Perceptual Rivalry as an Ultradian Oscillation.

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Introduction:

Perceptual rivalry alternations are switches in perception that occur despite a constant, if ambiguous, sensory input. Whilst being clearly and predictably influenced by the 'external' rivalry-inducing stimulus (Levelt, 1965; Mueller & Blake, 1989), these internally driven changes in perceptual state have been found to exhibit rhythmic properties (Carter & Pettigrew, 2003). It is this endogenously driven, externally influencable nature of perceptual rivalry that has motivated the following comparison with the self-sustaining circadian oscillations of biological systems, despite the significant differences in periodicity.

To date, research into binocular rivalry and related bi-stable phenomenon has largely focused on the mechanisms of suppression and awareness, with less consideration being directed toward the nature of the “switch” that drives the alternations in visual awareness. While the timing of the switches has been the subject of a number of studies (Borsellino, De Marco, Allazetta, Rinesi & Bartolini, 1972; Walker, 1975; Lehky, 1995), the switches themselves are generally considered to be a consequence of a reciprocal inhibition between competing neural populations (Blake, 1989; Wilson, Blake & Lee, 2001), with even the name “rivalry” implying direct competition. However, the observation that one can extend or truncate either the suppression or dominance phase durations independently, through appropriate manipulation of the stimulus (Levelt, 1965; Sobel & Blake, 2002), raises questions about the envisaged nature of such “reciprocal” interactions. Presented here is the thesis that binocular rivalry reflects the workings of an ultradian oscillator (an endogenously driven biological rhythm with a period of less than 24 hours). A key implication of this proposal is that the perceptual switches characteristic of rivalry are themselves generated by an oscillatory mechanism external to the level of perceptual representation. Previously proposed by Pöppel (1994), this is not a novel concept, but one that is being presented here with renewed vigour. While this is not the generally accepted viewpoint, a number of lines of recent

evidence support the idea that the perceptual alternations and the relevant reciprocal interactions are driven by such an oscillatory mechanism (Pettigrew, 2001). Furthermore, as binocular rivalry is becoming increasingly linked to other forms of bistable and multistable visual phenomenon (Carter & Pettigrew, 2003; Hupé & Rubin, 2003; see Rubin & Hupé, chapter 8 in this volume) and binocular rivalry is itself now being viewed as a process involving multiple brain regions (Blake & Logothetis, 2002), this proposal of a common oscillator for all forms of perceptual rivalries would seem well suited to unify and explain the present conglomeration of experimental results.

The thesis that perceptual rivalry alternations represent a form of ultradian oscillation was partly inspired by interactions at Caltech in the 1970s between one of the authors and Richard Feynman. Feynman conjectured, along with his friend David McDermott, that the brain might have a master oscillator, like the “clock” in a modern computer, which was responsible for coordinating all its rhythmic operations (e.g. Feynman, 1999). One corollary of Feynman’s conjecture is that timing should be linked at different levels of scale. In line with this, our suggestion is that perceptual rivalries exhibit ultradian rhythms that can be linked to circadian rhythms, despite their different periodicities.

The notion of perceptual rivalry as an ultradian biological oscillation is not widely accepted (see Pöppel,

1994) but many of the difficulties in accepting this idea are similar to the objections that were raised originally with regard to circadian oscillations. In this chapter we will discuss evidence from several sources supporting the idea that the period of perceptual rivalry rhythms reflects an underlying biological oscillator. Among these:

1. Rivalry alternations look more regular and more like “free running” biological oscillations when care is taken to minimise the potential “jitter” caused by *zeitgebers* (litterally meaning “time-givers” - the term *zeitgebers* will be used, in line with the biological rhythms literature, to refer to phase-shifting stimuli);

2. Despite considerable intra-individual stability, the rhythm of perceptual rivalries exhibits wide inter-individual variation (over a more than ten-fold range), similar to observed variations in circadian rhythms (Kerkhof, 1985);

3. The phase of a rivalry rhythm can be advanced or retarded in a manner analogous to the effects on circadian rhythms of *zeitgebers*, such as light;

4. Twin studies show that rivalry rhythms have high heritability but must involve a very large number of genes;

5. The seconds-long cycles of perceptual rivalry rhythms appear driven by subcortical interhemispheric oscillators (for review see Pettigrew, 2001) like the suprachiasmatic nucleus, the day-long circadian oscillator

that was also recently shown to be an interhemispheric oscillator (de la Iglesia, Meyer, Carpino & Schwartz, 2000).

Features of Circadian Rhythms:

The following discussion will pursue the relationship between circadian and perceptual rivalry oscillations by detailing the principal features of circadian rhythms mentioned above and examining the extent to which they can also be applied to the ultradian rhythms of perceptual rivalry.

The "free running" rivalry Period:

Many consider it unlikely that relatively irregular rivalry rhythms have an affinity with circadian rhythms when the latter repeat themselves so regularly. In the absence of any *zeitgebers,* free-running circadian rhythms have a regularity of minutes in 24 hours (<0.1%). The problem here may be that the changes in the visual system induced by rivalry stimuli have a dual role as both input and output in perceptual rivalry studies. This is in stark contrast to characteristics of circadian rhythms such as core body temperature (Refinetti & Menaker, 1992) and melatonin levels (Lewy, Wehr, Goodwin, Newsome & Markey, 1980) that can be

easily measured in the absence of light cues. The action of this changing visual input may be to constantly reset the rivalry rhythm despite the fact that the ambiguous stimulus itself is held constant (elaborated below in the section on *zeitgebers)*. Such an influence of external factors, however, should not be considered as evidence against the role of an intrinsic oscillator. For example, a jetsetter constantly changing time zones will show an irregularity of circadian period that is not a true reflection of the highly reproducible circadian rhythm obtained when the influence of *zeitgebers* is removed. If rivalry depends on the visual system for both input and output, it is impossible to consider the perceptual rhythms in isolation from the phase-shifting *zeitgebers* in a manner equivalent to the light controlled environments used to study circadian rhythms. A crucial point here is that the same *zeitgeber* has a completely different magnitude of effect, according to its timing, relative to the phase of rhythm. For example, there is a much greater effect of light at times when light is normally absent. If this also applies to rivalry, we would expect visual stimulation to act as a *zeitgeber* which would vary in its effect according to the rhythm’s phase, even though the stimulation were being held constant. A number of observations support this thesis of an underlying oscillator for perceptual rivalry whose stochastic qualities are a consequence of phase-dependent *zeitgeber*-like interactions with the visual input.

Firstly, if individual rivalry rhythms are measured under controlled conditions that recognise the possibility of phase-shifting inputs such as alterations in stimulus intensity and great care is taken to reproduce the stimulus conditions exactly (in respect to image size, contrast, luminance and even the testing procedure and location), test-retest reliability is 85% for the binocular rivalry rate of an individual (see Fig. 15.1) (Pettigrew & Miller, 1998). This level of reliability is impressively high for a psychometric measure and it is also true for the rate of alternation of Bonneh's motion-induced-blindness (MIB)(Bonneh, Cooperman & Sagi, 2001), a perceptual oscillation recently shown to share remarkable temporal similarities with binocular rivalry (Carter, 2001)(for an example of MIB see www.weizmann.ac.il/~masagi/MIB/mib.html). These two phenomena were thought to be related only distantly by the fact that each involves "suppression" of a stimulus that is continuously present. Our study suggests, however, that they may be united more fundamentally by a common oscillatory mechanism (Carter & Pettigrew, 2003). The proposal that a common oscillator may underlie all forms of perceptual rivalry has been further reinforced recently by the demonstration that plaid stimuli, a third kind of rivalry involving ambiguous motion, similarly shares a number of temporal characteristics with binocular rivalry (Hupé & Rubin, 2002; Hupé & Rubin, 2003. See chapter 8).

Secondly, extremely regular rivalry rhythms can be revealed by specific manipulations that appear to change the way in which visual input influences the oscillator. Perhaps the most extraordinary effect of this kind is the increased regularity of rivalry alternations that can be seen in the “rebound phase” after administration of hallucinogenic drugs such as LSD (Carter & Pettigrew, 2003) and psilocybin (Vollenweider, Hasler, Carter and Pettigrew, unpublished observations). This increased regularity, with multiple harmonically distributed modes, vividly suggests an underlying oscillator that the drug has revealed, conceivably, by reducing the impact of the “jitter” caused by visual input. This “harmonic oscillator” effect is seen in Fig. 15.2 where we show that it is exactly comparable in two different kinds of perceptual rivalry, Bonneh’s MIB and binocular rivalry. Work is continuing to try to unravel the mechanism of this striking increase in the regularity of the rivalry rhythm in subjects under the influence of these drugs. In the meantime, whatever the mode of action, the fact that the same drug can reveal an underlying harmonic oscillator in two different kinds of perceptual rivalry provides support for the thesis that perceptual rivalry represents an ultradian oscillation.

Inter-individual variability of period:

The circadian cycle typically runs over a period of 24 hours. However, in controlled environments – where the influence of *zietgabers* is minimised, there is a considerable degree of inter-individual variability in “free running” circadian cycles (for review see Kerkhof, 1985). The described range of circadian cycles is less than that described for rivalry cycles, however, the sample size is also smaller as measurement of this cycle is dependent on the subject spending many days within a light and temperature controlled environment. Nasal cycles in humans (another ultradian rhtythm that depends on the retrochiasmatic nucleus) vary from 20 min to 10 hours. This inter-individual variability is similarly observed in the period of perceptual rivalry cycles, where there is an approximately ten-fold variation between individuals (Pettigrew & Miller, 1998)(also see Fig. 15.1). Furthermore, while both long-period and short-period circadian mutants are known, naturally occurring long-period mutants are more common. Similarly, the frequency distribution of individual rivalry periods is not normally distributed but is skewed toward faster rhythms, with an extended tail towards slower periods. It has been customary in the field, with a few exceptions (e.g. (Leopold, Wilke, Maier & Logothetis, 2002) to ignore these inter-individual differences in rhythms through a process of “normalization” in which phase

durations are represented, not in absolute terms but as a fraction of the mean phase duration. Even when data is normalized within observers, the results are rarely, if ever, considered in respect to inter-individual variation.

Zeitgeber sensitivity can show phase-dependence:

The sensitivity of circadian rhythms to *zeitgebers* is phase-dependent, with greater sensitivity observed at times when the relevant *zeitgeber* stimulus is absent or low. This property is evident in the example of the circadian oscillator of the single cell organism *Gonyaulax* (Fig. 15.3). The circadian cycle of this organism governs photosynthesis on the surface of the ocean during the day and at night nitrogenous resources are harvested from the ocean depths (Roenneberg & Mittag, 1996). *Gonyaulax* has a precisely determined circadian cycle. If the *Gonyaulax* is deprived of nitrogen during the night, a late encounter with nitrogen will cause it to delay its ascent (Roenneberg & Rehman, 1996). In contrast to the earlier cycles where continuously present nitrogen has no effect upon the circadian rhythm, this fourth cycle (shown in Fig. 15.3) is phase delayed by the late encounter with nitrogen. This example also illustrates the importance of oscillation in dealing with ambiguity. The late encounter of the nitrogenous resource does not result in a compromise in

behaviour, but rather results in a phase delay of the switch from *“stay”* to “ascend”. In respect to the human circadian cycle similar phase specific effects of light can be observed. Under constant “free-running” environmental conditions light pulses presented against a background of constant darkness can cause shifts in the phase of these rhythms when presented during the animal’s subjective night, but not during the subjective day (Minors, Waterhouse & Wirz-Justice, 1991).

A recent set of experiments conducted by Leopold and colleagues (2002) showed the effectiveness of brief intermittent stimulus exposure in increasing the duration of one phase of perceptual rivalry. In this study it was found that if a rivalrous stimulus (for example a Necker cube or an ambiguously rotating sphere) was periodically removed for five seconds, the individual’s perceptual state could be maintained for prolonged periods, and in some cases perceptual alternations were prevented entirely. These results were reported to be evidence against an oscillator; however, reconsideration of the data shows otherwise. Specifically, a predictable relationship was found to exist between the individual’s rivalry rate (during uninterrupted stimulus presentation) and the probability that the same individual will experience a perceptual alternation during intermittent exposure of the stimulus (Fig. 15.4). Under the intermittent condition the stimulus (with five-second blank periods) the individuals who showed the greatest degree of

stabilisation were those with an average phase duration of more than five seconds (0.2Hz). This finding is exactly what would be predicted if rivalry alternations were driven by an endogenous oscillator that can be ‘phase shifted’ by late-phase stimuli in the manner that we are proposing.

Zeitgebers shift phase of perceptual oscillation:

Mammalian circadian rhythms are known to be driven by a network of endogenously oscillating neurons within the suprachiasmatic nucleus (Meijer & Rietveld, 1989). This bilateral nucleus is generally assumed to be synchronously active on both sides, but recent evidence shows that interhemispheric coordination of the paired nuclei can be asynchronous, or even 180deg out of phase (de la Iglesia, et al., 2000). The significance of interhemispheric circadian rhythms is yet to be fully elucidated, but this finding is consistent with the claim that binocular rivalry switching is associated with interhemispheric switching (Pettigrew 2001).

As mentioned above, external cues such as light and temperature influence the duration of the respective phases of the circadian cycles, with exposure to bright light during the early day advancing the circadian rhythm and exposure to the same light stimulus in the evening delaying the rhythm (for review see van Esseveldt, Lehman & Boer,

2000). In contrast to the detailed knowledge about the phase-shifting effects of *zeitgebers* on the circadian cycle, information is still emerging about the influence of different stimuli on relative phases of binocular rivalry rhythms. For example, until recently it was generally accepted that manipulating the “strength” of one of the rivaling figures through increases in motion (Breese, 1909), contrast (Mueller & Blake, 1989) or spatial frequency (Fahle, 1982) will affect its overall predominance not by prolonging its dominance phase, but rather by reducing its suppression phase duration (This is known as Levelt's second proposition. See Levelt (1965) and chapters 8 and 17 of this volume). However, recent work (Sobel & Blake, 2002) shows that the duration of dominance of one of the rivalling alternatives can also be increased directly by appropriate manipulations of the contextual salience of that phase (ie. adding contextual cues can disproportionately enhance the global “significance” of one of the rivalry targets). The phase-shifting effects of *zeitgebers* depend upon the phase in which they are applied. The new experiments showing these “anti-Levelt” effects provide evidence that rivalry is likewise phase-sensitive. This is particularly so if one considers MIB, where there is a simpler possible interpretation of phase than in BR where there is potential double confound (right eye “ON” is not strictly speaking synchronous with left eye “OFF” even if reciprocity is usually assumed). Plaid rivalry also reinforces the

importance of pinning down phase, with the result that contextual effects can be more firmly attributed to one phase, with the prediction that the effect might be reversed at the opposite phase. A detailed study of such context-specific reversals has been submitted for publication (Carter, Campbell, Wallis, Liu, & Pettigrew, submitted).

A possible unifying theme in the complicated interpretation of phase relations in biological rhythms is the idea that all may be interhemispheric rhythms with each phase corresponding to the dominance of a different hemisphere. Since each hemisphere exhibits well-recognised asymmetries in function (Nicholls, 1996; Tzourio, Crivello, Mellet, Nkanga-Ngila & Mazoyer, 1998; Perry, Rosen, Kramer, Beer, Levenson & Miller, 2001) and “cognitive styles” (Ramachandran, 1994), this phase-hemisphere correspondence could help elucidate phase changes. For example, in the case of Bonneh’s MIB, the disappearance phase can be reliably linked to the activity of the left hemisphere by experiments using trans-cranial magnetic stimulation (TMS), while similar experiments link the appearance phase to activity of the right hemisphere (Pettigrew & Funk, 2001). This assignment is in line with the left hemisphere’s “cognitive style” to ignore discrepancies (i.e. the stationary discs in the same depth plane and in complementary yellow colour) with the main hypothesis (the moving 3-D cloud of blue dots). The return of the yellow discs, in contrast, is consonant with the right hemisphere’s style to highlight

discrepancies. In this case, the phase effects are particularly clear. Perhaps this approach will also illuminate the context vs stimulus strength problem of phase in other perceptual rivalries. In any case, if due regard is paid to the difficulty of identifying the phase of perceptual rivalry, it is clear that stimulus conditions can shift the phase of perceptual rivalry just as they can shift the phase of a circadian rhythm.

High heritability of period - multiple genes:

An increasing number of “circadian clock” genes have been discovered since the initial discovery of the *per* gene in *Drosophila* (Konopka & Benzer, 1971). While review of this literature is beyond the scope of this chapter (for review see Helfrich-Förster, 1996), a number of features of circadian-rhythm genetics are relevant to the present comparison with rivalry rhythms. Firstly, even though there is much to learn about how the many “clock genes” contribute to the generation of stable ~24 hr rhythms, there is overwhelming evidence that the circadian period is highly heritable. Studies of twins, still in progress, reveal that the period of the binocular rivalry rhythm is highly heritable, with monozygotic twins showing a high concordance (0.55). In contrast, fraternal twins have a low concordance for binocular rivalry period, close to zero. Modelling of

these results is consistent with genetic determination of the rivalry rhythm involving a large number of genes. A larger sample size of twins will be needed to provide a more precise estimate of the number of genes that are likely to be involved, but the results so far support a high heritability and multigenic determination of rivalry rate, just as with circadian rate (Hansell, Wright, Martin, Pettigrew & Miller, In preparation).

It has been suggested that rivalry alternation rate reflects neural adaptation under control of specific transmitter mechanisms, that would similarly be expected to have a strong genetic influence. In response to this claim we would like to put forward an interesting prediction: that perceptual rivalry rate will be buffered against changes in body temperature. Given that the rate of a number of physiological process have been shown to be effected by temperature (Schoepfle & Erlanger, 1941; Hodgkin & Katz, 1949; Takeya, Hasuo & Akasu, 2002), those who adhere to “habituation” as a mechanism of rivalry would have to admit the possibility that increased metabolism would effect its physiology and that a temperature change would alter the rate of rivalry alternations. Whereas, a functional prerequisite for circadian pacemakers is that the oscillator is temperature-compensated so that time keeping will remain accurate over a range of physiological temperatures. Accordingly the circadian rhythms have been found to show a remarkable ability to compensate for increases or decreases

in temperature (Barrett & Takahashi, 1995; Huang, Curtin & Rosbash, 1995; Ruby, Burns & Heller, 1999).

Genetic coupling of circadian to ultradian periods:

A mysterious phenomenon links the genetics of both ultradian and circadian rhythms. A mutation that produces an increased period in a circadian rhythm (e.g. *per* long in *Drosophila*, ~30 hours) may produce a correspondingly increased ultradian rhythm in the same individual, such as the courtship rhythm in *Drosophila*, measured in seconds (Dowse & Ringo, 1987; Konopka, Kyriacou & Hall, 1996). This phenomenon has been observed in a number of systems, including *C. elegans* where the period of three different rhythms at three different scales have been shown to be linked in this way. Similar observations are seen in human perceptual rivalry:-

1. Individuals with a faster than usual rhythm measured on one form of perceptual rivalry, also show a faster than usual rhythm on a different form of perceptual rivalry. This has been shown for binocular rivalry vs monocular rivalry and binocular rivalry vs Bonneh's MIB (Carter & Pettigrew, 2003).

2. Rivalry rhythms are linked to nasal cycle rhythms, with individual's exhibiting a fast or slow nasal cycle similarly experiencing rivalry alternations at a rate

respectively faster or slower than the average (Pettigrew & Hekel, submitted).

Discussion: Feynman's Conjecture.

If the thesis that perceptual rivalries are ultradian oscillations is accepted for the moment, "How?" and "Why?" questions arise immediately. Perhaps the most difficult aspect of the present thesis is the "how?" component of the connection between ultradian rhythms of different scale. Specifically, how is coupling achieved between rhythms that are as far apart as binocular rivalry (seconds) and nasal cycle (hours)? We draw the reader's attention to a phenomenon that supports Feynman's conjecture whilst providing an explanation for the coupling of biological rhythms at all temporal scales. This remarkable discovery involves a redox enzyme, expressed on cell surfaces, that has an ultradian rhythm of around 21 min. If the gene for the enzyme is manipulated to produce an altered ultradian rhythm, the cell's circadian rhythm is altered in direct proportion. For example, a new enzyme with a 30 min ultradian period results in a circadian period of 30 hours instead of 24 hrs. This remarkable finding at the same time provides a biochemical mechanism for Feynman's conjecture and strong impetus for the present thesis linking the ultradian rhythms of rivalry to other biological rhythms (Morre, Chueh, Pletcher, Tang, Wu & Morre, 2002).

To answer the “why?” question, we would like to return again to the unpublished conjecture by Richard Feynman. As mentioned previously, Feynman and McDermott proposed that the brain should have a master oscillator that would synchronise its activities in a comparable manner to the internal clock of a modern computer. In such a scheme one would expect lawful temporal relationships between rhythms of different scales like the coupling that we observe between different rivalry rhythms and between these rhythms and the much slower nasal cycle. This scheme also explains how the recently proposed existence of both high- and low-level forms of binocular rivalry (for review see Blake & Logothetis, 2002) could be phenomenologically and temporally linked. While there is increasing evidence to support Feynman’s conjecture, acceptance has been limited by the lack of any plausible underlying basis for coupling oscillators of different scale.

One might also ask why visual perception should be influenced by "clocks" at all? Such a question arises naturally if one adopts the common view of vision as a relatively passive hierarchical sensory process that was widely promulgated as a result of the success of Nobel Laureates, Hubel and Wiesel. However, it is becoming increasingly clear that visual perception is necessarily bound to processes of visual decision-making, attention and other high-level processes that might require precise timing information. Feynman himself seemed to have recognised an

inextricable link between perception and timing in his early experiments. He was particularly struck by the varying influence that verbal and visual information can have on an individual's internal clock (see p. 218 in Feynman 1999).

Recent work has shown a strong link between efference copy magnitude in an individual and that same individual's rivalry rate, two apparently distant phenomena that are linked obviously only by their mutual reliance on temporal information (Campbell et al 2003). This precise, lawful relationship further strengthens the view that neural timing, as revealed by rivalry rhythm, is fundamentally determined.

In regard to the fundamental role of timing in perception, we draw attention to the work of Dale Purves on "inescapable ambiguity". Although ambiguity in visual perception is not a novel concept, his work emphasizes that ambiguity is often obligatory, and not a facultative issue that can ultimately be "solved" by, for example, bringing touch or other sensory information to bear upon the ambiguity. Faced with inescapable ambiguity, which is an inevitable property of the physical world, we propose that perception has evolved an oscillatory response. To help illustrate this role of perceptual oscillation in dealing with ambiguity, consider again the single cell organism, *Gonyaulax* that we show in Fig. 15.3. After a night at depth, on this particular dive, *Gonyaulax* is completely deprived of the sparsely-distributed nitrogenous substrates for which it

descends each evening. What does *Gonyaulax* “decide” to do if it encounters a patch of nitrogen just as its biological clock indicates that it is time to ascend? As Fig. 15.3 shows, the single cell is capable of a very adaptive response and delays its ascent to take advantage of the just-discovered resource. It is easy to imagine a variety of scenarios where different concentrations of nitrogenous resources interact at different times during the night to provide a variety of “ambiguous” situations when the outcome will be determined in a way that is difficult to determine in advance. The point is that the same sensory data concerning the nitrogenous resource will be “perceived” differently by *Gonyaulax* according to the phase of the circadian cycle, with a small signal triggering a phase delay if there has been a very low signal in the immediate past, while a large signal has no effect on behaviour if it occurs following recent large signals.

Similarly, we propose that an ultradian oscillation has been incorporated into the decision-making of visual perception in recognition of the fact that ambiguity cannot be escaped, but must rather be accepted in the early stages of processing instead of being “solved” at some later stage. If there are at least two different interpretations of the same sense data, as Purves and colleagues have shown for lightness, brightness, colour, motion, stereo depth and geometrical relations (Purves, Lotto, Williams, Nundy & Yang, 2001), we suggest that the ground state should reflect

this reality by oscillating between alternatives instead of assuming from the outset that there is a single “solution” that can be derived by the appropriate calculations. Andrews and Purves (1997) have themselves speculated that binocular rivalry reflects a mechanism evolved to deal with conditions of perceptual uncertainty. We would like to go further and suggest that oscillations are an inextricable component of all forms of visual perception. We think that widening the debate in this way may help generate further interest and expand the relevance of perceptual rivalry beyond the visual sciences. Current investigations into the rivalry process are focussed so intently on the neural correlates of visual suppression and awareness that there is a real danger of ignoring a more fundamental significance of the oscillatory aspect of the phenomena.

Figure Legends:

Fig. 15.1 Stability in time of perceptual rivalry rate when stimulus conditions are held constant:

Selected data on binocular rivalry rate from twenty-two individuals, all measured, over a period of years, using the same testing apparatus and in the same testing room (Pettigrew and Miller 1998). Note the remarkable stability of rivalry rate in each individual, despite the inter-individual variation.

Fig. 15.2 A harmonic rivalry oscillator revealed by LSD:

The existence of an underlying oscillator is strongly suggested by the greatly increased regularity in the phase durations, and harmonic modes, observed for a subject that had taken LSD 10 hours prior to being tested. The frequency histograms show the distribution of dominance phase durations for periods lasting between 0 and 12 seconds a, for binocular rivalry (grey = horizontal, black = vertical) and b, for MIB (grey = appearance, black = vertical). Fig c, Shows the frequency histogram corresponding to phase durations reported for MIB by the same subject retested two months later, when the subject was not under the influence of LSD (figure from Carter & Pettigrew 2003).

Fig. 15.3 Adaptability of the circadian oscillator of the single cell organism, Gonyaulax:

During the day the circadian cycle of *Gonyaulax* governs photosynthesis on the surface of the ocean, whilst during the night nitrogenous resources are harvested from the ocean depths. Note that *Gonyaulax* has a precisely determined circadian cycle, as shown by the first three cycles of daytime surface activity and nocturnal descents. Of great interest to the present discussion about biological oscillators, both circadian and ultradian, is the “decision” faced by *Gonyaulax* in the third cycle illustrated, when no nitrogenous resources are encountered until dawn, when it is time for the organism to return to the surface. This “decision point” is marked by an arrow. Will *Gonyaulax* delay its ascent to take advantage of the resource, or should the precision of the circadian clock determine the outcome by forcing the organism to return to the surface? The phase shift in the clock that is illustrated here shows the adaptability of the circadian rhythm, even in this simple organism.

Fig. 15.4 Replotted Data from the "Increased Persistence" Experiments of Leopold et al (2002):

For subjects that have fast rivalry switch rates (those on the right side of the dotted line), there is a linear relation between the rivalry rate under normal conditions compared with the rivalry rate during intermittent exposure. As indicated by the dotted line, this linear relationship intersects the x-axis at approximately 0.2 Hz (one switch per five seconds). These results were claimed by the authors to be evidence against the involvement of an oscillator. However, when one considers the potential phase shifting effects of intermittent stimulus exposure, the finding that perceptual "stabilisation" (after removal of the stimulus for five seconds) occurred predominantly in those individuals that normally required a period of greater than five seconds to switch, is compatible with the current thesis that there is an underlying oscillator driving perceptual rivalry.

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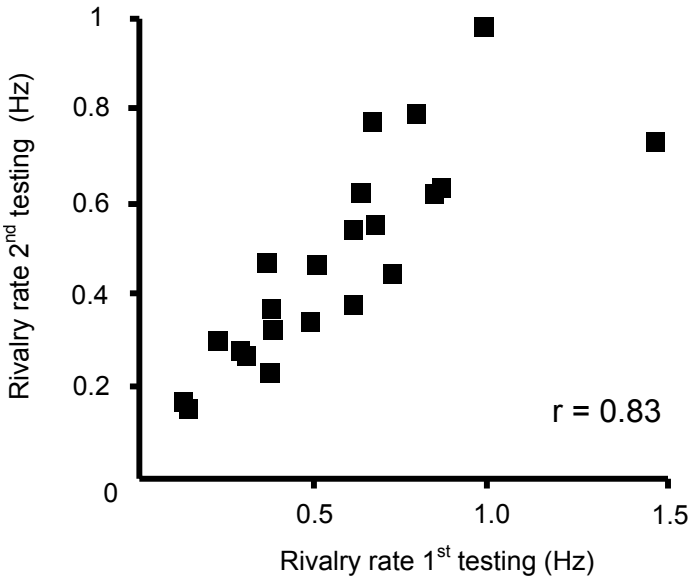
1
0.8
0.6
0.4
0.2
0
0.5
1.0
1.5
Rivalry rate 2nd testing (Hz)
Rivalry rate 1st testing (Hz)
r = 0.83

Fig. 15.1

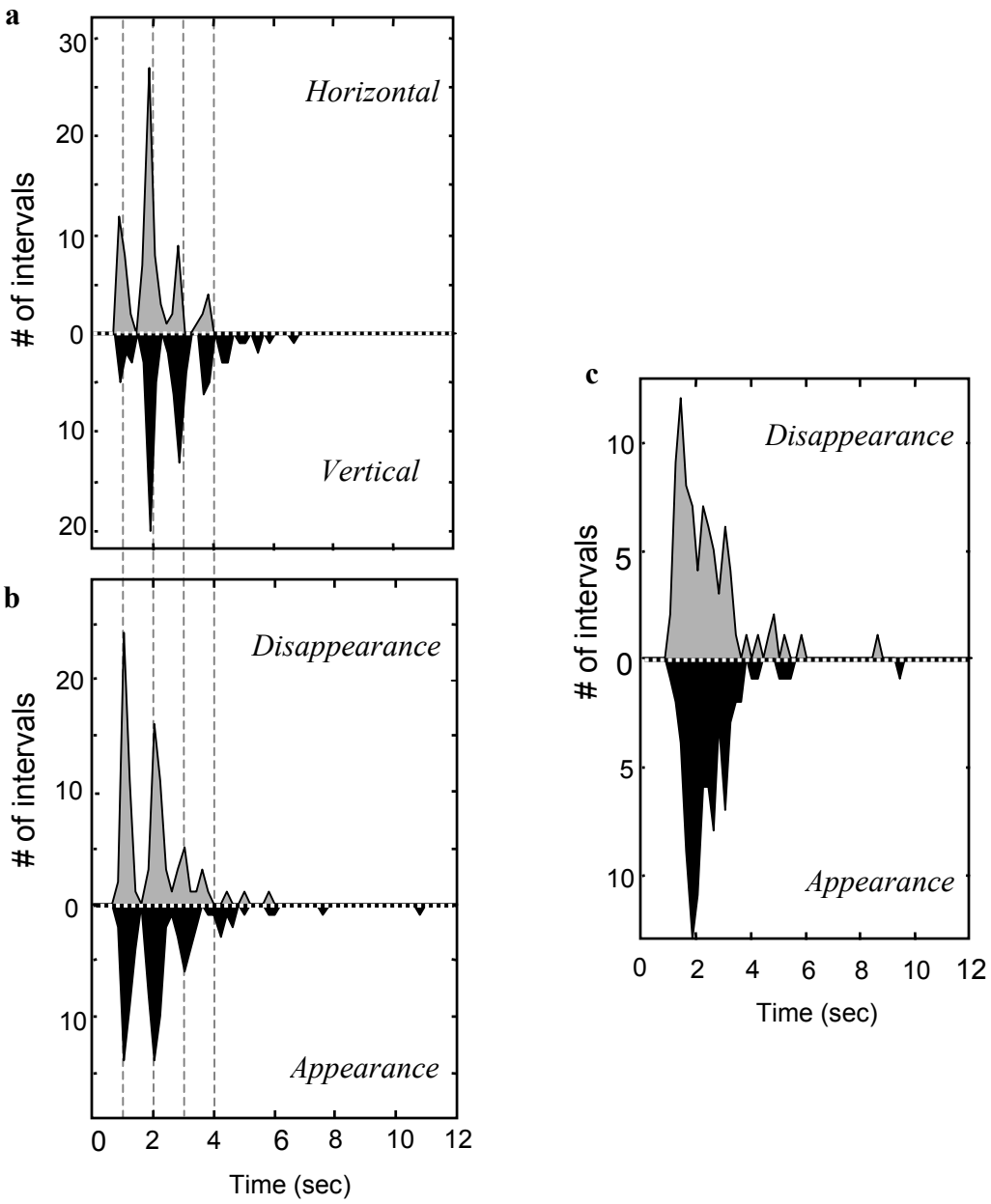
a
Horizontal
Vertical
# of intervals
30
20
10
0
10
20
b
Disappearance
Appearance
# of intervals
20
10
0
10
0
2
4
6
8
10
12
Time (sec)
c
Disappearance
Appearance
# of intervals
10
5
0
5
10
0
2
4
6
8
10
12
Time (sec)

Fig. 15.2.

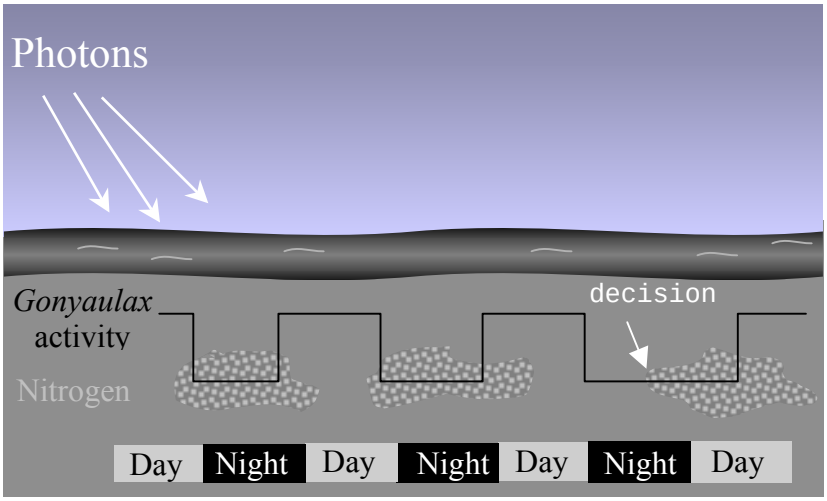
Photons
Gonyaulax
activity
Nitrogen
decision
Day
Night
Day
Night
Day
Night
Day

Fig. 15.3.

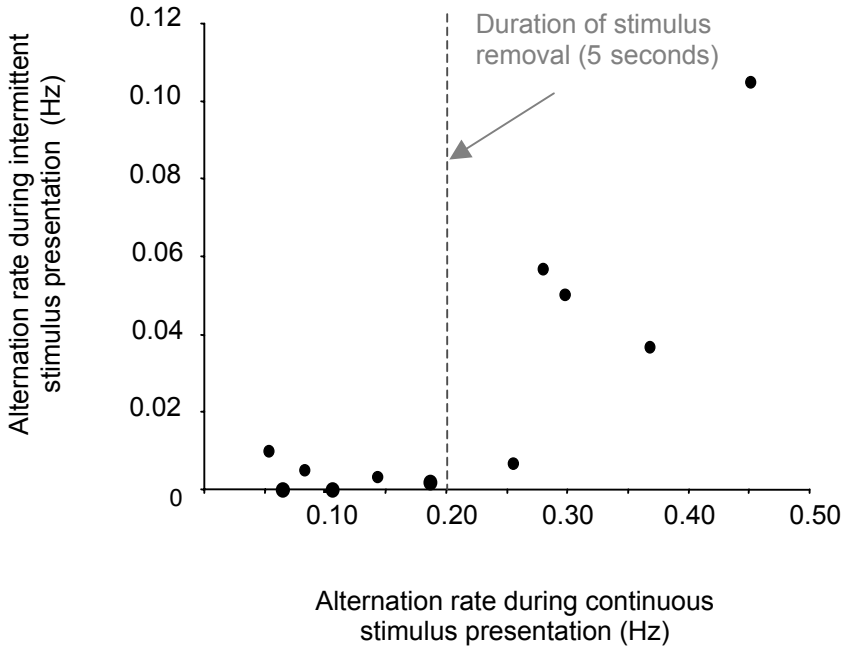
Duration of stimulus
removal (5 seconds)
Alternation rate during intermittent
stimulus presentation (Hz)
0.12
0.10
0.08
0.06
0.04
0.02
0
0.10
0.20
0.30
0.40
0.50
Alternation rate during continuous
stimulus presentation (Hz)

Fig. 15.4.