

# MODELING AS PART OF PERCEPTION: A HYPOTHESIS ON THE FUNCTION OF NEURAL OSCILLATIONS

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## Abstract

*We argue that the effectiveness of synchronization of oscillatory neural activities coding simple features, as it relates to perceptual organization, may originate in the temporal characteristics of resonance that develops in a two-stroke architecture of neural information processing – a cycling between bottom-up and top-down mechanisms. We provide empirical evidence to support the idea that resonance involves the generation and evaluation of ‘models’ of spatial and temporal stimulus attributes. By virtue of temporal modeling, temporally assisted spatial segmentation comes to be very precisely determined by the combination of both global and local stimulus phase.*

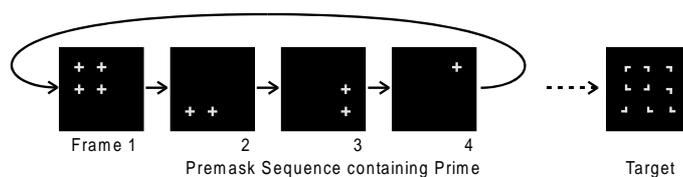
Neural oscillations in electrophysiological investigations are found throughout the cortex, at a wide range of frequencies and at every level of resolution. The extent to which the brain appears to employ oscillations and the complexity of the physiologically observed phenomena challenge any simple and somewhat more general explanation of their functional role. This situation is partly caused by the necessity to restrict electrophysiological investigation to certain segments of the cortex, certain frequency ranges and/or limited levels of resolution.

In this contribution we aim to show that the frequency locking of fast oscillatory activity between successive stages of processing promotes the segmentation of figure and ground. In addition we suggest a very general functional interpretation of the oscillations involved: They serve to: (a) generate interpretations of sensory attributes in bottom-up processing which are evaluated by (b) modeling prototypical sensory patterns to anticipate and match the sensory activities by means of top-down processing. It is important to note that, in contrast to hypotheses derived from electrophysiological investigations, we are able to reach this conclusion by examining the possible functions of neural oscillations from an information processing perspective only: i.e. by employing the psychophysical research agenda. In the historical context this is perhaps not remarkable: Fechner, who was the first to speculate about the role of oscillations in conscious perception, also demonstrated the first, but still puzzling empirical evidence for an oscillatory sensory function through demonstrations of color perception via the rapid and periodic alternation of black and white stimuli (i.e. Fechner’s Colors, see Fechner, 1838 and for a modern approach see Herrmann & Elliott, this issue). Fechner (1860) also suggested that the most likely neurophysiological process by which psychological events might be generated were neuronal oscillations.

Recent, empirical studies have revealed more specific evidence to suggest that perceptual mechanisms operate with very well defined temporal relations: Kristofferson, (1980, 1990) found that breaks in a stepwise-increasing discrimination function correspond to a successive doubling of the Weber fraction. Local invariances in absolute thresholds of very low

sinusoidal sounds (v. Békésy 1936) and of apparent motion (Geissler, Schebera and Kompass, 1999; Kompass & Geissler 2001) exhibit similar systems of preferred temporal intervals with a rich structure of simple integer size relations. It has been suggested that these phenomena can result from phase locking between coupled oscillators across a range of different, but necessarily related, frequencies (see e.g. Geissler, 1987; Geissler et al., 1999), although the timing of the apparent motion stimuli seems to indicate that temporal intervals may also play a fundamental role as units of perceptual processing. These results are complemented by a rapidly growing body of physiological data demonstrating a correspondence between particular perceptual experiences and zero-phase lag synchronisation of the neural activities coding elementary stimulus attributes (see Gray, 1999 for review).

One piece of psychophysical evidence in which these ideas converge is the synchrony-priming effects reported by Elliott and Müller (1998, 1999, 2000, 2001). In Elliott and Müller's experiments, a local, figurally-relevant priming stimulus was presented within the context of a flickering premask matrix of four frames, each presented at 10 Hz and, by virtue of frame-frame asynchronies of 25 ms with a global matrix frequency of 40 Hz (see Figure 1). The local 10-Hz priming frame was found to generate a prime with a 40-Hz structure, which, by Elliott and Müller's (2000) account may be explained if one considers local prime activity to have inherited the frequency of global frame presentations. Given that priming stimuli were not detected by observers and given that they did not promote the deployment of attention to the priming stimulus location in the flickering display, Elliott and Müller considered the priming effects to be generated very early in visual processing. Early visual mechanisms do not possess receptive fields with sufficient dimensions to be capable of responding to the entire premask matrix, although later cortical mechanisms do. Consequently, Elliott and Müller (2000) proposed that early and local neural activity might become primed at 40 Hz, by virtue of this temporal code being fed back from later mechanisms, responding at 40 Hz to the premask matrix as a whole. Successive phase shifts across this network of recurrency would serve to shift the phase of local neural activity coding the prime, such that it became temporally segmented from other activity coding distractor frames. Given that the priming frame is also located in a different place in the premask matrix relative to the distractor frames, temporal segmentation may be considered to spatially segment the priming frame, thereby leading to spatially-specific priming effects as reported by Elliott and Müller (1998).



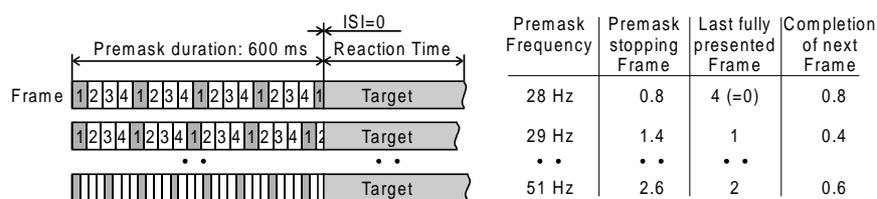
**Figure 1.** Example premask sequence containing a prime for the Kanizsa square and example target frame in the 'target present' condition. In the '40 Hz' condition every frame of the premask sequence is presented for 25 ms.

One question that arises from these studies is how recurrency, which presumably exists at the level of neural interaction, may be considered at the level of cognitive operation. In order to address this question, we examine the possible functions of recurrency with the following postulate: *Neural oscillations represent two different 'stages' of information processing, on the one hand 'model generation' with bottom-up information flow and on the other 'model*

*evaluation* which has *top-down direction*. ‘Models’, in this terminology, correspond to ‘hypotheses’ in the terms of Bayesian information processing. The activity of neural representations is interpreted as denoting the probability of the coded feature to be present. Complex representations are thought to be composed of simpler ones and several such compositions have to be evaluated according to their ability to match the sensory data. As an example, temporal modeling is part of Kristofferson’s (1977) ‘real-time criterion’ model of duration discrimination. In this scheme a standard of the interval to be discriminated is mentally generated at the onset of the external interval and the order of the offsets of the external and the mental internal are compared to judge the external interval. The internal standard can be seen as generating two hypotheses: ‘shorter’ and ‘longer’, the first being replaced by the second at the ending of the internal standard. In general, the notion that modeling occurs by means of oscillatory activity can be seen as a reinterpretation of Grossberg’s idea that the ‘resonance’ of bottom-up and top-down processes is a mechanism by which the ultimate perceptual experience of complex visual forms may be realized (see e.g., Grossberg and Grunewald, 1997; Grossberg, 1999). In the present context, the notion that ‘resonance’ serves as a medium for the realization of the modeling process appears more sufficient than the simpler notion of recurrency. While both concepts imply the co-activation of opposite processes, the role of time differs. Spatio-temporal modeling, which must occur in time as part of the resonant processing, includes the generation of temporally well-defined activities. Neural oscillations underlying resonance therefore are, in contrast to previous accounts, seen as a result of processing, not as a primary processing mechanism themselves. In the following section we aim to provide empirical support for this view.

### An experiment of Elliott and Müller

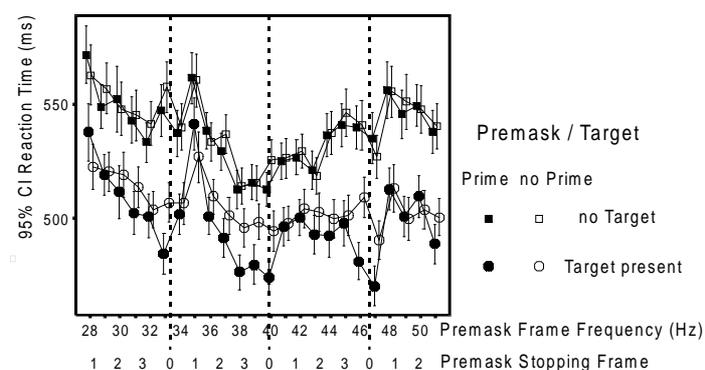
In the following experiment reported by Elliott and Müller (2001) detection of a Kanizsa-type square was preceded by premask-matrix presentation for 600 ms (this duration was found to generate the fastest and least variable RT performance, see Elliott, 1998). The premask consisted of a sequence of 4 frames, cyclically repeated with frame 1 containing four crosses, which might be presented in square arrangement (see figure 1). A measure of the magnitude of priming under these conditions was taken from reaction times to the target and relative to a premask condition in which the 4 crosses of frame 1 were not in square arrangement.



**Figure 2.** Timing of stimuli: Illustration of the co-variation between premask frequency and premask stopping frame resulting from a fixed overall premask duration of 600 ms. A premask stopping frame of 1.0, for example, denotes the situation that frame 1 is completely presented at the end of the premask (see premask illustration in Figure 1).

Given a fixed presentation time, different matrix-presentation frequencies determine a different spatio-temporal configuration at the termination of premask presentation. This we refer to as the ‘premask stopping frame’ (illustrated in figure 2). The integer part of this

variable is also called the ‘last fully presented frame’ in the premask (LFPF); the fractional part is called the ‘completion of the next frame’ (CNF). With a stimulus configuration of this type the effectiveness of the prime at a number of frequencies, or stopping frames respectively, was tested.



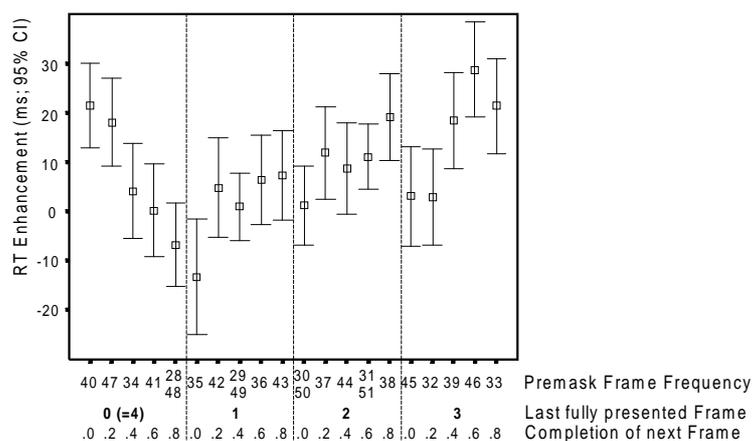
**Figure 3.** Reaction times (95% CI) plotted against frequency of the premask and/or the phase of premask ending in the four conditions target present/absent  $\times$  prime present/absent.

Analysis of the RT patternings by frequency in Figure 3 reveals that both frequency and the stopping frame variably influence RTs: For the general patterning in the RT  $\times$  frequency functions a generalized phase angle hypothesis (GPAH) was given which predicts local RT minima to occur for frequencies, which regularly converge in phase at multiples of  $138 \pm 2$  ms (for more precise details see Elliott & Müller, 2001). Although RT enhancements (i.e. priming effects) occur at the minima of the RT  $\times$  frequency function, they are confined to target-present trials, indicating that they are not immediately explicable by any term in the GPAH.

The assumption that resonance of bottom-up and top-down processes develops during presentation of the premask enables a different approach to analyse the data. Replacement of the premask sequence by the target, according to this assumption, should lead to a mismatch between top-down generated sensory prototypes – evaluated models – and the sensory activity. The extent to which the target matches or mismatches the modeled stimulus patterns should evoke benefits or costs in the target recognition. Analysis of the priming effects at different temporal configurations of premask termination should, by consequence, allow study of the temporal characteristics of the modeling processes.

Assuming simple priming without temporal modeling, a stopping frame value of 1.0, which corresponds to the situation that the prime was just completely present before the target, should enhance effectiveness of the prime most. The empirical results, however, show exactly the opposite: With stopping frame 1.0 the prime is most ineffective, the priming effect even reversed. Separate analyses of variance of RT enhancements by priming yielded highly significant ( $p < 0.001$ ) main effects of frequency and of LFPF in the target present condition and no significant effects when ‘no target’ was presented. LFPF however, a factor hierarchically above frequency, has a larger effect size (partial  $\epsilon^2 = 0.37$ ) than frequency (partial  $\epsilon^2 = 0.17$ ) thereby accounting for a statistically higher proportion of variance in the priming effects. Figure 4 displays this influence. RT enhancement is plotted against LFPF and CNF in the ‘target present’ condition. In particular, Figure 4 reveals that better completion of

the last frame in the premask (CNF) is beneficial for priming only if the last frame fully presented was 1, 2 or 3.



**Figure 4.** Reaction time enhancement by priming (95% CI) plotted against phase of premask stopping in the 'target present' condition.

The interaction of LFPF and CNF is highly significant ( $p \approx 0.001$ ). For LFPF = 1, 2 or 3 a CNF value of 0.0 implies significantly lower RT enhancement than any other value. These results may be summarized in terms of 3 particular patterns of effects:

1. The relative position of frame 1 (containing the priming stimulus) at termination of premask-matrix presentation determines whether it is an effective prime or not. If frame 1 is about to be presented, or was just set on, target RTs (relative to the non-priming frame) are maximally reduced.
2. The CNF has a negative effect on priming if frame 1 is just being completed at premask termination (LFPF = 4), and a positive effect otherwise.
3. Priming is (significantly) smaller if a frame different from priming frame 1 would be presented as the next premask frame (CNF = 0).

Pattern 1 clearly supports the assumption of a cyclical spatio-temporal modeling of the premask sequence, including top-down activation of the four positions being primed in frame 1, which possibly involves binding of the four crosses. Pattern 3 indicates that the modeling within resonant processing also includes the other frames. With CNF=0 these frames are not yet presented, instead the target follows a completed frame of the premask. Nevertheless reaction to the target is delayed.

With respects to the nature of resonance that develops during premask-matrix presentation, it might be considered sufficient to account for priming effects in terms of the resonances established by the local rhythms of the priming frame 1 and the other frames separately, but not in terms of the global rhythm of premask-matrix presentation. However, from experiments in which inter-stimulus intervals (ISIs)  $> 0$  were introduced between premask- and target-matrix presentation, Elliott and Müller (2000) found the magnitude of priming to regularly vary across ISIs with a modulation period equivalent to the frequency of premask-matrix presentation, a pattern derived solely from modulation of the RTs to targets

following prime-stimulus presentation. This result indicates that among the rhythms present in the premask (the cycle of frames in a gamma-frequency range and the cycle of the whole sequence which is in the alpha range) the fast rhythm is prominent in the representation of the prime after offset of the premask. The ISIs investigated however do not exclude the existence of a slow rhythm. That the priming stimulus may be characterized by both local and global premask-matrix rhythms strengthens the empirically driven argument given here (and the theoretical argument given in Elliott & Müller, 2000) that oscillatory synchronization occurs within the context of very finely tuned pattern of resonance between (at least) two functionally separable neural mechanisms, one of which exclusively codes the temporal structure of the priming stimulus and the other responsible for coding the temporal structure of the premask-matrix as a whole.

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