

Timing in Predictive Coding: The Roles of Task Relevance and Global Probability

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Abstract

■ Predictive coding models of attention propose that attention and prediction operate synergistically to optimize perception, as reflected in interactive effects on early sensory neural responses. It is yet unclear whether attention and prediction based on the temporal attributes of expected events operate in a similar fashion. We investigated how attention and prediction based on timing interact by manipulating the task relevance and a priori probability of auditory stimulus onset timing within a go/no-go task while recording EEG. Preparatory activity, as indexed via the contingent negative variation, reflected temporally specific anticipation as a function of both

attention and prediction. Higher stimulus probability led to significant predictive N1 suppression; however, we failed to find an effect of task relevance on N1 amplitude and an interaction of task relevance with prediction. We suggest the predictability of sensory timing is the predominant influence on early sensory responses where a priori probabilities allow for strong prior beliefs. When this is the case, we find that the effects of temporal prediction on early sensory responses are independent of the task relevance of sensory stimuli. Our findings contribute to the expansion of predictive coding frameworks to include the role of timing in sensory processing. ■

INTRODUCTION

The ability to anticipate forthcoming sensory events is crucial for selecting the most appropriate action. Expectations for future events can be formed based on the content of stimuli, but mounting evidence suggests that timing also plays a vital role in the anticipation of stimuli (Nobre, Correa, & Coull, 2007). Two primary sources of top-down anticipatory modulation, attention and prediction, have been shown to have dissociable influences on sensory processing. Stimuli with predictable attributes typically evoke attenuated neural responses compared with unpredicted stimuli, whereas attended stimuli evoke enhanced responses compared with relatively unattended stimuli. For nontemporal stimulus attributes, these mechanisms jointly optimize perceptual processing via a synergistic interaction whereby attention increases the precision of perceptual inference, reversing the attenuation of predictable, task-relevant stimuli (Hsu, Hämäläinen, & Wazak, 2014; Kok, Rahnev, Jehee, Lau, & De Lange, 2012). However, given that temporal expectations and spectral expectations have shown dissociable influences on sensory processing (Hsu, Hämäläinen, & Wazak, 2013; Costa-Faidella, Baldeweg, Grimm, & Escera, 2011), it is unclear how attention and prediction based on temporal information may jointly modulate sensory processing.

Predictive coding theory provides a physiologically plausible mechanism for the attenuation of sensory re-

sponses associated with prediction. Internal predictive models are thought to generate inferences of forthcoming sensory events (predictions) that are compared with incoming sensory signals from lower levels in a cortical hierarchy (Friston, 2008). The neurocomputational difference between predictions and actual incoming information (prediction error) is propagated in a feedforward manner to higher levels in the perceptual hierarchy to revise the internal model and minimize future prediction error (Friston, 2009). Neural activity during sensory processing measured by EEG/MEG are believed to primarily reflect this iterative process (Feldman & Friston, 2010; Garrido, Kilner, Kiebel, & Friston, 2007). The attenuation of sensory ERPs associated with accurate predictions can be explained in terms of reduced prediction error, and conversely unpredicted stimuli evoke larger responses due to the increased prediction error. This framework allows for a unifying interpretation of prediction effects across multiple experimental contexts (see Auksztulewicz & Friston, 2015; Schröger, Marzecová, & SanMiguel, 2015; Bastos et al., 2012; Bendixen, SanMiguel, & Schröger, 2012, for reviews).

In the temporal domain, prediction relies on the temporal regularity or learned temporal contingencies between events (Arnal & Giraud, 2012). Auditory stimuli highly predictable in their temporal onset due to rhythmic regularity (Schwartz, Farrugia, & Kotz, 2013; Costa-Faidella et al., 2011; Lange, 2009) or self-generation (Sowman, Kuusik, & Johnson, 2012; Lange, 2011) result in attenuation of the early N1 component of auditory ERPs. The passage of

time itself can also be used to actively predict the onset of events, as the conditional probability of stimulus onset increases as time elapses (Nobre et al., 2007). The modulation of the auditory N1 reflects the combination of a priori probability (the probability of sound onset at a given time) and the increasing conditional probability with time (Lampar & Lange, 2011; Lange, 2009, 2011).

Selective attention appears to have the opposite effect to prediction on early sensory processing—directing attentional resources selectively toward an event (based on timing, spatial location, or other stimulus attribute) enhances rather than suppresses sensory N1 amplitude (Lange, 2012a; Lange & Röder, 2006; Lange, Rösler, & Röder, 2003; Hillyard, Hink, Schwent, & Picton, 1973). As orienting attention toward a stimulus typically involves some inference regarding its attributes (spatial, temporal, etc.), this would appear at odds with the proposed effects of prediction, that is, a reduction in cortical responses. However, under a predictive coding framework, the generative model also actively infers the precision (the inverse variance) of prediction error (Feldman & Friston, 2010). Attentional selection has been proposed as a precision-weighting mechanism, increasing the gain of prediction errors resulting from more predictable stimuli. This view has gained empirical support from EEG and fMRI studies showing that attended, predicted stimuli elicit larger sensory responses than either unattended or unpredictable stimuli (Hsu et al., 2014; Kok et al., 2012). These findings suggest that attentional enhancement or, more specifically, gain modulations rely fundamentally on the predictability of stimuli.

When attention is oriented selectively to the expected time of stimulus onset (the temporal orienting of attention; Nobre et al., 2007), N1 modulation depends critically on the experimental task. When temporal orienting is induced by defining the task relevance of stimuli based on their temporal onset, task-relevant stimuli evoke enhanced N1 amplitudes compared with task-irrelevant stimuli (e.g., Lange & Schnuerch, 2014; Lange, 2012a; Sanders & Astheimer, 2008; Lange, Krämer, & Röder, 2006; Lange & Röder, 2006; Lange et al., 2003). In contrast, when attention is directed using cues indicating the most likely time of stimulus onset, only later ERP components associated with decision or response processes such as the P300 are enhanced for validly cued, expected stimuli (e.g., Lampar & Lange, 2011; Griffin, Miniussi, & Nobre, 2002; Miniussi, Wilding, Coull, & Nobre, 1999). Assuming that temporal probability and attention operate on the same underlying mechanism, the lack of an early attentional effect in probabilistic cueing paradigms may be due to the conflation of attention and prediction (Lange, 2013; Summerfield & Egnér, 2009). When temporal orienting is induced via expectations, the effect on N1 amplitude may be twofold—N1 enhancement from temporal attention and N1 suppression due to high predictability of onset, the net outcome being no discernable effect. This model is in contrast to the observed effects of attention and prediction when based on nontemporal stimulus attributes such as

spatial location or auditory frequency (Hsu et al., 2014; Kok et al., 2012), suggesting the mechanisms underlying timing operate distinctly from those operating on other stimulus properties. The joint roles of attention and prediction in timing have been investigated previously (Paris, Kim, & Davis, 2016). However, the use of predictive cueing in previous paradigms draws into question the generalizability of such local, trial-by-trial predictions to situations where global predictions, driven by longer-term learning, is the main underlying process.

To examine the interplay between attention and prediction in the temporal domain, we factorially manipulated the task relevance and probability of stimulus onset in an orthogonal design. Using EEG, we indexed preparatory activity via the contingent negative variation (CNV) before tone onsets as a measure of temporal expectancy and measured the auditory N1 and P3 components of ERPs evoked by nontarget stimuli. We hypothesized that N1 amplitude, our measure of early sensory processing, would reflect enhancement with task relevance and suppression with high probability in an additive manner. We expected that the P3 component, reflecting stimulus evaluation, would primarily be influenced by task relevance—a robust finding in temporal attention tasks (Lange, 2009; Lange et al., 2003, 2006). The orthogonal experimental design allows us to evaluate whether temporal attention and prediction induce opposite, additive effects on early sensory processing (Lange, 2013; Summerfield & Egnér, 2009). Alternatively, these processes may be reliant on one another to optimize perception, as observed in predictive coding models (Schröger, Marzecová, et al., 2015; Hsu et al., 2014; Kok et al., 2012).

METHODS

Participants

Twenty-nine participants were recruited using the University of Queensland Research Participation Scheme. The data from five participants were excluded from analysis as they responded to more than 33% of nontarget stimuli or failed to respond to 66% or more target stimuli. Data from two participants were excluded from analysis because of excessive artifact in EEG data. The final sample consisted of 22 data sets (10 men; mean age = 22.91; $SD = 3.15$). Inclusion criteria for participation were normal or corrected-to-normal vision, normal hearing, and no history of neurological or psychological disorder. Participants received monetary compensation for their time. The procedures outlined in this study were approved by the University of Queensland's medical research ethics committee, and all participants provided written consent.

Procedure

The experiment took place over two sessions, separated by 24–48 hr. Participants completed an attentional filter

task adapted for the temporal domain (Lange et al., 2003; Hillyard et al., 1973). Each trial began with presentation of a centrally displayed, nonpredictive cue (gray circle) for 200 msec, followed by either a short (1000 msec) or long (2000 msec) empty interval before a tone was presented. In 80% of trials, a low pitch (450 Hz) “standard” sine wave tone was presented, and in the remaining 20% of trials a high pitch (900 Hz) “deviant” sine wave tone was presented. Participants only responded to deviant tones and ignored all standard tones. All tones were presented for 100-msec duration and set at a comfortable volume, presented from two speakers located in front of the participant.

At the beginning of each block of trials, participants were informed that they would have to respond via speeded button response to high pitch (deviant) tones that occurred after a specific interval. Within each block, only deviant tones presented after short (short-relevant condition) or long (long-relevant condition) intervals required a response. Participants could orient attention to task-relevant points in time in preparation for possible deviant tones. All tones occurring at the task-irrelevant time need not be attended (see Figure 1). The task-relevant interval was alternated between blocks and was counterbalanced across participants. RTs were measured for responses to task-relevant deviant tones, whereas responses to standard and task-irrelevant tones, missed responses, and responses longer than 1000 msec were recorded as incorrect. A negative feedback cue (red circle) was presented for 400 msec following incorrect responses. Trials were separated by an empty intertrial interval with a duration randomly selected between 1500 and 2500 msec in 100-msec steps.

Each experimental session contained a different proportion of short and long interval trials. One session contained 75% short interval trials, whereas the other contained 75% long interval trials. This allowed for a separation of temporal predictability between session and minimized carryover effects between the two frequency distributions. The order of sessions was counterbalanced

across participants, and participants were not informed of the proportion of short and long interval trials.

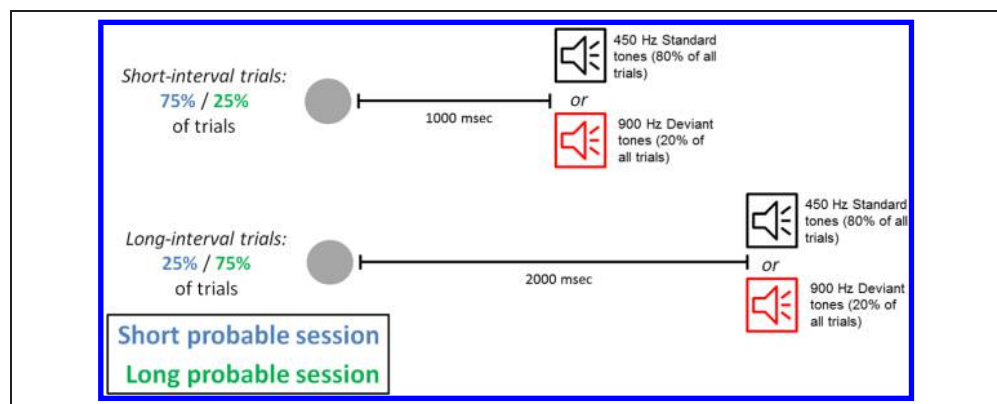
Each session contained 1000 trials, divided into 10 blocks. Each session began with a brief practice of 40 trials of each task relevance conditions. Participants were given feedback after each block, providing mean RT and response accuracy, and were allowed a self-paced break. Each experimental session ran for approximately 65 min, not including EEG setup. Stimuli were created and presented using Cogent toolbox software (Cogent 2000 toolbox: FIL, ICN, and Wellcome Department of Imaging Neuroscience) running in Matlab version 7.14 (www.mathworks.com).

EEG Recording and Preprocessing

EEG was continuously recorded at a sampling rate of 1024 Hz while participants completed the experimental task using a 64-channel Ag/AgCl ActiveTwo BioSemi system (Amsterdam, The Netherlands). EOG was recorded using Ag/AgCl electrodes positioned above and below the left eye and approximately 2 cm from the outer canthi of each eye. Two electrodes were placed on each mastoid for use in offline referencing. Data was analyzed offline using BESA Research 6.0 software (BESA GmbH, Gräfelfing, Germany). Continuous data were re-referenced to the combined average of mastoid electrodes and filtered between 0.01 and 45 Hz using high-pass and low-pass filters. Blink artifacts were corrected using the surrogate method (Berg & Scherg, 1994) as implemented by BESA by creating average blink topographies (minimum 50 blink artifacts) for each participant. Channels displaying excessive noise were interpolated, with no more than 10% of channels interpolated (mean = 1.60 channels).

Only trials containing standard (nontarget) tones were included in ERP averaging to avoid any contamination of sensory ERPs from response-related processes for deviant target tones. Averages were calculated separately for short- and long-interval trials, for each combination of

Figure 1. Diagram of trial types. In each trial a standard low pitch (450 Hz) tone (80% of trials) or an infrequent high pitch (900 Hz) deviant tone was presented after a short (1000 msec) or long (2000 msec) period of time following a cue (gray circle). Predictability was manipulated between experimental sessions, whereby short-interval trials were presented on 75% of trials (short probable session) or on 25% of trials (long probable session). Task



relevance was manipulated between blocks, whereby either short- or long-interval tones were task-relevant. Infrequent deviant tones (shown in red) only required a response when they were presented after the task-relevant interval. Note only trials with standard tones were included in EEG analyses.

task relevance (task-relevant/task-irrelevant) and probability (low probability/high probability).

To index preparatory activity before the time of tone onset (CNV analysis), ERPs were epoched from 100 msec before cue onset to 2200 msec after cue onset, baseline-corrected using mean activity -100 to 0 msec relative to cue onset. To evaluate the neural response to tones, tone-evoked ERPs were epoched from 100 msec before tone onset to 600 msec after tone onset and baseline-corrected using an epoch 0 – 50 msec relative to tone onset, to minimize carryover effects due to preparatory activity (Correa & Nobre, 2008). All ERPs contained a minimum of 60 artifact-free trials (difference between minimum and maximum amplitude per trial >120 μV).

Behavioral Analysis

Mean RTs and the percentage of correct responses to task-relevant deviant stimuli occurring after short and long intervals for each probability condition were calculated. Accuracy and RTs were submitted to separate 2×2 repeated-measures ANOVAs with factors of Probability (short probable/long probable) and Interval (short/long).

ERP Analysis

Mean amplitudes were calculated for the CNV across a 100-msec time window immediately before short- and long-interval tone onset times over central electrode Cz where CNV activity is typically maximal. CNV amplitudes for the early (900–1000 msec postcue) and late (1900–2000 msec postcue) time windows were submitted to separate repeated-measures ANOVAs with factors Task relevance (short relevant/long relevant), Probability (short probable/long probable), and Interval length (short/long).

Analysis of auditory evoked potentials to standard tones focused on the auditory N1 and P3. Time windows for calculating mean amplitudes were motivated by previous work: Mean N1 amplitudes were calculated from 90 to 120 msec after tone onset (see Lange & Schnuerch, 2014; Lange, 2012a, 2012b), and P3 amplitudes were calculated from 300 to 370 msec after tone onset (see Lange & Schnuerch, 2014; Lange, 2012b). To assess effects of topography, electrodes F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4 were each assigned one value of factor anterior–central–posterior (ACP) and one value of factor left–midline–right (LMR; see also Lange & Schnuerch, 2014; Lange, 2012a, 2012b; Lampar & Lange, 2011). As the absence of a tone after the short interval was predictive of a long-interval tone, regardless of probability manipulation, short- and long-interval tones were analyzed separately. Mean N1 and P3 amplitudes for short- and long-interval tones were submitted to separate repeated-measures ANOVAs with factors of task relevance (task-relevant/task-irrelevant), probability (high probability/low probability), ACP (anterior/central/posterior), and LMR (left/

midline/right). Sub-ANOVAs were used to investigate higher-order interactions where appropriate to hypotheses, with only effects involving task relevance and probability reported. The Greenhouse–Geisser correction was used when sphericity was violated. Corrected p values and degrees of freedom, as well as partial η^2 as a measure of effect size, are reported. Analyses were conducted using IBM SPSS v20 (Armonk, NY).

RESULTS

Behavioral Results

RTs to task-relevant tones were faster for long- than short-interval trials ($F(1, 21) = 17.347, p = .0004$, partial $\eta^2 = .452$). This reflects the reduced uncertainty of target onset at long intervals, as the passing of the short interval without a stimulus ensures that a long-interval tone will occur. Overall, responses were also faster when short-interval trials were more likely compared with when long-interval trials were more likely ($F(1, 21) = 8.42, p = .009$, partial $\eta^2 = .286$). There was no significant interaction between Probability and Interval on RTs ($F(1, 21) = 884, p = .358$), indicating participants did not respond significantly faster when a specific interval length was more highly predictable.

Participants responded with high accuracy to task-relevant deviant tones (hit mean = 0.92; false alarm mean = 0.12), showing they complied with task instructions. The high accuracy of responses suggests that participants were able to accurately orient their attention to task-relevant times to evaluate whether a response was required. Response accuracy differed according to both interval length and interval probability (Interval \times Probability interaction: $F(1, 21) = 6.52, p = .019$, partial $\eta^2 = .237$). Follow-up comparisons revealed accuracy for short-interval trials was significantly greater when they occurred with higher probability (.947) than lower probability (.898; $t(22) = 2.34, p = .029$). This effect was absent for long-interval trials ($t(22) = 1.06, p = .303$), where conditional probability ensured that tone onset was certain and therefore not affected by the probability manipulation.

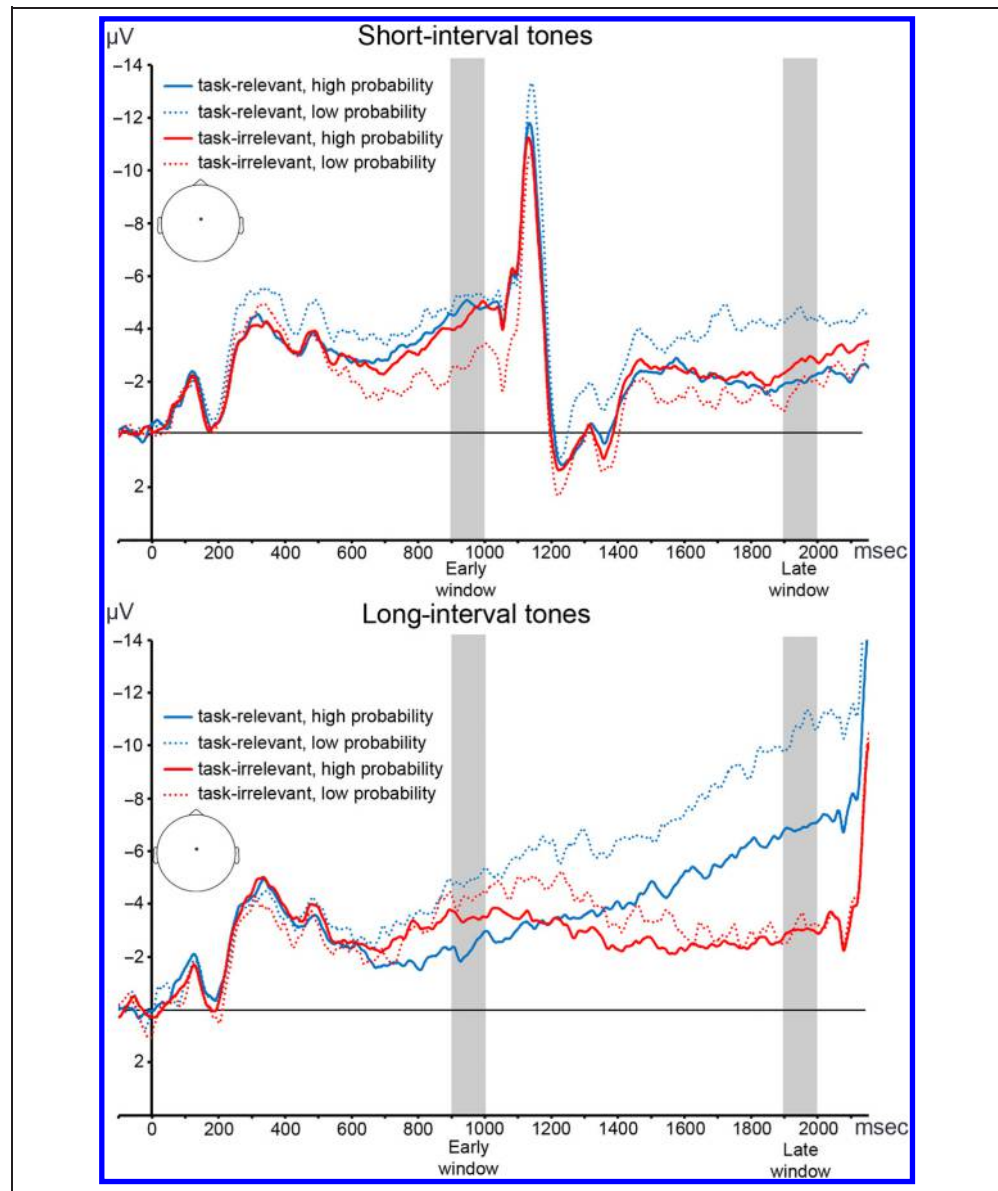
Cue-locked Preparatory Activity (CNV)

The grand-averaged activity across participants from the time of cue onset (0 msec) at central electrode Cz where CNV activity was maximal can be seen in Figure 2. The overall topography of the CNV at the (expected) times of stimulus onset can be seen in Figure 3.

Short-interval Epoch (900–1000 msec)

For both short- and long-interval tone trials, the activity at the early time window represents preparatory activity immediately before the time of short-interval tone onset. Interval effects were not observed because at this point, it

Figure 2. Grand-averaged preparatory CNV activity for short (top) and long (bottom) interval trials recorded from electrode Cz following cue onset (0 msec). The 100-msec time windows used to calculate mean CNV amplitudes before the expected time of short-interval tones (900–1000 msec) and late interval tones (1900–2000 msec) are highlighted in gray. CNV activity for task-relevant tones is shown in blue, task-irrelevant tones in red. Solid lines depict activity for high-probability tones; dotted lines depict low-probability tones. In this and all following EEG plots, negative voltage is plotted upward.



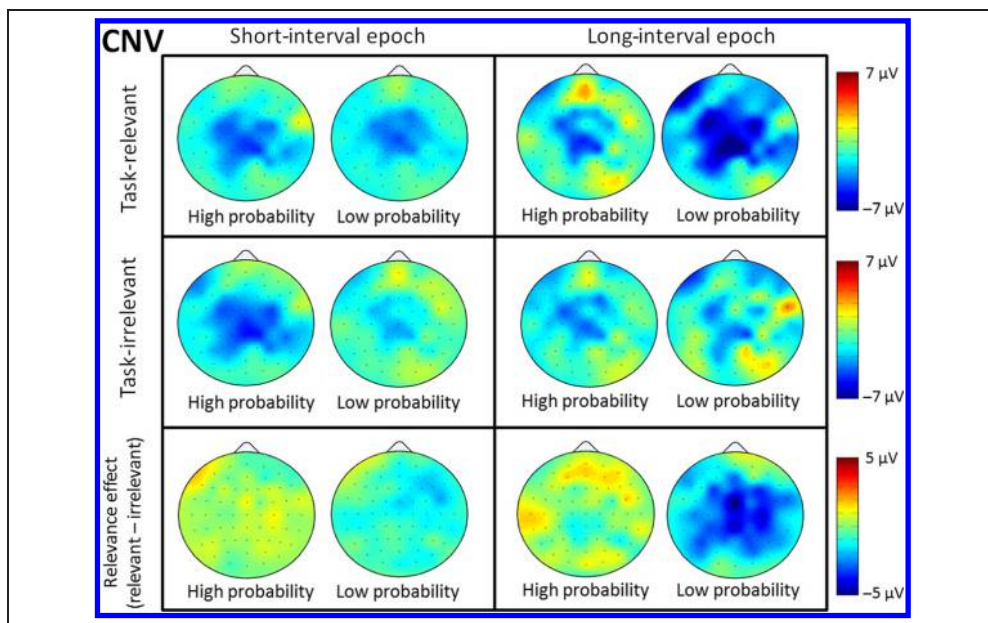
is unclear to participants whether a tone will occur at the short or long interval. The mean CNV amplitude varied according to interval probability and task relevance (Probability \times Task relevance interaction, $F(1, 21) = 1.790, p = .030$, partial $\eta^2 = .205$). Follow-up comparisons revealed CNV amplitudes were significantly lower if short-interval tones were task-irrelevant and occurred with low probability ($t(21) = 3.15, p = .005$). However, task relevance did not affect CNV amplitude when short-interval tones were highly probable ($t(21) = .289, p = .775$). In other words, CNV amplitude was only reduced when short-interval tones were both irrelevant and unlikely (see Figure 4, left).

Long-interval Epoch (1900–2000 msec)

In the time window immediately before the onset of long-interval tones, CNV amplitude was significantly

greater in trials with long-interval tones ($F(1, 21) = 9.631, p = .005$, partial $\eta^2 = .314$), reflecting a return toward baseline activity following the presentation of a tone in short interval trials. A significant main effect of Task relevance was also observed ($F(1, 21) = 8.997, p = .007$, partial $\eta^2 = .300$), showing overall greater CNV amplitude in the late time window when long-interval tones were task-relevant. This effect was qualified by a significant Interval \times Task relevance interaction ($F(1, 21) = 23.536, p = .00009$, partial $\eta^2 = .528$), with pairwise comparisons showing the increased amplitude when long-interval tones were task-relevant was only significant for long interval trials ($t(21) = 4.305, p = .0003$), but not when a short-interval tone had already occurred ($t(21) = 1.136, p = .269$). A significant Probability \times Task relevance interaction ($F(1, 21) = 5.143, p = .034$, partial $\eta^2 = .197$) indicated that across short and long interval trials, the effect of task relevance differed between probability conditions.

Figure 3. Average topography maps of the CNV at the time of stimulus onset for the short-interval epoch (1000 msec) and long-interval epoch (2000 msec) analysis windows. Topographies are displayed for averaged ERPs for each combination of interval, probability, and task relevance. Difference wave topographies (bottom) show the effect of task relevance (relevant – irrelevant), where negative (blue) values depict decreased amplitudes to task-irrelevant stimuli. Note different scaling for difference topographies for clarity of effects.



Post hoc comparisons revealed that when long-interval tones occurred with low probability, CNV activity was reduced for task-irrelevant tones ($t(21) = 3.306, p = .003$). No difference due to task relevance was observed when late interval tones were highly probable ($t(21) = .903, p = .377$; see Figure 4, right). Overall, CNV amplitudes in the late analysis window, where tone onset was predictable due to the presence or absence of a short-interval tone, were enhanced before task-relevant tones. Again, low-probability tones that were not task-relevant resulted in reduced CNV activity.

Post hoc Analysis

Finally, we conducted post hoc paired t tests (two-tailed) to ascertain whether the behavioral effects found in RT data were reflected in differences in CNV amplitudes. We collapsed mean CNV amplitudes in the 100-msec

time window before task-relevant tones in both probability conditions for short- and long-interval trials separately. CNV amplitude was significantly greater before task-relevant long-interval tones ($-9.09 \mu\text{V}$) compared with short-interval tones ($-5.07 \mu\text{V}$), $t(21) = 3.20, p = .004$. We also collapsed mean CNV amplitudes in the 100 msec time window before task-relevant tones across short- and long-interval trials for the short-probable and long-probable conditions separately. Comparing CNV amplitudes between short ($-7.98 \mu\text{V}$) and long ($-6.18 \mu\text{V}$) probability conditions found no significant difference, $t(21) = .933, p = .362$.

Auditory Evoked Potentials to Standard Tones: N1 and P3

ERPs evoked by standard (nontarget) tones separately for short- and long-interval tones, for electrode clusters

Figure 4. Mean CNV amplitudes for the short-interval epoch (900–1000 msec postcue) and long-interval epoch (1900–2000 msec postcue), averaged across short- and long-interval trials. Mean amplitudes are divided by the task relevance and probability of the epoch. Asterisks denote significant effects ($p < .05$).

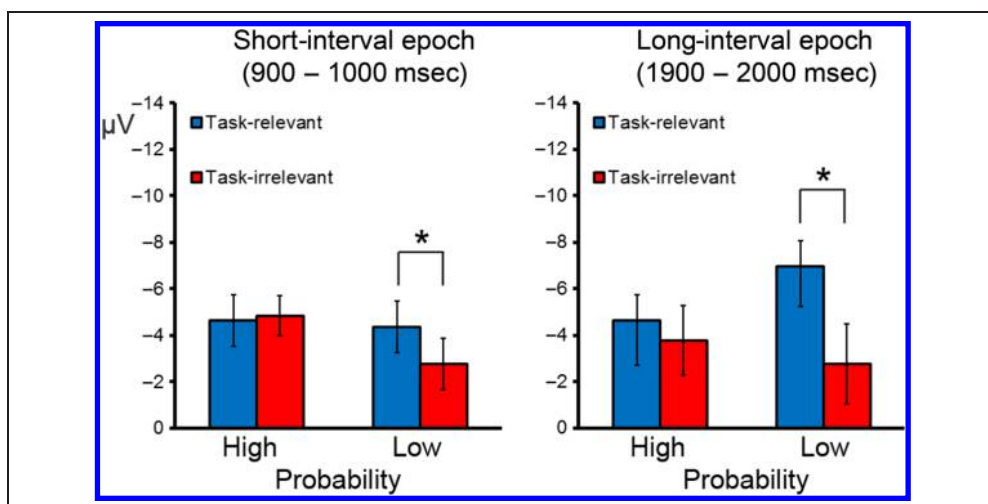
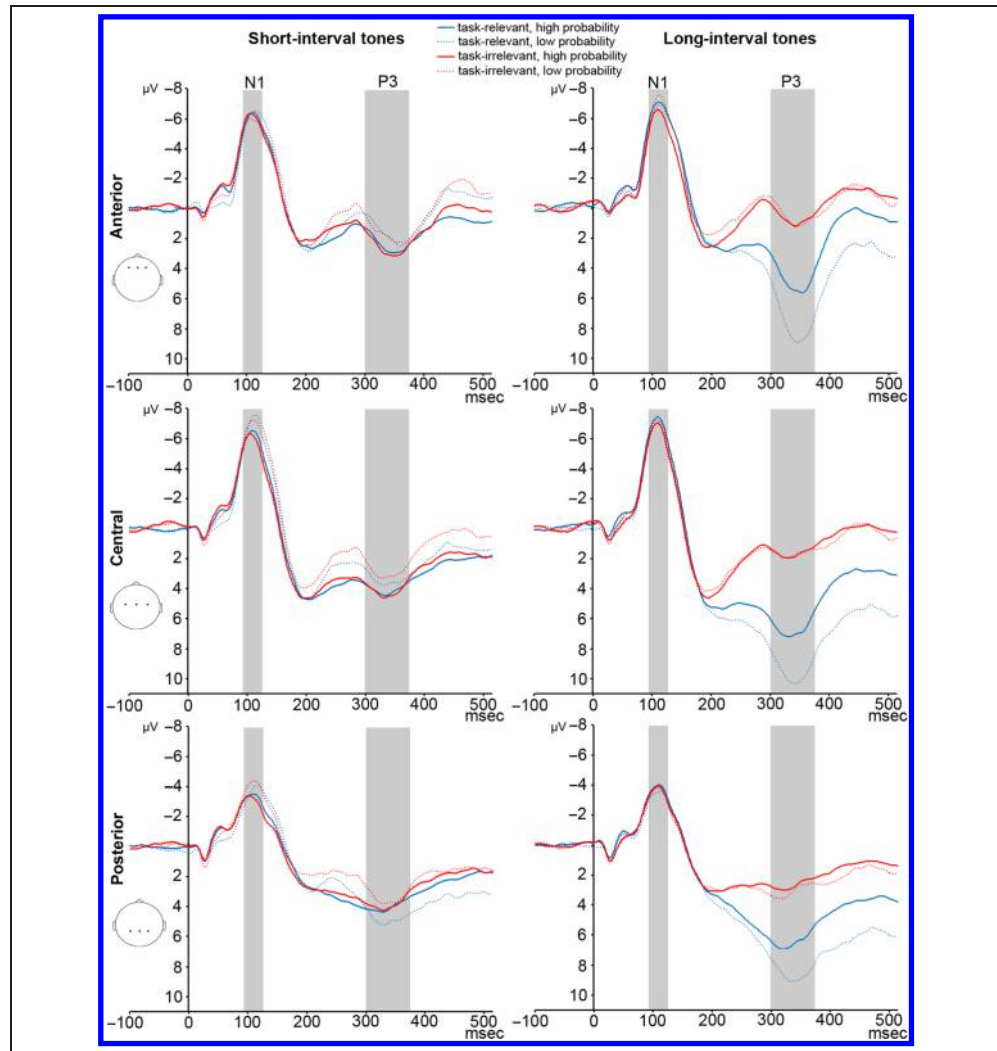


Figure 5. Grand-averaged ERPs evoked by standard (nontarget) tones for anterior, central, and posterior electrode clusters. ERPs for short (left) and long (right) are plotted separately. ERPs evoked by task-relevant tones are shown in blue, task-irrelevant tones in red. Solid lines depict ERPs evoked by high-probability tones; dotted lines represent low-probability tones. Time windows used for analysis of the N1 and P3 are highlighted in gray.



representing anterior, central, and posterior regions used in analysis are shown in Figure 5. Average topographies at 100 msec (N1) and 335 msec (P3) are shown in Figures 6 and 7, respectively.

N1 (90–120 msec)

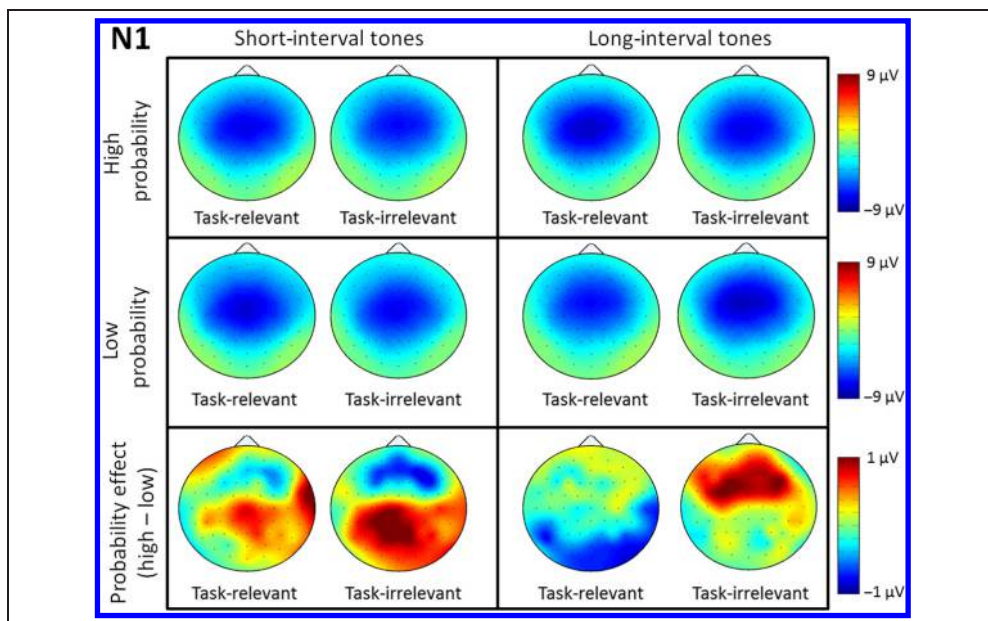
Significant N1 suppression effects were observed in short-interval trials. High-probability short-interval tones elicited lower N1 amplitudes compared with tones occurring at the same interval but with lower probability. This was shown by a significant Probability \times Anterior–Posterior interaction ($F(2, 42) = 7.848, p = .002$, partial $\eta^2 = .263$). Post hoc tests indicated significant N1 suppression for high compared with low probability in central and posterior regions ($t(21) = 2.809, p = .010$ and $t(21) = 2.17, p = .042$, respectively, see Figure 8, top). For long-interval trials, a significant Probability \times Task relevance \times LMR \times ACP interaction was found ($F(4, 84) = 2.841, p = .029$, partial $\eta^2 = .119$); however sub-ANOVAs at each electrode found no significant effects

of Probability or Task relevance (all $ps > .05$). No effect of Task relevance was found for either short- or long-interval trials, and no interactions between Task relevance and Probability were found (all $ps > .1$).

P3 (300–370 msec)

In short-interval trials, the effects of probability and task relevance interacted with the anterior–posterior factor (Probability \times ACP, $F(1.585, 33.285) = 4.184, p = .032$, partial $\eta^2 = .166$; Task relevance \times ACP, $F(1.381, 29.009) = 5.829, p = .014$, partial $\eta^2 = .217$; Probability \times Task relevance \times ACP, $F(1.463, 30.724) = 3.568, p = .053$, partial $\eta^2 = .145$). In posterior electrodes, P3 amplitude was enhanced when short-interval tones were task-relevant ($F(1, 21) = 4.575, p = .044$, partial $\eta^2 = .532$). A marginal effect of Probability \times Task relevance \times ACP ($F(1, 21) = 3.725, p = .067$, partial $\eta^2 = .453$) was followed by pairwise comparisons, showing the increased P3 amplitude for task-relevant tones was only present for low-probability tones ($t(21) = 2.270, p = .034$; Figure 8, bottom). No

Figure 6. Average topography maps for the N1 component at 100 msec after tone onset. Topographies are displayed for averaged ERPs for each combination of interval, probability, and task relevance. Difference wave topographies (bottom) show the effect of probability (high – low probability), where positive (red) values depict reduced amplitudes to higher probability stimuli. Note different scaling for difference topographies for clarity of effects.



effects of probability or task relevance were found in frontal and central electrodes.

For long-interval trials, P3 amplitude was greater when long-interval trials were task-relevant ($F(1, 21) = 26.706$, $p = .00004$, partial $\eta^2 = .560$), reflecting that P3 was practically absent for task-irrelevant tones. A significant Probability \times Task relevance interaction ($F(1, 21) = 7.221$, $p = .014$, partial $\eta^2 = .256$) was driven by larger P3 amplitudes for low- compared with high-probability late-interval tones when task-relevant ($t(21) = 2.215$, $p = .038$); however, this difference was not observed when late interval tones were task-irrelevant ($t(21) = .128$, $p = .899$; Figure 8, bottom).

DISCUSSION

Attention and prediction have dissociable effects on sensory processing—where attention typically increases neural responses to task-relevant stimuli, responses are attenuated when stimuli are highly predictable. The current study investigated how these top-down mechanisms interact in sensory processing by factorially manipulating the task relevance and prior probability of auditory stimulus timing. We found that temporal probability had a clear modulatory effect on early sensory processing indexed by the auditory N1; however, we failed to show an effect of task relevance on N1 amplitude in the presence of strong probabilistic manipulations. The effects of

Figure 7. Average topography maps for the P3 component at 335 msec after tone onset. Topographies are displayed for averaged ERPs for each combination of interval, probability, and task relevance. Difference wave topographies (bottom) show the effect of task relevance (relevant – irrelevant), where positive (red) values depict increased amplitudes to task-relevant stimuli. Note different scaling for difference topographies for clarity of effects.

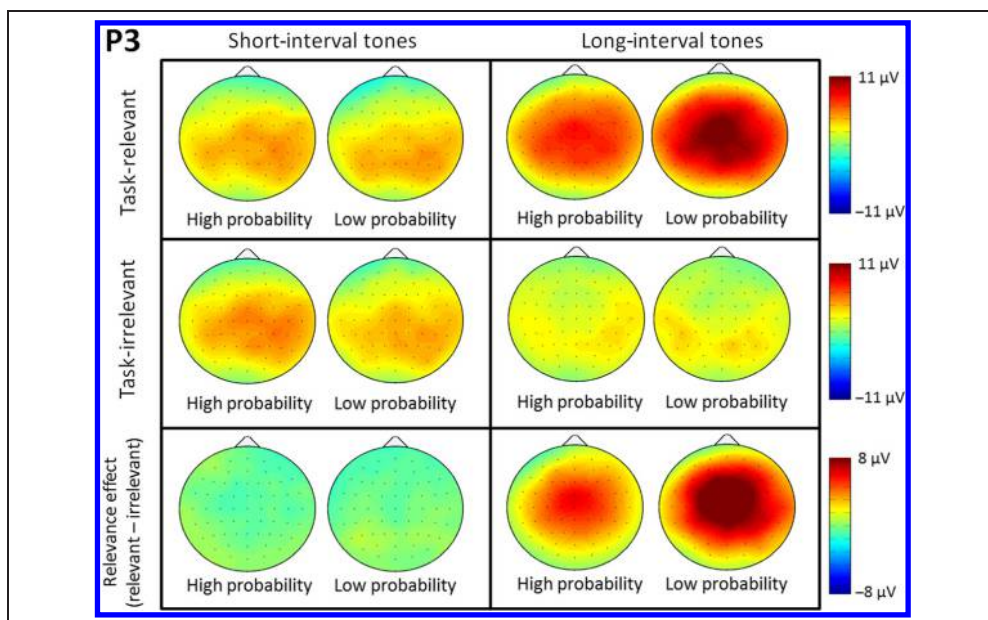
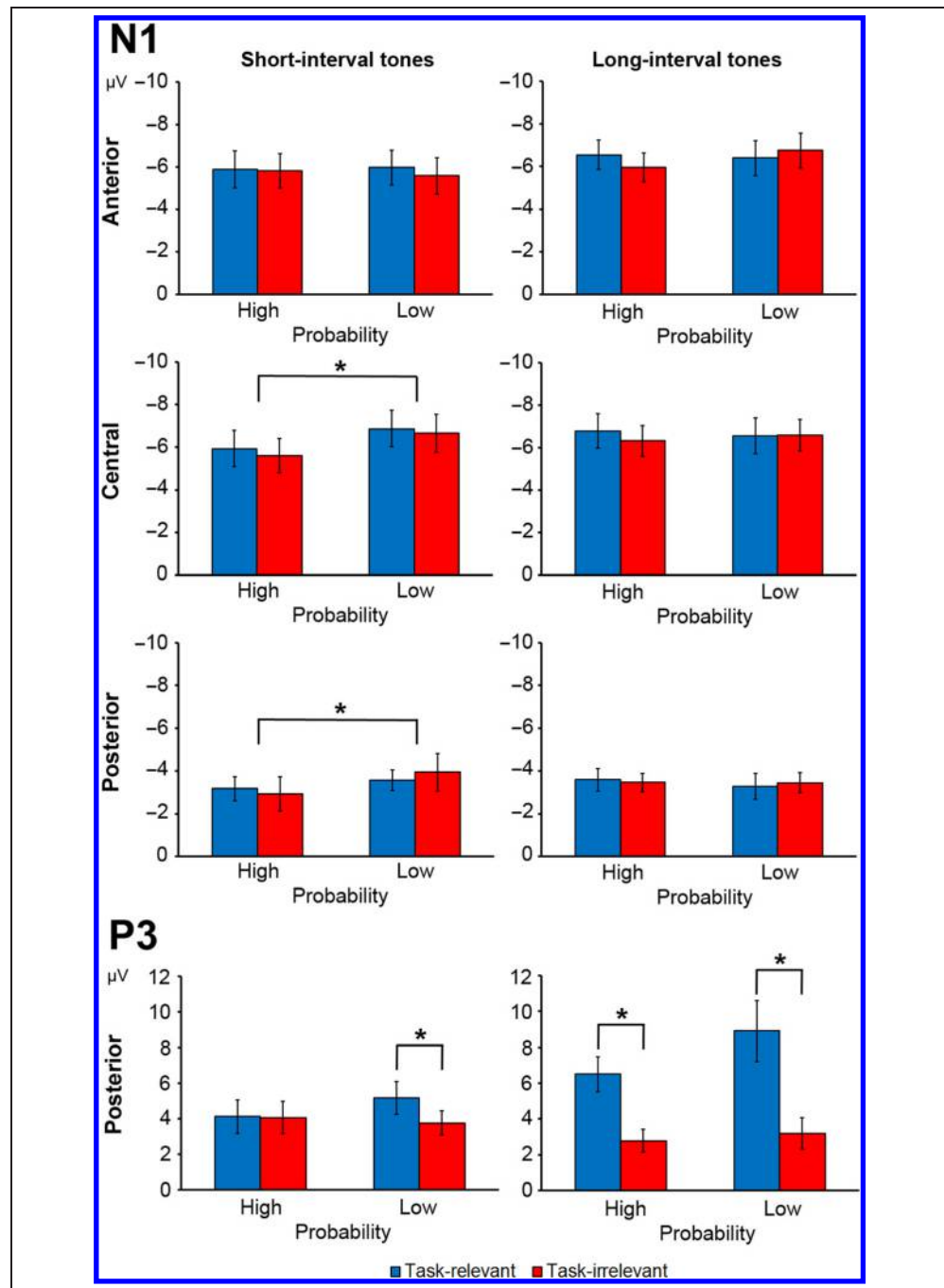


Figure 8. Mean amplitudes for N1 (top) and P3 (bottom) components evoked by standard (nontarget) tones. N1: Mean amplitudes across 90–120 msec poststimulus for short (left) and long (right) interval tones for anterior, central, and posterior regions. Amplitudes for task-relevant tones are shown in blue, task-irrelevant tones in red, separated for high- and low-probability tones. P3: As for the N1, with mean amplitudes taken from 300–370 msec poststimulus for the posterior region.



task relevance were restricted to preparatory activity before stimulus onset (CNV) and later sensory components of ERPs evoked by stimuli (P3), where they interacted with prior probability. Here, we discuss the implications for understanding the combined roles of attention and prediction in timing.

Our manipulation of a priori probability of stimulus onset reliably influenced early sensory processing, with auditory N1 amplitudes attenuated for tones occurring after short intervals when they were highly likely. N1 suppression has been observed when isochronous presentation of rhythmic stimuli reliably predicts subsequent stimulus

onset (Breska & Deouell, 2014; Schwartze et al., 2013; Costa-Faidella et al., 2011; Lange, 2009) and when self-generated sounds have predictable onsets (Lange, 2011; Bäß, Jacobsen, & Schröger, 2008). We extend upon these findings by showing larger a priori probability of onset using discrete intervals can induce similar N1 suppression. In line with predictive coding theory (Friston, 2009, 2010), when stimuli are presented after the short interval with greater frequency, the likelihood of stimuli occurring at that time increases and therefore prediction error for such stimuli is reduced, resulting in smaller N1 amplitude. Effects of a priori probability on N1 amplitudes

were absent for long-interval tones, reflecting the certainty of a long-interval tone after the omission of a short-interval tone. Interestingly, effects of probability on N1 amplitude did not depend on the task relevance of stimuli, reinforcing the notion of predictive processing as an automatic mechanism (Bendixen et al., 2012).

In contrast to proposed models of prediction of non-temporal stimulus attributes (Arnal & Giraud, 2012), the task relevance of stimulus onset did not appear to reliably modulate N1 amplitude and did not interact with the effect of probability at this early processing stage. Rather, task relevance affected the later P3 amplitude and preparatory activity before tone onset. The negative deflection of the CNV increased following cue onset leading up to the expected time of short-interval tone onset and declined following the omission of a task-relevant tone (Figure 2, task-irrelevant long interval trials). CNV amplitude in both early and late time windows (reflecting anticipation for short or long-interval tones, respectively) was enhanced when imminently expected tones were task-relevant or occurred with high probability. In contrast, CNV amplitude was lower in both analysis windows before onset times that were both task-irrelevant and unlikely. This corroborates previous findings that preparatory CNV amplitude is enhanced before highly probable stimulus onsets (Chennu et al., 2013; Mento, Tarantino, Sarlo, & Bisiacchi, 2013; Scheibe, Schubert, Sommer, & Heekeren, 2009), before cued stimuli (Correa, Lupiáñez, Madrid, & Tudela, 2006; Griffin et al., 2002; Miniussi et al., 1999), and before the onset of task-relevant stimuli (Lange, 2012a; Lange et al., 2003). The CNV is well known as a temporally sensitive measure of top-down expectation (Chennu et al., 2013; Nobre et al., 2007). Our results suggest that the manipulation of task relevance successfully caused participants to actively anticipate stimuli at task-relevant times and that either task relevance or high probability is sufficient to increase top-down expectation for stimulus onset.

CNV amplitudes immediately before stimulus onset are typically associated with greater stimulus detection (O'Connell et al., 2009; Rockstroh, Müller, Wagner, Cohen, & Elbert, 1993), which may be the result of increased selective attention (Wöstmann, Schröger, & Obleser, 2015). Our behavioral results indicated a small but significant increase in response accuracy during short-interval trials that occurred with greater probability; however, we failed to find an associated increase in CNV activity. Variation in CNV amplitude has similarly been related to RT performance, with larger negativities associated with faster responses (Trillenber, Verleger, Wascher, Wauschkuhn, & Wessel, 2000; Rockstroh et al., 1993). Our finding of faster RTs for long-interval tones was reflected in overall greater CNV amplitudes before these tones, compared with short-interval trials. However, performance benefits for high-probability short trials were not reflected in a similar difference in CNV activity when compared with high-probability long trials. This failure to find consistent

CNV variation corresponding to behavioral performance is likely due to the relatively small number of trials in which participants must respond to stimuli.

In line with our CNV results, effects in the time window of the P3 verified successful orienting of attention. Following tone onset, nontarget stimuli occurring at task-relevant times compared with task-irrelevant times elicited larger P3 responses, consistent with previous studies using task relevance to induce temporal orienting (Lange, 2012b; Lange et al., 2003, 2006). The topography of the P3 in short-interval trials was more pronounced in central-posterior sites and appeared slightly right-lateralized (see Figure 7), although this lateralization was not borne out in statistical analyses. Compared with the more central topography of long-interval trial P3 components, this may suggest that the relatively smaller positivity in this time window for short-interval trials may involve distinct processes, although this requires further research for any more firm conclusions. Although our P3 findings may partly be explained by response inhibition to nontarget stimuli at task-relevant times, this has been shown to be an insufficient explanation for temporal orienting P3 effects (Lange, 2012b). Importantly, prediction effects on P3 amplitude relied on attentional engagement—larger P3 amplitudes were observed for both short- and long-interval tones within low-probability contexts, but only when task-relevant. Modulation of the P3 by stimulus predictability is thought to reflect prediction errors occurring at relatively higher levels of the processing hierarchy, involved in updating internal models dependent on current task goals (Chennu et al., 2013; Wacongne et al., 2011). The pattern of P3 effects observed here likely reflect such model correction following an unlikely timed stimulus, akin to a mismatch response, occurring exclusively at this level for stimuli occurring at task-relevant time points.

The absence of N1 enhancement for task-relevant stimuli in the current task is somewhat surprising given the extensive literature showing attentional effects of early sensory processing (Schröger, Kotz, & SanMiguel, 2015; Fritz, Elhilali, David, & Shamma, 2007; Giard, Fort, Mouchetant-Rostaing, & Pernier, 2000). High accuracy in behavioral task performance may indicate that the task was relatively easy for participants and therefore not require the perceptual resources that demand attentional selection at the early N1 stage of processing. Indeed, past studies of temporal attention have shown greater attentional enhancement of the N1 with more challenging perceptual tasks (Lange & Schnuerch, 2014; Correa et al., 2006). However, experiments employing the same task relevance manipulation have produced attentional effects at N1 with similarly high behavioral performance (Los, Kruijine, & Meeter, 2014; Lange, 2012b; Lampar & Lange, 2011), making it unlikely that task difficulty alone can account for a lack of early attention effects. It should be noted that the effects of temporal attention on early sensory responses appear distinct from the classical effects of spatial attention. This disparity is evident from N1

effects shown in previous studies manipulating both spatial and temporal attention (Griffin et al., 2002) and when comparing the effects of attention and prediction based on timing (Paris et al., 2016) to those based on spatial location (Hsu et al., 2014). Furthermore, a study by Lange (2012a, 2012b) manipulating sound intensity and location while participants performed a temporal relevance task found the attentional N1 effect did not match the lateralisation of the sensory N1 and was independent of sound intensity. Lange argues that temporal attention may not increase sensory gain in the same manner that has been suggested for spatial attention (Hillyard et al., 1973) and that attention based on timing may operate on distinct subprocesses of the sensory response.

When temporal orienting of attention is induced by manipulating the task relevance of stimuli across equiprobable onsets, attended stimuli evoke enhanced N1 amplitudes (Lange & Schnuerch, 2014; Lange, 2012a; Sanders & Astheimer, 2008; Lange & Röder, 2006; Lange et al., 2003). In contrast, directing attention via probabilistic cues indicating the most probable time of stimulus onset typically elicits similar N1 amplitudes for attended (expected) and unattended (unexpected) stimuli (Lampar & Lange, 2011). In her model of the effects of temporal orienting on the auditory N1, Lange (2013) proposes that the lack of attentional enhancement in probabilistic cueing paradigms is due to the high predictability of attended stimuli, resulting in an attenuation of the N1. We provide evidence that high probability of stimulus onset in a discrete interval task can attenuate N1 responses; however, we failed to find the typical enhancement of N1 for stimuli occurring at task-relevant times. A contributing factor to this discrepancy may be the influence of strong a priori probabilities used to manipulate temporal predictions in the current task. Similar effects have been observed when task relevance was combined with probabilistic cues by Lampar and Lange (2011). In their task, predictive cues indicated on a trial-by-trial basis the most likely time (67% validity) of tone onset, whereas only tones occurring at cued times required a response (i.e., were task-relevant). The observed effect of task relevance in this study was smaller (albeit still significant) than reported in studies where tone onset was equally likely between intervals and the effect was limited to the left hemisphere rather than having a large central locus. Although our null result should be interpreted with caution, we suggest that strong a priori expectations may reduce or even abolish the early N1 effect of temporal task relevance on sensory processing.

Our findings are in line with those of a recent EEG study by Paris et al. (2016) that similarly investigates the potential interaction between temporal attention and temporal prediction. In their paradigm, the same task relevance manipulation (block-wise) was employed for short- and long-interval tones but manipulated prediction via a moving visual cue predicting auditory onset with 65.3% accuracy (predicted condition) or no moving cue was provided (unpredicted condition). Using a cluster-

based permutation approach to ERP analysis (Maris & Oostenveld, 2007), Paris and colleagues found frontocentral clusters of electrodes displayed a significantly reduced response for predicted relative to unpredicted short-interval tones when both task-relevant and task-irrelevant, in a time frame in line with our present N1 results. Task-relevant sounds were also shown to elicit larger responses than task-irrelevant sounds when they were not predicted by a visual cue; however, no effect of relevance was found when sounds were predictable. The authors proposed the prediction afforded by the visual cue makes attentional selection via task relevance redundant and therefore does not influence the evoked response. The N1 results reported here confirm that strong temporal expectations can abolish task relevance effects in early sensory ERPs. We further extend upon previous findings by providing evidence that manipulating prediction at the “global” level (manipulating overall onset probability) may operate in a similar fashion to “local” level prediction (cue-based manipulations) in early sensory processing.

It is important to consider that the findings from the current design may be limited by the experimental context, in so far as the neural mechanisms underlying temporal attention and prediction. Relatively static probabilities within sessions allowed for strong manipulations of stimulus predictability; however, such statistical relationships between stimuli in a real-world environment may be relatively rare. Different neural mechanisms may be employed in situations where predictive contexts change rapidly or involve greater volatility. Our findings contribute to a growing body of research that suggests prediction and attention in timing may involve similar underlying neural processes. Future research may provide insight into how dynamic these mechanisms are by investigating adaptation to changes in temporal relationships between stimuli within a single experimental session or by utilizing a broader range of temporal intervals.

The role of attention is addressed in predictive coding models as a mechanism that increases the inferred precision of predictions, increasing the synaptic gain of prediction error (sensory) units (Feldman & Friston, 2010). Precision in such models can be conceived as an estimate of the variance in the environment, with greater precision enhancing prediction error responses. Precision-weighting afforded by attentional selection is a plausible explanation for interactions between attention and predictability for nontemporal stimulus attributes, with findings of larger neural responses for attended stimuli when stimulus content is predictable (Hsu et al., 2014; Kok et al., 2012). The question remains as to why a similar interaction is not observed between the early sensory effects of attention and prediction in the temporal domain. One possibility is that temporal prediction and attention operate on the same process—namely the estimated precision of perceptual inference. In other words, increased predictability of event onset primarily affects inference on the precision of predictions, rather than on prediction

content. In line with this idea, omissions of temporally predictable auditory stimuli elicit error responses only when the identity of the stimulus is also predictable (Sanmiguel, Saupé, & Schröger, 2013), suggesting temporal expectations alone cannot elicit prediction errors. Rather, it appears that temporal prediction may affect the precision associated with preexisting stimulus-specific predictions. In temporal orienting paradigms, the joint effects of attention and prediction on the sensory N1 may therefore be explained in terms of the expected precision afforded by both a priori probability and task relevance. In tasks where stronger a priori probability at particular intervals provides greater precision (lower variance) of the time of stimulus onset, such as in probabilistic cueing paradigms (Lampar & Lange, 2011; Griffin et al., 2002; Miniussi et al., 1999) and the current task, temporal attention may have a reduced effect compared with when a priori probability is equal across potential onsets as in typical temporal filter paradigms (Lange & Schnuerch, 2014; Lange, 2012a; Sanders & Astheimer, 2008; Lange & Röder, 2006; Lange et al., 2003, 2006). The resulting effect on the N1 is enhanced responses to task-relevant (attended) stimuli in the context of greater temporal uncertainty. This notion more generally agrees with the model of N1 amplitude put forward by Lange (2013) but expands upon the role of a priori expectation on the enhancing effect of temporal attention—whereby expectations may increase attentional selection but also determine the extent to which prediction error responses are weighted by attention (via precision). This constitutes a functional interplay between attention and prediction in time, perhaps dependent on the most contextually reliable source of precision estimation. Selective attention in time might therefore only modulate the early stages of predictive processing when predictive inference is unreliable due to temporal uncertainty.

Our findings indicate that when the task relevance and probability of auditory stimuli are based on timing, attention does not appear to reverse the sensory silencing induced by prediction. We suggest the predictability and task relevance of stimulus timing may act upon the same mechanism, namely precision-weighting of prediction errors. Furthermore, predictability of stimulus onset is likely the predominant influence on early sensory responses where a priori probabilities allow for strong prior beliefs. In line with predictive coding frameworks, temporal prediction may primarily be a modulatory factor of prediction error, operating on preexisting predictions of stimulus content.

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