



# The role of perceptual expectation on repetition suppression: a quest to dissect the differential contribution of probability of occurrence and event predictability

Elia Valentini<sup>1,2\*</sup>

<sup>1</sup> Dipartimento di Psicologia, Sapienza Università di Roma, Roma, Italy

<sup>2</sup> Istituto di Ricovero e Cura a Carattere Scientifico, Fondazione Santa Lucia, Roma, Italy

\*Correspondence: elia.valentini@uniroma1.it

## A commentary on

### Human scalp electroencephalography reveals that repetition suppression varies with expectation

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Stimulus repetition is associated with an automatic reduction of cortical activity (e.g., Walter et al., 1964). This phenomenon, often termed repetition suppression (RS), has been reported at multiple spatial scales (Grill-Spector et al., 2006 for a review), from the level of individual cortical neurons in monkeys (e.g., Carandini and Ferster, 1997) to the level of electrical and hemodynamic changes in humans (e.g., Summerfield et al., 2008; Garrido et al., 2009). Traditionally, RS has been characterized either in terms of a process of habituation (Fruhstorfer et al., 1970; Fruhstorfer, 1971), such as that defined by the orienting response theory (Sokolov, 1963), or in terms of a process involving the refractory period of neural generators (Ritter et al., 1968; Budd et al., 1998). Such opposite interpretation is reminiscent of two main theoretical views on sensory representation: a *top-down* building of perceptual expectations from fronto-parietal cortices (Henson, 2003; Friston, 2005) and a *bottom-up* automatic tuning (e.g., sharpening mechanism) of perceptual information through sensory cortices (Desimone, 1996; Wiggs and Martin, 1998), respectively.

Importantly, a recent study attempting to replicate face-repetition effects on BOLD signal in the extrastriate visual cortex (Summerfield et al., 2008) reported no effect of RS on single inferotemporal neurons (Kaliukhovich and Vogels, 2011). This null finding provides indirect support to the idea that the effects of repetition would

be largely associated to neural adaptation mechanisms rather than to “perceptual expectation.” However, in a more recent fMRI study Larsson and Smith (2011) replicated Summerfield et al.’s (2008) and showed that when attention was diverted away from the stimuli the effects of stimulus expectation disappeared but a significant RS was still evident. Thus, it is entirely possible that RS, as indexed by fMRI adaptation paradigms, may reflect a combination of *bottom-up* automatic tuning of neuronal excitation and *top-down* building of perceptual expectation.

In a recent issue of *Frontiers in Human Neuroscience* Summerfield et al. (2011) tackled this challenging issue by testing RS effects on the human electroencephalogram (EEG) signal. They used a  $2 \times 2 \times 2$  factorial design comparing stimulus repetition (*repetition vs. alternation*) with expectation (*expect repetition vs. expect alternation*) and volatility (*volatile vs. stable*). Essentially derived from their previous study (Summerfield et al., 2008), this design had a new important exception: trials sequences were built in such a fashion that the probability of a repetition vs. an alternation changed between 0.2 and 0.8 every 10 trials (volatile condition) or 30–40 trials (stable condition).

By changing the *probability of occurrence* these authors aimed to test the hypothesis that the *repetition*  $\times$  *expectation* interaction should have appeared during stable periods rather than during volatile periods. Crucially, to test this hypothesis an original analytic approach was employed whereby a sequential Bayesian learner computed single-trial maximum likelihood estimates of the expected probability of repetition  $p(rep)$  and the volatility  $v$  for each subject, and subsequently used these single-trial estimates as regressors for EEG single-trial analyses. Aside from this innovative analytic method,

Summerfield et al. (2011) provided also a thorough analysis of both phase- and non-phase-locked EEG responses by computing both standard averaging of time-locked deflections and time–frequency decomposition of EEG oscillatory activity.

In sum, repetition effects were observed at parietal electrodes and at central electrodes between ~300 and 400 ms post-stimulus. In particular, at central electrodes (CP3, CP4, C3, C4, CPz, Cz) an interesting two-way *repetition*  $\times$  *expectation* interaction was detected by means of the Bayesian regression. This effect was accounted for by greater RS when repetitions were expected than when they were unexpected. Interestingly, the analysis of spectral power in the theta-band range (between 200 and 700 ms) was sensitive to the three-way interaction between repetition, expectation, and volatility: power was reduced during repetitions compared to alternations but only when repetitions were expected, and only when the probability of occurrence was stable. Therefore, expectation reliably modulated RS only during stable periods whereas no reliable modulation by expectation was observed during volatile periods.

Such finding has important implications for all the other electrophysiological studies of RS in other sensory modalities. For instance, recent studies on cortical responses elicited by repeated nociceptive stimuli of identical energy (Iannetti et al., 2008; Wang et al., 2010), showed that RS can be clearly observed in event related potentials (ERPs) evoked by nociceptive laser stimuli as well as observed in the auditory modality (e.g., Rosburg, 2004; Viswanathan and Jansen, 2010). In addition, it has been suggested that this phenomenon is strongly determined by the novelty (as function of saliency) of the eliciting stimulus (Wang et al., 2010; Valentini et al., 2011), rather than by neural refractoriness (Truini et al.,

2004, 2007). This view is in agreement with Summerfield et al.'s (2008, 2011) interpretation of their hemodynamic and electrophysiological findings. In addition, however, Valentini et al. (2011) suggested that the suppression of the EEG signal magnitude can be mainly explained by a lack of change (or deviancy – as function of novelty) in the sensory information contained in the repeated stimulus and less impacted by the fact that the change of incoming sensory information is unexpected.

Crucially, the ERPs literature seems to implicitly confer the same meaning to the two constructs of *novelty* and *uncertainty*: the occurrence of an unpredictable deviant event in the environment. However, as elegantly emphasized by Parmentier et al. (2011): novel sensory stimuli “are not only *rare* but also *unexpected*. *Probability* and *predictability* are often used interchangeably in oddball studies but these concepts are not synonymous.” In other words, *expected rare* events may not trigger the same amount of neural activation as that elicited by *unexpected rare* events. Similarly, the cortical modulation exerted by a change of a sensory feature (e.g., *modality change*) cannot be conceived as always representing novelty, as it is possible to have a change without it being novel.

In conclusion, Summerfield et al.'s (2011) study is an elegant first attempt to disentangle these conceptual and operational issues. Future research may focus on *how* and *when* both *bottom-up* and *top-down* variables differentially contribute to short-term habituation processes, and what are their neurophysiological underpinnings.

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