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# Repetition enhancement and memory effects for duration

Martin Wiener *, James C. Thompson

*Department of Psychology, George Mason University, USA*

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ABSTRACT

A remarkable aspect of conscious perception is that moments carryover from one to the next, also known as temporal continuity. This ability is thus crucial for detecting regularities, such as in speech and music, and may rely on an accurate perception of time. Investigations of human time perception have detailed two electroencephalographic (EEG) components associated with timing, the contingent negative variation (CNV) and late positive component of timing (LPCt); however, the precise roles of these components in timing remain elusive. Recently, we demonstrated that the perception of duration is influenced by durations presented on prior trials, which we explained by the creation of an implicit memory standard that adapts to local changes in sequence presentation. Here, we turn to the neural basis of this effect. Human participants performed a temporal bisection task in which they were required to classify the duration of auditory stimuli into short and long duration categories; crucially, the presentation order was first-order counterbalanced, allowing us to measure the effect of each presented duration on the next. EEG recordings revealed that the CNV and LPCt signals both covaried with the duration presented on the current trial, with CNV predicting reaction time and LPCt predicting choice. Additionally, both signals covaried with the duration presented in the prior trial but in different ways, with the CNV amplitude reflecting the change in the memory standard and the LPCt reflecting decision uncertainty. Furthermore, we observed a repetition enhancement effect of duration only for the CNV, suggesting that this signal additionally indexes the similarity of successive durations. These findings demonstrate dissociable roles for the CNV and LPCt, and demonstrate that both signals are continuously updated on a trial-by-trial basis that reflects shifts in temporal decisions.



## Introduction

One of the hallmarks of conscious experience is temporal continuity from one moment to the next (Pöppel, 1997). Indeed, James (1890) noted that temporal continuity was a necessary requirement for consciousness to flow. A critical feature of this continuity is that we can make predictions about upcoming events based on the statistics of prior experience, allowing for perceptual stability (Kiebel et al., 2008). Learning the rhythm of a song, or adjusting to the speed at which a person is speaking to better understand them are both examples of this remarkable ability. The ability to adapt to changes in temporal context depends on our perception of time (Ossmy et al., 2013; Rohenkohl et al., 2012). However, the neural mechanisms governing contextual effects in time perception are currently unknown.

Currently, our understanding of temporal processing within the human brain has been limited to a large number of neuroimaging studies exploring the localization of timing abilities to particular regions. Perhaps unsurprisingly, these studies have revealed a wide diversity of areas that may be implicated. In a recent series of quantitative, voxel-wise meta-analyses, we (Wiener et al., 2010) demonstrated that the neural regions responsible for timing could be fractionated on the basis of task context, including (but not limited to) the range of intervals employed, the motor requirements of the task and the attentional state of the subject. These findings suggested that separate yet overlapping neural circuits are flexibly recruited, depending on the nature of the timing task at hand. Crucially, our findings also demonstrated that the bilateral supplementary motor area (SMA) and right inferior frontal gyrus (rIFG) were activated across all task variations. Although these studies provide some insight to *where* timing functions may reside, they do nothing to answer *how* these regions are involved, a step that is necessary for a truly comprehensive understanding of timing functions and the potential impact of disruption from neural pathology.

A second area of recent interest in neuroscience is how sensory-based timing is processed within a larger temporal context. The temporal context refers to the separation between stimuli in time, as well as the distribution of experienced intervals in memory. Two common influences of temporal context are central tendency and carryover effects, both of which may rely on Bayesian integration (Shi et al., 2013). Central tendency, also known as Vierordt's Law, refers to a gravitation of timed responses to the mean of presented intervals (Jazayeri and Shadlen, 2010), whereas carryover effects refer to the influence of recently experienced intervals on a presently perceived one (Hellström, 1985).

* Corresponding author at: Department of Psychology, George Mason University, 4400 University Drive, Fairfax, VA 22030, USA.
*E-mail address:* mwiener@gmu.edu (M. Wiener).

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However, the neural bases of both effects for temporal perception have never been explored. Recently, we demonstrated that the perception of time is susceptible to carryover effects, such that the perception of duration on a given trial is influenced by the duration presented on the preceding one (Wiener et al., 2014). This influence depended on the difference between the present and prior interval, and was contrastive in nature, with longer prior intervals leading to shorter perceived durations, and vice versa. In order to explain these effects, we devised an implicit memory model that continuously updated an internal standard that was weighted by more recently presented intervals. Previous research has similarly demonstrated behavioral effects resulting from the order of presented intervals on time perception and memory mixing (Gu and Meck, 2011; Jones and McAuley, 2005; Taatgen and van Rijn, 2011; Dyjas et al., 2012). These findings are additionally consistent with a model of population-coding for duration, in which individual neurons are tuned to specific duration lengths (Ivry, 1996; Heron et al., 2012; Merchant et al., 2013a; Wiener et al., 2014). Such a mechanism would be expected to be susceptible to adaptive changes to repeated stimulus durations, resulting in repetition suppression (Grill-Spector et al., 2006) or enhancement (Segaert et al., 2013).

Recent experimental evidence suggests that the SMA interfaces with the basal ganglia and thalamus as an integrated circuit for predicting and measuring temporal intervals (Merchant et al., 2013a; Wiener et al., 2011), which exhibits duration-tuning properties (Mita et al., 2009; Merchant et al., 2013b). Activity in this circuit may also be probed in humans by frontocentral scalp EEG measurements of slow cortical potentials, such as the contingent negative variation (CNV) (Nagai et al., 2004; Fan et al., 2007; Scheibe et al., 2010). The amplitude of the CNV component has been hypothesized to relate to the output of an accumulator mechanism for time (Casini and Vidal, 2011); accordingly, pacemaker pulses are summated into an accumulator mechanism while subjects attend to duration (Gibbon et al., 1984). As such, longer durations are characterized by relatively greater accumulation and hence relatively larger amplitude CNV events (Wiener et al., 2012). However, the involvement of the CNV in temporal accumulation is complicated by recent findings suggesting that the CNV is additionally involved in memory (Macar and Vidal, 2003), decision making (Ng et al., 2011; Kononowicz and van Rijn, 2014; Mento et al., 2013) and response caution (Boehm et al., 2014). Among these findings is evidence demonstrating that the CNV amplitude, under certain task conditions, peaks when the standard interval in memory has elapsed (Macar and Vidal, 2003; Pfeuty et al., 2003; Ng et al., 2011), thus placing the CNV within the context of evidence accumulation accounts of decision-making (Balci and Simen, 2014).

A separate line of research has revealed that signal offset-related EEG activity may also index perceived duration and decision-making mechanisms (Kononowicz and van Rijn, 2014; Paul et al., 2011; Tarantino et al., 2010; Lindbergh and Kieffaber, 2013; Gibbons and Stahl, 2008). For example, Kononowicz and van Rijn (2014) demonstrated that sensory-evoked potentials associated with a stimulus marking the end of an interval were better predictors of perceived duration than the preceding CNV, suggesting that the CNV amplitude does not index the temporal accumulator, but rather preparatory processes. Similarly, Paul and colleagues (Paul et al., 2003, 2011; Gontier et al., 2009) have demonstrated a post-offset component, termed the late positive component of timing (LPCt), that is associated with decision-making and difficulty in temporal discrimination. Notably, the LPCt signal is similar to other positive components associated with decision making, such as the P3 (Polich, 2011; San Martin et al., 2013) and late positive deflection (Itthipuripat et al., 2014; Kelly and O'Connell, 2013; Hilyard et al., 1971).

In the context of the above ambiguities, carryover effects can serve as a means to disentangle the roles of the CNV and LPCt in time perception processes. If, for example, the CNV signal indexes the output of an accumulator, then it should not be influenced by preceding intervals, and should only reflect the output of the present interval (van Wassenhove and Lecoutre, 2015). However, if the CNV instead indexes memory mechanisms, then changes in the CNV amplitude should fluctuate on a trial-by-trial basis with the current value of the memory standard, which will be a product of recently experienced intervals. The same may hold true for the LPCt signal. Moreover, if the LPCt indexes decision-making, then it should covary with both the current choice and the influence of prior choices. In order to measure carryover, we adopted a continuous carryover design (Aguirre, 2007), wherein the presentation sequence of stimuli was first-order counterbalanced, allowing us to independently measure the effect of every duration in our stimulus set on the current trial and prior one. Continuous carryover designs with serially balanced stimulus sequences are suited to the characterization of "similarity spaces" in which the perceptual similarity of stimuli is related to the structure of neural representation (Fig. 1; Kriegeskorte et al., 2008). In our case, the similarity space is the stimulus duration, rather than any other stimulus property that may affect perceived duration (Matthews, 2015). As such, we may also index the neural effect of similarity between successive durations.

## Materials and methods

### *Participants*

A total of 15, right-handed participants (8 female; 18–33 years old) participated in the experiment. Participants were recruited from the population at George Mason University. Written informed consent was obtained from all participants, and the Institutional Review Board of George Mason University approved the study protocol. One subject was removed due to excessive noise in the recorded EEG signals, reducing the sample size to $N = 14$.

### *Task design*

Participants performed a temporal bisection task, (partition variant; Wearden and Ferrara, 1995), of a similar design to our previous study (Wiener et al., 2014). All participants sat in front of a Dell LCD monitor. On a given trial, participants heard a series of stimuli, one-at-a-time, that persisted for one of seven logarithmically spaced intervals of time, between 300 and 900 ms [300, 360, 433, 520, 624, 749, 900 ms]. On each trial, participants were required to judge whether the stimulus presented was "long" or "short", based on their own subjective feeling, and press one of two response keys for each choice; left and right-hand responses for short and long were counterbalanced between subjects. Participants were instructed to make each response as quickly, yet as accurately as possible, and not to over-think their responses. At the beginning of each run, participants were presented with three stimuli at the geometric mean of the stimulus set (520 ms) as an example of the average stimulus duration and for comparison purposes for the first few trials. Auditory stimuli were generated using Audacity, version 2.0 (http://audacity.sourceforge.net/), and consisted of a white noise burst (0.5 amplitude, 44,100 Hz digitization) presented via two speakers situated on either side of the monitor at a comfortable volume, individually adjusted for each participant (loudness range: [69–73 dB). Only one white noise burst was used for the entire experiment, differing only in duration. Stimulus timing and control were carried out using the Python programming environment with extensions provided by Psychopy, version 1.78 (Peirce, 2008). Each trial consisted of the presentation of a central fixation point for 500 ms, which then extinguished and was followed by the auditory stimulus of variable duration, followed by a blank screen that was terminated by a choice response.

The order of stimulus presentation was determined by a path-guided de Bruijn sequence (https://cfn.upenn.edu/aguirre/wiki/public:de_bruijn). de Bruijn sequences are modified Hamiltonian cycles through a stimulus set, such that every possible order combination of stimuli is presented (Aguirre et al., 2011). The path-guided process of the de Bruijn sequence allows the Hamiltonian cycle to be modified by

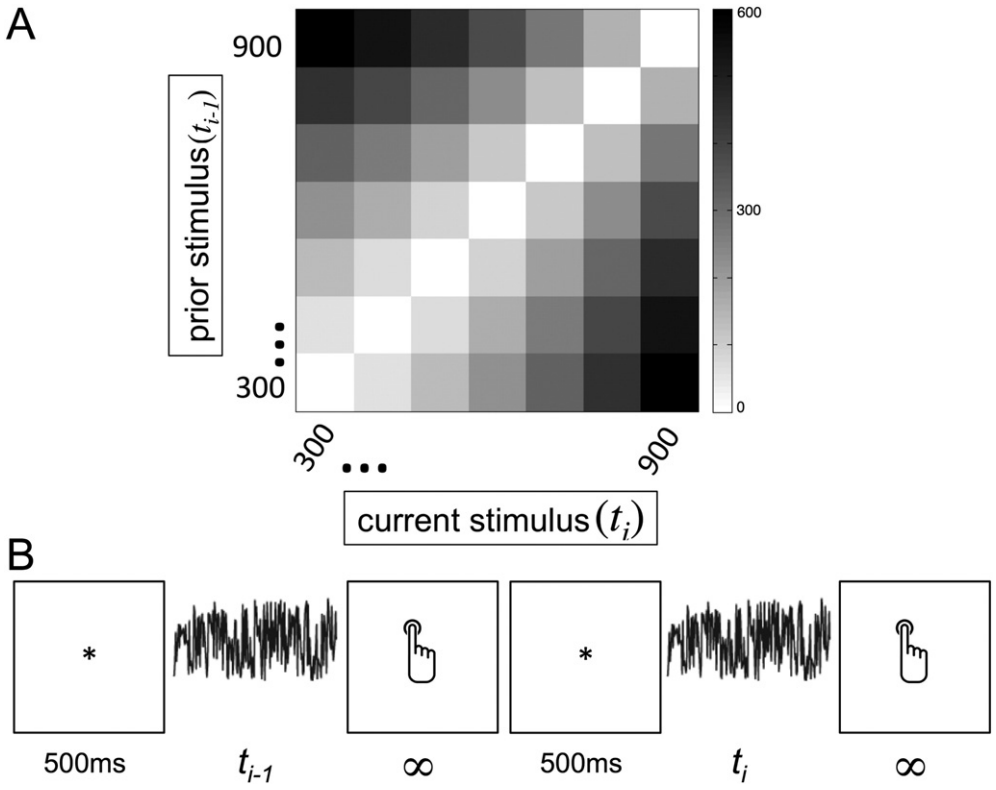


**Fig. 1.** Task design. (A) Temporal distance matrix for the stimulus set. The stimulus set included seven logarithmically spaced intervals between 300 and 900 ms. The presented matrix displays the distance, in ms, between every possible successive trial combination between current and prior durations. Direct effects are the influence of the present stimulus ($t_i$) on a response whereas carryover effects are the influence of the preceding trial stimulus ($t_{i-1}$). (B) Participants performed a 2AFC temporal bisection task, in which they were required to categorize whether an interval belonged to "short" or "long" categories. On a given trial, participants viewed a fixation point, followed by a burst of white noise, which persisted for one of seven durations. Participants were then required to respond as quickly but as accurately as possible which category the stimulus belonged to, which initiated the following trial.

a guide function, which can provide an underlying structure to the perceptually stochastic sequence in which stimuli are presented. The guide-function was modulated by a sum of sinusoids with random periods between 20 and 40 elements (unit labels). An additional label for null (empty) trials was added to the matrix, so as to include trials where no stimulus was presented; on null trials, subjects viewed a blank screen for 550 ms, followed by the appearance of the fixation point for the next trial. The resulting trial matrix consisted of 64 possible trial types and a sequence of 448 trials (excluding nulls). Each duration in the total sequence was presented 64 times. For each of the prior conditions, each duration was presented eight times. Three such de Bruijn sequences through the stimulus space were generated, leading to a total of 1344 trials. The time to run through a single sequence was ~16 min. Participants performed the task with each sequence in three separate runs, with a break between each run.

*Behavioral analysis*

As in our previous study, all trials were filtered by a RT cutoff of 1000 ms (Wiener et al., 2014), such that trials for which the RT exceeded 1000 ms were discarded. Psychometric and Chronometric curves were first generated for each participant based on the full dataset. Psychometric curves were generated by plotting the proportion of long response choices for each of the seven tested durations; these points were then fitted by a sigmoidal, logistic curve using the *psignifit* version 2.5.6 software package (see http://bootstrap-software.org/psignifit/) for Matlab, which implements the maximum-likelihood method described by Wichmann and Hill (2001a). Upper and lower thresholds, the approximate points at which the subject is 25% or 75% likely to judge the stimulus as long, were calculated using the bias-corrected bootstrap method implemented by *psignifit*, based on 1999 simulations (Wichmann and Hill, 2001b). The results of this analysis yielded the bisection point (BP; the time value at which subjects were equally likely to judge the stimulus as long or short), the difference limen (DL; the difference between the upper [75%] and lower [25%] threshold values divided in half), and the coefficient of variation (CV; DL/BP). The BP thus reflects the subjective midpoint of the range of tested durations, while the CV reflects the normalized variability of measurements. We note that our choice of nomenclature here reflects standard use among studies of time perception; BP is used here instead of the more common point of subjective equality (PSE), as the latter term implies an explicit comparison between two stimuli. Chronometric curves were constructed by plotting the RT for each of the seven possible durations.

For the exploration of carryover effects, trial types were divided up for each participant. Psychometric and Chronometric curves were again generated using the procedure outlined above. For perceptual carryover effects, participant responses were segregated into trials preceded by each of the eight possible prior trial types. A total of eight Psychometric and Chronometric curves were generated for each of the carryover conditions. To explore perceptual carryover, BP values from psychometric curves, and mean RT from chronometric curves, from each prior condition were entered into separate repeated measures ANOVAs, each with seven levels, one for each prior duration.

*EEG*

Continuous EEG was recorded from a 64 channel scalp Ag/AgCl electrode montage according to the international 10–20 system, relative to an online centroid reference, with horizontal and vertical electro-oculogram channels included to aid in the detection of eyeblinks (Neuroscan). Data were recorded with a Synamps$^2$ system

(Compumedics) at a sampling rate of 500 Hz, with an online bandpass filter of 0.1–100 Hz (Digitization rate: 500 Hz). Electrode impedance was kept below 5 kΩ, and was verified at the session start and between each run. Offline data analysis and subsequent analyses were all conducted in Matlab using extensions provided by EEGLAB (Delorme and Makeig, 2004) and custom scripts. Following acquisition, data were offline re-referenced to the average of two additional channels located at the mastoids. Noisy channels were interpolated with spherical spline interpolations. Continuous EEG data were epoched in two separate batches: one batch for onset-locked data (−400 to +1000 ms), and one for response-locked data (−1000 to +200 ms). A ±120 μV cutoff was used to discard trials where eye-blinks occurred; mean percentage range of trials removed per duration was 18%–20%, consistent with previous work employing this procedure (Kahn et al., 2010). Onset-locked data were additionally baseline-corrected by a 200 ms pre-stimulus window up to stimulus onset. No baseline correction was used for response-locked data, as the pre-response data were of interest; we note that an alternative method for baselining response-locked data, using the mean epoch voltage (Luck and Hillyard, 1990), produced qualitatively similar results. For this and all subsequent analyses, we averaged across frontocentral electrodes in an a-priori region of interest (F1, Fz, F2, FC1, FCZ, FC2, C1, Cz, C3), based on previous studies investigating temporal processing (Wiener et al., 2012; Macar and Vidal, 2004; Brunia et al., 2011).

Separate grand-average waveforms were generated for direct and carryover effects. Direct effects were interrogated by generating seven separate waveforms for each presented duration, whereas for carryover effects, the data were collapsed across all current durations and segregated by the seven possible prior trial durations. For transition distance effects, we segregated waveforms by the absolute distance between the present and prior trial duration (Fig. 1a). Mean amplitudes for each waveform were computed in separate time bins, spanning 200 ms each (0–1000 ms onset-locked; −800 to 200 ms response aligned). Separate analyses were conducted for each time bin. Additionally, we also segregated data based on the response made on the current or prior trial. In this instance, as the data were binary in nature, we conducted a repeated-measures ANOVA with time bin and response as within-subject factors. Significant effects were followed up with paired *t*-test comparisons. Notably, one subject is missing from the analysis of the prior response, due to a program error in data collection where these event codes were lost.

Single-trial regression of EEG data was conducted by constructing a general linear model (GLM), at the first level, for each individual subject (Kahn et al., 2010). EEG data consisted of the mean amplitude response from the CNV waveform in the 600 to 800 ms time bin for onset-locked data. The design matrix included seven regressors for the direct effects, one for each presented duration, and seven regressors for the carryover effects, one for each transition distance. β values for each regressor were extracted for each subject; at the second level, β values across subjects were concatenated and tested in separate repeated measures ANOVAs. This analysis shares many features with those commonly employed in continuous-carryover designs for fMRI (Aguirre, 2007), where GLM analysis are more commonly used. However, the GLM approach can provide an additional control over grand-averages, as direct and carryover effects may be simultaneously accounted for (Kahn et al., 2010).

## Results

### *Behavioral effects*

Psychometric curves constructed for participant performance demonstrated that participants were successfully able to categorize stimuli into short and long duration categories, with durations near the middle of the stimulus set categorized equally into both duration categories and the bisection point (BP) at the geometric mean of the stimulus set (Supplementary Fig. 1), consistent with previous studies (Kopec and Brody, 2010). Additional, chronometric curves constructed from reaction time (RT) data revealed that longer durations were associated with faster responses, consistent with recent findings [main effect of current duration: $F(6,78) = 108.729$, $p < 0.0001$] (Wiener et al., 2014; Balci and Simen, 2014) suggesting that, once participants have decided that the signal duration is longer than their internal standard, a response choice is prepared, leading to faster responses following longer durations, similar to perceptual decision-making findings in other domains (Palmer et al., 2005).

Consistent with our previous findings (Wiener et al., 2014), participant response choices were shifted by the duration presented on the prior trial. Accordingly, BP values were linearly altered by the prior duration, with longer prior durations inducing a rightward shift in the psychometric function (Fig. 2), characterized by fewer "long" responses, and shorter prior durations inducing a leftward shift [$F(1,13) = 7.847$, $p = 0.015$]. Chronometric functions were also linearly altered by the prior duration, with longer prior durations leading to an upward shift, characterized by progressively slower responses [main linear effect of prior duration: $F(1,13) = 8.392$, $p = 0.012$; interaction with current duration: $F(36,468) = 2.519$, $p < 0.001$].

### *Direct EEG effects*

Our use of a first-order counterbalanced sequence allowed us to divide our analysis into orthogonal "direct" and "carryover" effects, which independently characterize the effect of the present and prior stimulus, respectively. For the direct effect of stimulus duration, event-related potentials (ERPs) were constructed, timelocked separately to the onset of each stimulus and the response made following that stimulus. Although many studies of timing investigate the former ERP, relatively few investigate the latter. The use of both onset and response-locked effects thus allowed us to examine both encoding and decision-making mechanisms, and to examine effects that may be distorted by variable changes in RT (Luck and Hillyard, 1990).

ERPs for the onset of duration first exhibited a frontocentrally maximal positive waveform, likely reflecting auditory registration of the stimulus, that peaked at ~390 ms before abruptly shifting polarity into a broad, negative-peaked slow wave (CNV) (Fig. 3). Analysis of equally-spaced, 200 ms bins during the ERP epoch for each present duration revealed a significant linear effect of mean amplitude only during the CNV phase (600–1000 ms) [600–800 ms: $F(1,13) = 16.451$, $p = 0.001$; 800–1000 ms: $F(1,13) = 33.098$, $p < 0.001$] (Supplementary Fig. 3), with larger, broader CNVs for longer durations (all other bins $p > 0.05$), consistent with previous findings (Pouthas et al., 2000) (Fig. 3a). Notably, although statistically linear, CNV amplitudes plateaued after 520 ms, also consistent with previous research suggesting that CNV amplitude indexes the memory standard (Ng et al., 2011). For response-aligned waveforms, the effect of duration on the CNV was much more pronounced; longer duration stimuli were characterized by CNV waveforms that peaked earlier, relative to the choice-response. Notably, immediately following the decision, a late positive component (LPCt) developed whose amplitude scaled linearly, depending on the duration that had just been presented, with larger positive amplitudes associated with shorter durations [$F(1,13) = 25.483$, $p < 0.001$] (Fig. 3b). This finding is noteworthy, as the response made was binary in nature, and yet the ERP evoked by that response closely matched the length of the stimulus that had extinguished 450 to 650 ms previously; similar findings with fMRI have also demonstrated post-response increases in SMA activity during temporal expectation that also reflected the duration of the just-experienced trial (Cui et al., 2009). However, we note that this analysis segregates trials based on the objectively presented interval. In order to assess the effect of the subjective interval, we also segregated trials based on the response; that is, whether an interval was classified as long or short. Although binary in nature, these data mirrored the effects observed when segregating

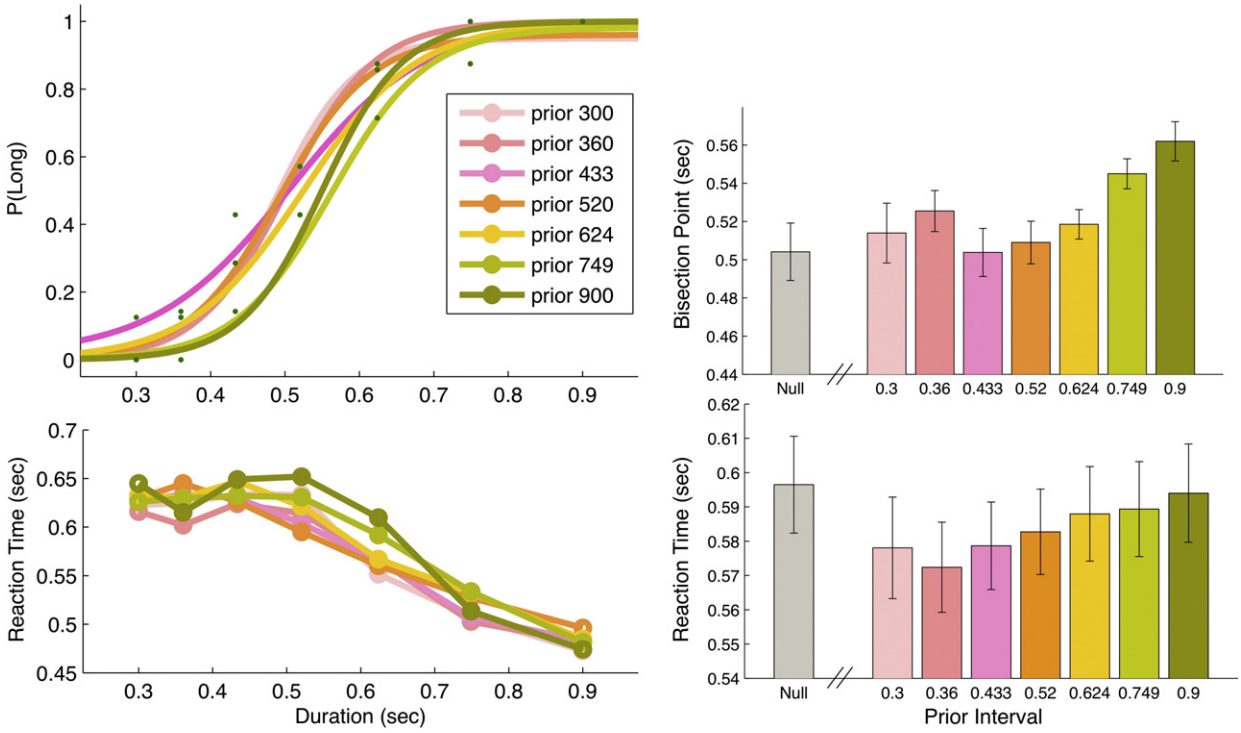


**Fig. 2.** Behavioral effects of perceptual carryover. Participant responses changed, depending on the length of the prior trial stimulus duration. At left, the top graph displays grand-average psychometric curves for each of the seven possible priors; psychometric curves were displaced linearly by the prior duration, with shorter perceived durations (characterized by fewer "long" responses) for trials preceded by a longer duration trial, and vice versa. At left, the bottom graph displays average chronometric data, exhibiting characteristic decreases in RT for longer duration stimuli (Wiener et al., 2014; Balci and Simen, 2014); longer prior durations linearly shifted RT upwards, with longer mean response latencies for trials preceded by longer duration trials. At right, the top graph displays the mean bisection point, as derived from psychometric curve fitting, as a function of the prior trial duration. At right, the bottom graph displays the mean RT, collapsed across present trial duration, and dependent on the prior trial duration. The mean BP and RT for trials preceded by null events are also displayed. Error bars reflect S.E.M.

by objective duration, with a larger CNV amplitude [onset-locked: choice by time window interaction $F(4,52) = 20.159$, $p < 0.0001$; significant post-hoc effects for 600–800 and 800–1000 ms, both $p < 0.05$) and smaller LPCt amplitude for durations classified as long and short [response-aligned; main effect of choice $F(1,13) = 79.482$, $p < 0.0001$; main effect of time window: $F(1,13) = 17.746$, $p < 0.0001$; interaction $F(4,52) = 11.526$, $p < 0.0001$; significant effects in every window, all $p < 0.05$, interaction driven by varying polarity of effects across windows], respectively (Supplementary Fig. 4). Taken together, both waveforms provide complementary pictures of the development of temporal encoding and decision-making. Furthermore, the change in CNV peak amplitude complements our RT data, suggesting that, when the presented duration has elapsed the internal standard, no additional encoding is necessary, leading to faster RTs.

These findings stand apart from the previous literature on the CNV in timing and temporal expectation, in that they provide a more nuanced view of the time course of neural activity during timing and decision-making. Although previous studies have described the LPCt as covarying during temporal processing (Paul et al., 2011; Tarantino et al., 2010; Gontier et al., 2009), these studies have only shown changes dependent on choice (i.e. perceived short or long), not for individual durations. We believe that the advantage of our study is that most previous EEG timing studies employ a low number of trials (<100), whereas we included a large number (>1200), allowing for a greater dissection of temporal differences between conditions.

Additionally, we examined if any of the direct-effects signals were correlated with our behavioral measures. First, in accordance with previous findings, we tested whether the CNV amplitude correlates with RT (Fan et al., 2007); this was done by concatenating the CNV and RT values for each presented duration and subject, to account for both within and between subject effects. We observed that both RT and CNV values plateau in their responses, with stable RTs *prior* to 520 ms, and stable CNVs *after* 520 ms, and reasoned that, if the inflection of RT values indexes when subjects have reached a decision that the signal is to be classified as "long", then the CNV amplitude and RT scores should be linked. Indeed, we found a significant positive correlation [Pearson $r = 0.239$, $n = 98$, $p = 0.018$; Spearman $r = 0.253$, $p = 0.012$] between the two values, with more negative CNV amplitudes (600–800 ms post-onset) associated with lower RTs. For the LPCt signal, we noted that these amplitudes matched the duration very well, and did not plateau, suggesting that they more closely matched choice probability. We thus found a significant correlation between LPCt amplitude and the probability of classifying a stimulus duration as long (Pearson $r$ and Spearman $r = -0.387$, $n = 98$, $p < 0.0001$). Notably, LPCt amplitude did not correlate with RT (Pearson $r = 0.072$, Spearman $r = 0.082$, $p > 0.05$), whereas CNV amplitude marginally correlated with choice probability (Pearson $r = -0.196$, $p = 0.053$ Spearman $r = -0.183$, $p = 0.072$). For these and all subsequent correlations, non-parametric permutation tests (10,000 randomizations) were run to confirm that Pearson and Spearman coefficients exceeded the critical alpha (two-tailed, 0.05), indicating that they did not occur by chance (Michaelis et al., 2014); the correlation between CNV amplitude and choice probability failed to exceed this threshold.

### *Carryover EEG effects*

To investigate carryover effects, we began by constructing onset and response aligned ERPs, but collapsed across all presented durations, with separate waveforms constructed for each of the seven possible prior durations. Due to the first-order counterbalancing, no changes observed as a result of the prior stimulus duration could be due to the duration presented on the present trial. For stimulus onset, waveforms exhibited the same characteristic shape, with a positive deflection followed by a negative CNV response (Fig. 4a). Markedly, we observed

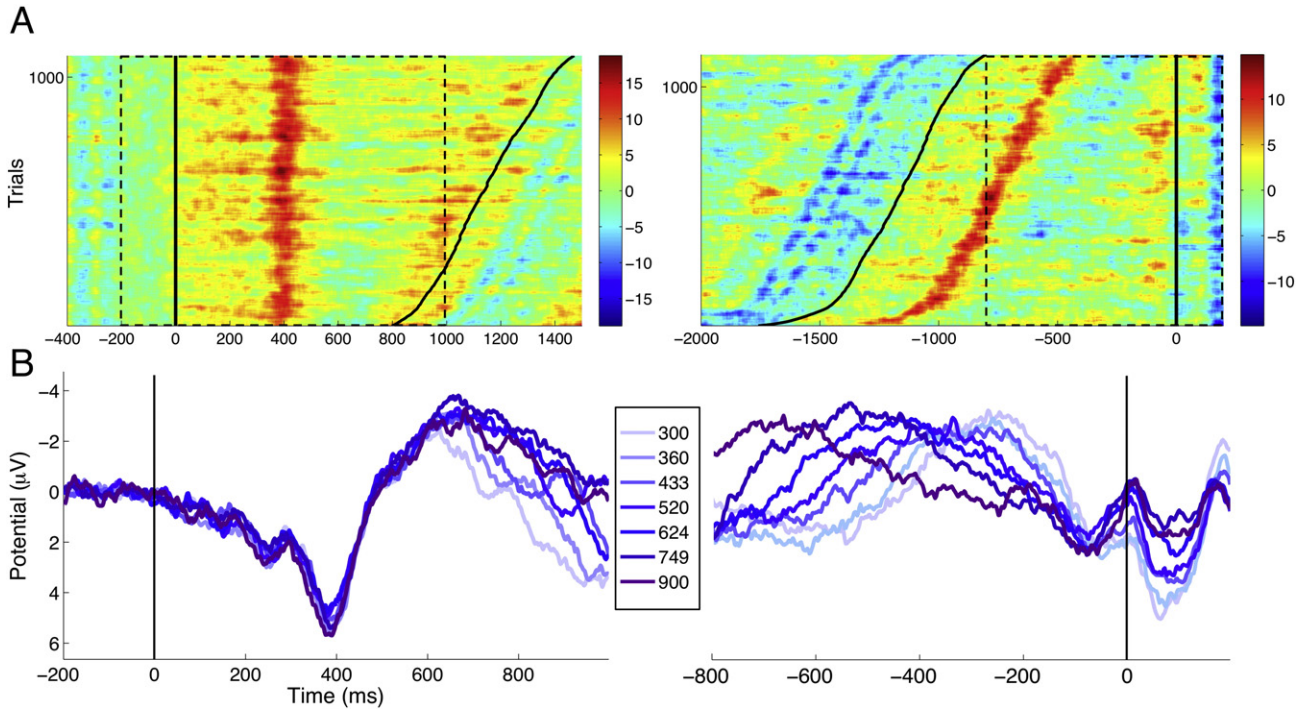


**Fig. 3.** Direct EEG effects of stimulus duration. (A) Single-trial amplitude images from a representative subject, displaying onset-locked (at left) and response-aligned (at right) data (FCz). Onset-locked trial data, sorted by RT (black solid sigmoid), display a sensory onset response, consistently phase-locked across trials, followed by a CNV signal that extended in time until a positive LPCt component. Response-aligned trial data, sorted by stimulus onset, displaying the staggering effect of onset response amplitude; here, CNV data can be seen to peak earlier, relative to the response. (B) Grand-averaged ERP waveforms for onset-locked and response-aligned data, from dashed insets above at frontocentral electrodes. Separate ERPs are displayed for each presented duration. Onset-locked data displayed larger (more negative) amplitudes for progressively longer duration stimuli. Dashed lines display the offset of each stimulus; notably, the CNV for longer duration stimuli reaches its maximum prior to stimulus offset. Response-aligned data similarly reveal that the CNV peak occurs earlier, relative to onset, for longer duration stimuli. The post-response LPCt signal additionally demonstrates a linear effect of duration, well after the stimulus has extinguished, with larger (more positive) amplitudes for shorter duration stimuli. Negativity is plotted upwards, for comparison with previous studies.

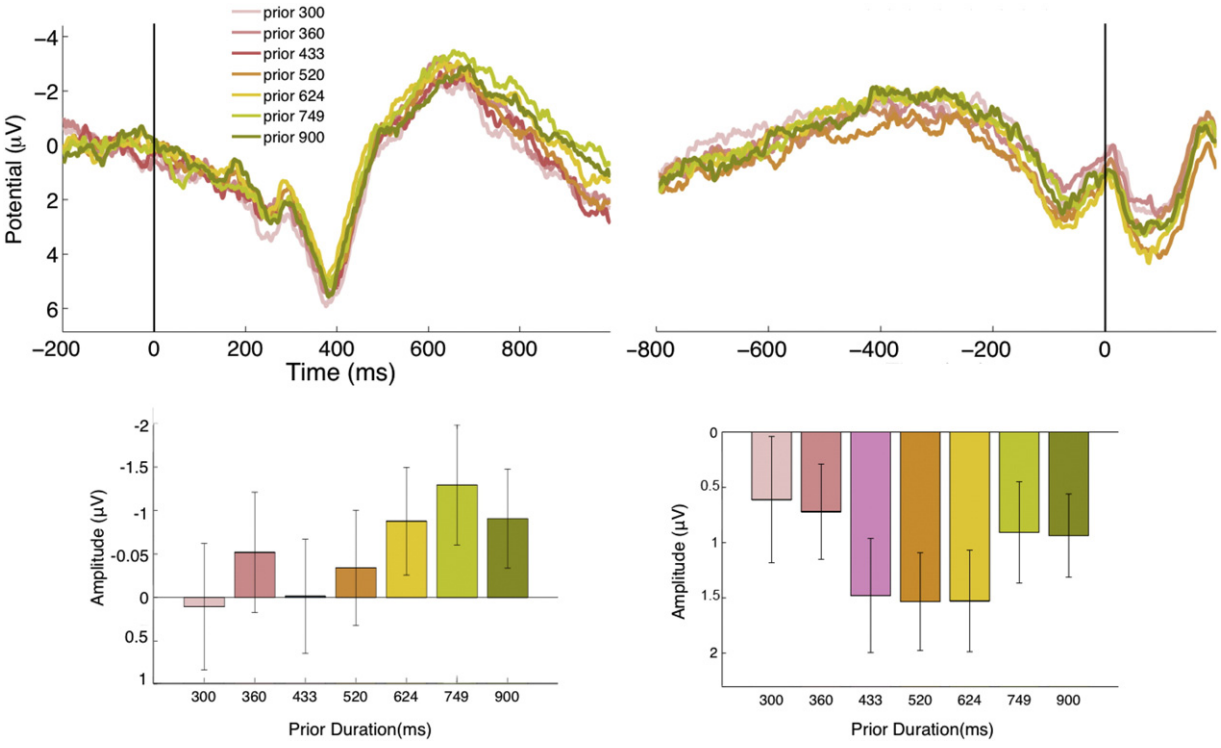


**Fig. 4.** Carryover EEG effects of duration. Top left displays onset-locked, frontocentral grand-average ERP waveforms, for each of the seven possible prior trial durations. CNV amplitudes were linearly shifted by the prior trial duration, with larger amplitudes on trials preceded by trials with longer duration stimuli. Bar graph below displays mean amplitudes within the 800–1000 ms, post-onset time window. Top right displays response-aligned activity, which revealed that the post-response LPCt exhibited a quadratic relationship with prior trial duration, with larger amplitudes for prior trial durations near the middle of the stimulus set (bottom graph). Error bars reflect S.E.M.

that the amplitude of the CNV response was influenced by the duration presented on the prior trial, with longer prior durations associated with higher negative amplitudes [800–1000 ms: $F(1,13) = 6.224$, $p = 0.027$]; this effect only occurred during the CNV portion of the waveform (Supplementary Fig. 5). For response-aligned data, the post-response LPCt was also modulated by the prior duration; however, in contrast to the linear effect observed in the CNV, the LPCt waveform exhibited a quadratic effect, with higher positive amplitudes associated with prior durations near the middle of the stimulus set [$F(1,13) = 5.418$, $p = 0.037$] (Fig. 4b).

Similarly, we also segregated our data based on the subjective perception of the prior interval; in this case, whether the prior interval was classified as long or short. For onset-locked data, although a slight offset in the waveforms was observed (Supplementary Fig. 6), no significant differences were detected (all $p > 0.05$). However, for response-aligned data, we detected a significant effect around the time of the response [time window x prior response $F(4,48) = 6.596$, $p < 0.001$; −200–0 ms $t(12) = 2.813$, $p = 0.016$; 0–200 ms $t(12) = 2.539$, $p = 0.026$]. Accordingly, if the prior trial was classified as long, the amplitude around the response of the following trial was greater, compared to trials on which the prior trial was classified as short. Of note, this pattern is opposite to that observed in the direct effects analysis, where long intervals are associated with *lower* post-response amplitudes.

The analysis of direct and carryover effects in our study demonstrated that the CNV amplitude on a single trial covaried with the duration presented on that trial and the prior one. Notably, this shift mirrors the contrastive effect of perception in our behavioral data, with longer prior durations associated with shorter perceived durations (Fig. 5a). Indeed, we found a significant negative correlation between individual subject CNV and psychometric BP values [Pearson $r = -0.2466$, Spearman $r = -0.2542$, $p = 0.012$], indicating that the prior-segregated CNV amplitude may serve as an index of the internal standard (Fig. 5b). For the LPCt, we detected a significant negative correlation between amplitude and the carryover effect of choice probability, defined as the average proportion of classifying the stimulus as "long", collapsed across all possible durations on the present trial [Pearson $r = -0.233$, $p = 0.021$; Spearman $r = -0.183$, $p = 0.071$], with larger positive LPCt amplitudes, which occurred for mid-range prior trial durations, associated with a lower probability of classifying a stimulus as long; however, the marginal Spearman correlation in this case did not exceed the permutation critical alpha. Finally, we note that CNV amplitude did not correlate with carryover choice probability [Pearson $r = -0.069$, Spearman $r = -0.081$, $p > 0.05$], and LPCt amplitude did not correlate with the carryover bisection point [Pearson $r = -0.165$, Spearman $r = -0.128$, $p > 0.05$].

### *Temporal distance effects*

An additional advantage of using a first-order counterbalanced sequence, as stated above, is that we could measure the similarity space of duration processing. In this framework, we could use as a metric the similarity of any perceived duration to the one on the preceding trial, which we term here the temporal distance. Our analysis thus turned to whether the CNV or LPCt signals covaried with the temporal distance. We constructed an additional set of onset and response-aligned ERPs, but with separate waveforms within each set for the temporal distance, characterized as the absolute difference between the present trial's duration and the prior one. By analyzing these waveforms, we could identify differences in the neural response when the same duration was repeated twice, versus the graded difference between successively larger temporal distances.

For onset-locked ERPs, we found a linear effect of temporal distance that was restricted to the amplitude of the CNV [400–600 ms: $F(1,13) = 7.808$, $p = 0.015$; 600–800 ms: $F(1,13) = 2.977$, $p = 0.011$; 800–1000 ms: $F(1,13) = 14.285$, $p = 0.002$] (Fig. 6). For response aligned data (Supplementary Fig. 8), we similarly found an effect of the pre-response CNV amplitude [−800–−600 ms: $F(1,13) = 13.678$, $p = 0.003$], but found no significant effect for any other window, including the LPCt (all $p > 0.05$). Interestingly, higher negative amplitudes were found for smaller temporal distances, with the largest amplitude response when the same duration was presented twice, thus exhibiting repetition enhancement.

### *Single-trial modeling*

Despite the effect of temporal distance observed in the CNV, we note that our analysis, which relied on grand-averaged waveforms, may not be ideal. That is, grand-average waveforms rely on averaging across a wide variety of trials, under the assumption of improved signal to noise ratios. However, they do not speak to whether activity on individual trials is sufficient to decode either the present stimulus duration or the temporal distance between pairs. In order to investigate the effect of temporal distance on the CNV further, we conducted single-trial modeling by constructing a GLM that simultaneously accounted for

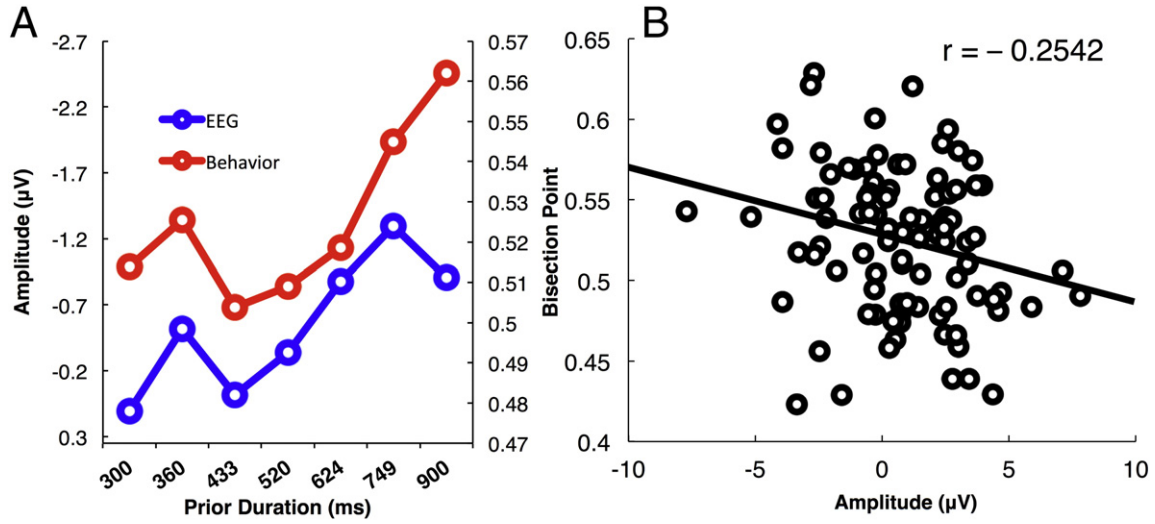


**Fig. 5.** Relationship between prior trial CNV amplitude and perceptual carryover effects. (A) Average bisection points from psychometric data and mean amplitudes from the CNV (800–1000 ms post-onset) both exhibited a similar magnitude of linear shift, dependent on the length of the duration presented on the prior trial. (B) Significant negative correlation between the bisection point and the amplitude of the CNV signal (800–1000 ms post-onset). Larger negative CNV amplitudes were associated with greater bisection points. Spearman *r* is presented.

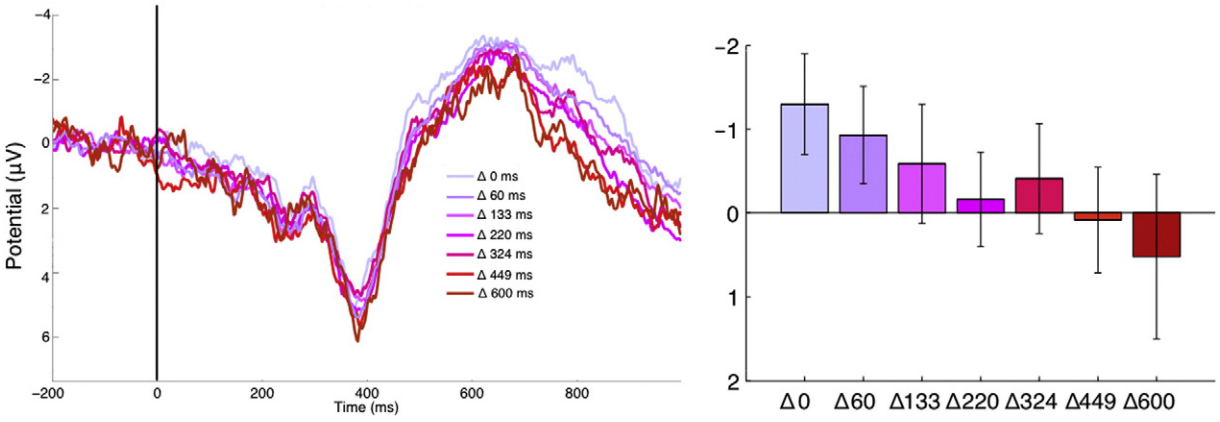


**Fig. 6.** Temporal distance EEG effects exhibiting repetition enhancement. Onset-locked CNV data exhibited a linear shift in amplitude, dependant on the absolute difference between the present and prior trial duration. Larger negative amplitudes were observed for smaller temporal distances, with the largest response when the same duration was presented twice. Error bars reflect S.E.M.

both the direct effect of every possible stimulus duration, and the temporal distance between pairings, with separate regressors (Aguirre, 2007; Kahn et al., 2010) (Fig. 7a).

Once constructed, we ran our GLM for each individual subject, using the mean amplitude data from the onset-locked CNV on each trial, and collected β values for each covariate. As shown in Fig. 7b, β values for direct and carryover effects recapitulated the effects observed in the grand-average waveforms, with linear effects for both the direct effect of stimulus duration on the present trial [$F(1,13) = 5.658$, $p = 0.033$], and the temporal distance effect between the present and prior trial [$F(1,13) = 5.824$, $p = 0.031$] that mirrored the patterns observed in the grand average data, including repetition enhancement for temporal distances. Overall, these findings bolster the results of our previous analysis; furthermore, as the GLM accounted for both the direct and

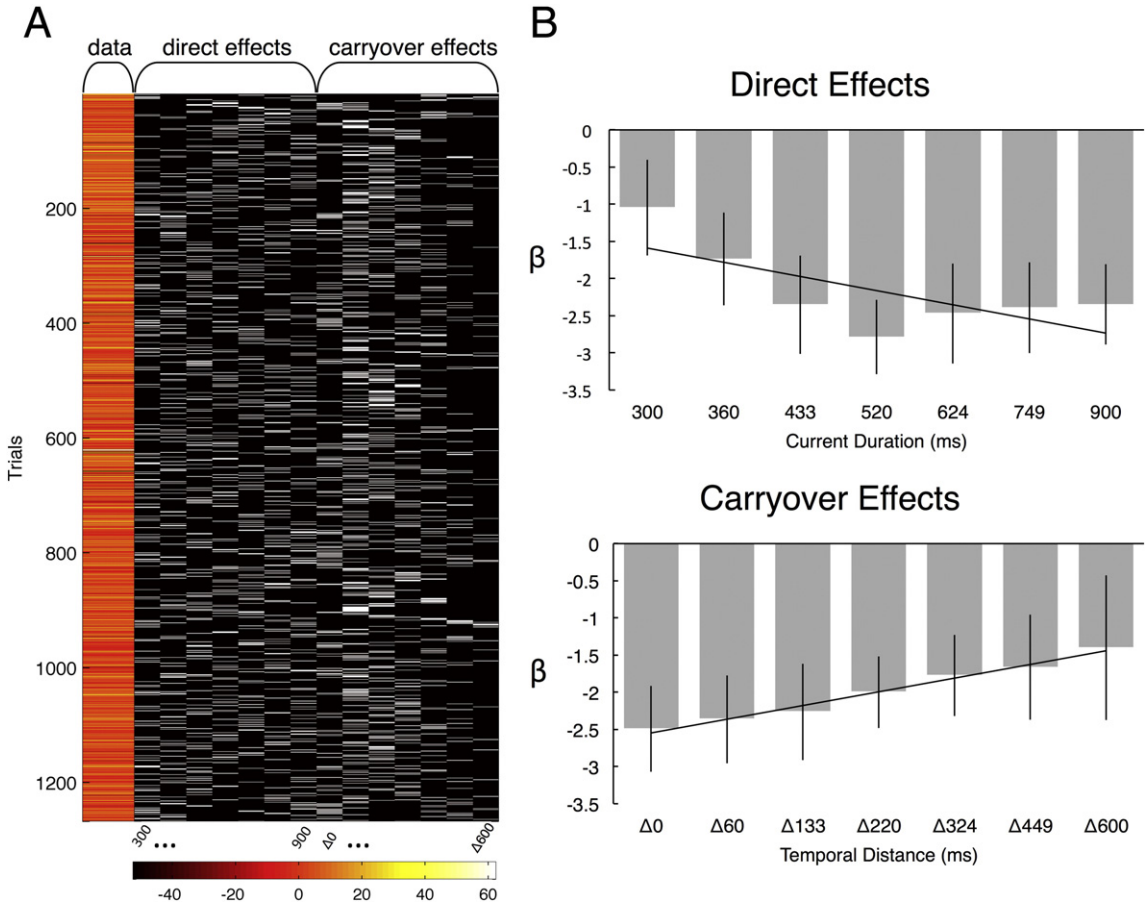


**Fig. 7.** Single trial modeling of direct and carryover effects in EEG data. (A) General linear model (GLM) design matrix for regressing direct and carryover effect. EEG data from frontocentral electrodes (data column) was regressed against fourteen separate regressors. Separate columns were constructed for each of the seven durations in the stimulus set, presented on each trial (direct effects); carryover effects were characterized by the seven possible transition distances between present and prior trial durations. Bottom scale depicts amplitude for EEG data. (B) β values for each single-trial regressor for direct and carryover effects. Both effects mirrored those observed in session averages, with larger (negative) β values for longer prior durations in direct effects, and larger (negative) β values for smaller transition distances in carryover effects, exhibiting repetition enhancement.

temporal distance effect, we suggest that the temporal distance effect could not have been driven by changes in amplitude resulting from the present stimulus alone. Finally, these findings suggest that there is sufficient information at the single-trial level to decode stimulus duration and temporal distance in the CNV.

## Discussion

In the present study, we have provided evidence of the neural indices of carryover effects for temporal perception. Our study reveals two EEG components that each reflects unique aspects of temporal perception. In the first signal, a slow negative-peaked deflection occurred that was parametrically modulated in length, amplitude, and peak time by the duration of the presented stimulus. This CNV signal has been previously implicated in a number of temporal paradigms, including preparation (Praamstra et al., 2006) and anticipation (Scheibe et al., 2010), as well as active duration encoding (Wiener et al., 2012). In the second signal, a transient positive peak occurred immediately following the choice response that was parametrically modulated in amplitude by the duration of the stimulus that had just been experienced. One noteworthy distinction of this LPCt signal from the CNV is that the CNV waveform could be argued to reflect simply the length of the stimulus duration, and so be driven by a sustained stimulus onset–offset profile (Sieroka et al., 2003); this argument would not hold for the LPCt, as the signal occurred well after the stimulus had extinguished.

The CNV and LPCt signals have both emerged in recent years as candidate signals for temporal perception, with both signals ascribed similar processing roles. The role of the CNV has been particularly contentious (van Rijn et al., 2011); however, the multifaceted aspect of the CNV is likely due to the mixture of neural signals and cognitive processes contributing at the level of the scalp (Philiastides et al., 2014). In the present study, we replicated previous findings demonstrating that the amplitude of the CNV signal plateaus once the geometric mean of the stimulus set has elapsed (Ng et al., 2011). This finding suggests that the CNV amplitude in our task indexes an evolving decision estimate for when the current stimulus has passed the criterion for classifying a stimulus as long (Wiener et al., 2014; Balci and Simen, 2014). Similarly, the CNV signal, has also recently been implicated in response caution, where subjects must integrate the tradeoff between response speed and decision accuracy (Boehm et al., 2014). Consistent with this explanation, response-locked activity demonstrated that the CNV peak occurred earlier in time for longer intervals, which were characterized by faster RTs, and CNV amplitude correlated with RT. The LPCt signal, in contrast, did not plateau following the geometric mean, but instead matched closely the previously experienced duration, and was correlated with choice probability. Importantly, the CNV signal did not correlate well with choice probability, whereas the LPCt signal did not correlate with RT. These findings suggest that the LPCt more closely matches the perceptual decision, whereas the CNV indexes the memory criterion.

Both the CNV and LPCt signal were also affected by the duration presented on the prior trial, but in different ways. For the CNV signal, we found that the amplitude of the response was linearly shifted by the length of the prior duration, with larger negative amplitudes for longer prior trial durations. For the LPCt signal, the amplitude exhibited a quadratic pattern, with larger positive amplitudes for prior trial durations near the middle of the stimulus set. These differences highlight distinct potential roles for each signal in temporal perception and decision-making. For the CNV signal, the linear shift in amplitude resulting from the prior duration indicates that this signal also indexes shifts in the internal memory standard resulting from the prior trial. We note that this pattern matches the expectations of our implicit memory model (Wiener et al., 2014; Dyjas et al., 2012), in which recently experienced durations are weighted more heavily in calculating the value of the criterion. Accordingly, if the prior interval was long (e.g. 749 ms), then the criterion will be shifted later in time; as such, the next interval is more likely to be judged as short relative to the criterion, and will have a slower mean RT. As for the criterion and CNV signal are linked, a larger criterion will be associated with a larger amplitude CNV on the next trial, which we found. Indeed, the carryover shifts of the BP and carryover amplitude of the CNV signal were correlated, further suggesting that these two are linked.

For the LPCt signal, it is more difficult to reconcile the finding of higher positive amplitudes associated with prior trials with mid-range. However, the implicit memory model again offers a potential explanation. Based on the present findings, modulations of the amplitude of the LPCt might reflect the difficulty of the decision regarding the duration of a temporal interval. The mid-range durations in our stimulus set (433–624 ms), are the more difficult durations to classify as long or short, because they straddle the criterion value. Notably, if the prior trial duration is one of these values, the implicit memory criterion will shift closer to the "true" BP of the stimulus set, at the geometric mean. When this occurs, the discrimination on the next trial becomes more difficult; this is evidenced by examining the choice probability distributions for each trial. For example, if the prior trial duration is very short (e.g. 300 ms), then the BP will shift closer to 300 ms; on the subsequent trial, given that all durations are equally probable to occur, the subject will be more likely to choose "long", as more durations in the stimulus set will now be longer than the BP, thus making stimuli around the middle of the stimulus set easier to discriminate. If, however, the BP is at the geometric mean, then the choices on the subsequent trial are equally split across the durations, leading the discrimination to be more difficult. Recent work has demonstrated that the amplitude of the LPCt component covaries with the difficulty of temporal discrimination (Paul et al., 2011; Gibbons and Stahl, 2008), suggesting that the carryover effect of LPCt reflects the difficulty of the discrimination. Further consistent with this model, we suggest that when comparing a stimulus against the geometric mean, subjects will be more likely to rely on their inherent bias. A documented strategy in this regard is the "choose-short" effect (Wearden, 1991; Lieving et al., 2006), in which subjects may be biased to classify a stimulus duration as short when they are uncertain. As such, if more positive LPCt amplitudes on the present trial indicate shorter durations, then if the prior trial leads to even more positive amplitudes, as shown for prior trials at mid-range durations, then this should indicate a bias to classify signals as "short". Consistent with this explanation, we found a correlation between LPCt amplitude and the carryover effect of choice probability.

In addition to the effect of prior stimulus, we also tested both signals for their sensitivity to the geometry of the stimulus space. That is, we tested if each signal is influenced by the temporal distance between the duration on the present and prior trial, regardless of the direction of that distance (longer or shorter). We found that only the CNV signal was sensitive to the transitory distance, and that this effect manifested as a linear change in amplitude. This suggests that the CNV signal can also index the deviance in duration between the prior trial and the present one, even when participants are not explicitly required to make this comparison. Of greater interest, the linear effect on CNV amplitude exhibited the neural phenomenon of repetition enhancement (Segaert et al., 2013), with greater amplitudes when the same duration was presented twice, and diminishing amplitudes for larger transition distances. This effect persisted in both grand-averaged waveforms and the regression of single-trial data, suggesting that the effect is both robust and decodable at granular levels.

Why might the brain exhibit repetition enhancement to repeated duration, instead of repetition suppression? The source of repetition enhancement effects, similar to repetition suppression, has been debated in the wider neuroscience literature (Grill-Spector et al., 2006). We suggest a possibility: the detection of temporal stability. Previous research and theory suggest that the brain acts as a prediction engine, in order to minimize energy expenditure, wherein expected outcomes predicted by a forward model elicit smaller responses than unexpected ones (Knill and Richards, 1996; Friston, 2005). A vital

aspect of this is the search for temporal stability, whereby temporal patterns are identified. In the present experiment, the pattern of presented stimuli was perceptually stochastic, in which no discernible pattern existed.[1] However, in a chaotic environment, the brain likely seeks to reduce uncertainty by attempting to detect an underlying pattern. As such, in our paradigm, when the same duration is presented twice, this may serve as a salient exogenous cue signaling regularity (Zhao et al., 2013), and thus elicits a larger neural response. Indeed, neural repetition effects have been suggested to underlie perceptual expectations and predictive coding mechanisms (Summerfield et al., 2008). Notably, in temporal oddball tasks, wherein detection of a novel, temporally deviant stimulus elicits a larger activation than repeated stimuli the size of the neural response to an oddball duration reflects the deviance of that duration from the standard, regardless of the direction (van Wassenhove and Lecoutre, 2015; Jaramillo et al., 2000), the opposite finding of our results. In this regard, our paradigm serves as the converse to a temporal oddball task; in our task, it is the repeated stimuli that appear novel. We further predict that in our task, following repetition, if the same stimulus duration were to be additionally repeated, the repetition enhancement effect would gradually diminish, shifting to repetition suppression; similar findings have been demonstrated with fMRI and face-stimuli (Muller et al., 2013). However, the data in the present experiment, while demonstrating repetition enhancement, cannot demonstrate with certainty that the results were driven by predictive coding. A method to test this would be to have subjects perform a timing task where repetitions in stimulus duration were either rare or common. A prediction for this experiment is that the CNV signal would be higher for rare, unexpected repeats than for common, expected ones, similar to other stimulus domains (Todorovic et al., 2011). Similarly, differences in the rarity of non-temporal stimulus repetition have been found to affect duration processing (Matthews, 2015). Furthermore, we suggest that common repeats should be associated with a reduction in variability, as repeated stimulus durations would reduce the variability of the memory standard, thus leading to easier discrimination (Ivry and Hazeltine, 1995; Dyjas et al., 2012). In our study, we could not test for a difference in perceptual variability (CV), as some temporal distance conditions (Δ324, Δ449, Δ600 ms) did not have enough present trial durations to construct a psychometric curve.

Regarding the source of the EEG activity observed in the present study, our data do not permit us to state with certainty, in the absence of structural data for source localization. However, we note that the CNV signal we describe shares many characteristics with the recently described CPP component (O'Connell et al., 2012), which has been interpreted as an index of accumulator-to-bound decision-making. However, regarding the shape of the waveform, it is noteworthy that a similar profile was observed across the wide range of durations tested. Indeed, whether the duration was 300 ms or 900 ms, a similar overall pattern was observed, with an onset response peaking at ~390 ms, followed by a large negative deflection. Given this profile, it is unlikely that the CNV signal here reflects an accumulation or auditory ramping process, where we would expect to see an effect occurring prior to 300 ms (van Wassenhove and Lecoutre, 2015). As such, the signal we observe here more likely reflects a decision process, which can occur either before or after an interval is complete. Our classification of the observed signal as the CNV was due to the polarity and spatial location of the signal. However, we suggest that the boundary between the CNV and CPP is fluid, and so our choice to classify the signal we observed as the former is not a strict definition. Indeed, recent work on the CPP has noted that, without spatial filtering of the data, which may greatly change scalp electrical topography (Cohen and Gulbinaite, 2014), the CPP more closely resembles the CNV (Kelly and O'Connell, 2013). Regardless of the definition, however, we note that our study demonstrates two EEG signals, one pre-response and one post-response, that covary with duration on both the present and prior trial.

In summary, our data provide additional context for understanding the multiplexing of EEG signals during temporal processing. Our results support the hypothesis that the CNV and LPCt signals during a temporal bisection task reflect memory and decision-making mechanisms, respectively. Furthermore, we demonstrate that the CNV signal is sensitive to the similarity structure of the range of presented durations, on a trial-by-trial basis, and in a manner consistent with repetition enhancement and predictive coding. We end by suggesting that the signals we observe allow for temporal continuity by continuously updating the statistics of environmental temporal stimuli, in order to construct a stable percept in conscious perception.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.03.054.

[1] Of note, human participants are generally biased to identify temporal patterns, even when none exist (Kareev, 1995), further suggesting that the brain is continually attempting to identify stability in uncertain environments.

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