Neuropsychologia 51 (2013) 2548–2555

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Temporal expectation and spectral expectation operate in distinct fashion on neuronal populations

Yi-Fang Hsu [a,b,*], Jarmo A. Hämäläinen [c], Florian Waszak [a,b]

[a] Université Paris Descartes, Sorbonne Paris Cité, 75006 Paris, France
[b] CNRS, Laboratoire Psychologie de la Perception, UMR 8158, 75006 Paris, France
[c] Department of Psychology, University of Jyväskylä, 40014 Jyväskylä, Finland

ARTICLE INFO

Article history:
Received 24 March 2013
Received in revised form
7 August 2013
Accepted 6 September 2013
Available online 14 September 2013

Keywords:
Temporal expectation
Spectral expectation
EEG
ERPs
Low-frequency neuronal oscillations

ABSTRACT

The formation of temporal expectation (i.e., the prediction of “when”) is of prime importance to sensory processing. It can modulate sensory processing at early processing stages probably via the entrainment of low-frequency neuronal oscillations in the brain. However, sensory predictions involve not only temporal expectation but also spectral expectation (i.e., the prediction of “what”). Here we investigated how temporal expectation may interrelate with spectral expectation by explicitly setting up temporal expectation and spectral expectation in a target detection task. We found that reaction time (RT) was shorter when targets were temporally expected than when they were temporally unexpected. The temporal expectation effect was larger with than without spectral expectation. However, this interaction in the behavioural data did not result from an interaction in the electroencephalography (EEG), where we observed independent main effects of temporal expectation and spectral expectation. More precisely, we found that the N1 and P2 event-related potential (ERP) components and the entrainment of low-frequency neuronal oscillations were exclusively modulated by temporal expectation, whilst only the P3 ERP component was modulated by spectral expectation. Our results, thus, support the idea that temporal expectation and spectral expectation operate in distinct fashion on neuronal populations.

1. Introduction

Most research on predictive processing is anchored in the formation of temporal expectation (i.e., the prediction of “when”). It was suggested that temporal expectation can modulate sensory processing at early processing stages (Bendixen, SanMiguel, & Schröger, 2012). Electroencephalography (EEG) studies showed that temporal expectation is associated with the enhancement of certain event-related potential (ERP) components, particularly the N1 amplitude (Astheimer & Sanders, 2011; Lange, 2013). The N1 amplitude was found to be enhanced when the stimulus onset asynchrony (SOA) was extended (Wastell, 1980; Näätänen & Picton, 1987). The enhancement of the N1 amplitude with mounting SOA was believed to reflect the increase in temporal uncertainty of when the stimulus will occur in time, which can also be understood as the accumulation of temporal expectation of the occurrence of the stimulus. Later research also found significant enhancement in the N1 amplitude for stimuli presented at the attended moment in time, when there was high temporal expectation (Lange, Rösler, & Röder, 2003; Sanders & Astheimer, 2008; Astheimer & Sanders, 2009). Such N1 enhancement from high temporal expectation was more pronounced for task-relevant stimuli (Lange & Röder, 2006). On the other hand, some research suggested that temporal expectation can be associated with the enhancement of the P3b amplitude in the attentional blink paradigm in which the stimuli consisted of a rapid series of sounds (Shen & Alain, 2011, 2012).

It was proposed that temporal expectation in audition may involve a division of labour between the cerebellum and the basal ganglia. Whilst the cerebellum may be associated with the automatic encoding of event-based temporal structure, the basal ganglia may be associated with the attention-dependent evaluation of temporal information (Schwartze, Tavano, Schröger, & Kotz, 2012). Such predictive mechanism concerning temporal expectation may be embodied in low-frequency neuronal oscillations which reflect the rhythmic shifting of neuronal excitability instrumental in sensory processing (Engel, Fries, & Singer, 2001; Lakatos et al., 2005; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Schroeder & Lakatos, 2009; Busch, Dubois, & VanRullen, 2009; Arnal & Giraud, 2012). Recent research found that the attentional effect on low-frequency oscillatory entrainment can increase with

* Corresponding author at: Laboratoire Psychologie de la Perception, UMR 8158, 45, rue des Saints-Pères, 75006 Paris, France.
Tel.: +33 1 42 86 43 11; fax: +33 1 42 86 33 22.
E-mail addresses: yi-fang.hsu@cantab.net (Y.-F. Hsu), jarmo.a.hamalainen@jyu.fi (J.A. Hämäläinen), Florian.waszak@parisdescartes.fr (F. Waszak).

0028-3932/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuropsychologia.2013.09.018

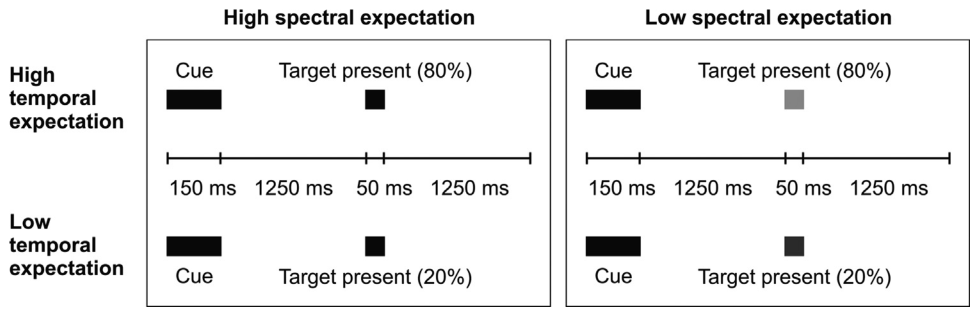

Fig. 1. Experimental design.

temporal expectation (Besle et al., 2011). Stefanics et al., (2010) also found that the oscillatory entrainment in the delta frequency range increased when the stimulus was more probable to appear at certain time point. The temporal expectation effect suggests that the cortical network can be tuned to the temporal dynamics of behaviourally relevant stimuli to boost perceptual inferences (Rohenkohl, Cravo, Wyart, & Nobre, 2012; Vangkilde, Coull, & Bundesen, 2012).

Note that sensory predictions involve not only temporal expectation but also spectral expectation (i.e., the expectation of "what") (Arnal & Giraud, 2012). However, how temporal expectation may interrelate with spectral expectation is largely unknown. Literature on sound feature detection and the mismatch negativity (MMN) response suggested that temporal information and spectral information are processed at least partly by different neuronal networks. Both EEG and magnetoencephalogram (MEG) studies on MMN showed that the foci of the neuronal activity in the brain differ between responses to sound duration, frequency, and intensity deviations (Giard et al., 1995; Verkindt, Bertrand, Perrin, Echallier, & Pernier, 1995; Rosburg, 2003). One the other hand, at the MMN time window, different sound features are also rapidly integrated as suggested by research using sound feature conjunctions (Näätänen, Paavilainen, Rinne, & Alho, 2007). This raises the question whether the expectation of temporal information and spectral information modulates sensory processing in a similar way.

To dissociate the influences of temporal expectation and spectral expectation on sensory processing, we explicitly manipulated these two factors in a target detection task using EEG. One possibility is that the anticipatory processing for temporal information and spectral information are tightly connected such that both temporal expectation and spectral expectation can influence perceptual analysis (Lange, 2009). Another possibility is that temporal expectation and spectral expectation operate in distinct fashion on neuronal populations (Rimmele, Jolsvai, & Sussman, 2011; Arnal & Giraud, 2012). It is this latter scenario that turned out to be corroborated by our data. In particular, we found that the N1 and P2 ERP components extracted from a temporal principal component analysis (PCA) and the entrainment of low-frequency neuronal oscillations were exclusively modulated by temporal expectation. Spectral expectation did not have any effect until later processing stages. Our results suggest that temporal expectation and spectral expectation operate in distinct fashion on neuronal populations.

2. Materials and methods

2.1. Participants

Fifteen healthy volunteers (average age 29; six males; all right-handed) with no history of neurological, psychiatric, or hearing impairments participated in the experiment. Participants gave written informed consent and were paid for participation. Ethical approval was granted by the Comité de Protection des Personnes (CPP) Ile de France II. Participants were excluded from EEG analysis if they had more than 10 electrodes showing extensive artefacts in the recording and/or less than 30 artefact-free trials in any of the conditions of interest. For the analysis of EEG activity before presumable target onset, there were thirteen participants in the final sample (average age 29; six males; all right-handed). For the analysis of EEG activity after presumable target onset, there were twelve participants in the final sample (average age 29; five males; all right-handed).

2.2. Stimuli

Sinusoidal tones with a loudness of 80 phons were generated using Matlab. Two cue tones of distinct frequencies (1318 Hz and 1046 Hz; 150 ms duration; 10 ms rise/fall times) signalled the probability (80% and 20%) of the target tone to appear after 1250 ms, creating the conditions of high and low temporal expectation. In the block of high spectral expectation, the frequency of the target tone was always 1975 Hz (50 ms duration; 10 ms rise/fall times) so that participants can be certain of the identity of the upcoming target tone. In the block of low spectral expectation, the frequency of the target tone was chosen in the range of 1725–1925 Hz and 2025–2225 Hz with 50 Hz steps (50 ms duration; 10 ms rise/fall times) so that participants cannot be certain of the identity of the upcoming target tone. Note that the target tone frequency in the high spectral expectation condition was sandwiched in between the target tone frequencies in the low spectral expectation condition to control for the stimulus-driven effect on the EEG. In other words, the target tone frequency in high spectral expectation condition was higher than half of the target tone frequencies and lower than half of the target tone frequencies in low spectral expectation condition. Such design thus counterbalanced the "mean" frequency as well as the frequency distance between the cue tone and the target tone in the high/low spectral expectation condition, which in turn minimised the probability that stimulus-driven effects can account for possible spectral expectation effects. The target tone was followed by a 1250 ms inter-trial interval (Fig. 1).

2.3. Procedures

A total of 1200 trials were presented in twelve blocks of 100 trials. Within each block, there were equal proportions of trials for the high/low temporal expectation conditions. The arbitrary mapping of the two cue tones and the probability of the target tone to appear after 1250 ms was counterbalanced across participants. There were a total of six blocks of high spectral expectation and six blocks of low spectral expectation. The order of blocks was counterbalanced across participants. Participants listened to the stimuli delivered binaurally through headphones (Sennheiser PX200). They were made aware of the meaning of the cue tones and were instructed to press a key for target tone as soon as possible.

2.4. Data recording and analysis

2.4.1. EEG recording and pre-processing

EEG was recorded with 64 electrodes (actiCAP, Brain Products GmbH, Germany). The sampling rate was 500 Hz and an online bandpass filter of 0.01–100 Hz was used. The data was recomputed to average reference offline. For the analysis of EEG activity before presumable target onset, epochs extended from −100 ms to 1400 ms relative to cue onset, using a 100 ms baseline prior to cue onset. For the analysis of EEG activity after presumable target onset, epochs extended from −1400 ms to 1300 ms relative to presumable target onset, using a 100 ms baseline prior to presumable target onset. Ocular artefact correction was conducted with independent component analysis in EEGlab (Delorme & Makeig, 2004). Epochs containing voltage deviations exceeding ±90 μV relative to baseline at any of the electrodes were rejected. The trial numbers after artefact rejection in each condition were listed in Table 1.