantum unit according to (H3a) is implemented as a “fuzzy”bipolar sinusoidal cycle resulting from superposition of carriers of slightly different cycle durations (cf. Geissler, 1985, 1987). Note that, after initial synchronization (rectangular

![Fig.1. Illustration of the TQM assumptions H1, H2 and H3. Note that in the picture at the top random phase differences are depicted as eight waves of equal distances.](image)
frame at the top left), in accordance with H3 phase jittering spreads linearly as time elapses after initial synchronization (dashed vertical line with arrows). It does so up until the “coherence limit” of $N_{max}$ cycles (here arbitrarily assumed to be 12) is reached where it completely erases detectable periodicities and thus no phase coding of information would anymore be possible. Consequently, $N_{max}$ is the only resulting limit that can be identified with the upper range bound M according to H1. Note that this identification brings something new beyond H1 and H2 as such. It follows automatically that M and C can be reduced to only one constant, the uncertainty interval of the operative modular unit. When assuming uniform phase distribution, this is tantamount to the testable prediction that $C \sim 1/M$ should hold. The approximate inverse relation between the estimates for M and C, never taken notice of in the literature, fits in well with this prediction.

It is now easy to capture an important consequence of H3b: Unlike the other hypotheses that are stated in relative terms, $Q_0$ provides a basis to specify ranges in absolute terms, which is big news in psychology. A straightforward consequence is the existence of an absolutely shortest range $R_1$ of possible multiples of $Q_0$. When adopting the ideal estimates $Q_0 = 4.57$ ms (for adults) and $M = 30$, this “base range” extends from durations of 4.57 ms to 137.1 ms. A compelling requirement for mental timing as a whole is that ranges of different absolute extensions up to the respective Weber resolutions must be compatible within sub-ranges of overlap. In the middle part of Figure 1, this property is illustrated for $R_1$ and $R_2$ by bidirectional arrows connecting the lower chain to the next larger compatible chain above it. Accordingly, integer-ratio relations should hold between ranges of different sizes in order to meet the compatibility condition. By generalization, there follows a proper cascade $R_1$, $R_2$, $R_3$, $...$, etc., of admissible ranges resulting from $R_1$ by magnifications through integer factors.

Motivation of the experimental inquiry

That much about TQM; let us now return to our main objective: What have temporal range structures to do with phase-frequency relations and their connection to oscillatory mechanisms, the two central issues of this paper? For phase and frequency, the answer is straightforward: According to H1, quantized cycle times are evenly spaced by physical measures of time. If, for the sake of simplicity fuzziness is ignored, this property implies a simple relation between cycles and phase positions. Possible phase positions can, across all admissible cycles, be expressed as multiples of the same modular unit as the cycle itself within which phase positions are marked out. As one can easily imagine, this relationship enormously simplifies extraction and computation of complex information across different frequencies. By contrast, there would be no such simple rules on which processing can rely if cycles could take on any value or were uniformly spaced in terms of frequency.

What about oscillatory mechanisms? Superficially, it might appear that range structures of cycles uniformly spaced in time logically contradict customary oscillator concepts, as they typically ascribe an analogous privileged role to multiples of natural frequencies of oscillators, which amounts to segmentation of largest rather than concatenation of smallest cycles. However, reality is much subtler. In fact, analyses of inner regularities of quantal structures such as were first described by von Békésy (1936) for low-frequency sound and by Latour (1967) for eye movements and their relations to EEG frequencies have revealed exactly that hierarchical segmentation property. The hypothesis that it holds simultaneously with the time-quantum assumption H3 is among the earliest suggestions of TQM (Geissler, 1985). For full ranges, i.e. for modular multiples $1 \leq N \leq M = 30$ as hypothesized, it can be stated as follows:

The Double-constraint hypothesis (H4)

Admissible processing cycles are both integer multiples of the respective operative modular cycles and integer fractions of larger multiples if there are any.
Thus H4 agrees in one basic respect, the “segmentation property”, with common oscillator concepts. However, it differs from them by two properties with crucial consequences for the main issues of the present article:

(A) As illustrated at the bottom of Figure 1 for two different segmentations of a macro cycle of 24 times a modular unit, the potential manifold of possible segmentations becomes narrowed down to a strictly limited set of hierarchies. More exactly, ignoring fuzziness, hierarchical segmentation can be reduced to decompositions following the mathematics of alternative ordered factorizations of integers 1 to M.

As a consequence of (A), the above indicated uniform relations of within-cycle phase positions across admissible cycles translate into concrete relations between cooperating, hierarchically phase-coupled carriers of cyclic activity of different frequencies.

(B) Different from common biological concepts, there are no fixed oscillators or clock mechanisms implied. Instead, each multiple $1 < N \leq M$ can in principle assume the position of the top element in one or more segmentation hierarchies.

Note that (B) thus delimits the manifold of available options and does not say anything about their employment in the representation and processing of information. Accordingly, TQM accounts for task- and stimulus-specific processing through fast progressive selection from a large number of initially co-activated options, functions that in common oscillator implementations are ascribed to adaptive tuning to stimulus conditions and task demands.

So far the strongest empirical evidence in support of (A) and (B) that offers a direct link to the objectives of this paper can be seen in the success of two predictions. One relates to a long-known global physiological regularity, the other to stochastic properties of a class of ambiguity phenomena. Due to lack of space, we can here provide only a sketchy description: The first prediction springs directly from property (A): As a consequence of prime factorization, the set of possible multiples $N \leq M = 30$ falls apart into four subsets of mutually disjunctive elements. In application to $R_1$, this decomposition reveals a perplexing congruence with the empirical definitions of EEG bands in terms of frequency values (see Appendix). What is important in the present context is that the even spacing of EEG bands on a logarithmic scale corroborates the even-spacing assumption for possible cycle durations.

The second prediction relates to superficially irregular multimodal distributions of breakdowns of apparent motion (cf. Geissler, 2009). The relevant predictions derive under the premise that for the weakly-constraining conditions of the experiment all possible options are activated with equal probability. Although modified variants seem possible, the high correlations found for more than 20 degrees of freedom should hardly allow for completely different explanations. What bears on the objectives of this paper is that the predictions rely on the above progressive constraining principle and thus contradict plain oscillator notions.

While the evidence quoted in favor of the quantal-timing claims is fairly encouraging, one may still doubt their generality. Against the power of the EEG prediction one may object that it is not a forecast of a hitherto unknown phenomenon but a re-production of a familiar structure that as such is suspicious of depending, at least partly, on technical conventions. An obvious limitation of the second example is its limited scope: Due to inherent constraints of the phenomena investigated, Beta and Gamma Motion, predictions apply to ISIs up to 250 ms, a bit below the upper bound of $R_2$, which corresponds to the lower limit of the Theta band.

Thus it remains desirable to demonstrate broad validity of the assumptions more directly, for a much larger range of variation of temporal parameters and within a paradigm building on robust effects providing a strong test. Another highly desirable requirement is that the paradigm employed should psychophysically and physiologically be well studied – quite in accordance with Fechner’s ideal goal of establishing “Inner Psychophysics” through linking psychophysical and physiological evidence.
Proposed mechanisms and choice of paradigm

A goal thus set raises the question what the physiological basis of the curious double-constraint condition might be. A cue to answer the question is provided by a comparison of different interpretations of the same psychophysical principle as illustrated at the bottom of Figure 1 (cf. Geissler, 1994). When considering that scheme, the irresistible primary interpretation is one in terms of two alternative hierarchies marking cycles of four phase-coupled oscillations whose largest members are of equal duration. However, alternatively, the hierarchies can be conceived as two different segmentations of one and the same chain of elementary cycles or intermittencies, \( x \), into chunks according to

\[
(((xxx)(xxx))((xxx)(xxx)))(((xxx)(xxx))((xxx)(xxx)))
\]

or

\[
\]

The important difference between the two modes is that implementation in terms of oscillations in either case involves participation of four different oscillations, whereas in the chunking interpretation the resulting structure somehow “consists” of sub-chunks as constitutive parts: if one of it is dropped the total chunk is no more of the same length. In fact, while prediction (B) implies transient generation of full hierarchies, it is inconceivable how (in the example) four different oscillations could be generated fast enough and brought to precise phase coincidence. Moreover, in the face of well-known properties of non-linear oscillators, it remains a puzzle how the configuration could be kept stable and frequency floating avoided. Quite differently, whatever chunking exactly means, in the second version stability is not a question of precise coordination, for sub-chains are constitutive parts of the whole. Also, it appears no principal problem to add new sub-chains or replace a particular decomposition by another one.

Considerations like the latter have led to the suggestion that the neural basis of temporal quantization lies in precisely timed chains of neural delays (cf. Kompass & Geissler, 2003; Kompass, 2004) or “synfire chains” as first postulated on the basis of findings of super-precise timing on the neuron level in the forebrains of monkeys (Abeles et al., 1993). The resulting hypothesis thus is that the physical basis of the quantal property is given by recurrent neural delays that by imposing their constraints upon neuronal mass activity co-determined by informational constraints control the emergence of transient resonant states of cyclic activity. For details of possible implementations the reader is referred to Kompass (2004).

The mechanism assumed gives rise to expectations on which experimental tests can be based. The functioning of the “invisible” delay mechanism should be robust even under quite artificial conditions. This should make possible psychophysical tests over much larger ranges of variation of temporal parameters than can be realized within the confines of spontaneous temporal organization induced solely by task-related performance. Other experimental situations to be taken into consideration are given by a large class of driving procedures in which normal performance is altered through enforcing external rhythms either by cyclic presentation of stimuli in addition to task-related target stimuli or by cyclic variation of the intensity of the target stimuli. Obvious physiological parallels for possible comparisons are stimulus regimes as are employed in studying steady-state EEG responses. In psychophysical timing research the application of driving techniques has received a major boost through pioneering work by Treisman and coworkers demonstrating pronounced driving exerted by series of clicks upon judged durations (e.g. Treisman, Faulkner, Naish, & Brogan, 1990). An important further step was made by Burle & Bonnet (1999, 2000). Crucially, by fine-graded variation within in a small interval of frequencies, these authors found in Sternberg’s task and in a Simon paradigm across several conditions the same modulation effect in form of a near-sinusoidal wave. Different from their expectations, this function cannot, however, be explained by physical driving acting on an oscillator controlling timing, because it again steeply crosses the axis where it should relax to it. Important for interpretation within the framework of TQM was the finding of Kompass (2004) that the distance of the outer knots of
the wave agrees quite closely with \( Q_0 \), later complemented by the observation of their agreement with multiples 10 and 11 (Geissler, 2009).

In order to explore the even-spacing assumption in a large range of presumed intermittencies, binocular rivalry was adopted as paradigm. To demonstrate fine-grained modulations of Dominance Time (DT), here defined as the period of time during which one of the mutually excluding images is continuously perceived, stimuli were cyclically interrupted. This choice of conditions is a challenge from the viewpoint of the \( Q_0 \)-related modulations described, because DTs are of the order of seconds as compared to latencies never exceeding a few hundred milliseconds obtained in the RT-paradigms so far studied. Inclusion of high interruption rates is also a challenge, because for rates above the so-called critical fusion frequency (CFF) non-monotonic effects have never been observed. To avoid complexities concerning differential effects of light intensity, the lower bound of interruption rates was set at 50 Hz. To permit a clear decision about the hypothesis of even spacing of fine-grained modulations in time, the range of driving rates was extended up to 125 Hz.

Working hypotheses

Although as yet very little is known about the precise nature of the observed modulations, TQM allows for rough expectations. In the experiment by Burle and Bonnet (2000), RT effects of task-related stimulus variation of maximally 150 ms, i.e. of about the extension of \( R_1 \) corresponded to driving modulations of \(~5\) ms. Kompass’ observation of a driving cycle roughly equal to \( Q_0 \) perfectly fits into this frame. Thus these figures suggest that driving causes essentially stochastic delays or accelerations of no more than one quantal epoch within \( R_1 \). For binocular rivalry, the respective critical intervals are of the order of one to several seconds and they comprise three generally accepted stages all of which may be sensitive to cyclic driving. As a consequence, we may expect driving effects ranging from minimally \(~50\) ms up to \(~100\) ms and more. In addition, we should expect a mixture of effects ranging from contributions of \( Q_0 \) and \( 2Q_0 \) to possibly \( 16Q_0 \). Still, if the gating assumption is valid, near uniformity in time should hold in every case.

Experiment

Subjects

Four subjects of normal or corrected-to-normal vision participated in two to three sessions, in the following indicated by DN, RB, NK, and LO. For simplicity, cardinal numbers of sessions and eye sides (L, R) will be attached to these acronyms. Thus, for example, DN3L relates to data obtained for subject DN, for his left eye in the third session.

Apparatus, stimuli and design

In a completely darkened room subjects were exposed to transparent slides mounted in a Wheatstone stereoscope and lighted by PC-controlled white LEDs (of \(~60\) cd/m\(^2\) luminance). Black bars \((1.7^\circ \times 0.6^\circ)\) were presented to the left and right eye against white backgrounds at 45° counter clockwise and clockwise orientations, respectively. The slides were lighted asynchronically with equal presentation and interruption times with an accuracy of \(~5\) \(\mu\)s. Subjects were asked to press a button as soon as an alteration of the perceived bar orientation occurred. Responses were automatically registered and Dominance Times computed for each eye separately. One session consisted of 17 blocks, each for one fixed value \( t_i \) randomly chosen from presentation times spaced at millisecond distances from \( t_1 = 4 \) to \( t_{17} = 20 \) ms. A block lasted about three minutes. For two participants (DN, NK), the number of sequential key pressings, in the following referred to as trials, was fixed to 50, for each eye side. For the other two participants, as usual in similar experiments, a time limit was set leading to variable numbers of trials between 37 and 50. Blocks were separated by short breaks of three to five minutes of rest.
Results

Fine-grained systematic modulations could be confirmed for all participants and sessions with block means of DT, differing significantly at least between opposite extremes. Most strikingly, absolute elongations were found to be up to 50 times as large as those established in other driving paradigms. However, at the same time large differences resisting any type of standard analysis were evident not only in apparent periodicity but also in absolute elongations, between subjects and eyes as well as within subjects between sessions. In a process of careful stepwise exploration, uniform dynamic properties could be dissociated from striking unpredictably occurring dynamic-shift phenomena of yet unknown origin. In that way basic driving characteristics could be isolated. A key to reach this goal was provided by cases in which clear periodicities of the anticipated type were obvious. A pronounced example is shown in Figure 2: While the data from the first session of subject DN (DN1) in the left panel show a base level about three times as high as those from the first session of RB in the right panel, a strong periodic modulation is found for the left-eye side of RB. With elongations of maximally 0.4 s to both sides, it covers about one third of the entire range. Two clearly visible bipolar waves point to a cycle as a function of presentation time of 4 to 5 ms, which is of the expected order.

Another finding contributing to the disclosure of basic dynamic effect properties is shown in Figure 3. Namely, when computing the averages across sessions and eyes for the subjects whose first-session data are shown in Figure 2 it turns out that in either case about the same periodicity appears as the one seen for the left-eye data at the right of Figure 2. This holds with one striking exception: the completely reversed trend within range $t_1 = 4$ ms to $t_6 = 9$ ms. For convenience of illustration, in Figure 3 this section is mirrored at the overall mean which is put to zero and contrasted with the rest of the function using open diamonds and dashed lines. Comparison with a sinusoidal function of 4.5 ms cycle duration (dotted lines) makes two things obvious: First, both the empirical functions are of roughly that period and, second, the overall course in both cases is that of a damped oscillation becoming increasingly flatter for presentation times $t_i > 14$ ms. Via generalization encouraged by similar observations, these findings lead to two modifications of the original hypothesis on the course of the induced effects, which was derived from the trend obtained by Burle and Bonnet for a much smaller interval of driving rates: (1) Amplitudes may vary and even change signs depending on organismic state variations. (2) They tend to decrease and get more variable as stimulus cycles increase. Note that knot positions along the $t$ axis remain invariant.

Results like those raise the question whether a periodicity of this order is inherent to the entire data set. Motivated by experience from work in color-space representation (Fomin, Sokolov & Vaitkevicius, 1979), factor-analytic techniques were applied.

Fig. 2. DT for DN1 and RB1 plotted against flash duration. Vertical bars denote 95% confidence intervals. Filled and open symbols denote left eye and right eye data, respectively.
Fig. 3. Mean DT trends across sessions relative to the overall means for subject DN (open and filled diamonds, see text) as compared with subject RB (filled squares).

To eliminate the dominant influence of the large base-level differences between individuals, session means of DT were subtracted from block means for each eye separately. From the resulting profiles of relative DT values a 20 × 20 correlation matrix was computed and subjected to Principal Component Analysis (PCA). From the four main factors accounting for 80% of the total variance, the third in the order of variance contribution (F3) turned out to exhibit a strikingly periodic loading structure (Table 1). Rotation of the factor space revealed no crucial change in this patterning. Also, the corresponding coordinates on a dimension obtained through a complementary DMS analysis replicated essentially the same structure. Fitting a sinusoidal function to the F3 loading profile enforcing zero phase shift and using the criterion of maximum correlation revealed a cycle of ~4.45 ms.

Table 1. Load of factor F3 as a function of presentation times $t_i$ (in ms)

<table>
<thead>
<tr>
<th>$t_i$ (ms)</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Load</td>
<td>-0.367</td>
<td>0.703</td>
<td>0.609</td>
<td>-0.638</td>
<td>-0.504</td>
<td>-0.220</td>
<td>0.120</td>
<td>0.011</td>
<td>-0.385</td>
</tr>
<tr>
<td>$t_i$ (ms)</td>
<td>13</td>
<td>14</td>
<td>15</td>
<td>16</td>
<td>17</td>
<td>18</td>
<td>19</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Load</td>
<td>-0.155</td>
<td>0.085</td>
<td>0.400</td>
<td>-0.118</td>
<td>-0.148</td>
<td>0.158</td>
<td>0.414</td>
<td>0.160</td>
<td></td>
</tr>
</tbody>
</table>

Although the regularity of the F3-load structure is robust enough to appear as a cyclic modulation even in the one-factor solution obtained when entering analysis with unreduced data, the result is not fully satisfactory on two major counts. First, F3 absorbs only about 20 percent of the variance covered by the remaining factors. Closer inspection in accordance with (1) and (2) above reveals as likely reasons volatile fluctuations and a steep decline of amplitudes with increasing stimulus presentation times. Both features will drastically attenuate correlations and as a result the contribution to overall variance. The second reason consists in what appears an irregular structure of the eigenvectors of the remaining three factors. The expected contributions of $Q_0$ and its multiples larger than $2Q_0$ are not visible.

To find a solution, we have to first assign the above estimate of cycle duration in terms of presentation time to a hypothetical intermittency in the brain. The standard answer suggesting itself is based on the observation first reported by Sherrington (1904) that effects of alternating and synchronous monocular interruptions do not differ for high presentation rates. The common conclusion is that only the monocular rate is relevant. In application to factor F3, this implies that the underlying physiological cycle should be of the duration $\sim2 \times 4.45\,\text{ms} = 8.9\,\text{ms}$, i.e. of the order of the “Vanagas quantum” mentioned above. An intuitive further consequence would be that that value marks the lower limit of resolution, which would be at variance with former findings such as those of Burle and Bonnet (1999, 2000) amounting to an operative lower limit of $\sim4.5\,\text{ms}$, i.e. of the order of $Q_0$. 

105
To resolve this puzzle, recall that the equivalence assumption of alternating and synchronous stimulation is based on monotonous dependencies and thus does not include periodic modulations even of ~9 ms. In this perspective, therefore, stimulus on- and off-sets across both eyes can be very well established at central parts of the brain rhythms of twice that rate. Note that for intermittencies thus short effect variation between sessions as described by (1) may even be more volatile and decline with increasing presentation time correspondingly steeper. This would explain the lack of any direct trace in the factor structures and call for regression procedures as a viable alternative. Yet, instead of standard procedures, complex iterative strategies will be required; because fixed zero crossings at integer multiples $q$ of $Q_0$ seem to be the only reliable constraints for sinusoidal approximations. As a first move in this direction, session means for the first eight presentation times from $t = 4$ to $t = 11$ ms, corresponding to the segment of highest correlations with F3, were fitted to linear combinations of the form

$$\psi = \sum_{i} a_i \sin(2\pi t / 2^n Q_0) + b_0. \quad (1)$$

In addition, the empirically founded doubling rule $q = 2^n$ and an upper limit of $n = 3$ were adopted as pragmatic constraints. Furthermore, the estimate $Q_0 \approx 4.45$ ms obtained from fitting the F3 eigenvector was used for all computations – a rather strong simplification. Note also that $b_0$ and the expressions for $n = 2$ and 3 may in effect merely play the role of functions taken as customary for non-linear trend reduction. Due to possible differential variations within sub-cycles, no particularly good quantitative fit was to be expected. However, substantial correlations of, on average, $r = 0.62$ justified the attempt. Since in ten of the twenty cases the contributions of $Q_0$ turn out to be larger than those of $2Q_0$, structural agreement with the data can rarely be attributed to the inclusion of higher-order multiples. Above all, the excellent fit of particularly irregular structures of which three striking examples are shown in Figure 4 speaks for a genuine role of $Q_0$.

**Discussion**

**Basic findings**

Figure 5 illustrates the probably most important result of the foregoing analysis. In the panel at the top, the plot against presentation time of the F3 load structure (black diamonds) together with the computed sinusoidal approximation (open squares, dotted lines) makes the basically even cycle-spacing apparent. These modulations established for a range of rate variation as large as 25 Hz to 125 Hz clearly speak in favor of the real-time nature of the presumed quantal mechanism, despite some imperfections of the detected regularity. By comparison, the panel below, in which the same data are re-plotted as functions of the reciprocal presentation rate, is striking because of an accelerated compression toward the right side. It thus reemphasizes on a purely qualitative basis the relevance of the even-spacing feature getting visible in the time domain.
In conclusion, this basic finding supports the notion that two different principles are at work in joint action, shaping the temporal regimes of information processing throughout the brain. Of these, the one reflected by the driving structure seems to ensure under natural conditions precise and undisturbed timing by gating and supporting the stable structuring of wave-like oscillatory activity that is governed by the second principle, the segmentation of longer periods into smaller ones.

We appreciate a similar earlier idea of dual pacing suggested in an insightful paper of Burle and Bonnet (2003). However, an adequate comprehensive implementation must go beyond clock-like mechanisms as the basis of cyclic timing. Neither the progression of maxima, as would have to be expected in accordance with Treisman et al. (1990), nor that of the zero crossings in the middle of each full cycle as considered by Burle and Bonnet agree with harmonics of a wherever located natural oscillator frequency. In addition, modulation amplitudes are the higher the higher the driving rates, a horror to any plausible pure oscillator implementation. But this feature fits nicely in with TQM if one assumes that a driving rhythm elicits fuzzy carriers of cycles corresponding to the boundaries $N \times Q_0$ and $(N+1) \times Q_0$ of the interval into which the driving cycle falls, because the amplitudes of the superimposed carriers added together will be the higher the smaller the zones of fuzziness.

![Fig. 5. Top: F3 loading structure (filled diamonds) and predictions from fit of a sinusoidal function (open squares), plotted against presentation time. Bottom: same, against rate.](image)

We can only in passing mention here that the evidence supporting the validity of H1 and H2 not just for time but also for intensity suggests that the assumed time-based principle also applies to intensities in the brain. This agrees with the mechanism described in Fries et al. (2007) for recoding spike-train coding of intensities into temporal phase coding within the cycle of gamma activity. One may thus speculate that spike trains are intimately related to the second principle of oscillator-like action.

In accordance with the focus of this paper, we have so far concentrated on relational properties. In a more general perspective, it is no less important that our data support basic tenets of TQM with respect to the order of magnitude of the elementary time unit assumed. Whether one agrees to the proposed precise value of the lower limit and its assumed role or
not, the cycle identified in the F3 load structure and the results of the above regression analysis argue against the theoretical relevance of intermittencies as large as some tenths of milliseconds, which are often adopted as fundamental units. Instead, they argue in favor of smaller units far below conscious discrimination. From the TQM perspective, it is this subtle graining in the first place that provides room for fast processes whose automatic underpinning renders possible conscious cognition.

The significance of driving procedures
Mere confirmation of the even-spacing hypothesis does by far not exhaust the returns from the experiment. Of significance for a deeper understanding of the assumed quantal-timing mechanism are two general dynamic properties of driving effects already found in Burle and Bonnet’s data and again confirmed in the present experiment: First, it is the interpolated zero-crossings that coincide with range-specific multiples as predicted, whereas the space between them is filled with up-and-down variations. Qualitatively identical bipolar courses found for driving rates from 25 to 125 Hz indicate robust and invariant functioning of one and the same mechanism along the whole range and probably beyond. This requirement is plausibly met by the delay-based implementation hypothesized in Geissler & Kompass (2003) and its possible neural specifications (cf. Kompass, 2004).

The second feature of importance in the present context springs from comparison with features of spontaneously emerging quantal structures. What is characteristic of the latter is selective prominence of subsets of quantal multiples in accordance with H4. In fact, in driving profiles such preferences are completely lacking. In other words, driving rhythms seem to completely override this constraint and instead enforce themselves as the dominant rhythms. As we have seen, the working hypothesis that this is due to superposition of elicited fuzzy carriers seems to provide a good description of this fact. It remains an open question how this can be expressed in terms of the assumed timing principles.

Are there benefits for research in binocular rivalry?
To complete the picture, we should address the question of possible benefits for research in the field of binocular rivalry (BR). Two facts through which our results bear on current theorizing on the phenomenon are fairly obvious: First, none of the accounts of BR have so far led to the expectation of fine-grained systematic driving effects as those reported here. Second, our findings give testimony to temporal characteristics in the millisecond range by which different individuals agree within margins of a few percent. To the best of our knowledge, nobody working experimentally in the field of BR has as yet even tried to demonstrate such commonalities. Too large are the individual differences in BR to encourage such an endeavor. Yet, as is well known, failing recognition of a regularity inherent to a complex structure may render detection of others difficult or impossible. In this context, it is of interest that TQM not only offers estimates of the invariants to be accounted for, but also gives advice on how individual differences can be included without loosing the foothold of invariance. Just to mention two cases: In the wave scheme of Figure 1 ideal initial synchronization can be replaced by phase spreads specific to individuals, causing a reduction of the observable coherence limit to an “operative” value $M^* < M$. Similarly, individuals may differ in the $Q_0$ modular multiples adopted for otherwise identical processing stages which could explain the observed large base-level differences. There is no space here to explore those or any further options. Suffice it to say, even combinations of such modifications remain testable provided the basic invariants are left untouched.

There are indeed various indications giving evidence that, beyond the observed fine-grained modulations, the known characteristics of BR are in close accord with fundamental invariants as are suggested by TQM. Most straightforward is the apparent correspondence between shortest ranges according to TQM and persistence times of early stages of
information representation and processing: Referring to analogous earlier findings by Engel (1970) O’Shea and Crassini (1987) report a ubiquitous upper bound of about 100 ms common to stereopsis and binocular rivalry and a persistence of a second stage of integrated binocular information of ~300 ms. According to TQM, information can be first represented in $R_1$ with a maximum precision of ~4.5 ms. When the coherence limit is reached at ~135 ms, this precision is lost and cannot be recovered. The next finest possible resolution is ~9 ms and the pertaining ideal upper limit is ~ $30 \times 9 = 270$ ms. These figures agree quite closely with the empirical persistence characteristics and therefore suggest congruence between assumed range structure and physiological stage organization as a reasonable hypothesis. To further check this hypothesis a comparison with estimates obtained by modeling full DT distributions would be desirable. As a first attempt, we here refer to a model of Manousakis (2009) because of its unprecedented data fit with a small number of parameters, which does not imply we share his quantum-physical interpretation. In its mathematical form, the model closely resembles an earlier suggestion by Atmanspacher (e.g. Atmanspacher et al., 2004). Crucial for testable predictions is the theoretical forecast of a slowing-down of state transitions, the quantum “Zeno Effect”. Interestingly, fit of three well-documented cases yields intervals of 300, 280 and 100 ms that can be conceived of as persistence times. According to Manousakis, the intervals are multiples of micro-event times of 5 or 10 ms. This is an obvious analogue to the relation between modular units $Q_0 \approx 4.5$ ms and $2Q_0 \approx 9$ ms and the respective coherence limits $30 \times 4.5$ ms = 135 ms and $30 \times 9$ ms = 270 ms. Furthermore, of two long-term characteristics, one, referred to as $T_b$ and ranging from 0.4 to 0.9 seconds, is of the order of magnitude required for the generation of micro cycles (Geissler, 1991), the second, referred to as $T(s)$ and ranging from 3 to 6.2 seconds and more, is of the size of maximum “shells” (Geissler, 1992), ensuring access to information on the sensory level. Thus the least one can say is that available evidence in BR conforms with the logic successfully applied in designing our experiment and extracting regularities from the data obtained.

**A challenge to physiology**

Considered as a general program the greatest potential of TQM may be seen in the fact that the structural and numerical invariants on which it builds are neutral against the choice of theoretical language and data basis from the realms of psychology or physiology. This provides the unique chance of convergent modeling based upon canonc parameterization. However, one should not underestimate the methodological difficulties involved in such an endeavor: TQM invariants relate to the necessary and sufficient basis of mental activity which Fechner once termed “the Psychophysical Process” (PP). Clearly, the machinery below and behind PP, necessary for its implementation, is beyond the scope of psychophysical experimentation and theorizing. More difficult to accept seems to be that substrate-oriented research in mental activity is reliant on the aid of psychophysical constructs when pinpointing and validating physiological equivalents of PP. The rationale of TQM is fairly radical in this respect. For example, while physiologically founded theories have rightly suggested that mental activity operates at the boundary of stability, TQM with the constant internal Weber Law according to H3 sets a quantitative norm for the transition from near-deterministic performance to chaotic activity, and it does so with the provisional claim of universal validity that can be refuted only by psychophysical means. Search for physiological equivalents of psychophysical constructs, if accepted as a reasonable goal, puts a heavy burden onto physiology, because substrate-oriented research is confronted with a degree of signal variability in general much larger than that found in psychophysical experiments. Therefore, dissociation of the relevant fractions of variability and even more so the identification of those properties that are invariant across the brain seem impossible without a psychophysical target structure and carefully controlled backward-search starting from psychophysical information. Mutatis mutandis, the same applies to our suggestion of a delay-based timing principle for
which new massive complementary evidence has been presented in this article. It appears that corresponding mechanisms have so far generally not even been considered because the relevant transmission delays are inconspicuous by comparison with recordable oscillatory brain potentials. Demonstration of their presence and their relevance as a basis of timing mechanisms in different areas of the brain is a difficult aim certainly not to be pursued without related psychophysical evidence and at least rough estimates of their quantitative characteristics. But here they are.

Appendix

Integers $N \leq M = 30$ fall apart into the four subsets (in descending order) $S_1$: {30, 29, 28, 27, 26, 25, 24, 23, 22, 21, 20, 19, 18, 17, 16}; $S_2$: {15, 14, 13, 12, 11, 10, 9, 8}; $S_3$: {7, 6, 5, 4}; $S_4$: {3, 2} plus unity such that no element of one of these sets is divisor of another element of the same set. With the ideal estimate $Q_0 = 4.57$ ms, one obtains as corresponding sub-ranges of $R_1$ the intervals: $R_{11}$: $[30Q_0, 16Q_0]$, $R_{12}$: $[15Q_0, 8Q_0]$ and $R_{13}$: $[7Q_0, 4Q_0]$ and $R_{14}$: $[3Q_0, 2Q_0]$. Expressed in frequencies (in Hz) this corresponds to: $R_{11}$: $[7.3 \leq f \leq 13.7]$; $R_{12}$: $[14.6 \leq f \leq 27.4]$; $R_{13}$: $[31.9 \leq f \leq 54.5]$; and $R_{14}$: $[72.9 \leq f \leq 109.4]$. Of those, $R_{11}$, $R_{12}$, and $R_{13}$ agree surprisingly well with standard definitions of the EEG alpha, beta and gamma bands, respectively. From the property of $R_{11}$ as the set of intermittencies from which all others can be generated follows the hypothesis of a privileged position of the alpha band. Figure 6 illustrates how good the predicted band width agrees with employed alpha-band definitions.

Fig. 6. TQM prediction for $R_{11}$ (bold bar, dashed vertical line) as compared to alpha band definitions from the literature (1-21: after Klimesch et al. (2007), 22: after Livanov (1971)).

Acknowledgments

This contribution is based on an international cooperation launched in 2006 during a visit by H.-G. Geissler at Vilnius University and sponsored by grant 436 LIT 18/1/06 from the German Research Council DFG. The reported experimental research was funded by grant MIP-015/2011 from the Research Council of Lithuania. The draft of this paper was written and finalized by H.-G. Geissler. He takes responsibility also for details of theoretical interpretation. We thank Algirdas Bastys for technical assistance and Hanna Geissler for communication and help with the language. The first author wishes to thank Lawrence Ward for a stimulating chat.

References


†This paper is dedicated to Michel Treisman, Boris Burle and Michel Bonnet for their pioneering contributions to our knowledge on timing in the brain.