

Temporal structure and inner psychophysics: A glimpse of equilibrium?

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Abstract

It has been suggested that the synchronization of spatially distributed neural assemblies at fast frequencies in the range 20 - 80 Hz (the 'gamma' band) is instrumental for binding the separate feature-elements of a figure or object. In agreement with this we have shown that reaction times to a display matrix containing a target Kanizsa square (an illusory square consisting of grouping 90° corner junctions) are expedited when the target is preceded at its location by a synchronous priming stimulus. This stimulus comprises four crosses presented simultaneously within a matrix of otherwise asynchronously presented premask crosses, but only if the premask display flickers at key frequencies within the range 27.75 – 67.5 Hz. We have previously argued that this can be partly explained as a function of the return phase of the priming stimulus, suggesting that one of the primary functions of repeated stimulus presentation is the formation of a pattern of anticipatory activity, and it is presumed a pattern of recurrent activity, which relates to the precise timing of the stimulus. However stimulus timing cannot entirely explain the relationship between stimulating frequency and the timing of the anticipatory response. Rather and as is suggested from subsequent data, repeated stimulus presentation provides a means of access to a rich, but as yet not fully circumscribed structure of temporal relations within the receiver.

Oscillatory priming has been shown to relate to important aspects of perceptual coding, such as judged figural complexity (Shi & Elliott, 2007) and has been shown to be realized as a function of inhibitory inter-neuron modulation (Elliott, Becker, Boucart & Müller, 2000; Elliott, Giersch & Seifert, 2006) in circuits under concurrently active anterior and posterior brain circuits (Elliott, Conci & Müller, 2003; Conci., Elliott, Becker Wendt & Müller, 2004). Nevertheless, the fact that priming occurs at one or more specific frequencies (Elliott & Müller, 1998, 2004) remains a puzzle.

Elliott and Müller (2004) presented a set of experiments in which premask matrices were presented at frequencies in the range 30 – 50 Hz. These experiments extended upon the original finding reported by Elliott and Müller, (1998, 2000, 2001) in that they showed priming was not confined to premask flickering at 40 Hz, but that effects are also found when premask matrices flicker at 33 Hz and 46-47 Hz. Following on from the initial findings, Kompass & Elliott (2001) proposed that priming varied in magnitude (or was or was not found) for frequencies according to the time of target presentation expressed in terms of the phase of premask frame presentation (the Return Phase Hypothesis). In fact priming was maximal for targets presented slightly ahead of the time the priming stimulus would have been presented – of premask matrix presentation had continued. This indicates priming to be an effect of protention established by the rhythm of premask matrix presentation. Premask matrices were presented for 600 ms and were followed by static target matrices with an ISI of < 1 ms.

A number of subsequent experiments examined premask-presentation frequencies in various ranges and at various resolutions (in 1 Hz and/or ¼ Hz intervals with premask matrices presented for 600 ms) across various sections of the broad range 27.75 Hz – 67.5 Hz. (Note for full methods see Elliott & Müller, 1998, what varied in the experiments described here were only premask-matrix presentation time and presentation i.e. flicker frequency Priming was indexed by significant Target x Synchrony interactions that often also interacted with Frequency. For short ranges at which there were no priming effects, e.g. 27.75 – 29.5 Hz, a Target main effect was taken as indicator of experimental validity). The mean RTs are presented in Figure 1, in which it is clear that in addition to priming frequencies at 33, 38-40 and 46-47 Hz, priming also occurs when premarks were flickered at 53, 59 and at 66 Hz, while RT minima are evident at 33, 46 and 59 Hz

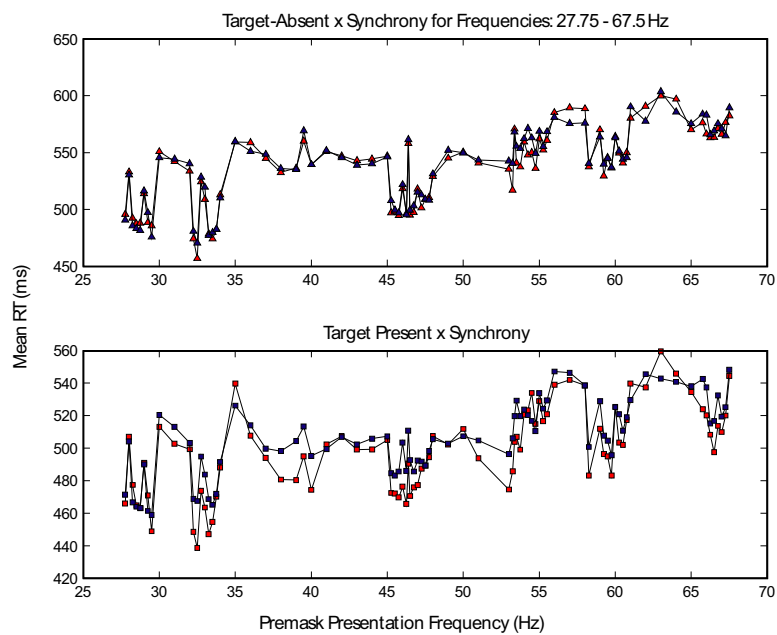


Figure 1

Priming is evident for frequencies separated by 6.49 Hz and this provides inexact but broadly consistent support for the Generalized Phase Angle Hypothesis (Elliott & Müller, 2004 – actually Hans Geissler personal communication), which suggests that priming occurs for stimuli that would regularly interact in phase, every 154 ms, with slower rhythm within the EEG theta band. This is also supported when it is considered that a similar, and related Return Phase Hypothesis could describe the regular phase synchronization of premask stimuli presented at frequencies for which RTs are fastest (e.g. every 77 ms, and for 33, 46 and 59 Hz). However caution is required with this interpretation as it applies singularly to priming given the clear and near identical modulatory patterning in all RT x frequency functions (rank order correlations $r > .9 < .97$). The generalized phase angle hypothesis may thus describe the RT x frequency relation, but something else is required to describe the priming x frequency relation.

Is the return phase hypothesis a more suitable description of priming? Figure 2, which re-plots the RT data shown in Figure 1 as a function of the of target presentation time, expressed in terms of its offset in phase relative to the frequency of premask presentation, would seem to suggest so.

But there is a problem of confusability between this hypothesis and that of the Generalised phase angle, brought about because premask matrices were all presented for 600 ms, irrespective to frequency. Eight * 77 ms (4 * 154 ms) is close to the time of premask-presentation termination (616 vs. 600 ms). Perhaps some or all priming frequencies are favoured due to the interaction of premask-matrix presentation with the slower (77 ms/ 13 Hz or 154 ms/6.49 Hz) rhythm.

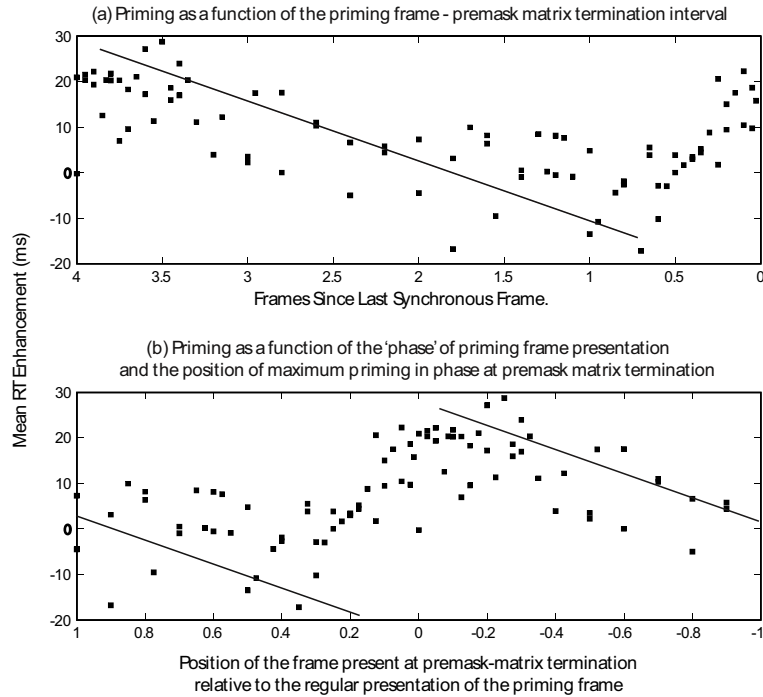


Figure 2

Are the effects of protention revealed for an ordinary range of frequencies (28 – 51 Hz in single Hertz steps) when premask-matrix presentation lasts for some other duration – say 700 ms?

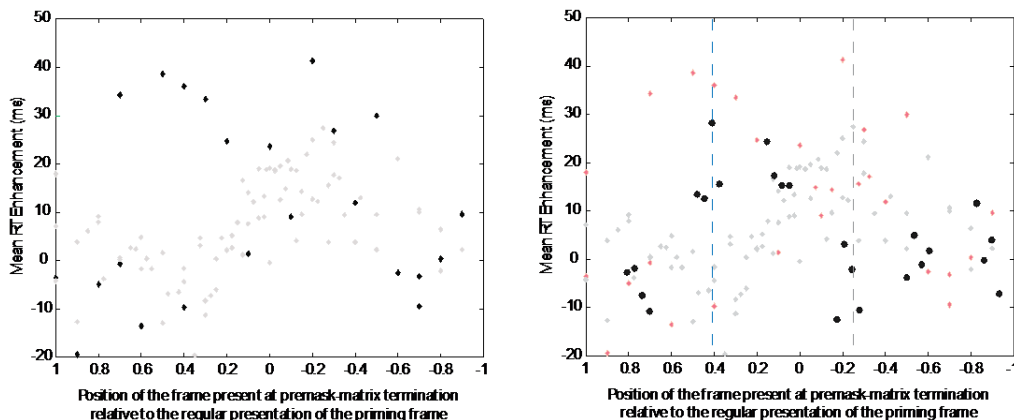


Figure 3

In Figure 3 (left panel – darkest data points) one can see that the pattern is shifted: some frequencies prime in anticipation, but for many others priming occurs retroactively or retentively. However, 700 ms is also very nearly $9 * 77 \text{ ms} (= 693 \text{ ms})$. In a third experiment, premask

presentation time was set to 655 ms (frequencies were 28 – 51 Hz). Figure 3 (right panel – darkest data points) shows the results of this experiment and a clear shift in the location of priming over frame phase with protentive effects now entirely absent. The same data expressed in terms of RT over premask presentation frequency (Figure 4), also show that altering presentation time has an effect on stimulating frequency: specifically, effects are now located at 31 – 32 Hz, 37 – 38 Hz, 43 – 44 Hz and 49 – 50 Hz, a shift of between 1 – 4 Hz relative to the data reported by Elliott and Müller (2004), although at frequencies still separated by ~6.7 Hz.

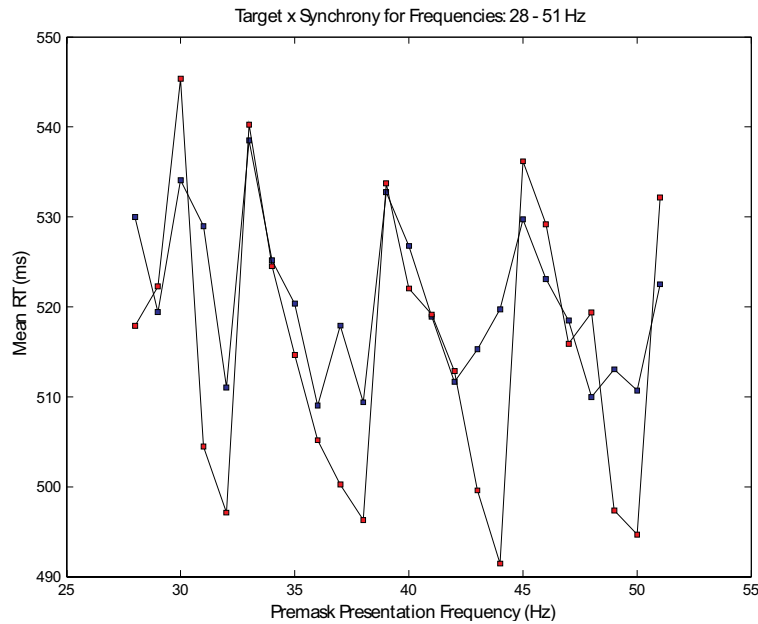


Figure 4

These data have several implications for the priming accounts of Elliott and Müller (1998, 2004) and Kompass and Elliott (2001), the Generalized Phase Angle and Return Phase Hypotheses, respectively. Contrary to the claims of Elliott and Müller, priming is not exclusive to either 40 Hz nor is it specific to the fixed series of frequency bands separated by 6.49 Hz described by them. In addition, it is not exclusively protentive and can prime targets presented at a phase shift after that of priming stimulus presentation, and thus, while frequency-specific priming occurs according to the time of target presentation expressed in terms of the phase of premask frame presentation (i.e. return phase is important), priming is not necessarily protentive.

Both the protentive nature and specific frequency of oscillatory priming depend upon the relationship between the time of target-matrix and the phase of premask-matrix presentation: priming may either occur, or not occur for a given frequency and where it occurs may be protentive or retentive according to this relation. However, considering these dependencies alone, we are unable to determine any causal relationship between frequency and phase and because of the reciprocity of these factors are unable to say for sure that protentive processing arises as a consequence of priming at this frequency or that this frequency ‘appears’ to prime because the character of the processing involved is protentive (for example).

Significantly however, the precise priming frequencies do seem to be organised relative to one another such that they are separated by around 6.5 – 6.75 Hz, irrespective to which frequencies appear to prime and how one might characterise priming (pro- or retentive). This would lend support to the Generalized Phase Angle Hypothesis. However support must acknowledge two caveats: the first of these states that the hypothesis is strictly ‘general’. In other words, one has to accept that a phase separation of 6.5 - 6.75 Hz will obtain between priming frequencies and that this separation may indicate interaction with a slower endogenous rhythm of the that frequency, irrespective to the phase at which premask-presentation frequencies and slow frequency interact. The second caveat states that the hypothesis will remain theoretically ‘general’ until the theoretical relationship between the RT x Frequency functions and priming is resolved. This account and in particular the data shown in Figures 3 and 4 also tends to suggest that a definitive account of priming should consider entrainment phase and phase interaction as opposed to the precise frequency of premask matrix presentation, or at least that this frequency, while prognostic of priming does not provide an explanation for it.

As this concerns the effects of priming, it is perhaps unsurprising that premask-matrix or entrainment frequency is not ultimately critical. Instead, perceptual processes of the sort described by Elliott and colleagues and perhaps in particular Shi and Elliott (2007) – and even perhaps motor response processes – may be dependent upon interactions in phase between premask matrix and endogenous rhythms . Shi and Elliott showed that priming is not merely a data-driven effect but also involves processes responsible for form or figural computation with the corollary that figural information is held and deployed in short-term iconic memory. Elliott et al., (2003) seem to show something similar, or at least that more than one mechanism is engaged in the brain during premask-matrix presentation, with the implication that these mechanisms are bound by virtue of their concurrent activation. If, this is so then phase locking may be a critical feature of their concurrent activation.

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