Dissociable neural indices for time and space estimates during virtual distance reproduction

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A R T I C L E   I N F O

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A B S T R A C T

The perception and measurement of spatial and temporal dimensions have been widely studied. Yet, whether these two dimensions are processed independently is still being debated. Additionally, whether EEG components are uniquely associated with time or space, or whether they reflect a more general measure of magnitude quantity remains unknown. While undergoing EEG, subjects performed a virtual distance reproduction task, in which they were required to first walk forward for an unknown distance or time, and then reproduce that distance or time. Walking speed was varied between estimation and reproduction phases, to prevent interference between distance or time in each estimate. Behaviorally, subject performance was more variable when reproducing time than when reproducing distance, but with similar patterns of accuracy. During estimation, EEG data revealed the contingent negative variation (CNV), a measure previously associated with timing and expectation, tracked the probability of the upcoming interval, for both time and distance. However, during reproduction, the CNV exclusively oriented to the upcoming temporal interval at the start of reproduction, with no change across spatial distances. Our findings indicate that time and space are neurally separable dimensions, with the CNV both serving a supramodal role in temporal and spatial expectation, yet an exclusive role in preparing duration reproduction.

1. Introduction

The perception and production of time in the milliseconds to seconds range, known as interval timing, is of fundamental importance to our everyday lives. Temporal processing underlies such capacities as walking, talking, singing, and playing sports (Buhsui and Meck, 2005). Furthermore, the ability to predict upcoming events requires an accurate perception of time (Chang and Jazayeri, 2018; López-Moliner et al., 2019). Similarly, the perception of space is a requirement for navigating through the world, manipulating objects, and accurately attending to distinct locations (Epstein et al., 2017; Issa et al., 2020). From a combined perspective, time and space should both then be necessary for situating oneself within the world and deciding where and when to move, and is thus critical for planning. However, whether or not these dimensions rely on shared or separate neural circuits remains unknown (Marcos and Genovesio, 2017; Cai and Connell, 2016; Robinson et al., 2019). Previous studies have used a variety of methodologies and behavioral paradigms to provide evidence of a symmetrical or asymmetrical relationship between the perception of space and time (Buets and Walsh, 2009; Cai and Connell, 2016; Martin et al., 2017). Among these studies, evidence has been found both for and against shared neural processes between each dimension.

On a broader scale, areas of the brain such as the prefrontal cortex and the right parietal cortex have been implicated in different types of magnitude processing (Buets and Walsh, 2009) especially in regard to the perception of time and space. Additional studies have provided ample evidence of the role of the right dorsolateral prefrontal cortex, supplementary motor area (SMA), basal ganglia and inferior frontal gyrus as being involved in the estimation and encoding of temporal duration through the use of fMRI (Wiener et al., 2010; Hayashi et al., 2018). Other studies have shown a neural distinction between space and time in which spatial and distance related tasks largely activate more posterior regions including the parahippocampus, anterior hippocampus, and retrosplenial complex (Cona et al., 2019; Gauthier and Wassenhove, 2016; Kim and Maguire, 2018; Peer et al., 2019), whereas time exclusively invokes the SMA (Coull et al., 2015). More recently, a combined meta-analysis of neuroimaging studies of time and space revealed partially overlapping regions of activation likelihood across the SMA, right inferior parietal lobe, and right inferior frontal gyrus, forming gradients from one dimension to another (Cona et al., 2020).

One well-studied neural signal associated with the measurement of temporal intervals is the Contingent Negative Variation (CNV), an event-Related Potential (ERP) component putatively driven by the SMA and corticothalamic circuitry (Nagai et al., 2004). Previous studies on...
the CNV have shown a more negative amplitude pattern during different aspects of temporal processing as well as a variety of timing tasks involving subjective duration estimates. (Macar and Vidal, 2003; Monofort et al., 2000; Pfeuty et al., 2003; Ruchkin, McCalley, and Glaser, 1977). However, other experiments have called to question the specificity of the CNV for time, instead suggesting the CNV may reflect a more general neural signature for different types of magnitude processing (Kononowicz and Penney, 2016; Schlichting, de Jong, and Rijn, 2020). Indeed, the CNV has demonstrated sensitivity to a general sense of expectation, in which the probability of upcoming stimuli occurring in time is encoded (Scheibe et al., 2009; Mento and Vallesi, 2016; Breska and Deoull, 2017; Boet et al., 2020). Expectations would also be critical during navigation, in which a moving agent has to generate expectations about where, and when, things will occur. However, the CNV has not as far as we are aware been investigated in studies of spatial processing or navigation. We further note that the CNV can be decomposed into so-called “initial” and “termination” CNV portions, reflecting increases in amplitude at the beginning and end of the interval (Tecce, 1972) and which only become apparent with longer, supra-second intervals, over sub-second ones (Nagai et al., 2004). Notably, the CNV in particular has previously been associated with attentional and arousal processes in task engagement (Tecce, 1972; Nagai et al., 2004; Fan et al., 2007), as well as time perception (Ng and Penney, 2014; Kononowicz et al., 2018).

One reason for the difficulty in teasing apart temporal and spatial dimensions is the natural correlation of each; longer distances naturally take more time, following time’s arrow (Riemer, 2015). Indeed, previous research has demonstrated that humans have great difficulty attending to spatial information without also considering temporal information (Glasauer et al., 2007; Kolesari and Carlson, 2018; Zach and Brugger, 2008). However, more recent studies utilizing virtual reality (VR) environments have demonstrated that time and space can effectively be decoupled from one another (Petzschner and Glasauer, 2011; Deuk et al., 2016; Wiener et al., 2016; Thurlby and Schild, 2018; Bansal et al., 2019; Robinson et al., 2019). Petzschner and Glasauer had subjects perform a virtual distance reproduction task, in which subjects walked for an unknown distance, and then were required to reproduced that same distance again. To dissociate time, the speed at which subjects walked varied between the initial, distance estimation phase and the subsequent, distance reproduction phase. Additional studies have successfully demonstrated this strategy allows for a “decoupling” of spatial and temporal estimates (Wiener et al., 2016; Kautzky and Thurlby, 2016; Thurlby and Schild, 2018). Previous research using this paradigm has also demonstrated that subject estimates of distance exhibit a central tendency effect, wherein reproduced distances gravitate to the mean of the stimulus set, and so the shortest and longest distances are over and under-estimated, respectively (Petzschner and Glasauer, 2011). This central tendency effect has also been observed frequently in studies of time perception (Shi et al., 2013), and has been characterized as a Bayesian process, wherein the uncertainty in distance reproduction is mitigated by relying on the prior distribution of experienced distances. Whether the priors used exist “globally”, across time and space, or are specific to each dimension, remains unknown, yet should be correlated if they rely on the same underlying process (Petzschner et al., 2015).

The advantage of studying virtual distance reproduction in this way is that it can provide important insights into visual path integration mechanisms (Bremmer and Lappe, 1999; Gramann et al., 2005). Indeed, path integration, in which subjects must incorporate idiothetic information during locomotion, is a critical aspect of navigation and survival (Mittelstaedt and Mittelstaedt, 1986; Klitzky et al., 1990). Previous work has demonstrated that time and distance information are both encoded during visual path integration (Mossio et al., 2008), but that subjects are more accurate at measuring distances (Durgin et al., 2009). Yet, interference while subjects travel different distances disrupts both the sense of time and distance traveled, suggesting shared mechanisms (Glasauer et al., 2007).

In the present study, we sought to disentangle time and space processing during the estimation and reproduction of intervals from each dimension. We employed the virtual distance reproduction task as described above. As a crucial extension, subjects performed separate versions of the task in which they were asked to reproduce either the time, or distance, that they had just walked. Concurrently recorded EEG was used to measure the CNV across encoding and reproduction of both dimensions. By manipulating the speed between estimation and reproduction phases, we could thus scramble the arrival times across all of the tested distances. In this way, we could investigate if the CNV oriented to both the time (regardless of distance) and distance (regardless of time). If the CNV served a cross-domain role, then orienting responses should be observed for both. However, if the CNV is exclusive to time and temporal information, then only an orientation to time should be observed. We found evidence for both general and exclusive properties of the CNV, suggesting a difference in processing modes, depending on the phase of the task.

2. Methods

Subjects: Sixteen subjects (11 females), ages 18–35 years old from George Mason University participated in the study. Informed consent was obtained from all participants prior to the experiment and all protocols were approved by the University Institutional Review Board. All subjects were right-handed, healthy individuals without any history of neurologic or psychiatric illness and normal or corrected-to-normal vision.

Task: Subjects performed temporal and spatial reproduction tasks within a virtual reality environment. The environment for the task was modified from an earlier version employed in our lab (Robinson et al., 2019; Wiener et al., 2016), based on a paradigm devised by Petzschner and Glasauer (2011) and designed using the Python-based software Vizard 5.0 (Worldviz). The VR environment resembled a desert with a textured ground, 20 scattered rocks in the distance, and a clear, sunny sky. The sky was a simulated 3D dome included in Vizard software, a black and white noise image was used to create the ground texture, and a single rock was modified and imported from SketchUp 3D (Trimble Navigation) and replicated within the VR script. The construction of the VR world was such that environmental distance cues were either absent or unreliable: the initial location of the viewpoint and the position and orientation of each of the rocks was randomized at the start of every trial, and the 3D sky was such that the horizon always appeared to be a constant distance away. Participants sat in front of a 32" LCD Monitor (Cambridge Research Systems Display++) running at 120 Hz refresh rate with 1920 × 1080 resolution at a distance of ~70 cm. Participants controlled the movement of the viewpoint with a hand-held gaming controller (Xbox, Microsoft); the eye height of the VR viewpoint was set to the approximate eye height of the participant.

On a given trial, subjects were primed to walk forward, by pressing forward on the controller joystick, towards a red sphere presented on the horizon, constituting the estimation phase of the trial (Fig. 1). Once moving, subjects were stopped after a particular distance had been reached. On spatial reproduction trials, this distance was selected from seven linearly-spaced intervals [4 – 10 m]. On temporal reproduction trials, the distance was determined such that the time needed to reach it varied across seven linearly-spaced intervals [1 – 5 s]. In either case, the speed at which the subject traveled was randomly selected from a uniform distribution between 1 and 3.6 m/s. These speeds were chosen such that the possible range of durations experienced on spatial reproduction trials closely matched those presented in temporal reproduction trials (see Supplementary Materials). After the specified distance was reached, movement of the viewpoint was stopped automatically, the horizon sphere disappeared and the environmental lighting was dimmed. The words “REPRODUCE DISTANCE/TIME” were displayed in the center of the screen. After a delay of 3 s, the words disappeared, and the normal lighting resumed. Participants were allowed to simu-
late walking forward again (reproduction phase) and pushed a button on the controller when they judged they had reproduced the same distance or duration as during the estimation phase. Crucially, the simulated walking speed was randomly altered between the estimation and reproduction phases so that the participant could not use the time spent simulating walking as a measure of the distance traveled in distance trials, or the distance walked as a measure of time traveled in time trials. For each trial, the reproduction phase simulated walking speed was modified such that it was noticeably faster or slower than the production phase speed (maximum ±60% estimation speed, drawn from a normal distribution). Subjects were not informed about the range of distances or times, and were additionally instructed not to count or tap during the task (Rattat and Droit-Volet, 2012).

Following a response, subjects were provided feedback on the accuracy of their reproduction in the form of the horizon sphere, which reappeared either as green (accurate) or red (inaccurate). Accuracy was adaptively determined on each trial by adjusting a feedback constant (k), such that the reproduced interval had to lie within a window [interval/k]; the constant was updated in a 1-up/1-down rule with a step size of 0.015. Separate values of k were measured for time and spatial reproduction tasks, and the initial value for each was 3.5 (Jazayeri and Shadlen, 2010).

**Procedure**: Subjects performed the time and distance reproduction tasks in separate blocks, with 105 trials in each block (15 trials/interval); subjects performed a single block of each task. All subjects additionally performed a practice version of the task beforehand, with 10 trials of the time and distance reproduction tasks, to familiarize themselves with the task requirements. Task order was randomly counterbalanced between subjects. To analyze behavioral data, the average reproduced interval was measured for each task. In addition, we also separately calculated the coefficient of variation (CV) for each tested interval, by dividing the standard deviation of reproduced intervals by the average reproduced interval; for example, the CV for 5 s was calculated by dividing the standard deviation of reproduced times for the 5 s interval, divided by the average reproduced time for 5 s. We additionally calculated the average value of the feedback constant k for each subject. To further analyze reproductions, we calculated the slope and intercept of a simple linear fit to reproduced intervals against the tested intervals (Reproduced Interval = slope * Tested Interval + intercept). The slope can provide an estimate of uncertainty, as a slope closer to 1 represents veridical reproductions, whereas a slope of 0 indicates the reproduction of the same interval across all tested intervals. Lastly, to ensure that the non-attended dimension did not influence responses, we conducted an analysis similar to our previous study (Wiener et al., 2016). Specifically, we conducted non-parametric Spearman partial correlations, for each subject, in which we correlated the change in speed experienced on every trial with the reproduced distance or time, while controlling for presented interval. An increase of speed in the time reproduction task would indicate that subjects would travel a longer distance while reproducing time, whereas in the distance reproduction task this would indicate subjects would travel for a shorter amount of time while reproducing distance. By controlling for the interval subjects were supposed to reproduce, we could examine if the change in the non-attended dimension influenced the reproduced one.

**EEG**: EEG was recorded using an actiCHamp amplifier (Brain Products GmbH, Germany) and a 64-channel actiCAP slim active electrode...
montage (international 10–20 system), with FCz as the online reference and an online bandpass filter of [0.1 – 100 Hz]. BrainVision Recorder (v. 1.20.0801) was used to digitize the EEG at a sampling frequency of 1000 Hz. Electrode impedances were kept below 20 kΩ. Offline filtering was performed using EEGLAB for Matlab. Data were re-referenced to the mastoid channels (TP9, TP10) and down sampled to 500 Hz. A low-pass Hamming windowed since finite impulse response (FIR) filter was applied at 50 Hz. Electrodes with excessive noise were detected using automated methods in the pop_rician function, removed, and interpolated. The continuous EEG data was then decomposed using Infomax Independent Components Analysis (ICA); eye-blinks and other artifact components were visually determined and removed from the data. Continuous data were then epoched into separate sets for the estimation and reproduction phases of the temporal and spatial reproduction tasks, respectively. Estimation and reproduction phases were both time-locked to the initiation of movement, as this was under volitional control of the subject, in segments of [−1 – 5 s].

For the examination of event-related potentials (ERPs) we focused on the CNV signal, as described above. For this, the average of a fronto-central cluster was used, consisting of electrodes [Fz, FC1, Cz, FC2, F1, C1, C2, F2, and FCz] (Wiener and Thompson, 2015). To measure significant differences between ERPs, we used the cluster-based permutation statistic by Mariëls and Oostenveld (2007), as implemented in Fieldtrip, with an alpha level of 0.05, using the maximum sum paired-samples t-tests at each time point.

3. Results

Behavioral: All subjects performed the task without any difficulty. On both tasks, subjects exhibited the classic pattern of central tendency, such that the shortest interval was overestimated, and the longest interval was underestimated (Petzschner et al., 2015) (Fig. 1). Notably, this pattern was shifted slightly on the temporal reproduction task, with a greater propensity to over-estimate durations. Consistent with this finding, we also observed a significantly lower average value of the feedback constant k for the temporal reproduction task ([τ=3.635, p = 0.002, d = 0.91], indicating that the adaptive feedback window was wider for temporal than spatial estimates. However, no significant difference was detected between the slope of reproduced intervals for temporal and spatial reproduction tasks [Paired t-test: τ=0.651, p = 0.525], suggesting that despite the difference in veridicality, the degree of central tendency was the same; further, no correlation between slope values was observed [Pearson r = −0.239, p = 0.374], suggesting that a common mechanism did not underlie central tendency effects observed across both tasks (Martin et al., 2017). Additionally, when analyzing CV values, a repeated measures ANOVA with task (2 levels: duration/distance) and interval (7 levels: each tested duration/distance) as factors detected a main effect of task ([F(1,15)=14.425, p = 0.002, η²p = 0.49] but not interval ([F(1,15)=1.079, p = 0.381] or interaction ([F(1,15)=0.552, p = 0.768]; when collapsing across duration, this effect was shown to be due to a higher CV for the temporal reproduction task ([τ=−3.798, p = 0.002, Cohen’s d = 0.95], indicating that subjects were less precise in their reproductions of temporal than spatial intervals. Finally, in comparing the influence of the non-attended dimension (space or time), we verified that our speed manipulation was successful in mitigating the effect of the secondary dimension on primary task responses (see supplementary figure 1). Specifically, the mean impact of speed changes on distance estimates was [Spearman’s ρho = −0.096 ± 0.05], consistent with our previous study (Wiener et al., 2016). For the impact of speed changes on time estimates, we observed a lower influence [Spearman’s ρho = −0.027 ± 0.037]; indeed, while the impact of each dimension on the other was low, the impact was significantly higher for time-on-distance than distance-on-time ([τ=2.37, p = 0.032], an effect previously noted in similar versions of this task (Thurley and Schild, 2018; Kautzky and Thurley, 2016).

EEG: Our analysis of EEG signatures of temporal and spatial processing began by examining the CNV signal at frontocentral electrodes. For ERPs time-locked to the onset of movement initiation, we initially observed a strong negative deflection 500 ms prior, reflecting the readiness potential (Brunia et al., 2012). Following this, the EEG signal rapidly returned to baseline before again exhibiting a negative peak ~500 ms after movement initiation that was maximal at frontocentral sites (Fig. 2). This deflection matches the iCNV signal. Notably, the iCNV observed here was significantly larger for temporal than spatial reproductions, as determined by a non-parametric cluster test ([340–598 ms] p<0.05). No other significant clusters were detected. Further, no differences were observed during the estimation phase, where both waveforms exhibited similar time courses and amplitudes.

The observance of a difference in the iCNV signal between temporal and spatial reproduction suggests a difference in processing between these tasks; further, the fact that this difference was observed immediately after movement initiation suggests a difference in the orienting of attention to time over spatial ones (Minnussi et al., 1999; Nobre, 2001). However, one alternative possibility may relate to lower accuracy in the temporal reproduction task, which may have driven greater effort (Casini et al., 1999). To explore this difference further, we divided the ERPs by the intervals presented during the estimation phase (duration or distance). Here, we observed a striking dissociation between the iCNV signal between tasks: While the iCNV for spatial estimates remained the same, the amplitude for temporal estimates covaried with the length of the interval that the subject was about to reproduce (Fig. 3). To quantify this effect, we averaged the amplitude within the window identified previously by the cluster test for each subject, and then calculated the slope of a linear regression between mean amplitude and the estimated interval. We observed that the slope of iCNV amplitudes for temporal estimates ([0.68 ± 0.18 s.e.m.]) was significantly different than zero (onestarmer t-test, τ=3.851, p = 0.002), whereas for spatial estimates ([−0.04 ± 0.18]) it was not ([τ=−0.256, p = 0.801]; additionally, the slopes for temporal estimate amplitudes were significantly greater than for spatial estimate amplitudes ([τ=2.625, p = 0.019]. Interestingly, we note that the amplitudes for longer temporal intervals were associated with smaller iCNV amplitudes, a point we return to in the discussion.

The results of the above ERP analysis reveal distinct differences during the reproduction and estimation of temporal intervals. In particular, the pronounced CNV difference between temporal and spatial reproduction tasks, further distinguished by the interval-specific effects, suggest differential processing modes for the reproduction of temporal intervals. However, we note that the ERP comparison may have obfuscated any findings related to spatial, as opposed to temporal intervals. In particular, we note that in the spatial reproduction task the time needed to reach any of the distance intervals was scrambled such that any distance could be reached within a range of possible times matching the distribution used in the temporal reproduction task. As such, the time-course from onset to interval terminus is meaningless for spatial intervals, and although the CNV effects for reproduction all occurred at onset and were not distinct in terms of latency, it is possible that this difference in tasks obscured other effects.

Given the above issues, we conducted two additional analyses. First, for spatial reproduction, we divided the data not by the spatial distance reproduced, but by the time taken to reach that distance. Specifically, for each subject, we generated 7 ERPs by dividing trials according to the time taken to reach each distance into 7 equally-spaced bins. From each bin, we averaged the iCNV signal within the same window as before. Notably, the distributions of reproduced times did not differ between the time or space reproduction tasks, indicating that the iCNV difference observed was not likely driven by a propensity of shorter durations in the time task (supplementary figure 2). Further, no significant difference was observed for iCNV amplitudes across the 7 bins ([F(6,90) = 1.262, p = 0.283], suggesting the iCNV effects observed in the temporal task condition were not driven by preparatory responses, nor was the lack

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Fig. 2. Grand-average ERPs from frontocentral electrodes time-locked to the initiation of movement in the estimation (A) and reproduction (B) phase. A negative deflection was observed ~500 ms following movement, putatively reflecting the CNV, that was significantly larger on the temporal reproduction task, only during reproduction and not estimation; the gray bar reflects significance as determined by a non-parametric cluster test at \( p < 0.05 \). Inset presents topographic maps within the significant window, demonstrating a larger frontocentral negativity for time. Shaded regions represent standard error.

Fig. 3. Temporal estimates change the amplitude of initial CNV. Grand average ERPs from Fig. 2 are presented here based on the distance (A) or duration (B) about to be reproduced. For time reproduction, faded EEG traces represent the portion of the interval from beyond when the interval ended, on average. Middle panels present the mean CNV amplitude, averaged from gray bar regions in left panels. While the CNV does not differ strongly for spatial estimates, there is a linear gradient response for the CNV amplitude in temporal reproduction (bottom panel), with longer estimates associated with a lower amplitude, that is not observed on the space task. Orange lines depict a simple linear fit. Insets depict scalp distribution of average slope values, with the highest slope values in a frontocentral region during the time task. Right panel displays a scatterplot of slope values for each task and subject; dashed line indicates identity, orange line a simple linear fit. Error bars represent standard error.
of an effect in the spatial task (supplementary figure 2). Second, we generated a new set of ERPs, instead time-locking to the point where subjects completed the interval – either the offset during the estimation phase, or the response in the reproduction phase – so as to align each time-course to the moment when subjects completed either interval. All timeseries were mean centered, as the baseline portion was of interest (Wiener and Thompson, 2015). For the reproduction phase, we observed in both tasks a gradual negative buildup prior to the response. This signal corresponds to the so-called “late” or terminal CNV (tCNV), which underlies response preparation and anticipatory responses (Brunia et al., 2012). Notably, no differences were observed between tasks in this signal, as assessed by a cluster-based permutation test. Similarly, in the estimation phase we also observed a tCNV buildup prior to the offset, with no significant differences between tasks. However, when further separating these epochs by duration, we found a noticeable difference between estimation and reproduction phases: While in reproduction no differences were observed as a function of interval in either task, in the estimation phase we observed that the CNV prior to offset varied by the interval presented for both tasks. Here, the CNV exhibited a negative peak shift, such that the peak occurred earlier in time for longer intervals in both space and time that was also lower in amplitude (Fig. 4A).
To quantify these effects, we conducted an ERP peak analysis, using routines provided by Liesefeld (2018). Briefly, individual subject average ERPs for each interval and task were scanned for the largest negative peak deflection (100 ms peak width) in the pre-onset/response window, from which the latency and amplitude were calculated. For the estimation phase, a repeated measures ANOVA on peak latencies with task and interval as within-subject factors found a linear main effect of interval \([F(1,14)=8.277, p = 0.012, \eta^2_p = 0.372]\) and a task by interval interaction \([F(1,14)=16.39, p = 0.001, \eta^2_p = 0.539]\), but no effect of task \([F(1,14)=0.444, p = 0.516]\), characterized by a linear general dispersion of peak latencies in the duration task. Similarly, for peak amplitude, a linear effect of interval \([F(1,14)=11.844, p = 0.004, \eta^2_p = 0.458]\) and task by interval interaction \([F(1,14)=5.509, p = 0.034, \eta^2_p = 0.282]\), but no effect of task \([F(1,14)=1.606, p = 0.226]\) was observed in which peak amplitudes decreased with increasing interval magnitude and a larger difference for time than for space reproduction. For the reproduction phase, no significant effects were observed for peak latency or amplitude across any interval or task (all \(p > 0.05\)).

We additionally noted that, for the estimation phase of the time task, the alignment of peaks may not have entirely included EEG portions from within the interval, as our analysis included the entire period pre-offset. In particular, we noted that the average peak for the 1 s interval occurred before the interval even began. To address this, we conducted a second peak latency analysis for the time estimation task phase, including only the EEG data from within the interval. Here, we observed no major differences between the peaks detected using either portion, except for the 1 s interval (supplementary figure 3), which now reliably shifted to when the subject was estimating it. We further observed that the peaks themselves were linearly shifted away from their respective onset times, with a progressively later peak from onset for longer intervals \([F(1,15) = 4.284, p < 0.001, \eta^2_p = 0.733]\), a finding similar to that observed in another timing task (Wiener and Thompson, 2015).

4. Discussion

In the present study, subjects completed a temporal and spatial reproduction task within a virtual reality environment, presented on a desktop computer screen. In this study, we analyzed EEG signatures first by examining the CNV at frontocentral electrodes and found a strong negative deflection prior to the onset of movement, followed by a strong negative deflection after movement initiation. The initial negative deflection, or iCNV, which has been associated with time perception, attention and arousal during task engagement, was significantly larger for temporal reproduction than spatial reproduction. As previously noted, the temporal and spatial reproduction tasks exhibited a difference in the iCNV signal, specifically at the start of the reproduction phase of each trial, suggesting that subjects needed to orient their attention to temporal over spatial features. (Liu et al., 2013; Taatgen et al., 2007).

Critically, there was a dissociation within the iCNV signal between tasks where the amplitude for temporal estimates covaried with the length of the interval the subject was planning on reproducing, while no difference in the iCNV for spatial estimates was observed. A central framework of timing continues to be the pacemaker-accumulator model in which the brain contains a pacemaker whose pulses are integrated by an accumulator to process measures of time (Allman et al., 2014). Included within this theory is the notion of climbing of neural activity over time that is associated with the SMA and is indexed by the CNV (Coulil et al., 2016). Notably, our results are in contrast to the assumptions of climbing neural activity, where the accumulation of temporal information should be directly related to a larger increase in CNV amplitude. Instead, our results point to a scaling of the CNV signal for both space and time. While these findings may seem counterintuitive, they accord with recent electrophysiological recordings from rodents (Matell et al., 2011), monkeys (Renoult et al., 2006; Lebedev et al., 2008; Jazayeri and Shadlen, 2015) and a single study in humans (Pfeuty et al., 2019) demonstrating that firing rates scale to match the temporal inter-

val. Further, a recently developed firing-rate theory of time perception posits that an accumulation regime can be characterized as opponent firing rate processes between neuronal populations that also scale to the temporal estimate (Simen et al., 2011). Consistent with this theory, recent work has shown that, at the onset of a reproduction interval, the amplitude of population firing (Jazayeri and Shadlen, 2015), as well as the overall dynamic configuration of that network (Wang et al., 2018; Remington et al., 2018), vary with the length of the interval. Indeed, our own findings of iCNV amplitude scaling support this “pre-planning” hypothesis, in which the to-be-reproduced interval is set in advance.

Yet, while the reproduction phase CNV signal demonstrated clear dissociations between tasks, the estimation phase CNV did not. Indeed, here we observed that the CNV signal again scaled with the measured interval, such that the peak in amplitude was linearly shifted earlier in time from the interval offset, regardless of time or distance. Importantly, subjects were not aware of the interval they were measuring on any given trial. This finding accords with recent work on anticipation, in which the probability of the interval offset grows with the elapsed interval, mathematically expressed as a hazard ratio (Nobre et al., 2007). Previous work has demonstrated that the CNV signal is sensitive to the probability of upcoming events and can be an index of hazard rate (Scheibe et al., 2009; Mento and Vallesi, 2016; Breska and Deoull, 2017; Boetcher et al., 2020). However, all of these studies have shifted upcoming events in time; in our present study, we found that the CNV can also account for the elapsed distance as well. Crucially, as time was scrambled across possible distances by randomly varying the speed gain, the CNV estimates of distance probability cannot be accounted for simply by elapsed time. This finding suggests that the CNV can account for both elapsed distance and time, and for space specifically indexes the probable distance to the target.

These finding suggests the CNV signal can index both time and space, two critical components for path integration (Glaser et al., 2007). Yet, why are distance estimates not also pre-planned? While it remains possible that a pre-planning signal for distance exists, but was not observed in the present study, an alternative possibility is that pre-planning was not crucially necessary for distance reproduction. Indeed, path integration mechanisms may critically rely on accumulating information retroactively from optic flow regions (Chrstal et al., 2019; Zajac et al., 2019). However, when landmarks, even distal ones, are present, the brain may utilize these for prospectively orienting to the goal location (Brown et al., 2016; Ekstrom et al., 2017). It is also crucial to note that while the current paradigm included a change in speed that may have discouraged the subject from planning, we cannot rule of the possibility that our CNV results reflected an inability vs ability to plan as opposed to time vs space. We hope that the results presented here will provide a framework for further research to help address this critical question. Given this alteration, we suggest that, if subjects are given an indicator of where they must travel to in advance, either via a landmark or a remembered location, then the CNV would likely show an orientation to the appropriate distance.

Furthermore, our results suggest an asymmetric and possible disentangled relationship between the perception of spatial and temporal information in that measuring intervals of time and space require different attentional processes and therefore, rely on separate neural systems (Brunet et al., 2017; Jafarpour and Spiers, 2017; Robinson et al., 2019). Yet, we note that a large aspect of the distance reproduction task that we employed here relied on estimates of optic flow from the observer. That is, in the absence of available landmarks for navigation, subjects had to rely to some degree on the rate of visual change while moving forward. Optic flow has previously been demonstrated to impact duration estimates (Seno et al., 2011). Yet, due to the speed manipulation in the present experiment, optic flow would provide an unreliable estimate of duration; as such, it is possible that subjects actively suppressed visual information during time estimation and reproduction, driving the observed CNV effects. Yet, if subjects were actively suppressing distance (or optic flow) on time trials, this would not explain the covarying ef-
fect of the CNV at reproduction onset with the duration of the to-be-reproduced duration, nor would it explain the parametric increase in CNV amplitude and shift in CNV peak latency as subjects approached the likely distances during the estimation phase.

Regarding further neural mechanisms for the observed effects, it is certain that the CNV signals represent a network of activation across various regions (Nagai et al., 2004), including motor and premotor regions, as well as subcortical structures within the basal ganglia. We further suggest, in the context of the present task that navigation-related regions are also likely engaged. Indeed, we have previously demonstrated that the retrosplenial cortex and hippocampus, two critical regions for navigation, are both engaged in the distance reproduction task employed here (Wiener et al., 2016). Recent work has focused on the interdependence of time and space processing (Cona et al., 2020; Issa et al., 2020), with particular attention to so-called “time cells” within the hippocampus (MacDonald et al., 2011). The integration of temporal and spatial information further provides a unifying account of the encoding of experience, in which multiple networks serve to integrate experience (Tao et al., 2018).

As a limitation to the present study, we note that the task as designed only addresses distance reproduction along a single, straight axis. This was chosen to adhere to previous implementations of this task (Wiener et al., 2016; Petzschner and Gläsauer, 2011), and to further dissociate time and distance within a single design. As an extension to this task, alternative paths along different shapes could be explored, to see how alterations might shape the perception of time or distance. Recent work has demonstrated that turns along a path increase the perceived duration of that path (Brunec et al., 2020), whereas routes that require circumnavigation shorten the perceived path duration while increasing perceived path length (Brunec et al., 2017), whether such effects depend on the shape and trajectory of the path could further be explored using path deviations in the present task. Indeed, path navigation studies have frequently employed triangle-completion, in which a subject must indicate a homing vector to return to a starting point, or circular paths in which they must indicate if they traveled back to the same location (Wolbers et al., 2007; Arnold et al., 2014; Chrastil et al., 2015). A natural extension would be to test if subjects also integrate the time necessary to return to the starting location.

An additional qualifier to the task used here is that 1) the task was tested in a blocked design, and 2) it relied on virtual, rather than actual, movement. To the former, the observed lack of a correlation between central tendency measures for each task could be due to a shifting of strategy from one block to another, as subjects were aware of that every trial in a given block would be of the same task type (distance or duration reproduction); had the task varied from trial-to-trial, correlated performance may have been observed. Yet, central tendency measures for other tasks, such as distance reproduction and angular rotation, do exhibit correlations between blocks (Petzschner and Gläsauer, 2011). To the latter, marked differences exist between virtual and real-world navigation, especially with regards to idiothetic cues that may be crucial to path integration (Taubé et al., 2013). Indeed, hippocampal activity in mice exhibits distinct differences between virtual and real-world navigation (Chen et al., 2018). However, in humans, recent work has also suggested that spatial memory is independent of the modality, virtual or real, in which it was acquired (Huffman and Ekstrom, 2019), and so the present findings may carry over to real-world settings.

Overall, our findings demonstrate both specialized and generalized properties within the CNV signal during distance reproduction. Under this framework, the CNV generally indexes the probability of upcoming spatial and temporal intervals, but specifically the planning of reproduced times. These results broadly support separate yet overlapping processing regimes for time and space, with distinct networks and operating modes for each stimulus dimension. Further, they accord with recent work demonstrating that time and space exist along a gradient similarity representation across several brain regions (Cona et al., 2020), wherein time and distance are both integrated during navigation. In a larger context, the question of whether temporal and spatial intervals are calculated conjointly or separately is at the heart of how humans navigate, and so our study can provide possible insights into those computations. In a more practical sense, interdependent computations may explain why faster driving speeds are associated with longer intervals of time (van Rijn, 2014), or that time intervals while driving through complex environments appear longer (Leiser and Stern, 1988; Baldauf et al., 2009). Altogether, our work supports time/space interdependence during an aspect of visual path integration, suggesting time is a critical feature of navigation (Gläsauer et al., 2007).

Declaration of Competing Interest

The authors declare no competing financial interests.

Credit author statement

MW and EMR designed the research, programmed the task, conducted analyses of behavioral and electrophysiological data, and wrote and edited the manuscript. EMR tested all subjects and collected behavioral and EEG data.

Supplementary materials

Supplementary material associated with this article can be found in the online version, at doi:10.1016/j.neuroimage.2020.117607.

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