Abstracting time in memory

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Abstract

Planning the future relies on the ability to remember how long events last, yet, how durations are stored in memory is unknown. Here, we developed a novel *n-item delayed duration reproduction task* to assess whether elapsed time is stored as a continuous feature or as a discrete item in memory. In three experiments (N = 58), participants listened to non-rhythmic sequences composed of empty time intervals (durations), which they had to reproduce as precisely as possible following a delay period. We manipulated the number of time intervals (n-item) and the overall sequence duration to separate their effects on recall precision. In Experiment 1, the number of items and the sequence duration affected the precision of temporal reproduction (recall). In Experiment 2, orthogonalizing the number of items and the duration of the sequence, demonstrated that the *precision* of temporal reproduction systematically decreased with an increasing number of items, but not with sequence duration. Experiment 3 confirmed the decrease in precision with a larger number of items. Altogether, our results suggest that durations can be compressed and itemized in working memory.

Keywords: time perception, duration, sequence, precision, symbolic

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Statement of Relevance

The temporary storage of information in working memory is central to theoretical models of consciousness, and holds a foundational status in all subfields of psychology and neuroscience including timing and memory. Coding and temporarily storing the durations of episodic experiences are vital to prediction and foresight, yet, the status of duration storage in memory is currently unknown.

Herein, we investigate the format in which durations may temporarily be stored, contrasting a continuous to a discrete coding hypothesis. Our findings suggest that the number of time intervals, not their duration *per se*, determines recall precision, commonly taken as a measure of working memory load. Our work provides a novel empirical approach for tackling the issue of the nature of representation for duration in support for the lack of isomorphism between the cognitive representation of duration and clock duration.

1. Introduction

The estimation of duration involves attention and memory: attention regulates the perceived flow of events, and memory maintains the access to stored events. Empirical evidence has shown that in the range of seconds to minutes, which constitute the phenomenological present, paying attention to time significantly lengthens perceived duration, while diverting attention away from time shortens it (Brown, 1985; Fortin & Schweickert, 2016; Polti et al., 2018). Whereas the relation between attention and timing has received ample consideration (Nobre & Coull, 2010), the systematic link between time and memory remains less studied. Seminal models of duration perception (Buhusi & Meck, 2005; Gibbon, 1977; Gibbon et al., 1984; Treisman, 1963) include a working memory component, posited to enable the comparison between just encoded durations, and stored durations in long-term memory. Yet, neither time perception models, nor time memory models (Friedman, 1993) provide clear predictions as to the representation of duration in memory.

The representation of a duration as a quantity, detached from the spatial, temporal, and sensory contingencies initially constraining the coding of elapsing time would constitute an discrete or symbolic form of duration storage (Gallistel & Gelman, 2000; Gallistel & King 2011; van Wassenhove, 2009). A discrete representation of duration is not coded in real time, nor grounded in the sensory evidence or internal dynamics that marked the initial duration, but instantiated as a mental magnitude which has no direct temporal attributes (Gallistel & Gelman, 2000; Martin et al. 2017; Walsh, 2003).

Discrete representations of duration are not explicitly accounted for by current timing models, like state-dependent networks (Paton & Buonomano, 2018). In state-dependent networks, latent variables, proposed to operate silently in working memory (Stokes, 2015), capture the dimensions of a neural population code. The hidden states of a neuronal network affect the trajectories a neural population can take in response to inputs: the network dynamics are thus constitutive of a latent representation of the temporal pattern of the inputs (Wang et al. 2018). In humans, using a task requiring the self-generation of a duration, showed that latent variables in a state-dependent network pre-determine the network trajectories and constitute the basis for a metacognitive readout (Kononowicz et al, 2018). Hence, state-dependent networks can instantiate a latent representation of duration in real time, but the specification of a readout mechanism is necessary to explain how the network dynamics can be abstracted to form an explicit representation of duration (van Wassenhove, 2009; Zhou et al 2020; Cueva et al. 2020).

Herein, we set out to explore the behavioural consequences of positing a continuous representation of duration (e.g. the trajectory of a state-dependent network) versus a discrete code (e.g. a symbol) for duration in working memory. For this, we designed a set of experiments testing whether working memory for duration follows the same principles as working memory for sensory events. Working memory is classically defined as a limited resources system dedicated to the temporary storage and manipulation of information during complex cognitive tasks (Cowan, 2001; Miller, 1956). While working memory has long been regarded as a temporary store with a fixed number of slots to which information can be allocated, recent work has proposed flexible resource allocation without a fixed item limit (Ma et al., 2014). According to these recent models, memory precision decreases when more items need to be retained, but there is no fixed upper limit for the number of items to be memorized. In support of this assumption, previous studies used parametric measures of recall to evaluate working memory capacity, such as choosing the color of a visual item or the frequency of an auditory tone on a scale, rather than a binary measurement like judging whether an item had been presented before (Bays and Husain, 2008; Kumar et al., 2013; Ma et al., 2014). The results of these studies show that recall precision decreases with working memory load, i.e. the number of items, and thus serves as a means to measure working memory capacity.

By analogy, we developed two working hypotheses for the representation of durations in working memory, using recall precision as an index for memory load. Under the *continuous coding hypothesis*, the longer the total duration to be maintained, the larger the memory load, and the lower recall precision is predicted to be. Under the *discrete coding hypothesis*, the number of duration items, not their magnitude, should impact working memory load and thus reduce recall precision. To compare these two working hypotheses, we developed a novel paradigm using sequences of durations, which varied along two dimensions: the total duration of the sequence and the number of duration items in the sequence. To illustrate this, let's imagine two sequences composed of two durations: A is a 5 s long sequence composed of a 2 s and a 3 s time interval, and B a 7 s long sequence composed of a 3 s and a 4 s time interval. Under the *continuous coding hypothesis*, the recall precision for the 3 s item should be more precise in A as compared to B, because the short sequence A (5s) should take up less working memory load than the long sequence B (7s). Under the *discrete coding hypothesis*, the recall precision of an item depends on the number of items in the sequence, not on the overall duration of the sequence. Thus, the recall precision for 3 s should be comparable across sequences A and B.

A number of previous studies tested for factors that affect the precision of working memory for durations and reported working memory interferences with the number of duration items in a sequence, but none directly compared the effect of duration and number of items. Fraisse (1942) observed that the variability of duration reproductions in a rhythmic context depended on the number of intervals. Teki & Griffiths (2014) found a decrease in recall precision with decreasing rhythmicity, as well as with the number of items (up to four). The effect of the number of items was found only for sub-second items, and was not replicated in a second study (Teki & Griffiths, 2016). Manohar & Husain (2016) consistently found a decrease in recall precision with the number of items (up to five); the authors also reported primacy and recency effects, in one out of three experiments. In a study using a match-to-sample task, increasing the number of items was found to decrease participants' accuracy (Chen & Huang, 2016). Fan and Yotsumoto (2018) found a decrease in recognition performance with higher working memory load for visual and temporal items (up to three), and reported similarity effects for temporal items so that items closer in duration interfere and provoke false memory reports. Finally, Yarrow et al. (2020) found evidence for a shared storage of the duration of visual and auditory filled durations (up to eight), which favors an abstract code. In sum, although the reported effects of the number of items on recall precision and recognition align well with the discrete coding hypothesis, existing reports are very heterogeneous in their measurement of working memory load, and no study has yet systematically contrasted the effects of sequence duration and number of duration items on recall precision.

In this context, we designed a set of three behavioural experiments using a novel *n-item delayed reproduction task*: participants listened to a sequence of empty durations delimited by short tones and, as in a serial recall procedure, had to reproduce the sequences as precisely as possible. To dissociate the continuous vs. discrete coding hypotheses, the number of items and the duration of the sequences were varied, and we measured the precision of recall. The design allowed comparing the recall precision between single items and items embedded in a sequence. We hypothesized that a decrease in precision as a function of sequence duration would support the continuous coding hypothesis, while a decrease in precision as a function of the number of items would favor discrete coding of duration items in working memory.

It is important to clarify the measure of precision, which varies across studies: visual working memory studies quantified precision as the standard deviation of the reproduction errors (see also Luck & Vogel, 2013, Gorgoraptis et al., 2011, but see also Teki et al. 2014), a measure which is independent from accuracy. An observer with a consistent bias would show

highly precise reproductions yet could be off the true value. Similarly, here, we quantified precision separately from accuracy to measure the variability of duration reproductions, that is the capacity of an observer to reproduce durations reliably. Furthermore, in the case of timing, we needed to account for scalar variability (Gibbon, 1977), namely the scaling of variance with the mean. In contrast to the timing studies cited above, the larger range of durations we chose to test (0.3 – 4.5 s) made this correction crucial. Therefore, we divided the reproduced duration by the target duration before computing the standard deviation across reproductions.

2. Methods

2.1. Data and Code Availability

Upon acceptance for publication, the analysis code and anonymized data for all experiments will be made publicly available with a link included in the final version of the paper. The studies were not pre-registered.

2.2. Participants

58 participants took part in three behavioural experiments (Experiment 1: 22 participants, mean age = 23.0 y.o. (SD = 4.2), 1 left-handed, 10 females, 11 males; Experiment 2: 14 participants, mean age = 30.1 y.o. (SD = 7), 1 left-handed, 6 females, 8 males; Experiment 3: 22 participants, mean age = 23.7 y.o. (SD = 4.9), 3 left-handed, 14 females, 5 males). Sample sizes were chosen for convenience, and because they match those from previous studies.

To detect outliers, we calculated the correlation between participants' reproductions and the items to reproduce: participants with a correlation below 0.6 were excluded from the analyses (one participant in Experiment 1 ($r = 0.52$) and three participants in Experiment 3 ($r = 0.54, 0.50, 0.05$)). Hence, a total of 54 participants were analyzed. Participants had normal hearing and no history of audiological or neurological disorders. Participants were naive as to the purpose of the study and received monetary compensation for their participation. Prior to the study, all participants signed a written informed consent in accordance with the Ethics Committee on Human Research at Neurospin: CPP n° 100049 (Gif-sur-Yvette, France) and the Declaration of Helsinki (2013).

2.3. Stimuli

All stimuli were created digitally using Psychtoolbox (Brainard, 1997) under MATLAB (2017a, The Mathworks), at a sampling rate of 44.1 kHz, played with a 16-bit resolution soundcard. Acoustic tone sequences were played via the speakers of the computer at a comfortable loudness, fixed for all participants. Testing took place in a sound-proof room.

Stimuli consisted of a sequence of pure tones (1 kHz, 50 ms duration including 10 ms onset and offset ramping), which demarcated empty time intervals (thereafter referred to as “items”). Items varied from 0.3 s to 4.5 s duration across all three experiments, resulting in irregular (non-rhythmic) sequences. The number of items composing an acoustic sequence varied from 1 to 3 in Experiments 1 and 2, and 1 to 5 in Experiment 3. The total duration of the sequence varied from 0.3 s to 6.35 s (Table 1 and Figure 1). The order of items within each n-item sequence was randomized within each experiment.

Since it was not possible to orthogonalize the number of items, the item duration, and the sequence duration in one experiment, we systematically varied those factors across experiments. In Experiment 1, a set of fixed durations was assigned to sequences of variable lengths, which resulted in sequences with more items lasting longer. In Experiments 2 and 3, we orthogonalized the number of items and the duration of the sequences, resulting in a fixed sequence duration regardless of the number of items, but shorter individual items in sequences with more items (Figure 1B).

2.4. General Procedure (all Experiments)

In all experiments, one trial comprised four successive phases: encoding, retention, reproduction, and feedback (Fig. 1A). We refer to this experimental design as an *n-item delayed temporal reproduction* task. During encoding, a red fixation dot was displayed on the center of the screen and participants listened to a sequence of tones demarcating time intervals of different durations (e.g. three tones demarcating two duration items), while. The durations are typically referred to as “empty intervals” in timing research; herein, we call them “item” or “duration item”. Following the encoding period, and 500 ms after the last tone in the sequence, an orange fixation

dot signalled the onset of the retention period (3.5 s in Experiment 1 and 2, and 4.5 s in Experiment 3). Following the retention period, a green fixation dot prompted participants to reproduce the full sequence using the spacebar of their keyboard. Participants had unlimited time to initiate their reproduction, and no sound was played when they pressed the spacebar.

	# Items	Item duration (ms)	Sequence duration (ms)
Exp. 1	1	300, 450, 633, 675, 950, 1337, 1425, 2006, 3008	300, 450, 633, 675, 950, 1337, 1425, 2006, 3008
	2	[300; 450], [300;675], [450;675], [633; 950], [633; 1425], [950;1425], [1337; 2006], [1337; 3008], [2006; 3008]	750, 975, 1125, 1583, 2058, 2375, 3343, 4345, 5014
	3	[300; 450; 675], [633; 950; 1425], [1337; 2006; 3008]	1425, 3008, 6351
Exp. 2	1	2000, 3000, 4500	2000, 3000, 4500
	2	[666; 1333], [1000; 2000], [1500; 3000]	2000, 3000, 4500
	3	[444; 666; 888], [666; 1000; 1333], [1000; 1500; 2000]	2000, 3000, 4500
Exp. 3	1	1882, 4500	1882, 4500
	2	[1800; 2700]	4500
	3	[947; 1421; 2132]	4500
	4	[554; 831; 1246; 1869]	4500
	5	[341; 512; 768; 1152; 1727]	4500

Table 1 : Stimuli sets used in all three experiments. Sequences were composed of up to five time intervals, which we refer to as *items*. The number of items co-varied with the sequence duration (Exp. 1) or was orthogonalized to the sequence duration (Exp. 2 and Exp. 3)

To reproduce the sequence, participants pressed the key as many times as there were tones in the sequence (e.g. 3 key presses for 2 items demarcated by 3 tones), trying to reproduce each item as precisely as possible. Visual feedback was displayed on the screen 500 ms after the last button press, lasting for 1 s, and followed

by a variable inter-trial interval sampled from a uniform distribution ranging from 2 s to 3 s. The feedback indicated the performance for each item in the sequence, presented as a vertical bar, whose height represented the relative temporal reproduction error for the item, and whose direction (up/down) indicated whether the item was under- or over-estimated. The relative temporal reproduction error was computed as:

$$\text{relative temporal reproduction error} = \frac{(\text{item reproduction} - \text{item duration})}{\text{item duration}}$$

The more positive the relative temporal reproduction error, the more participants overestimated the duration of the item; the more negative the relative temporal reproduction error, the more participants underestimated the duration of the item.

Experiment 1 and Experiment 2 consisted of 6 blocks of 54 trials each; each block lasted ~13 minutes. Experiment 3 consisted of 7 blocks of 36 trials each, and each block lasted ~10 minutes. Participants could take a break between blocks if they wanted to. Each experiment lasted overall ~90 minutes. Before the main experiment, the researcher explained the task to the participants, and provided them with written instructions. Participants could then start a training block composed of eight trials. The training was repeated if a participant failed on more than half of the trials with a failed trial defined as an average relative temporal reproduction error over all items in the sequence below - 0.5 or above + 0.5. Data from the training session were not included in the analyses. Participants were monitored during the training to ensure that the task was understood. Once a participant passed the training block, the experiment started and the experimenter left the soundproof room.

2.5. Specific designs of individual experiments

Experiment 1: In Experiment 1 (Fig. 1A), we asked whether both the number of items and the duration of the sequence increased working memory load. To this end, we created sequences with one item (e.g. 1.3 s) that served as a reference, and manipulated the number of items by combining these to sequences of variable length (e.g. 1.3 s and 2s for the 2-item sequence). By doing so, we could measure the precision of reproduction for a single item (in our example, 1.3 s) as a function of the number of items in a sequence. In addition to manipulating the number of items, this

time interval was played in sequences of varying durations resulting from combining several items. For instance, the 1.3 s item was played in a 1.3 s, 3.3 s, 4.3 s, and 6.4 s sequence duration. Hence, we could measure the precision of temporal reproduction of the 1.3 s item as a function of the full sequence duration it was embedded in, as well as the number of items to be retained concurrently. If the number of items or the sequence duration increased working memory load, the precision of reproduction should decrease parametrically with increasing number or with sequence duration. In this design, the number of items and the full sequence duration covaried.

Experiment 2: In Experiment 2 (Fig. 1B), the number of items and the duration of the sequence were orthogonalized. Three sequence durations were tested (2 s, 3 s and 4.5 s) and the number of duration items was 1, 2 or 3 for each sequence. With this design, we could measure the precision of temporal reproduction as a function of the number of items and, independently, of the full sequence duration. Again, we could test whether: (i) the precision of reproduction decreased parametrically with an increasing number of items, and (ii) with sequence duration, which were orthogonal factors in this experiment.

Experiment 3: In Experiment 3 (Fig. 1C), we extended our experimental approach to sequences of up to 5 items. This time, the sequence duration was kept identical at 4.5 s (single items of 1.9 s duration had originally been added, but were not included in the analysis) while the number of items composing the sequence varied. We could thus measure the precision of temporal reproduction as a function of the number of items ranging from 1 to 5. We expected a parametric decrease of precision with an increasing number of items.

Item position: In Experiment 1 and 2, the position of each item was counterbalanced, such that each item in a sequence appeared equally frequently in the 1st, 2nd and 3rd position. In Experiment 3, too many trials would have been required to counterbalance the position of each possible item but we ensured that within each block of 36 trials, each item was played at least once in every possible position (1st to 5th). This manipulation allowed assessing the effect of item position on precision.

A) Experiment 1

B) Experiment 2

C) Experiment 3

D) Example Trial

Figure 1: n-item delayed reproduction task. Panels A–C depict the individual items and sequences used in Experiment 1, 2, and 3, respectively. Black dots represent 1 kHz tones. All numbers are durations in seconds. (A) The set of sequences used in Experiment 1, in which the number of items in a sequence and the full sequence duration covaried. A sequence was composed of 1, 2 or 3 items, and its duration varied from 0.3 s to 6.3 s. (B) In Experiment 2, the number of items and the sequence duration were orthogonalized. A sequence was composed of 1, 2 or 3 items with sequence duration fixed to 2 s, 3 s, or 4.5 s irrespective of the number of items composing it. (C) In Experiment 3, a sequence was composed of 1 to 5 items. Only two sequence durations were used (1.9 s and 4.5 s). (D) Example trial. In all experiments, each trial was composed of four phases: First, participants listened to a sequence of pure tones demarcating time intervals of varying duration. Following a retention interval, participants were asked to reproduce the temporal sequence as precisely as possible. In the example depicted here, the sequence was composed of two items. Following the reproduction (green), feedback was provided showing the relative temporal reproduction error for each item in the sequence.

2.6. Statistical analyses

All analyses were conducted using R (R Core Team, 2019). We collected the reproduced duration per item as the time elapsed between the two key presses. Trials in which participants had pressed a button during the retention interval were labelled as errors and removed. Then, we removed the single item reproduction outliers defined as reproductions that exceeded 3 standard deviations above or below a participant's mean reproduction. This procedure resulted in the removal of 0.69 % (SD = 0.34), 0.62% (SD = 0.47), and 1.7% (SD = 0.54) of all items in Experiments 1, 2, and 3, respectively.

We quantified the relative temporal reproduction per item as: $relative\ reproduction = \frac{item\ reproduction}{item\ duration}$. The use of *relative* reproduction enabled the aggregation of temporal reproductions across items irrespective of their duration, despite the large range of durations used. As a measure of *recall precision*, we assessed the standard deviation (SD) of relative reproductions for single items, computed per participant over bins per number of items, sequence duration, and item position in the sequence. As a measure of accuracy, we computed the *mean* of the relative reproductions in the same bins.

We chose not to aggregate the measures within a sequence of several items to control for motor noise: in a 3-item sequence, participants pressed the key four times during reproduction whereas in a 1-item sequence, participants pressed the key only twice. The aggregated reproduction of a 3-item sequence would *a priori* yield more motor noise than the reproduction of a 1-item sequence, which is why we chose to compute SD and mean at the item level.

All statistical analyses were performed using the values of SDs, but in the subsequent text, as well as in the figures, we will refer to 'precision' as the inverse of the relative SD: $precision = \frac{1}{SD(relative\ reproduction)}$. Our precision index differs from previous work (Teki & Griffiths, 2014) in which it was computed as a function of timing errors, allowing us to conserve the directionality of the estimation, that is under- or over-estimation of the item.

We carried out parallel statistical analyses for all Experiments: first, we assessed the recall precision for single items only as a function of item duration, to test whether the scalar variability was met at the single item level (Figure 2, Table 2). Scalar entails that the variance of a given estimate is proportional to its mean, a hall-mark feature of interval timing.

Second, and only for Experiments 1 and 2, we computed a 2-way ANOVA on single item SDs (using R's `aov` function), with the factors **number of items** (categorical) and **sequence duration** (continuous), plus their interaction (Figures 3, 4, Table 3). The error terms were specified for all factors, and allowed to vary per participant. For Experiment 3, we computed a 1-way ANOVA with a single factor, **number of items**, and for the 4.5 s sequences only (Figure 5, Table 3).

Using all items together, there were proportionally more items in the 3-item sequences than in the 1-item sequences (*i.e.*, three times as many). To confirm that the effects were not due to such imbalances, we performed the same ANOVA on the first item of each sequence, and the last item of each sequence separately (supplementary Tables 1, 2). For single item sequences, the single item was used, both as first and last item.

Third, for all experiments, we assessed the position effects on precision for sequences with more than one item, using a 1-way ANOVA per n-item sequence with the factor position (*e.g.* first, middle, last for a three-item sequence). In addition, for all three experiments, we computed the main ANOVA (factors: n-item, sequence duration) using mean or standard deviation of the relative reproductions as dependent variables (Figure 6, Table 4).

The effect sizes of all ANOVAs were measured by eta-squared (η^2); the effect sizes of t-tests were measured by Cohen's *d*. According to (Cohen, 2009), η^2 s of .01, .06, and .14 and Cohen's *ds* of 0.20, 0.50, and 0.80 are considered small, medium, and large, respectively. Statistical results for all experiments are summarized in Tables 2 – 5.

Originally, we had planned to measure the precision of temporal reproductions by computing the coefficient of variation: $CV = \frac{SD(\text{relative reproduction})}{\text{mean}(\text{relative reproduction})}$, which provides an index of the variability in memory representation around its true value, and is

commonly used to quantify timing performance. However, we observed a strong central tendency effect in the reproductions, namely that longer intervals were underestimated, commonly observed in interval timing (“Vierordt’s law”; Vierordt, 1868; see also Lejeune & Wearden, 2009). This is problematic, as assuming that the relative standard deviations of short and long intervals are roughly equal (the scalar property of timing, see Table 1), the shorter reproductions for longer items (relative mean < 1) would bias the estimate of CV, making the combined measure difficult to interpret.

Hence, we decided to report the accuracy, and SD as a measure for precision separately. Results for CV are nevertheless displayed in the Supplementary Materials.

3. Results

3.1. Assessment of the scalar variability for single items

First, we examined the data collected for the 1-item sequences (Figure 2, Table 2) and showed that, overall, participants complied with the task instructions as their temporal reproductions correlated linearly with the objective item duration (Figure 2A). We then computed participants' relative temporal reproductions by dividing each reproduction of an item by the actual item duration. Reproduction precision was computed as the standard deviation over the relative reproductions of all 1-items per participant (Fig. 2B). For illustration, relative density profiles for exemplary item durations are displayed in Figure 2C.

To test whether the reproduced durations complied with the well-established scalar property of interval timing, in which the variance scales with the magnitude, we tested for an effect of item duration on the precision with which single items were reproduced (Table 2). In Experiment 1, we found a significant effect of item duration on precision, reflecting a violation of the scalar property, likely due to the large range of durations used in Experiment, including sub-second durations (0.3 – 6.35 s ; Lewis & Miall, 2009). In Experiments 2 and 3, participants' temporal reproduction precision scaled with the item duration (Figure 2, Table 2). We also observed the classical underproduction of longer durations ("Vierordt's law"; Vierordt, 1868; see also Lejeune & Wearden, 2009). Overall, these results show that participants performed the timing tasks as expected, displaying classical signatures of magnitude estimations such as regression effect, scaling, and range effect (Petzschner et al, 2015).

<i>Item duration</i>	<i>F(df)</i>	<i>p</i>	<i>η^2</i>
Experiment 1	10.58 (1, 185)	0.001	0.045
Experiment 2	0.21 (1, 38)	0.649	0.005
Experiment 3	1.68 (1, 34)	0.203	0.032

Table 2: Effect of single item duration on precision. Bold values indicate a significant effect of item duration on relative SD ($p < 0.05$).

A) Reproduced durations (mean)

B) Precision (1 / SD)

C) Density of relative reproductions

Fig. 2. Reproduction and precision of 1-item durations. Only single-item sequences are shown. **A)** Absolute temporal reproduction as a function of the item duration, per Experiment. The dashed identity line represents a perfectly accurate reproduction. Grey dots show single participants' data. Overall, participants' 1-item reproductions increased linearly with the objective durations, with a systematic underproduction of longer intervals. **B)** Precision (inverse of relative SD) as a function of item duration. Statistically, the precision of the 1-item reproduction was affected by item duration in Experiment 1, but not in Experiments 2 and 3. **C)** Distributions of relative reproduction for three exemplary items in Experiments 1 and 2. In Experiment 2, the relative reproductions displayed comparable precision.

Accuracy		F(df)	p	η^2
Experiment 1	n-item	0.34 (2, 744)	0.72	0.000
	sequence duration	150.39 (1, 744)	< 0.001	0.088
	n-item x sequence duration	8.81 (2, 744)	< 0.001	0.010
Experiment 2	n-item	2.39 (2, 240)	0.094	0.013
	sequence duration	29.90 (1, 240)	< 0.001	0.083
	n-item x sequence duration	0.36 (2, 240)	0.701	0.002
Experiment 3	n-item	7.10 (4, 275)	< 0.001	0.072
Precision		F(df)	p	η^2
Experiment 1	n-item	4.23 (2, 744)	0.015	0.009
	sequence duration	17.99 (1, 744)	< 0.001	0.019
	n-item x sequence duration	3.81 (2, 744)	0.023	0.008
Experiment 2	n-item	8.66 (2, 240)	< 0.001	0.051
	sequence duration	0.02 (1, 240)	0.887	0.000
	n-item x sequence duration	0.87 (2, 240)	0.420	0.005
Experiment 3	n-item	18.79 (4, 275)	< 0.001	0.119

Table 3. Effects of n-item and sequence duration on the accuracy (mean of relative reproductions) and precision (SD of relative reproductions) of temporal reproductions. Bold values indicate a significant effect ($p < .05$).

3.2. Experiment 1

To investigate whether the number of items and the sequence duration affected the maintenance of durations in working memory, we calculated the precision (relative SD) of temporal reproduction for each item in a sequence as a function of the total number of items comprised in the sequence and the sequence duration (Figure 3, Table 3). A 2-way ANOVA showed a significant effect of the number of items on precision ($F(2, 744) = 4.23$, $p = .015$, $\eta^2 = 0.009$), a main effect of sequence duration ($F(1, 744) = 17.99$, $p < .001$, $\eta^2 = 0.019$), and an interaction between number of items and sequence duration on precision ($F(2, 744) = 3.81$, $p = .023$, $\eta^2 = 0.008$). Computing the same ANOVA only for the first or last items yielded a significant effect of sequence duration, as well as an interaction between sequence duration and n-items for and the

first item ($p < .01$; $p = 0.017$), and a sequence duration effect only for the last item ($p < .001$; Supplementary Tables 1, 2).

The accuracy of the reproductions (relative mean, Figure 3C, Table 3), showed a strong effect of sequence duration ($F(1, 744) = 150.39$, $p < .001$, $\eta^2 = 0.088$) and an interaction between number of items and sequence duration ($F(1, 744) = 8.81$, $p < .001$, $\eta^2 = 0.010$).

We further calculated the precision of reproduction as a function of the position of the items (1st to 3th) for 2- and 3-item sequences only. Results indicated no significant effect of position in the 2-item or in the 3-item sequences (Table 4; Fig. 6).

Position effect on precision		<i>F</i> (df)	<i>p</i>	η^2
Experiment 1	2-item sequence	0.44 (1, 374)	0.508	0.001
	3-item sequence	0.41 (2, 183)	0.667	0.004
Experiment 2	2-item sequence	0.43 (1, 80)	0.514	0.005
	3-item sequence	0.35 (2, 120)	0.702	0.006
Experiment 3	2-item sequence	1.51 (1, 34)	0.228	0.096
	3-item sequence	0.06 (2, 51)	0.944	0.002
	4-item sequence	1.72 (3, 68)	0.171	0.063
	5-item sequence	3.59 (4, 85)	0.01	0.133

Table 4: Serial position effect for all experiments. Bold values indicate a significant effect of position on precision ($p < 0.05$).

Experiment 1

A) Relative reproductions

B) Precision (1/SD)

C) Accuracy (mean)

Figure 3. Precision is affected by the number of items and sequence duration in Experiment 1 (N = 21). **A)** Relative reproductions (all participants), density. Grey shades indicate 1-item, 2-item, and 3-item sequences, indicating a lower precision for sequences with more items. **B)** The precision of individual items for all sequences as a function of the number of items (x-axis) and their duration (color coded). The mean duration of the 1-item sequence was by design shorter than that of the 2-item, itself shorter than the 3-item sequence. Transparent shapes are individual data points. Error bars indicate 95% confidence intervals. The precision decreased with the number of items in the sequence, and showed a quadratic variation with sequence duration in Experiment 1. **C)** The accuracy, indicated by the relative mean of reproductions (1 indicates perfect accuracy) per number of items (x-axis) and sequence duration (color coded). Accuracy showed a strong decrease with increasing sequence duration in Experiment 1.

3.3. Experiment 2

In Experiment 2, we orthogonalized the number of items and the sequence durations to ensure that the precision of reproduction was a function of either the number of items or the sequence duration (Fig. 1B). Results (Fig. 4, Table 3) indicated a significant effect of the number of items on precision ($F(2, 240) = 8.66$, $p < .001$, $\eta^2 = .051$), but no main effects of sequence duration ($F(1, 240) = 0.02$, $p = .887$, $\eta^2 = .000$), nor any interactions. Hence, likely due to the orthogonalization of the number of items and the sequence duration in Experiment 2, we found that only the

number of items but not the sequence duration, impacted the precision of temporal reproductions. When computing the same ANOVA on the first and the last items only, the effect of the number of items was consistently found ($p \leq .01$; Supplementary Tables 1, 2).

As in Experiment 1, we found that the sequence duration affected accuracy ($F(2, 240) = 29.90$, $p < .001$, $\eta^2 = .083$).

We further calculated the precision of reproduction as a function of the position of the items (1st to 3th) in the 2- and 3-item sequences. As in Experiment 1, no position effects were observed (Figure 6, Table 4). Therefore, as in Experiment 1, we found no robust primacy or recency effect in the precision of temporal reproduction.

Experiment 2

A) Relative reproductions

B) Precision (1/SD)

C) Accuracy (mean)

Fig. 4. Precision decreases as the number of items increases in Experiment 2 (N = 14). **A)** Relative reproductions (all participants), density. Grey shades indicate 1-item, 2-item, and 3-item sequences. **B)** The precision of individual items for all sequences as a function of the number of items (x-axis) and duration (color coded). Here, the mean durations of 1-item, 2-item, and 3-item sequences were equal. Transparent shapes are individual data points. Error bars indicate 95% confidence intervals. The precision decreased with the number of

items in the sequence, but was not affected by duration. **C)** The accuracy, indicated by the relative mean of reproductions (1 indicates perfect accuracy) per number of items (x-axis) and sequence duration (color coded). The accuracy showed a strong effect of sequence duration in Experiment 2, but no significant effects of number of items.

3.4. Experiment 3

In Experiment 1 and 2, we found no effects of item position in the sequence. We reasoned that a maximal set of three items may not be sufficiently taxing for participants to observe robust effects of item positions. In Experiment 3, we thus increased the number of items to 5, and kept the sequence duration constant to 4.5 s (the 1.9 s sequence was not included in the analyses). The precision was calculated as in the two previous experiments, and remained comparable across all item durations (Table 2). A 1-way ANOVA with factor of number of items showed, as in previous experiments, a robust effect of number of items on precision ($F(4,275) = 18.79$, $p < .001$, $\eta^2 = .119$; Figure 5, Table 3 Experiment 3). The accuracy was also affected by the number of items ($F(4,275) = 7.10$, $p < .001$, $\eta^2 = .072$).

We then calculated the precision of reproduction as a function of the position of the item (1st to 5th) for 2-, 3-, 4- and 5-item sequences (Fig. 5B). Unlike in Experiment 1 and 2, but as predicted by the experimental design, our results indicated a significant effect of position for the 5-item sequences ($F(4, 85) = 3.59$, $p = .01$, $\eta^2 = 0.133$; Table 4; Fig. 6).

3.5. Effect sizes

Combining the effects on precision observed in all three experiments (independent participant samples), we observed, for the factor n-item effect sizes (η^2) of 0.009 (Exp. 1), 0.051 (Exp. 2), and 0.119 (Exp. 3), which confirms that the effect is sufficiently robust, and that the chosen sample sizes were sufficient to reliably reproduce the effect. The effect size for sequence duration on precision (significant only in Exp. 1) was in the lower range (0.019). The effects of sequence duration on accuracy were robust (0.083 – 0.088).

3.6. Effects on the coefficient of variation

Since we had originally planned to analyse the coefficient of variation (CV) as a measure of timing precision, and to reach the wider timing community, we report the

results of the number of items and sequence duration on CV in Supplementary Table 3 and Supplementary Figure 1. Overall, the above described effects on accuracy and precision lead to a pattern of results on the CV that is more intricate to interpret. In Experiment 1, only the number of items had a significant effect on CV ($F(2, 744) = 8.30$, $p < .001$, $\eta^2 = 0.016$) as the effects of sequence duration on both the SD and mean cancelled each other out. In Experiment 2, CV was affected by both the number of items and the overall sequence duration ($F(2, 240) = 9.02$, $p < .001$, $\eta^2 = 0.056$; $F(1, 240) = 9.84$, $p = .002$, $\eta^2 = 0.031$). In Experiment 3, we observed an effect of the number of items on CV $F(4, 275) = 9.35$, $p < .001$, $\eta^2 = 0.077$.

Experiment 3

A) Relative reproductions

B) Precision (1/SD)

C) Accuracy (mean)

Fig. 5. Precision decreases as the number of items increases in Experiment 3 (N = 19). **A)** Relative reproductions (all participants), density. Grey shades indicate sequences with 1 – 5 items. **B)** Precision of individual items for all sequences that were tested as a function of the number of items (x-axis). We tested only one sequence duration. Error bars indicate 95% confidence intervals. Precision decreased with number of items in the sequence. **C)** Accuracy, indicated by the relative mean of reproductions (1 indicates perfect accuracy) per number of items (x-axis). Accuracy showed a strong effect of number of items n in Experiment 3.

Position effects (Precision)

Fig. 6. Experiments 1 – 3: Effects of item position on recall precision. **Experiment 1:** no position effects were observed, neither in 2- nor 3-item sequences. **Experiment 2:** again, no position effects were observed. **Experiment 3:** we observed a position effect for 5-item sequences, namely higher recall precision for items presented earlier in the sequence.

4. Discussion

We assessed working memory for duration in three independent behavioural experiments, using a novel *n-item delayed temporal reproduction task*, in which we manipulated the number of items and the duration of a sequence orthogonally. Precision of recall, serving as an indicator of working memory load, was quantified as the standard deviation of *relative* reproductions. Contrary to accuracy, which we quantified independently, the precision of recall measures the reliability of reproductions across trials, separately from possible biases that may affect accuracy.

In all three experiments we found that maintaining a larger number of duration items (1 to 5 items) decreased the *precision* of recall for all items. The sequence duration only affected precision in Experiment 1, where sequence duration and number of items were not orthogonalized. Accuracy was affected by sequence duration in Experiments 1 and 2, and by the number of items in Experiment 3 (no variation of sequence duration). Below we discuss the implication of our novel observations on the nature of duration storage in working memory.

4.1. Continuous vs. discrete durations in working memory: The number of duration items affects precision

We contrasted the continuous coding hypothesis, which predicted that sequence duration should systematically impact the precision of recall, with the discrete coding hypothesis, predicting that the precision of recall should be mostly affected by the number of items and not by the magnitude of the items. To test this, we assessed the precision of recall by measuring the temporal reproduction of sequences with varying number and duration of items maintained in memory.

The most robust and consistent effect in this set of experiments is a decrease of recall precision with the number of items in a sequence. This was observed for sequences in which the number of items co-varied with the sequence duration (Experiment 1), as well as for sequences whose duration was independent of the number of items (Experiments 2 and 3). This pattern was predicted by the discrete coding hypothesis, with the implication that durations may be maintained as discrete items in working memory. The decline in precision with an increasing number of items suggests that

available resources are distributed flexibly amongst all items to be maintained, which is compatible with recently proposed models of working memory (Ma et al., 2014).

Under the continuous storage hypothesis, the duration of the whole sequence was expected to affect memory load. This prediction was observed in Experiment 1, in which we found that precision decreased with increasing sequence duration. Possibly, this effect results from a confounding factor linked to the covariation of the number of items and of the sequence duration, *i.e.* the shortest sequences (sub-second) were also more likely to be single items in Experiment 1. The significant interaction between the number of items and sequence duration on precision in Experiment 1 further suggests that these factors were not independent. In Experiment 1, we also found a violation of the scalar variability for single items, likely due to the large range of durations tested (Lewis & Miall, 2009). Taken together, it is possible that participants may have used a different strategy to reproduce the sequences in this experiment.

Previous studies (Teki & Griffiths, 2016) have reported somewhat inconsistent effects of the number of items on recall precision. A major paradigmatic difference between these studies and ours is their use of quasi-rhythmic sequences, which might have involved beat-based mechanisms (Grube et al., 2010). Previous work also required participants to recall only one cued item, whereas our experimental paradigm required the reproduction of all items in the sequence. Crucially, however, in our analyses we compute precision for single items, not for sequences, which otherwise might have led to a confound between recall precision and motor noise due to the larger number of button presses for more items. Another set of studies (Manohar & Husain, 2016) used non-rhythmic sequences and found an effect of the number of items, consistent with our results. However, their use of “filled durations” may have led participants to use a maintenance strategy of auditory features such as intensity, as opposed to duration *per se*, considering the classical trade-off between apparent duration and auditory intensity (Berglund *et al.*, 1969). As maintenance in working memory involves brain circuits that code for events themselves (Postle, 2006), we deliberately used empty intervals demarcated by identical tones such that no sensory feature but only the duration itself could be used to recall the different items.

The gradual decrease in precision with increasing working memory load aligns well with a previous study (Politi et al., 2018) showing that increasing visual working

memory load decreased the precision of a concurrent duration estimation. From an information-theoretic standpoint, dual task effects show that duration estimation competes for working memory resources, a competition that can be partially alleviated by deliberately paying attention to time (Zakay & Block, 1996). Considering we chose a prospective timing paradigm which makes time ‘the foreground’ (MacDonald, 2014), the precision effects depicted here are specific to the temporal dimension. Importantly, the time-scale invariance represented by the absence of an effect of sequence duration on recall precision in Experiment 2 in which number of items and sequence duration were independently varied, further strengthens the interpretation of a symbolic code for duration storage (Gallistel & Gibbon 2001).

In sum, our results suggest duration can be *discrete items* in working memory, favouring a discrete and symbolic representation of duration. Such representations appeal to the notion of a magnitude system so that pre-verbal magnitudes and symbolic quantities can be manipulated, and possibly represented in a common magnitude system (Gallistel & Gelman, 2000; Martin et al. 2017; Walsh, 2003).

4.2. Context effects: reproduction accuracy is biased towards the mean

The accuracy of temporal reproductions was affected by the sequence duration in Experiments 1 and 2. In line with our findings, previous studies (Chen et al, 2015; Yu et al. 2017) reported a decrease of accuracy with increasing durations in a duration working memory task but reported no measure of precision. Such central tendency or regression effects are well known in the timing literature (Vierordt, 1868; Lejeune & Wearden, 2009), and have more recently been described to originate from a noisy Bayesian estimation of elapsed time (Jazayeri & Shadlen, 2010; Petzschner et al., 2015; Ren et al., 2021). In more details, such context dependence of duration estimates appears to result from the integration of noisy measurements of single time intervals with previously encountered ones, reflecting the maintenance of statistics beyond the intervals observed on the current trial, compatible with mental magnitudes (Petzschner et al, 2015; but see Sohn et al. 2019).

Our choice to separate the analyses of precision (standard deviation) and accuracy (mean) has provided us with a direct measure of reliable timing performance, independent from possible biases that affected accuracy. This distinction could not

have been achieved if we had only quantified the coefficient of variation, which remains a disputed measure in timing research, with important theoretical and neuroanatomical implications regarding the existence of a unique or multiple clocks (Buhusi & Meck, 2005; Gibbon, 1977; Gibbon et al., 1984; Treisman, 1963). In our series of experiments, the index of precision is used not to evaluate timing *per se*, but maintenance, once empty intervals have been encoded as durations in memory.

4.3. From serial position to contiguity effects in time

We found no robust evidence for serial position effects for item duration in Experiments 1 and 2. Experiment 3, in which the number of items was closer to posited working memory limits yielded a primacy but no recency effect: recall precision gradually decreased with item position only in the 5-item sequences. The primacy effect may have been caused by the serial allocation of memory to subsequent items, since participants did not know how many items they would be presented with throughout the sequence. Alternatively, the decrease in precision over time may reflect an asymmetric temporal contiguity effect, previously described in free recall and episodic memory (Murdock, 1962), and which may be particularly relevant in the context of memory for episodic time (Kahana, 1996; Healy et al., 2018). To robustly demonstrate the existence of such an effect, a dedicated design would be needed to counterbalance forward and backward transitions between duration items. As previously mentioned, while similar tasks have reported primacy and recency effects (Manohar & Husain, 2016; but see Fan & Yotsumoto, 2018), the use of filled durations may have relied on dimensions such as frequency or loudness for storage whereas such strategies were prevented here and participants could solely rely on the duration of events.

4.4. Storing time in memory

Despite a host of studies showing that temporal delays are coded with events and can be used for efficient recall (Gallistel & Gibbon, 2000; Tsao et al., 2019), and the strong assumption of a working memory component in seminal internal clock models (Gibbon et al., 1984), there is to date no consensual account of whether and how durations are stored in memory (Friedman, 1993).

As outlined in the introduction, the intrinsic dynamics of brain circuits that represent a duration could in principle provide the code for its maintenance in working memory (Paton & Buonomano, 2018), for instance through re-activation of the network trajectory during the delay period via replay mechanisms to insure its maintenance (Huang et al., 2018). State-dependent networks account well for the continuous coding of elapsed time predicting that the longer the durations, the less precise the recall should be (Laje et al., 2011), but require additional explanations to account for an abstraction of temporal information for storage in memory, possibly through a set of orthogonal codes (Zhou 2020; Cueva et al. 2020), providing information to downstream readers.

Our observations are also consistent with recent work suggesting that rodents keep a detailed report of the sequence of durations they have just experienced (Kheifets et al., 2017). These findings suggest that sequences of durations may be encoded and stored to form the basis for episodic memory of sequences, including the temporal dimension of these events. It appears that maintaining multi-item sequences over short and long temporal scales requires a qualitative change in memory mechanisms, which blurs the conceptual borders between working and episodic memory (Bellmund et al., 2020; Palombo et al., 2020). A number of models from the episodic memory literature explicitly discusses the nature of the temporal features in memory (Friedman, 1993; Brown et al., 2007; Shankar & Howard, 2010), highlighting two distinctive features of time memory: order and temporal distance. As neuroimaging studies shed light on how the brain tracks and stores temporal distances between events (Eichenbaum, 2014; Heys & Dombeck, 2018; Tsao et al., 2018; Gauthier et al., 2020), a convergence of coding strategies for temporal features may inform on the transition from the real-time and online coding of elapsing time between events to their abstracted representations, as previously alluded to in a two-stage model for the representation of time (van Wassenhove, 2009).

4.5. Conclusions

In conclusion, we here described a novel experimental paradigm using minimalist sequences of empty intervals, which provide sufficient and necessary temporal statistics to assess working memory for duration. Our analyses point to the

important distinction between reproduction biases that are captured by accuracy, and decreased precision which indexes working memory load. Altogether, our findings suggest that durations can be stored as discrete items *in* working memory rather than reflecting fully analog constituents *of* memory. However, in some intriguing aspects, our findings diverge from typical working memory effects as we found no robust evidence for serial position effects, suggesting that working memory for duration may not fully align with working memory for sensory stimuli.

Author contributions

V.vW, S.K.H, and T.W.K developed the research concept and all authors contributed to the study design. Coding was performed by S.K.H., I.M., and T.W.K.. Testing and data acquisition was performed by I.M. I.M. performed the data analysis under the supervision of T.W.K and S.K.H.; S.K.H and V.vW finalized the analysis and wrote the manuscript. All authors approved the final version of the manuscript.

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Supplemental Information

First item SD		F(df)	p	η^2
Experiment 1	n-item	2.22 (2, 429)	0.110	0.008
	sequence duration	11.02 (1, 429)	0.001	0.019
	n-item x sequence duration	4.08 (2, 429)	0.017	0.014
Experiment 2	n-item	7.76 (2, 114)	< 0.001	0.083
	sequence duration	0.00 (1, 114)	0.963	0.000
	n-item x sequence duration	0.29 (2, 114)	0.746	0.003
Experiment 3	n-item	3.58 (4, 85)	0.009	0.056

Supplementary Table 1: First item only

Last item SD		F(df)	p	η^2
Experiment 1	n-item	0.97 (2, 429)	0.378	0.003
	sequence duration	13.57 (1, 429)	< 0.001	0.024
	n-item x sequence duration	2.16 (2, 429)	0.117	0.008
Experiment 2	n-item	7.03 (2, 114)	0.001	0.070
	sequence duration	0.53 (1, 114)	0.467	0.003
	n-item x sequence duration	0.70 (2, 114)	0.496	0.007
Experiment 3	n-item	21.53 (4, 85)	< 0.001	0.236

Supplementary Table 2: Last item only

CV, all items included		F(df)	p	η^2
Experiment 1	n-item	8.30 (2, 744)	< 0.001	0.016
	sequence duration	1.88 (1, 744)	0.171	0.002

	n-item x sequence duration	1.61 (2, 744)	0.201	0.003
Experiment 2	n-item	9.02 (2, 240)	< 0.001	0.056
	sequence duration	9.84 (1, 240)	0.002	0.031
	n-item x sequence duration	0.83 (2, 240)	0.439	0.005
Experiment 3	n-item	9.35 (4, 275)	< 0.001	0.077

Supplementary Table 3: Effects on CV: n-item and sequence duration for all experiments.

Coefficient of Variation

Supp. Fig.1 Coefficient of variation (CV) for all three experiments. Inverse CV as a function of the number of items composing the sequences, separately for different sequence durations for Experiment 1 (left) and Experiment 2 (middle). The sequence durations were fixed in Experiment 3 (right). In Experiment 1, CV was modulated by number of items only, in Experiment 2 by number of items and item duration, and in Experiment 3 by the number of items.