Brain Structure and Function (2020) 225:149–159
https://doi.org/10.1007/s00429-019-01993-8

ORIGINAL ARTICLE

Modality-specific sensory readiness for upcoming events revealed by slow cortical potentials

V. Bianco[2] · R. L. Perri[1,3] · M. Berchicci[1] · F. Quinzi[2] · D. Spinelli[1] · F. Di Russo[1]

Received: 1 July 2019 / Accepted: 22 November 2019 / Published online: 29 November 2019

Abstract

Human brain activity allows to anticipate future events and to prepare the next action accordingly; consistently, event-related potential (ERP) studies found action preparatory brain activities in the premotor and prefrontal cortex. In the present study, we investigated the preparatory activity in the sensory cortical regions. Slow cortical potentials were recorded during passive tasks, i.e., subjects expected for a sensory stimulus and no motor or cognitive response were required. In particular, we tested the hypothesis that perceptual anticipatory cortical mechanisms were modality specific. Three groups of 21 young adults underwent passive perceptual tasks in different sensory modalities (visual, auditory, or somatosensory). We confirmed the presence of a visual negativity (vN) component for the visual modality starting about 800 ms before stimulus with source in extrastriate areas and we found novel modality-specific sensory readiness components for the auditory and somatosensory modalities. The auditory positivity (aP) started about 800 ms before stimulus with source in bilateral auditory cortices and the somatosensory negativity (sN) started about 500 ms before stimulus with source in the somatosensory secondary cortex, contralateral to the stimulated hand. The scalp topography and intracranial sources of these three slow preparatory activities were mirrored with inverted polarity at early post-stimulus stage evoking the well-known visual P1, auditory N1, and somatosensory P100 components. Present findings contribute to widening the family of slow wave preparatory components, providing evidence about the relationship between top–down and bottom–up processing in sensory perception.

Keywords Sensory anticipation · Predictive coding · Perception · Prediction · Perceptual inference

Introduction

Although the best and the worst things in life occur unexpectedly, most of the events we experience every day are actually predictable and our brain is continually committed to anticipate future events to prepare the best next move. The brain anticipatory functions have been extensively investigated using the event-related potentials (ERPs) technique, because, due to its high temporal resolution, it represents a suitable tool to investigate the dynamics of predictive brain processes. Early studies showed slow-growing potentials in the premotor areas, namely the Bereitschaftspotential (BP, Kornhuber and Deecke 1965), initiating well before movement execution and preparing for any voluntary action and in response to incoming (imperative) stimuli (Jahanshahi et al. 1995). If cues are displayed before the onset of an imperative stimulus, an anticipatory slow potential is recorded at frontal-central scalp in the period between the cue and the stimulus, called the contingent negative variation (CNV). This anticipatory ERP consists of two separate functional

✉ V. Bianco
biancovalentina86@gmail.com

R. L. Perri
perri.rinaldo@gmail.com

M. Berchicci
m.berchicci@gmail.com

F. Quinzi
fquinzi@libero.it

D. Spinelli
donatella.spinelli@uniroma4.it

F. Di Russo
francesco.dirusso@uniroma4.it

1 Department of Movement, Human and Health Sciences, University of Rome “Foro Italico”, Rome, Italy

2 IRCCS Fondazione Santa Lucia, Rome, Italy

3 University of Rome “Niccolò Cusano”, Rome, Italy

components: the frontal early CNV, considered an orienting response and the central late CNV, described as a motor preparation component (e.g. Gomez et al. 2003). Further, a slow potential named stimulus-preceding negativity (SPN; Damen and Brunia 1985) was observed over frontal areas in the case of perceptual anticipation in tasks not requiring a motor response and limited to cognitive activities such as waiting for receiving a feedback about past performance or instruction about future performance, waiting for probe stimuli in arithmetic tasks or for affective stimuli (see van Boxtel and Böcker 2004 for review). Although the morphology and scalp distribution of the SPN was different in each of these experimental conditions, there is general agreement that an underlying network, including the anterior cingulate cortex (ACC), the parietal cortex, and the insular cortex might contribute to the occurrence of the SPN (see Kotani et al. 2017 for review). Overall, since the 60 s, the ERP technique has been used to investigate the anticipatory cortical activities and different slow potentials have been described (for review see Van Boxtel and Böcker 2004).

In purely passive paradigms, where no motor or cognitive actions are required, no preparatory/anticipatory brain activity has been reported in ERP literature, but we recently found that sensory preparation can be recorded in the pre-stimulus phase also in purely passive vision task. Prior to the appearance of visual stimuli (not requiring discrimination or motor response and not having any cognitive or affective value), a slow-rising occipital negativity (called visual negativity, vN) was recorded and interpreted as perceptual readiness activity (Di Russo et al. 2019). The presence of a pre-stimulus activity of the visual areas is consistent with both functional magnetic resonance (fMRI) studies (e.g. Kastner et al. 1999), describing activity from the extrastriate and the striate cortex during the expectation of attended stimuli and EEG studies showing that increased pre-stimulus alpha phase alignment is associated with enlarged post-stimulus P1 (e.g. Fellinger et al. 2011). Indeed, the occipital-parietal alpha rhythm, likely generated by thalamo-cortical afference, is actively involved in shaping forthcoming perception of visual events (e.g. Romei et al. 2010). These findings are in line with the thalamic gating theory (Skinner and Yingling 1976; Brunia 1993) and with the threshold regulation theory (Rockstroh 1989; Birbaumer et al. 1990) postulating the presence of sensory-specific anticipatory activity in modality-specific cortical areas. Further, several recent functional magnetic resonance imaging studies have reported increased blood oxygenation level dependent (BOLD) responses in modality-specific cortices due to the mere presence of stimuli from another modality. These interactions have been found between visual and auditory cortices (e.g. Lehmann et al. 2006), auditory and somatosensory cortices (Schürmann et al. 2006), visual and somatosensory cortices (Dionne et al. 2010; Staines et al. 2014), demonstrating that information relevant to behavior enhances modality-specific excitability in cross-modality experimental settings. However, although fMRI studies describe a selective modulation of baseline activity during visual, auditory, and somatosensory stimulus expectation (Langner et al. 2011), ERP evidence of such anticipatory sensory activity is limited to the visual domain (van Boxtel and Böcker 2004; Di Russo et al. 2019) and it seems important to extend this investigation also to other sensory modalities.

The aims of the study were (1) to confirm the presence of the vN component in passive visual tasks and (2) to extend the notion of sensory readiness to other modalities such as the auditory and the somatosensory modalities. In the present study, we sought to enlarge the family of slow wave preparatory components investigating a "purely" perceptual readiness. To this aim, we used passive paradigms to exclude (or maximally reduce) any task-related cortical activities, such as cognitive processing of information of the incoming stimulus (as in the case of cues, feedbacks or probes) or motor preparation, inhibition, and decision making, typically present in any response tasks.

Methods

Participants

Sixty-three young adults participated in the study. Inclusion criterion was the absence of any reported neurological or psychological disorders. Participants were divided into three gender- and age-matched groups: the first group ($N=21$, 10 females, mean age ± SD = 22.3 ± 1.8 years) performed the experiment in the visual modality, the second group ($N=21$, 10 females, mean age ± SD = 21.7 ± 1.2 years) in the auditory modality, and the third group ($N=21$, 8 females, mean age ± SD = 22.1 ± 2.0 years) in the somatosensory modality. All participants were right-handed (Edinburgh Handedness Inventory, Oldfield, 1971) and were naïve about the aim of study. Written informed consent was obtained from all participants according to the Declaration of Helsinki; the project was approved by the Santa Lucia Foundation Ethical Committee.

Procedure

Participants were seated in front of a screen placed 114 cm from their eyes with their arms positioned palm down on the armrests. During the whole run, the fixation point was displayed in the center of the computer screen and consisted of a yellow circle (diameter 0.15 × 0.15° of visual angle) over a black background. Participants were instructed to remain silent and inactive during stimulus delivering and to maintain their gaze on the fixation point (always present on the screen) throughout the run. Four or five runs and 320–400 trials in total were presented in each of the three experiments. The duration of each run was approximately 2.5 min. The recording session duration was about 15 min. For all stimulation modalities, stimuli were presented with a variable stimulus-onset asynchrony (SOA) of 1–2 s to avoid ERP overlaps between trials. As recently shown (Quinzi et al. 2019), this SOA is enough long and variable to avoid ERP overlaps from the previous trial even in the case of complex tasks evoking late components as the P3 peaking between 600 and 800 ms after the stimulus onset. In addition, as shown in Berchicci et al. 2016 (Fig. 6), the 1000 ms SOA jittering is large enough to strongly attenuate all the activities not related to the current stimulus: indeed, the post-stimulus P3 component of the $n-1$ trial is largely reduced compared to the P3 amplitude of the n trial as an effect of the variable SOA.

For the visual modality, the stimuli were four squared configurations made by vertical and horizontal bars subtending 4×4° (two exemplificative configurations are shown in Fig. 1, panel a), which were randomly displayed for 250 ms with equal probability ($p=0.25$).

For the auditory modality (see the schema of the experiment in Fig. 1, panel b), stimuli were presented for 250 ms binaurally through two loudspeakers placed symmetrically on each side of the computer screen. The stimulus loudness was adjusted to a comfortable level for each subject (around 65–70 dB). Stimuli consisted of four binaural complex tones with the following features: 10 ms rise and fall, 16 harmonic components, 44.100 Hz sample rate, 16-bit sound depth, stereo master, 60 dB SPL, WAV audio file format.

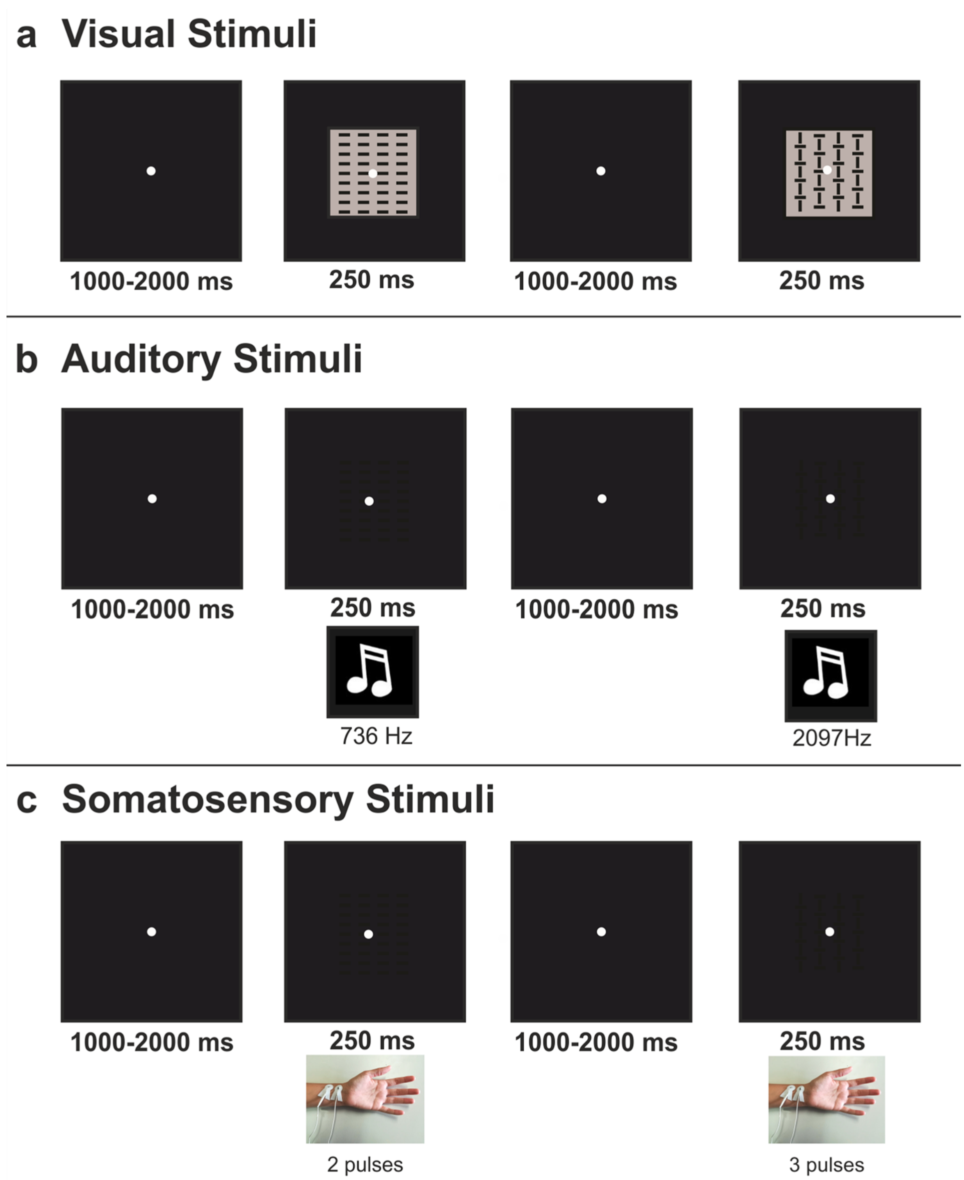

Fig. 1 Schematic representation and sample stimuli of the three paradigms adopted in the present study for the visual (**a**), auditory (**b**), and somatosensory (**c**) modality

For sound synthesis, it was used Praat open source software by Boersma and Weenik (http://www.fon.hum.uva.nl/praat). The following fundamental sound frequencies were adopted: 740 Hz (i.e. F#5), 1046 Hz (i.e. C6), 2093 Hz (i.e. C7), and 2960 Hz (i.e. F#7). The four stimuli were administered randomly with equal probability.

To obtain reliable somatosensory evoked potentials (SEP) by electrical pulses (see the schema of the experiment in Fig. 1, panel c) stimuli consisted of 0.5 ms constant current square-wave pulses delivered by means of a constant tension stimulator (STM 140, HTL, Udine, Italy). The median nerve of the left wrist was stimulated via bipolar electrodes with the cathode placed at 2 cm proximal to the wrist crease and the anode placed 2 cm distal to cathode. For each participant, the intensity of the stimulation was adjusted to produce a moderate thumb twitch (mean intensity = 12 ± 2 mA). The stimuli consisted of a train of two or three pulses to limit the stimulus duration. The two stimuli were administered randomly with equal probability.

All experimental sessions were part of a larger experimental design: after the passive task, which was always performed at the beginning of each session, all participants also performed other two cognitive tasks using the same stimuli. Given the high volume of data from the other experiments and the novelty and originality of the design, the results will be treated properly elsewhere in a specific paper.

EEG recording and analysis

All participants were individually tested in a sound attenuated dimly lit room using a 64-channel EEG system (Brainamp™ amplifiers) with active electrodes (Acticap™) and software (Recorder 1.2 and Analyzer 2.1) all by BrainProducts GmbH (Munich, Germany). The electrodes were mounted according to the 10-10 International System and referenced to the left mastoid. Horizontal and vertical electrooculogram (EOG) was monitored by bipolar recordings. For the visual and auditory modalities, the EEG was digitized at 250 Hz. For the somatosensory modality, the EEG was digitized at 1000 Hz, and then resampled at 250 Hz. In all modalities, the EEG was filtered with 0.01–70 Hz bandpass, including a 50 Hz notch filter. Continuous data were processed offline to reduce EOG artifacts using ocular correction procedure based on the independent component analysis (ICA) tool of the Brain Vision Analyzer software. Semi-automatic artifact rejection was performed prior to signal averaging to discard epochs contaminated by other signals exceeding the amplitude threshold of ± 60 μV. The signal was segmented in epochs starting 1100 ms prior the stimulus onset and lasting for 2000 ms. For the pre-stimulus analysis, ERP components were measured with respect to a −1100/−900 ms baseline (see Di Russo et al. 2016 for the rationale of this baseline). For the post-stimulus stage, ERP activity was measured with respect to the standard −200/0 ms baseline (Handy 2005). Voltage and current source density (CSD, all in one view, 120°, nose top) mapping were used to show scalp topography. CSD maps result from mathematical algorithms, which transform the scalp-recorded ERP into estimates of radial current flow at the scalp: the positive values represent the current flow from the brain toward the scalp (i.e. sources) and the negative values represent the current flow from the scalp into the brain (i.e. sinks; e.g., Nunez and Srinivasan 2006). Compared to voltage, CSD maps are reference-free and reduce the negative impact of volume conduction, which often blurs the scalp-recorded EEG signal.

Spatiotemporal source analysis of the pre-stimulus ERP in the three sensory modalities was performed using the BESA research 6.1 system (MEGIS, Germany). The average reference was used for these analyses. Three independent unseeded models were obtained fitting both dipole locations and orientation on ERP data using a pair of symmetrical dipoles. Each source model was first fitted in the pre-stimulus grand average ERP to obtain a stable model, which was then optimized on each individual ERP. Lastly, source locations, orientations, and time courses (dipole moment) were averaged to obtain the final model.

Statistical analysis

To verify the pre-stimulus ERP activity in the three sensory modalities that did not reflect noise, *t* tests against zero were performed for all scalp electrodes on every sample point between − 900 to 0 ms for each modality. For each sensory modality, the specific time interval during which the brain activity recorded at the peak electrode was significant after correction for multiple comparisons (Bonferroni) is reported in the results. The same statistics were applied to the dipole moment of the source analysis.

Results

Using different colors, Fig. 2a) shows the pre-stimulus ERP waveforms for three sensory modalities. For each sensory modality, thick lines represent the most relevant waveforms at the most representative electrode. Figure 3 shows the peak electrode in each condition with the respective standard error indicating the reliability of the pre-stimulus activity.

In the passive visual condition, the first detectable activity started at about − 800 ms on parietal-occipital electrodes (see PO8) as a negative slope peaking just after stimulus onset; this activity has been previously labeled as visual negativity or vN (Di Russo et al. 2019). *T* test against zero in the pre-stimulus phase at PO7 and PO8 electrodes showed that differences were significant from − 784 to 0 ms, $p < 0.005$. Figure 4 reports the statistical map of the *t* test against zero showing the whole scalp topography in the epochs, where *t* test was significant.

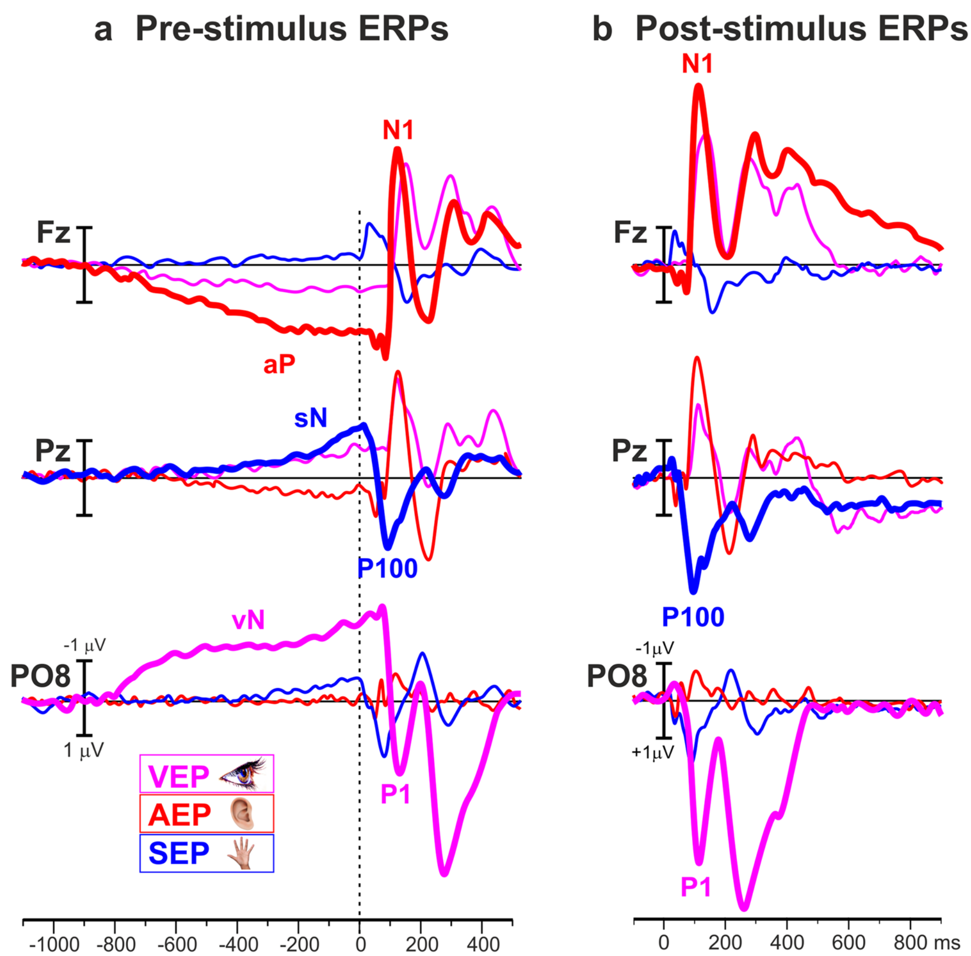

Fig. 2 **a**, **b** Pre- and post- stimulus activities in three passive paradigms. In different experimental settings three sensory modalities were considered: visual, auditory, and somatosensory (see the inset of the figure for the color code of visual evoked potentials, VEP; auditory evoked potentials, AEP; somatosensory evoked potentials, SEP). Grand averaged ERP waveforms are reported for pre-stimulus stage (**a**) and post-stimulus stage (**b**) overlapped for the three modalities. Thicker lines enhance the largest activity at each electrode. In the pre-stimulus stage, the auditory positivity (aP at Fz), the somatosensory negativity (sN at Pz) and the visual negativity (vN at PO8) are indicated

For the passive auditory condition, a positive slow-rising voltage shift emerges at −800 ms over medial frontal sites and peaks after stimulus onset; we named this activity auditory positivity (aP). *T* test against zero at Fz and FCz electrodes showed that differences were significant from −720 to 0 ms, $p<0.05$ (for statistical map, see Fig. 4).

For the somatosensory passive condition, a slow negativity initiated approximately at −500 ms over medial parietal scalp; we labeled this activity as somatosensory negativity (sN). *T* test against zero at Pz and CPz electrodes showed that this activity was different from zero in the interval from −450 to 0 ms, $p<0.05$ (for statistical map, see Fig. 4).

The post-stimulus ERP waveforms for the three conditions are shown in Fig. 2b at the same electrodes were the pre-stimulus activity was maximal but using the −200/0 ms interval as baseline.

The first large evoked activity in the visual modality (VEP) in parietal-occipital sites was the P1 component with a peak latency of 110 ms. For the auditory modality, on medial frontal sites, the earliest evoked activity (AEP) was the N1 component peaking at 110 ms. For the somatosensory modality, the first major evoked (SEP) component at medial parietal sites was the P100 peaking at 95 ms.

Figure 5 shows voltage (a) and CSD (b) maps for both pre- (−200/0 ms) and post-stimulus (90–120 ms) intervals, which were chosen to emphasize the occurrence of similar scalp distributions for pre- and post-stimulus cortical activities. For the visual modality in the pre-stimulus stage, the vN focused at parietal-occipital sites with a wide radial negativity present at both left and right hemispheres (larger on the right side); then, in the post-stimulus stage, the P1 showed a similar topography, but with opposite polarity. CSD maps confirm the parietal-occipital topography and emphasize the bilateral topography for both the vN and the P1 components (with a tendency toward higher activity at the right side).

For the auditory modality, the auditory positivity (labeled aP in the figure) emerged as radial positive voltage distribution in the pre-stimulus interval, peaking at medial frontal sites. The post-stimulus N1 showed a similar distribution, but opposite polarity. CSD maps revealed the involvement of bilateral temporal areas, in both pre- and post-stimulus intervals. The medial frontal voltage focus (Fig. 5a) results from two temporal dipolar activities pointing inward and anteriorly.

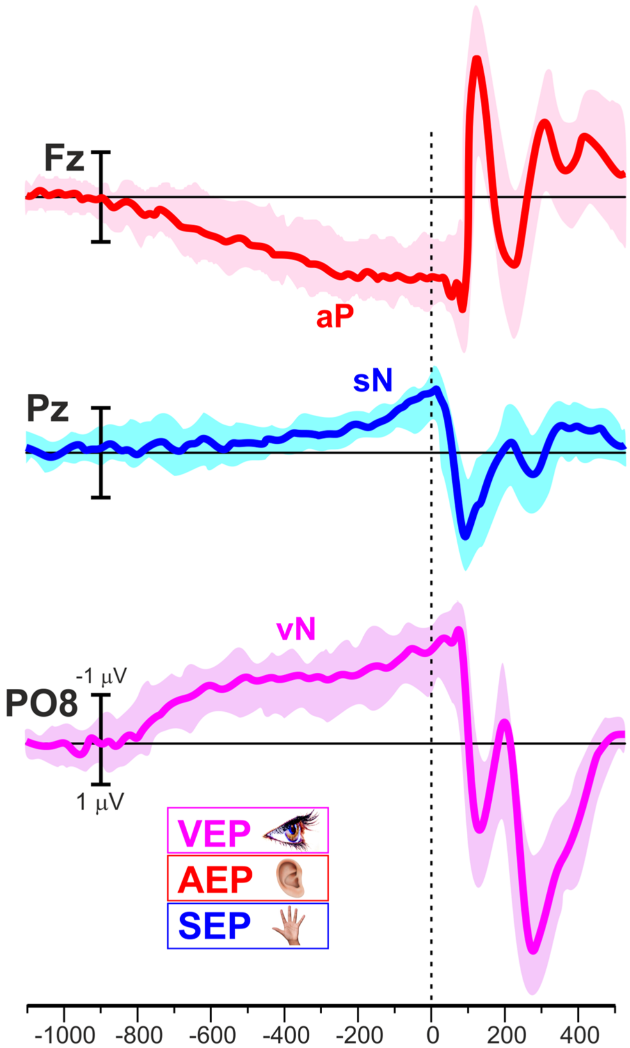

Fig. 3 Pre-stimulus ERP at peak electrodes showing, for each condition, the respective standard error of the waveform

For the somatosensory modality, the "somatosensory negativity" (labeled sN in the figure) was present in the pre-stimulus interval, as a tangential distribution with a negative pole over medial central-parietal electrodes and a small positive pole over right temporal areas. In the post-stimulus stage, as in the case of visual and auditory modalities, the somatosensory P100 showed a distribution similar to that characterizing the pre-stimulus stage, but opposite polarity. Similar distributions were also detected with pre-stimulus and post-stimulus CSD maps. Moreover, both voltage and CSD maps highlighted a post-stimulus stronger activity contralateral to the stimulated (left) wrist, consistent with lateralization of somatosensory processing at parietal level (Hari et al. 1993). Further, a large prefrontal negativity emerged on prefrontal sites in the pre-stimulus period.

Figure 6a shows the dipole locations and orientations of the pre-stimulus ERP sources found for each sensory modality, plotted on the same head template. Figure 6b shows the time course of these dipoles.

The source analysis of the visual activity (the vN) localized the dipole pair in bilateral extrastriate visual cortex (Talairach coordinates: $xyz = \pm 24, -80, 4$) with a residual variance (RV) of 4.14% in the −700/0 ms range, where *t* test against zero was significant ($p < 0.0023$). The dipole time course of the sources of the vN well represents also the P1 and the P2 post-stimulus components.

The dipole pair fitted in the pre-stimulus auditory activity (the aP) was localized in bilateral auditory cortex (Talairach coordinates: $xyz = \pm 51, -18, 12$) with a RV of 4.83% in the −660/0 ms range, where *t* test against zero was significant ($p < 0.0041$). In addition to the aP, the dipole time course of these sources well represents also the N1 and the P2 post-stimulus components.

The dipole pair fitted in the pre-stimulus somatosensory activity was localized in bilateral somatosensory cortex within secondary cortex (S2), Talairach coordinates: $xyz = \pm 17, -35, 46$. In this case, the *t* test against zero in the −470/0 ms range was significant for the right hemisphere dipole ($p < 0.0079$) only, contralateral to the stimulated hand. The RV of this model was 4.36%. In addition to the sN, the dipole time course in the right hemisphere well represents also the P100 post-stimulus component.

Discussion

The present study considered ERPs recorded in passive tasks during which visual, auditory, or somatosensory stimuli were administered to the participants. The main purpose was to investigate the scalp-recorded anticipatory slow waves for each sensory modality. We found that each modality has a distinctive pre-stimulus component; in addition, according to topographical and source analysis, the same secondary sensory areas were active during both pre-stimulus and post-stimulus processing stages.

As for the visual modality, we confirm the presence of the recently described component named visual negativity (vN; see Di Russo et al. 2019), a slow-rising negative activity starting about 800 ms before stimulus. We also confirm its extrastriate origin, which supports the interpretation of the vN as electrophysiological correlate of visual anticipation. Moreover, we suggest that vN might be related to a negative wave found at posterior sites in the S1-S2 interval in some CNV studies (e.g. Kutas and Donchin 1980). Also, the vN might be related to the pre-stimulus posterior increased alpha power previously reported in magnetoencephalographic study (Van Dijk et al. 2008) and to enhanced pre-stimulus alpha phase alignment (Fellinger et al. 2011) and power (Brandt and Jansen 1991) in EEG studies pointing to a modulation of the upcoming stimulus perception (see

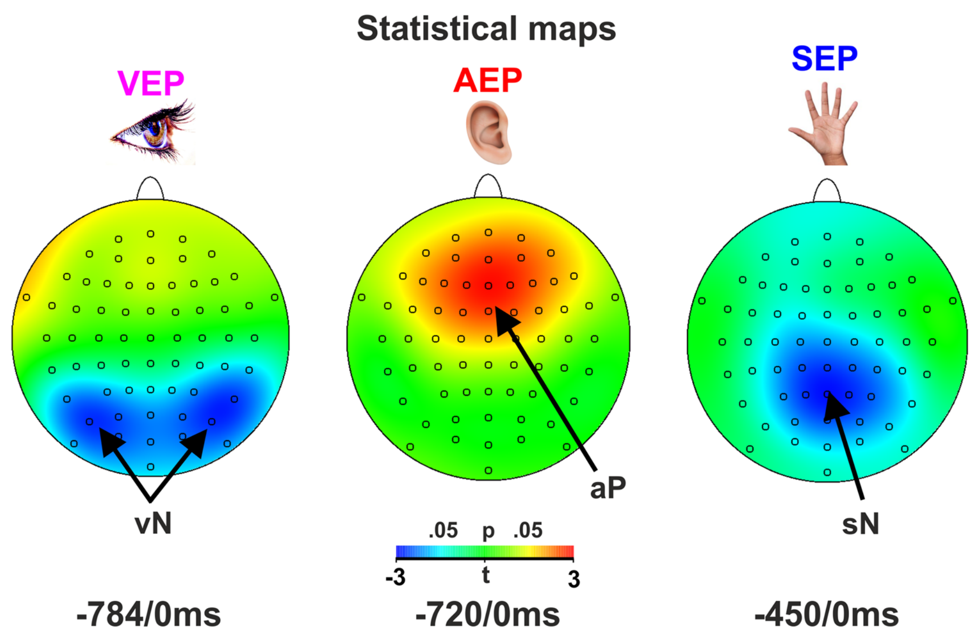

Fig. 4 Statistical maps (*t* test against zero) of the pre-stimulus ERP for the three modalities

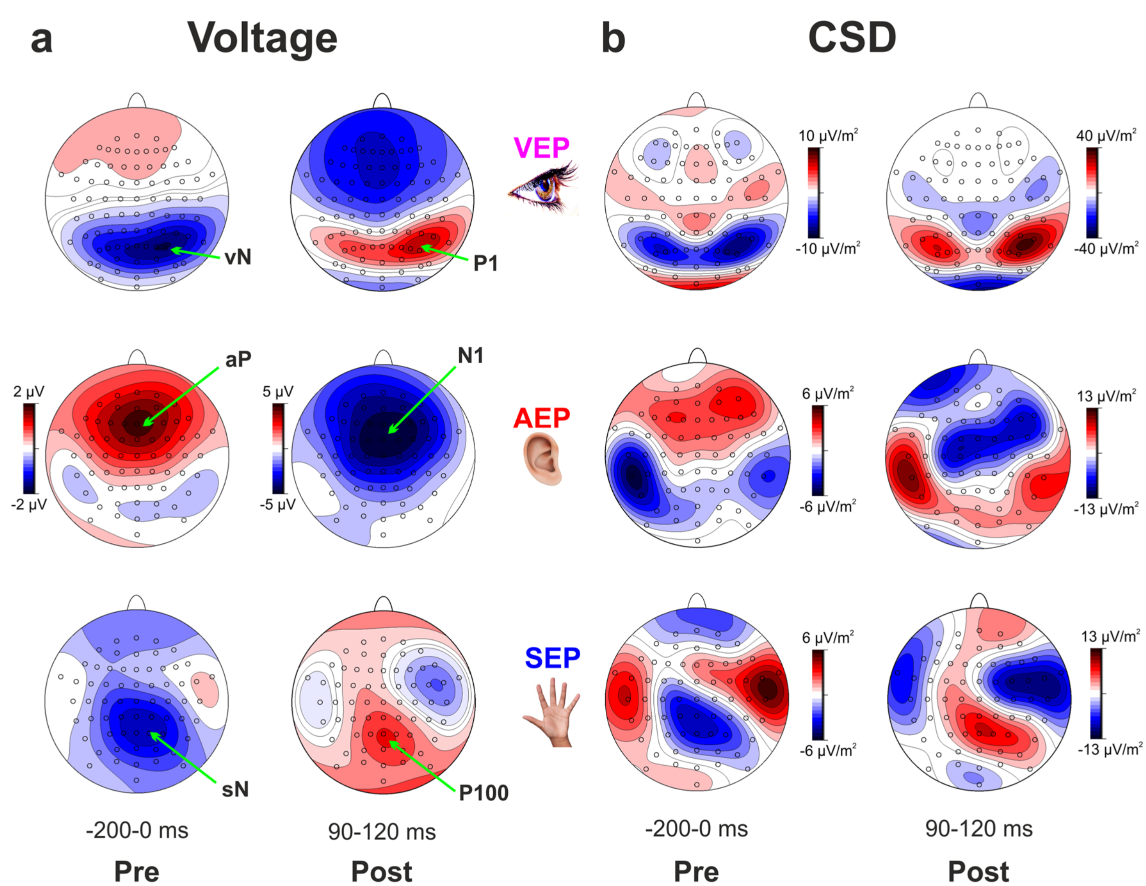

Fig. 5 Topographic distributions of activities in the pre-stimulus (from −200 to 0 ms) and post-stimulus (90–120 ms) stages. **a** Voltage topography. **b** Current source density (CSD) topography

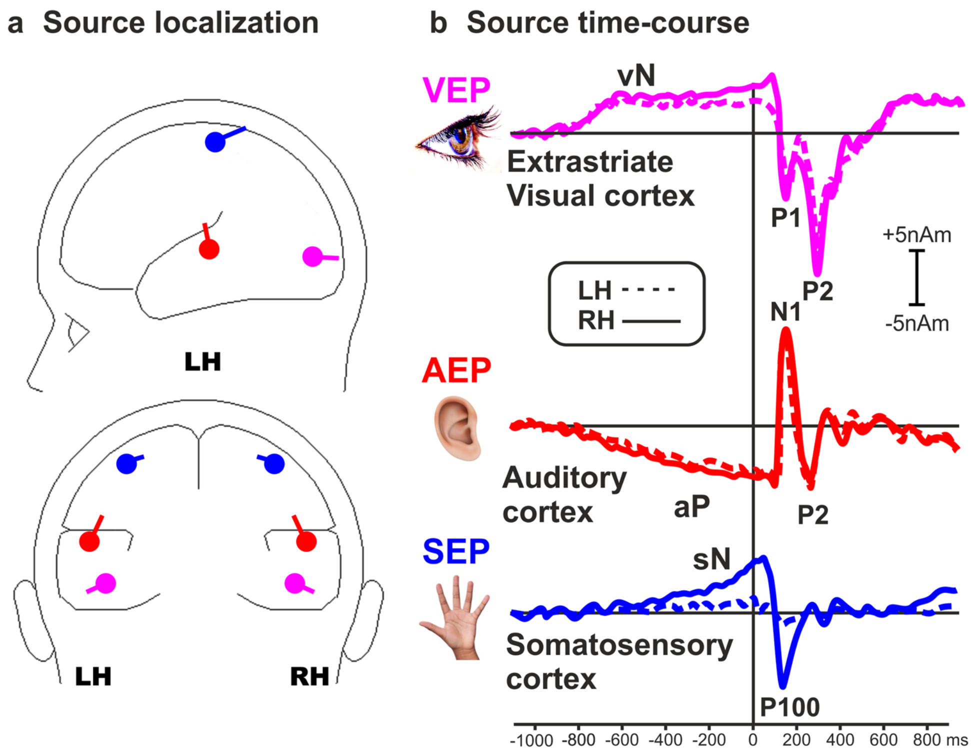

Fig. 6 Source analysis of the pre-stimulus interval. **a** Source localization and orientation, **b** source time course (dipole moment). *LH* left hemisphere, *RH* right hemisphere

Romei et al. 2010). Following visual stimulus presentation, the scalp-recorded negative activity inverts its polarity, producing the P1 component, a well-known component representing the cortical activity evoked by visual stimulus at parietal-occipital electrodes (e.g. Hillyard and Anllo-Vento 1998). The source of the P1 component is the secondary (extrastriate) visual area, as shown by ERP-fMRI combination studies (for a review, see Di Russo and Pitzalis 2013). Overall, extrastriate areas are the cortical sources of both the vN and the P1 components.

In the auditory modality, a positive slope was evident at the most frontal electrodes, starting at about 800 ms before stimulus (timing similar to that recorded for the visual modality). To the best of our knowledge, this activity has never been described before. In auditory CNV or SPN studies (e.g. van Boxtel and Böcker 2004), negative activities were generally reported during the stimulus fore-period; however, in those studies, the analyses did not consider anterior electrodes. Further, fMRI evidence showed that primary and secondary auditory cortices were active during passive listening (Binder et al. 1994; Grady et al. 1997). The herein described auditory Positivity (aP) component might possibly be related to the tau rhythm (6.5–9.5 Hz), a sub-band of the alpha range found in a MEG study (e.g. Bastiaansen et al. 2001), which predicts an activation of auditory areas during anticipatory attention for knowledge of results (KR) presented with auditory feedback in a time estimation paradigm. Present findings suggest that the aP might represent the correlate of auditory anticipation. As in the case of the vN (with a similar timing, but with opposite polarity), the aP slowly grows, reaches its maximum just after stimulus presentation, then the same topography, but with opposite polarity, the N1 shares the same intracranial sources. The auditory N1 component is thought to mainly reflect primary and secondary auditory cortex activities related to processing of the physical features of sensory stimuli (e.g. Key et al. 2005; Zouridakis et al. 1998). Overall, it is likely that auditory areas contribute to both the aP and the N1 components that was described in the present study.

In the somatosensory modality, a slow-rising negativity (called somatosensory Negativity, sN) started half a second before stimulus onset on medial central-parietal electrodes; this activity was associated with a tangential configuration, having positive focus over lateral frontal-central sites (contralateral to the stimulated wrist). The presence of tangential scalp distributions in post-stimulus SEP has been reported from early studies (Desmedt and Robertson 1977) and associated to neural generators in the post-central gyrus, within the somatosensory area. However, information about the pre-stimulus stage is lacking. This somatosensory anticipatory activity may relate to pre-stimulus event-related desynchronization (ERD) detected by Bastiaansen et al. (2001) during electrical stimulation applied to the right calf muscle. The anticipatory sN peaks at a time close to stimulus onset, then the activity changes polarity maintaining a similar topography and produces the P100 component. The origin in secondary somatosensory areas found in the present study for the P100 is consistent with a long-standing literature (e.g.

Goff et al. 1977; Kakigi 1986; Larrea et al. 1992). Overall, it is likely that the activity in the somatosensory areas is the source for both the sN and the P100 components.

According to present findings, slow-rising preparatory activities characterize the pre-stimulus stage for each sensory modality; the same sensory regions are active some time later, after stimulus onset, reflecting stimulus processing. These slow potentials are specific to each sensory modality in line with the thalamic gating theory (Skinner and Yingling 1976; Brunia 1993) and the threshold regulation theory (Rockstroh 1989; Birbaumer et al. 1990). These theories predict the activity related to sensory-specific anticipation in the specific cortical areas: the slow waves vN, aP, and sN might represent the electrophysiological correlate of top–down modulated perceptual preparation, which in turn facilitates bottom–up post-stimulus early processing (the P1, N1 and P100). Present findings corroborate a previous fMRI study on preparatory modality-specific expectancy-induced attention, which showed that activities were mostly found in areas specialized for processing input of the respective sensory channel (Langner et al. 2011). Our results suggest that secondary sensory areas activation is present before stimulus presentation, representing a sort of sensory-specific preparation for upcoming stimulus detection. Therefore, present findings may offer a contribution to highlight the role played by expectations in determining the way we perceive the environment, activating the selected sensory cortex for input processing from the respective stimulus modality (see De Lange et al. 2018).

Regarding the pre-/post-stimulus polarity inversion of scalp-recorded activity observed for the three modalities, present results are consistent with the evidence that top–down connections involves superficial cortical layers, while bottom–up connections occur in deep cortical layers (Lawrence et al. 2017). The polarity shift between pre-stimulus and post-stimulus activities might be explained by different laminar activities in the two time intervals. Present results are in line with the proposal that post-stimulus evoked cortical activity can be considered as a part of a general recognition process, where prior expectations and sensory information interact according to a predictive model (e.g. Knill and Richards 1996; Mamassian et al. 2002). At cortical level, present findings may support the predictive coding theory (Friston 2005; Rao and Ballard 1999) proposing that neurons in the superficial layers represent top–down predictions sensory inputs, while neurons in deep layers encode bottom–up sensory inputs.

Present results may be also be relevant for researchers investigating pre-stimulus readiness potential (RP) within the ideomotor theory (Shin et al. 2010); a frame with implication also for clinical populations (e.g. Ford et al. 2013) and explaining suppression of self-generated sensory stimulation (Blakemore et al. 1998; Sanmiguel et al. 2013). In these studies, the passive condition is often used as a control condition. Consistent with the theory, in the active condition, when the subject expected auditory consequences of their actions, the RP amplitude was larger compared to RP recorded, when the same action was not expected to produce sensory consequences (Reznik et al. 2018); moreover, the RP was absent in the non-motor control condition, in which the subject simply waited for auditory stimuli (a condition similar to the present passive condition). The authors concluded that the action's modulatory effect at the RP level could not be attributed to expectation of an auditory event, because expectation of an auditory event did not produce RP. Other studies with a similar paradigm but using visual instead of auditory stimuli replicated (Vercillo et al. 2018) or did not replicate (Hughes and Waszak 2011) the RP results. The present work may contribute to this frame showing that in passive condition, the "sensory" RP is indeed present in the sensory but not in the motor cortices. One may also speculate that this preparatory sensory activity may add up on the scalp in correspondence of electrodes over the motor cortices, with results that may vary according to intensity and polarity.

Although participants were instructed not to respond or perform any cognitive task on the upcoming stimulus, it is possible that they directed their attention to the stimulus spatial region (in the visual modality) or to the auditory channels or to the portion of the body to be stimulated (in the somatosensory modality). Substantial research has shown attention regulation of processing before stimulus in visual-spatial attention tasks (Fu et al. 2001; Liu et al. 2014; Sauseng et al. 2005; Simpson et al. 2011). However, the tasks in these studies were different from the present one, because mostly used CNV paradigm with motor activities (e.g. button press) after the second cue; this might have interfered with the exploration of a genuine "passive" condition. In the present study, spatial attention was not directly manipulated; future research will explore this point. Further, future studies might also consider replicating our results by means of 128 or 256 EEG channels and magnetoencephalography (MEG) technique to enhance spatial resolution.

In conclusion, using passive sensory stimulation paradigms, the present study confirms the presence of perceptual readiness ERPs in the visual modality and extends knowledge of preparatory slow waves to auditory and somatosensory modalities.

Acknowledgements The study was supported by the University of Rome "Foro Italico" and Santa Lucia Foundation.

References

Bastiaansen MC, Böcker KB, Brunia CH, De Munck JC, Spekreijse H (2001) Event-related desynchronization during anticipatory attention for an upcoming stimulus: a comparative EEG/MEG study. Clin Neurophysiol 112(2):393–403

Berchicci M, Spinelli D, Di Russo F (2016) New Insights into Old Waves. Matching Stimulus- and Response-Locked ERPs on the Same Time-Window. Biol Psychol 117:202–215

Binder JR, Rao SM, Hammeke TA, Yetkin FZ, Jesmanowicz A, Bandettini PA, Hyde JS (1994) Functional magnetic resonance imaging of human auditory cortex. Ann Neurol 35(6):662–672

Birbaumer N, Elbert T, Canavan AG, Rockstroh B (1990) Slow potentials of the cerebral cortex and behavior. Physiol Rev 70(1):1–41

Blakemore SJ, Goodbody SJ, Wolpert DM (1998) Predicting the consequences of our own actions: the role of sensorimotor context estimation. J Neurosci 18(18):7511–7518

Brandt ME, Jansen BH (1991) The relationship between prestimulus alpha amplitude and visual evoked potential amplitude. Int J Neurosci 61(3–4):261–268

Brunia CH (1993) Waiting in readiness: gating in attention and motor preparation. Psychophysiology 30(4):327–339

Damen EJP, Brunia CHM (1985) Slow brain potentials related to movement and visual feedback in a response timing task. Biol Psychol 20(3):195

de Lange FP, Heilbron M, Kok P (2018) How do expectations shape perception? Trends Cogn Sci 22(9):764–779

Desmedt JE, Robertson D (1977) Differential enhancement of early and late components of the cerebral somatosensory evoked potentials during forced-paced cognitive tasks in man. J Physiol 271(3):761–782

Di Russo F, Pitzalis S (2013) EEG-fMRI combination for the study of visual perception and spatial attention. Cognitive electrophysiology of attention: signals of the mind. Academic Press, New York, pp 58–70

Di Russo F, Lucci G, Sulpizio V, Berchicci M, Spinelli D, Pitzalis S, Galati G (2016) Spatiotemporal brain mapping during preparation, perception, and action. NeuroImage 126:1–14

Di Russo F, Berchicci M, Bianco V, Perri RL, Pitzalis S, Quinzi F, Spinelli D (2019) Normative event-related potentials from sensory and cognitive tasks reveal occipital and frontal activities prior and following visual events. NeuroImage 196:173–187

Dionne JK, Meehan SK, Legon W, Staines WR (2010) Crossmodal influences in somatosensory cortex: interaction of vision and touch. Hum Brain Mapp 31(1):14–25

Fellinger R, Klimesch W, Gruber W, Freunberger R, Doppelmayr M (2011) Pre-stimulus alpha phase-alignment predicts P1-amplitude. Brain Res Bull 85(6):417–423

Ford JM, Palzes VA, Roach BJ, Mathalon DH (2013) Did I do that? Abnormal predictive processes in schizophrenia when button pressing to deliver a tone. Schizophr Bull 40(4):804–812

Friston K (2005) A theory of cortical responses. Philos Trans R Soc Lond Biol Sci 360(1456):815–836

Fu KMG, Foxe JJ, Murray MM, Higgins BA, Javitt DC, Schroeder CE (2001) Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. Cogn Brain Res 12(1):145–152

Goff GD, Matsumiya Y, Allison T, Goff WR (1977) The scalp topography of human somatosensory and auditory evoked potentials. Electroencephalogr Clin Neurophysiol 42(1):57–76

Gomez CM, Marco J, Grau C (2003) Preparatory visuo-motor cortical network of the contingent negative variation estimated by current density. Neuroimage 20(1):216–224

Grady CL, Van Meter JW, Maisog JM, Pietrini P, Krasuski J, Rauschecker JP (1997) Attention-related modulation of activity in primary and secondary auditory cortex. NeuroReport 8(11):2511–2516

Handy TC (ed) (2005) Event-related potentials: a methods handbook. MIT press, Cambridge

Hari R, Karhu J, Hämäläinen M, Knuutila J, Salonen O, Sams M, Vilkman V (1993) Functional organization of the human first and second somatosensory cortices: a neuromagnetic study. Eur J Neurosci 5(6):724–734

Hillyard SA, Anllo-Vento L (1998) Event-related brain potentials in the study of visual selective attention. Proc Natl Acad Sci 95(3):781–787

Hughes G, Waszak F (2011) ERP correlates of action effect prediction and visual sensory attenuation in voluntary action. Neuroimage 56(3):1632–1640

Jahanshahi M, Jenkins IH, Brown RG, Marsden CD, Passingham RE, Brooks DJ (1995) Self-initiated versus externally triggered movements: I An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. Brain 118(4):913–933

Kakigi R (1986) Ipsilateral and contralateral SEP components following median nerve stimulation: effects of interfering stimuli applied to the contralateral hand. Electroencephalogr Clin Neurophysiol 64(3):246–259

Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron 22(4):751–761

Key APF, Dove GO, Maguire MJ (2005) Linking brainwaves to the brain: an ERP primer. Dev Neuropsychol 27(2):183–215

Knill DC, Richards W (eds) (1996) Perception as Bayesian inference. Cambridge University Press

Kornhuber HH, Deecke L (1965) Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: bereitschaftspotential und reafferente Potentiale. Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere 284(1):1–17

Kotani Y, Ohgami Y, Yoshida N, Kiryu S, Inoue Y (2017) Anticipation process of the human brain measured by stimulus-preceding negativity (SPN). J Phys Fit Sports Med 6(1):7–14

Kutas M, Donchin E (1980) Preparation to respond as manifested by movement-related brain potentials. Brain Res 202(1):95–115

Langner R, Kellermann T, Boers F, Sturm W, Willmes K, Eickhoff SB (2011) Modality-specific perceptual expectations selectively modulate baseline activity in auditory, somatosensory, and visual cortices. Cereb Cortex 21(12):2850–2862

Larrea LG, Bastuji H, Mauguière F (1992) Unmasking of cortical SEP components by changes in stimulus rate: a topographic study. Electroencephalogr Clin Neurophysiol Evoked Potentials Sect 84(1):71–83

Lawrence SJ, Formisano E, Muckli L, de Lange FP (2017) Laminar fMRI: applications for cognitive neuroscience. Neuroimage 197:785–791

Lehmann C, Herdener M, Esposito F, Hubl D, Di Salle F, Scheffler K, Seifritz E (2006) Differential patterns of multisensory interactions in core and belt areas of human auditory cortex. Neuroimage 31(1):294–300

Liu Y, Bengson J, Huang H, Mangun GR, Ding M (2014) Top-down modulation of neural activity in anticipatory visual attention: control mechanisms revealed by simultaneous EEG-fMRI. Cereb Cortex 26(2):517–529

Mamassian P, Landy M, Maloney LT (2002) Bayesian modelling of visual perception. Probabilistic models of the brain. MIT Press, Cambridge, pp 13–36

Nunez PL, Srinivasan R (2006) Electric fields of the brain: the neurophysics of EEG. Oxford University Press, USA

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychol 9(1):97–113

Quinzi F, Berchicci M, Bianco V, Perri RL, Di Russo F (2019) The independency of the Bereitschaftspotential from previous stimulus-locked P3 in visuomotor response tasks. Psychophysiol 56(3):e13296

Rao RP, Ballard DH (1999) Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat Neurosci 2(1):79

Reznik D, Simon S, Mukamel R (2018) Predicted sensory consequences of voluntary actions modulate amplitude of preceding readiness potentials. Neuropsychologia 119:302–307

Rockstroh B (1989) Slow cortical potentials and behaviour. Urban & Schwarzenberg

Romei V, Gross J, Thut G (2010) On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? J Neurosci 30(25):8692–8697

Sanmiguel I, Todd J, Schröger E (2013) Sensory suppression effects to self-initiated sounds reflect the attenuation of the unspecific N1 component of the auditory ERP. Psychophysiology 50(4):334–343

Sauseng P, Klimesch W, Stadler W, Schabus M, Doppelmayr M, Hanslmayr S, Birbaumer N (2005) A shift of visual spatial attention is selectively associated with human EEG alpha activity. Eur J Neurosci 22(11):2917–2926

Schürmann M, Caetano G, Hlushchuk Y, Jousmäki V, Hari R (2006) Touch activates human auditory cortex. Neuroimage 30(4):1325–1331

Shin YK, Proctor RW, Capaldi EJ (2010) A review of contemporary ideomotor theory. Psychol Bull 136(6):943

Simpson GV, Weber DL, Dale CL, Pantazis D, Bressler SL, Leahy RM, Luks TL (2011) Dynamic activation of frontal, parietal, and sensory regions underlying anticipatory visual spatial attention. J Neurosci 31(39):13880–13889

Skinner JE, Yingling CD (1976) Regulation of slow potential shifts in nucleus reticularis thalami by the mesencephalic reticular formation and the frontal granular cortex. Electroencephalogr Clin Neurophysiol 40(3):288–296

Staines WR, Popovich C, Legon JK, Adams MS (2014) Early modality-specific somatosensory cortical regions are modulated by attended visual stimuli: interaction of vision, touch and behavioral intent. Front Psychol 5:351

Van Boxtel GJ, Böcker KB (2004) Cortical measures of anticipation. J Psychophysiol 18(2/3):61–76

Van Dijk H, Schoffelen JM, Oostenveld R, Jensen O (2008) Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. J Neurosci 28(8):1816–1823

Vercillo T, O'Neil S, Jiang F (2018) Action-effect contingency modulates the readiness potential. NeuroImage 183:273–279

Zouridakis G, Simos PG, Papanicolaou AC (1998) Multiple bilaterally asymmetric cortical sources account for the auditory N1 m component. Brain Topogr 10(3):183–189