**The effect of an unexpected modality on time reproduction:
Clock speed or memory mixing?**

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Abstract

The pacemaker-counter model (PCM) has been the core architecture of scalar expectancy theory for decades. PCM assumes the same timing mechanism applies to every stimulus input, regardless of modality, and has been used to explain differences between perceived durations. In violation, previous studies demonstrate a robust effect of memory-mixing, occurring when the memory trace of a previous time interval influences perception of upcoming ones. We examined the influence of unexpected modality for a trained duration on temporal reproduction, using auditory/visual stimuli with short/long (500/1000ms) standard durations—testing the PCM pure ‘clock speed’ prediction against the memory-mixing account. Here, we report different outcomes of unexpected modality on time reproduction based on modality assignments with specific intervals. When the short interval was trained with an auditory stimulus, and long interval with a visual stimulus, unexpected presence of the opposite modality led to a memory-mixing pattern, in which reproductions shifted toward the other interval. However, no such effect occurred when the short interval was trained with a visual stimulus and long interval with an auditory stimulus. We propose that durations stored in reference memory retain its paired modality, but that during averaging durations are combined based on both their modality and relative duration.

Keywords: time perception, duration reproduction, sensory modalities, reference memory, crossmodal timing

Introduction

The validity of our sense of time depends on the memories of intervals we have perceived in the past (Droit-Volet et al., 2004; Gamache & Grondin, 2010; Ivry & Spencer, 2004; Ogden et al., 2008; Ogden et al., 2010; Penney et al., 1998; Penney et al., 2000), yet, little is known about how memory content and limits shape the accuracy of how humans perceive time. Over the past two decades, a large array of research has addressed different influences on how we perceive the passage of time, specifically, how we perceive time across different senses, i.e., vision and hearing (Allman et al., 2014; Matthews & Meck, 2016).

The prominent theory in timing in psychology is scalar expectancy theory (SET; Gibbon, 1977), which identifies a series of sequential processes that contribute in different ways to variability in the accuracy of temporal processing. The model attributes timed behavior to underlying processing involving internal clock, memory, and decision mechanisms. The pacemaker-counter model (PCM) has been the core architecture of SET's internal clock mechanism (Gibbon et al., 1984), assumes that the same timing mechanism applies to every stimulus input, regardless of modality, and has been used to explain differences observed between perceived temporal durations. Various components of the 'clock', or pacemaker-accumulator device, include assumptions that pulses generated accumulate in a counter; thus, temporal experience comprises the number of pulses accumulated (Treisman, 1963). Furthermore, assumptions of the pacemaker-accumulator clock include filtration of emitted pulses through a switch mechanism permitting pulses to reach the counter in either smaller or larger numbers. Thus, content of the accumulated pulses within the counter is then processed in working memory, allowing retrospective comparisons between stored interval representations within reference memory (Gamache & Grondin, 2010).

SET thus proposes two memory stores: (1) working memory, which reflects the contents of the accumulator, and (2) reference memory of temporal standards (Gibbon, 1977). The temporal reference memory component of the SET model has two functions: (1) stores memories of standard durations essential for the current task, remaining constant over time, and (2) generates in part the scalar property of timing (Jones & Wearden, 2003). However, models following the storage logic of reference memory fail to account for the variability of temporal references on behavior. Jones and Wearden (2003) propose that reference memory is not an extensive storage of previous experience but is built up by the collection of separate instances of experiences of reinforcement at the time a standard duration is represented. This finding implies that the reference memory store is smaller than previously theorized, either containing a single item or as a single item with upper and lower boundaries, modulating subsequent changes as a result of new experiences.

As early as 1868, Vierordt first remarked on the differences in auditory and visual stimuli duration estimates (see for review Lejeune & Wearden, 2009). Many studies since have proposed that the pacemaker runs faster for auditory stimuli than for visual stimuli, or that auditory stimuli are quicker at attracting attention (Bratzke & Ulrich, 2019; Gibbon et al., 1984; Meck, 1984; Penney et al., 2000; Ulrich et al., 2006; Wearden et al., 1998; Wearden et al., 2006), as sounds are often judged as having lasted longer than lights. Different modalities specifying short and long durations, for example, may contribute to these differences, as modality differences in clock speeds as well as latency to begin timing have been observed previously (Droit-Volet et al., 2007; Meck, 1984; Penney et al., 1998; Penney et al., 2000). These differences in internal clock rate violate the PCM assumption that the same timing mechanism applies to every stimulus input, irrespective of sensory modality.

By testing this critical limitation of the PCM, the persistence of temporal representations (auditory/visual) after encoding, we can examine the characteristics of the reference memory component. One way to test this is to consider the robust effect of memory mixing, which occurs when the memory trace of a previous time interval influences the perception of upcoming time intervals (Coull et al., 2013; Droit-Volet et al., 2007; Gamache & Grondin, 2010; Grondin & Rousseau, 1991; Jones & Wearden, 2004; Penney et al., 1998; Penney et al., 2000; Swanton & Matell, 2011; Wearden et al., 2006; Wiener et al., 2014). Evidence from temporary memory distortions can occur as a function of differences in signal modalities and by the encoding of multiple signal durations associated with different timing tasks into a single memory distribution (Gu & Meck, 2011). Moreover, visual temporal reference memory may be more stable than auditory reference memory, such that auditory temporal information and visual temporal information do not mutually interfere in reference memory (Ogden et al., 2008; Ogden et al., 2010), and auditory memories are more susceptible to changes following new duration exposures (Gamache & Grondin, 2010; Wiener et al., 2014). By examining proactive interference effects from previous trials using signal duration categorization, we can elucidate observed changes in temporal context (e.g., duration ranges), as well as for Vierordt's law.

Interval categorization is often used to investigate the memory mixing phenomenon, i.e., temporal generalization or bisection tasks. Typically, a series of intervals are assigned to one of two categories (short or long) with blocks of trials marked by either auditory or visual signals. Results from research utilizing these methods suggest a common memory representation of intervals marked by different sensory modalities (Filippopoulos et al., 2013; Grondin, 2005; Penney et al., 2000), with the memory trace of one interval type influencing the other for at least a few minutes hence (Gamache & Grondin, 2008). Therefore, both modality-specific and

modality-independent timing components may exist (Stauffer et al., 2012), with different modality-specific ‘clocks’ producing the initial duration representations, followed by transformation into an amodal form if these representations become identified as standards (Filippopoulos et al., 2013).

The current work expands upon previously observed differences in auditory and visual signals on clock speed and temporal memory, using a temporal reproduction task similar to the one used by Bratzke and Ulrich (2019), but with marked differences, such as adding a standard duration cue before modality reproduction and no inclusion of a comparison stimulus. Our design is further inspired by an early study by Meck (1984) in which rats were trained to time two durations using different modalities, each associated with a unique cue stimulus, and then tested on the same duration but with an unreliable (80% accurate) cue and either modality possible. Rats demonstrated a remarkable ability to time the trained duration, regardless of the modality used, but with sounds generally timed as faster than lights, supporting a clock-speed effect.

Here, we tested if the same effect would occur in humans, but with two possible outcomes depending on the level of interaction between remembered and experienced stimulus modalities. Wearden et al. (2006) suggested that memory mixing may be avoidable if the experimental design allows a clear distinction between the standards for different conditions, hence our inclusion of two duration standards, with subjects trained to associate the auditory stimulus with one duration standard (either 500ms or 1000ms) and the visual stimulus with the other duration standard, before testing. Our primary focus of interest is whether temporal reproduction will be affected by the modality of duration standards in incongruent trials: in particular, when the trained standard duration for one modality influences the perception of another modality presented incongruently (unexpected modality for the standard duration cue), suggesting that memories of standard

122 durations in the congruent blocks (modality presented matches standard duration cue) may
 123 influence temporal reproduction in the incongruent blocks (modality presented does not match the
 124 standard duration cue), thus altering performance. Based on previous findings, we predicted an
 125 interference of memory would occur based on modality congruency, as a result of the robust
 126 memory mixing phenomenon (see Figure 1 for predicted results).

127
 128 *Figure 1.* Predicted results for mean reproductions (ms) for the clock-speed pattern (left panel) and memory pattern
 129 (right panel) as a function of modality congruency for short (500ms) and long (1000ms) standard durations. Under a
 130 clock pattern effect, the presence of the secondary (incongruent) cue should lengthen or shorten reproduced duration
 131 depending on its modality, with auditory stimuli leading to under-reproduction (due to a faster clock) and visual
 132 stimuli leading to an over-reproduction (due to a slower clock). Note that, under a clock pattern, the effect of the
 133 incongruent modality should be larger for longer intervals. Under a memory pattern effect, the presence of the
 134 secondary (incongruent) cue should shift reproduced time toward the interval associated with that modality,
 135 regardless of whether it is auditory or visual, leading to an over/under reproduction pattern. Here, no difference in
 136 the size of the shift is predicted between primary and secondary modalities.

137 Method

138 Subjects

139 Forty healthy, right-handed volunteers participated in the experiment (27 women, 13 men, $M =$
 140 20.1 years)¹. They reported normal hearing and normal or corrected-to-normal vision, and

¹ Previous results by Ulrich and Bratzke (2019) revealed an interaction of modality and congruency on temporal reproduction performance in a design similar to ours ($F = 39.27$; $\eta^2_p = .36$). A power analysis for obtaining this

received course credit. All provided written informed consent prior to the experiment and met all inclusionary criteria. The experiment procedure was approved by the George Mason University Institutional Review Board before data collection.

Design

A 2x2x2 mixed factorial design was used with two within-subject variables, *standard duration* (short, long) and *congruency of modality* (congruent, incongruent) and one between-subject variable, *modality assignment* ($T_S|L_L$; $L_S|T_L$). Each group consisted of 20 randomly assigned subjects whose training of standard durations, modalities, and duration reproduction cues was counterbalanced based on the assigned group.

Apparatus and stimuli

Stimuli were generated and controlled by PsychoPy version 1.85.6 (Peirce, 2009) on a PC (Microsoft Windows 10). The sensory signals marking time were either visual or auditory. The visual stimulus was a 5x5 cm white gaussian blue that appeared on a gray background presented on the center of a 24-inch LED computer monitor (Dell model S2417DG, 2560x1440 pixel resolution, 100Hz refresh rate). The auditory stimulus was a single continuous tone provided by PsychoPy and was presented binaurally through wired silicone-tipped earplug headphones (Plugfones) at an intensity of 70 dB SPL during the simultaneous presentation of a gray background on the computer monitor. Subjects sat in front of the computer monitor with a viewing distance of about 68-cm. Subjects pressed the space key with their right index finger to initiate the modality for temporal reproduction, then pressed it again to terminate reproduction.

effect, using the BUCCS package for R (Andersen et al., 2017), which adjusts for publication bias and uncertainty, revealed that a sample size of at least $n = 23$ participants would be necessary to achieve 80% power with an assurance of 0.8 and an alpha of 0.05.

Keypresses were recorded via a mechanical keyboard with a 1000Hz polling rate (CORSAIR K70 MX Red).

Procedure

Before starting the session, subjects were randomly assigned to one of four groups, with all condition types counterbalanced to eliminate order effects. Based on group assignment, subjects were trained to associate a duration reproduction cue (x or +) with the short (S) standard duration (500ms) and its modality—auditory (A) or visual (V)—and the other duration reproduction cue with the long (L) standard duration (1000ms) and the other modality. Before beginning the training phase, subjects were instructed not to count the time (for methods used to prevent counting, see Rattat & Droit-Volet, 2012).

(a) Training Segment 1: Exposure trials

(b) Training Segment 2: Reproduction trials

Figure 2. Schematic of training phase segments. Top (a): example of training segment one exposure trail. Bottom (b): example of training segment two reproduction trial.

Training Phase

During the training phase, two blocks were presented: one block for the auditory stimulus and one block for the visual stimulus, presented in a counterbalanced order based on the assigned group. Each block consisted of two segments (for example, see Figure 2).

In the first segment, subjects learned the modality duration and associated reproduction cue through 10 exposure trials per duration standard. Subjects were instructed to press a key to initiate the next trial when "Press any key to view duration" appeared on the screen. Next, the same black fixation mark (x or +) would appear in the center of the screen for 500ms, representing the duration cue for that block. Then, the same stimulus type (auditory or visual) was presented for the duration of the standard interval (500 or 1000ms). The intertrial interval (ITI) was 1500ms (as in Bratzke & Ulrich, 2019). No responses were made during the first segment.

In the second segment, subjects practiced reproducing modality durations immediately after each exposure for a total of 50 practice trials. During the second segment, each trial started with the presentation of a black fixation mark in the center of the screen with "Reproduction duration" appearing above it. Subjects were instructed to press a key when "Reproduce duration" appeared to initiate the exposure stimulus duration. After the interstimulus interval of 1000ms (as in Ulrich et al., 2006), a white fixation mark matching the previous black fixation mark type would appear. When the white fixation mark appeared, subjects were instructed to press a key to initiate the stimulus duration, then terminate the stimulus duration with another key-press when the duration of the stimulus appeared to be equal to the duration of the standard. Subjects received feedback to reinforce duration reproduction training, receiving either the message "Great!" when the reproduction was accurate or "Wrong Time" when inaccurate. Feedback for accuracy/inaccuracy was determined by a feedback constant (k), such that the response had to be within the tested duration divided by k . An initial value of $k=3.3$ was chosen, such that responses had to be within ~150ms for the short standard duration and within ~300ms for the long standard duration. Feedback (k) was adjusted within increments of ± 0.15 for every accurate/inaccurate reproduction. The ITI was 1500ms.

For the two experimental groups, different modalities were associated with each duration. In the first group, “Tone Short, Light Long” ($T_S|L_L$), subjects were trained to associate the auditory stimulus with the short duration ($A-S$), then the visual stimulus with the long duration ($V-L$). The second group, “Light Short, Tone Long” ($L_S|T_L$), subjects learned the opposite association. The cues associated with each duration (x or +) were randomly assigned to each subject within each of these groups.

Testing Phase

During the testing phase, subjects were instructed to reproduce the learned standard intervals based on their associated reproduction cue (x or +) while simultaneously ignoring the stimulus modality being presented; 80% of the trials presented matched the modality for that reproduction cue during the training phase (congruent trials), while 20% of the stimuli did not match (incongruent trials). Subjects received two iterations of the same reproduction blocks. Each iteration consisted of two blocks: one for the short standard and one block for the long standard, with 100 trials per block (400 trials total). After the first block, a brief break was allowed, followed by the second block. After completing the first iteration, a refresher block followed, consisting of the exposure trials experienced during the first segment of the training phase. Immediately after the refresher block, the second and final reproduction iteration was administered. The two duration reproduction cues were presented in fixed blocks, i.e., one block contained the “x” cue, and the other the “+” cue. Each trial started with the presentation of a white fixation mark (x or +) in the center of the screen, with the words “Reproduce duration” above it for 1000ms. When “Reproduce duration” appeared, subjects were instructed to press a key, after which either the auditory or visual stimulus was presented. This first key-press initiated the stimulus duration. The second key-press terminated the stimulus duration when the subject judged it to be equal to the duration of the standard for that

cue, regardless of stimulus modality. The ITI was 2000ms. No feedback was provided. The experimental procedure can be viewed in Figure 3.

Figure 3. Graphical representation of experimental procedure. Top (a): example of trained standard durations (500ms vs 1000ms) for Group 1 (top row), with their associated duration reproduction cue (x vs +) and matching modality (auditory vs visual). Based on previously learned standards for the group, here we demonstrate all possible congruent trials (middle row) and all possible incongruent trials (bottom row). Bottom (b): timeline of the experimental session; standard duration, duration reproduction cue, and stimulus modality were counterbalanced across subjects/blocks.

Data analysis

We analyzed the mean reproduced time for each condition. For variability, we calculated the coefficient of variation (CV), as the standard deviation of reproduced times divided by the mean.

Data from two subjects were excluded from the (L_s|T_L) group due to a high coefficient of variation (CV>1) for the long standard duration condition. All statistical analyses were conducted in SPSS (v. 19, IBM Corporation) with an alpha level of 0.05. Separate analyses of variance (ANOVAs) with the within-subjects factors *standard duration* (short vs. long) and *congruency of modality* (congruent vs. incongruent) and the between-subjects factor *group* were conducted on mean reproduced durations and CV of reproductions. In addition to group assignment, more in-depth analyses into duration order and modality order were conducted.

Results

Mean reproduction. Overall, there was a significant main effect for standard duration, $F(1,36) = 6.23, p = .017, \eta^2_p = .148$: notably, subjects notably were far less accurate for the short duration standard than the long duration one. A significant interaction between standard duration and congruency of modality occurred, $F(1,36) = 6.43, p = .016, \eta^2_p = .152$: reproduction of the *S* standard duration congruent trials were shorter on average (736 ± 50 ms) compared to incongruent trials (844 ± 60 ms); reproduction of the *L* standard duration congruent trials were longer on average (998 ± 50 ms) compared to incongruent trials (918 ± 49 ms). The main effect for group was not significant, $F(1,36) = 0.26, p = .613, \eta^2_p = .007$ (Figure 4).

Figure 4. The pattern of mean reproductions (in seconds) and variability aggregated across modality pairings. Left panel: mean reproduction between congruent and incongruent intervals demonstrated an over-reproduction of the short duration (S) and under-reproduction of the long duration (L). Right panel: mean coefficient of variation (CV) results between short and long duration pairings, in which no significant differences were observed between either interval length or congruency. Error bars represent standard error.

When examining the effect of modality-assigned groups, there was a significant three-way interaction between standard duration, congruency of modality, and modality/duration assignment, $F(1,36) = 10.263, p = .003, \eta^2_p = .222$. When investigating this three-way interaction, two different patterns were observed for the different modality-assigned groups (Figure 5). In the ($T_S|L_L$) group, mean reproductions for incongruent trials were longer ($847 \pm 69\text{ms}$) than for congruent trials ($735 \pm 86\text{ms}$) for the S duration standard, and for the L duration standard were shorter ($935 \pm 100\text{ms}$) for incongruent trials than congruent ones ($1048 \pm 82\text{ms}$). However, in the ($L_S|T_L$) group, little difference was observed between the S (737ms vs 745ms) and L (942ms vs 997ms) duration standards. Separate repeated-measures ANOVAs for each group confirmed this effect, with an interaction between standard duration and congruence for the ($T_S|L_L$) group $F(1,19) = 10.31, p = .005, \eta^2_p = .352$, and no interaction for the ($L_S|T_L$) group $F(1,17) = 0.91, p = .354, \eta^2_p = .051$.

Figure 5. Mean reproduction and variability between modality pairing groups. Top: different patterns emerged depending on the interval/modality pairings in both groups. Subjects in the Tone Short, Light Long group demonstrated an over-reproduction of the short duration and an under-reproduction of the long duration with incongruent stimuli, while subjects with the opposite modality pairing (Light Short, Tone Long) exhibited no effect of the incongruent stimulus. Bottom: CV results between groups, with no significant difference between interval or modality pairing in either group. Error bars represent standard error.

To further investigate the difference between groups, we compared reproduced durations for individual duration lengths and congruent vs incongruent modalities, depending on whether the modality tested was auditory or visual (Figure 6). Here, we observed that, when subjects expected a tone, but were presented with a light, the interval was over-reproduced, but only for

the S duration standard [$t(19) = 3.06, p = .006, d = 0.68$] and not the L duration [$t(17) = 1.44, p = .17, d = 0.34$]. Likewise, when subjects expected a light, but were presented with a tone, the interval was under-reproduced, but only for the L duration standard [$t(19) = 3.08, p = .006, d = 0.69$]. Notably, the size of the shift in under and over-reproduction between short and long duration standards was equivalent, with subjects over-reproducing the S duration standard by 220ms and under-reproducing the L duration standard by 201ms. Finally, when measuring the size of the shift between conditions, we observed no difference in the change in duration reproduction between interval ranges [$t(19) = 0.55, p = .59, d = 0.12$].

Figure 6. Mean reproduction performance (same as Figure 5), but presented as a function of modality congruence across groups. Here, when the incongruent stimulus was a light (left panel), time was over-reproduced, but only for the short duration. In contrast, when the incongruent stimulus was a tone (right panel), time was under-reproduced, but only for the long duration stimulus.

Variability of reproductions. The variability of reproductions was not significantly modulated by group [$F(1,36) = 1.59, p = .21, \eta^2_p = .04$], standard duration [$F(1,36) = .74, p = .39, \eta^2_p = .02$] nor by congruency [$F(1,34) = 1.68, p = .2, \eta^2_p = .04$]. Additionally, there was no

significant interaction between standard duration, congruence, and group assignment, $F(1,36) = 2.96, p = .094, \eta^2_p = .07$].

Discussion

This study examined the influence of an unexpected modality for a trained duration standard on crossmodal temporal reproduction. Specifically, we tested the pure ‘clock speed’ predictions of the PCM against the memory mixing phenomenon. According to the PCM assumption that the pacemaker runs faster for auditory stimuli than for visual stimuli (Penney et al., 2000; Ulrich et al., 2006; Wearden et al., 1998), it was predicted that when an unexpected stimulus modality is presented, the interval should be over or under reproduced, depending on the modality presented. Specifically, when timing for a standard interval associated with an auditory stimulus, if an unexpected visual stimulus is presented, an overproduction of duration will occur, due to a slower clock speed for visual stimuli. Conversely, when timing for a standard interval associated with a visual stimulus, if an unexpected auditory stimulus is presented, an underproduction of duration will occur, due to a faster clock speed for auditory stimuli.

When first analyzing these data, the pattern of results observed matched that predicted by a memory mixing account. That is, duration for the short and long durations were over and under-reproduced when the incongruent cue was presented. However, for a true memory mixing account to be present, this pattern should exist regardless of the modality of the incongruent stimulus. When dividing the data depending on modality/duration pairing, we found that a shift in duration reproduction for incongruent stimuli was only present in those subjects in which the short duration was cued with a tone, and the long duration was cued with a light; in the opposite paired group, no differences were found between congruent and incongruent modalities. This finding suggests that

a memory-mixing account cannot entirely explain our results, and further suggests that there is a difference in how modality-pairings influence duration reproduction.

Why might the interval-pairing in the Tone-Long group show little effect of incongruent modality? It is difficult to provide an exact mechanism with our present data. However, it should be noted that previous work has demonstrated that auditory and visual modalities exhibit different properties when retrieved from reference memory. Swanton and Matell (2011), in a replication of their memory mixing effects observed in rats timing a compound cue (Swanton et al., 2009), found that rats differentially weighted durations when timing an average of the two, depending on which interval (long or short) was paired with which modality (tone or light), such that relatively equal averaging only occurred when the tone was associated with the short duration, with rats showing a greater impact of the visual interval than the auditory one, particularly when the visual stimulus was long. Consistent with this finding, in humans, it has been shown that visual stimuli exhibit greater “persistence” in memory, such that more exposures of a different interval are necessary to shift the memory of a visual interval (Gamache & Grondin, 2010; Ogden et al., 2010; Wiener et al., 2014). The greater persistence of visual intervals in reference memory may be due to the greater variability in their processing. Indeed, recent Bayesian accounts of temporal reproduction suggest that greater measurement noise leads to a higher reliance on prior statistics (Jazayeri & Shadlen, 2010). However, these findings cannot entirely account for the difference between groups, as 1) any difference in processing fidelity should be observed regardless of the modality-duration pairings, and 2) no differences in the CV were observed across any conditions.

A second possible explanatory factor is the difference in duration length between the two intervals. Recent work suggests that different processing regimes exist depending on whether the intervals tested are sub-second or supra-second. In the present study, the intervals tested were 500

and 1000ms, and so the difference between over and under reproduction between modality and interval may have been due to a difference in how 500ms and 1000ms signals are processed. However, this would suggest that visual stimuli are weighted more in memory-mixing effects at supra-second intervals, whereas auditory stimuli are more weighted more at sub-second intervals, a finding which is unlikely, given that visual stimuli generally exhibit greater weights across both duration ranges (Takahashi & Watanabe, 2012).

A third possible explanation, following on the work of Matell and colleagues (Matell & Kurti, 2014; Matell et al., 2014) is that, when retrieved from reference memory, intervals are combined based on both their modality and prior probability associated with interval. In the original formulation of PCM, the retrieval from reference memory involves the selection of an exemplar, represented as a sample from a distribution of previously reinforced times. In the present experiment, the cue stimulus should lead to this retrieval process, but, on incongruent trials, the wrong modality should lead to the retrieval of a second sample. However, distinct weights could be applied to each sample when averaging. To explain the present findings, one could construct a prior in which tones are more likely to be short in duration, and lights are more likely to be long (De Corte & Matell, 2016; Stocker & Simoncelli, 2006). In this framework, short-duration tones and long-duration lights should be weighted more in memory. Thus, in the Tone-Short group, memory-mixing is observed, but in the Tone-Long group, the weight of the incongruent modality durations has been substantially reduced. Further work to test predictions of this account across more intervals will be necessary to test this mechanism.

We note that our findings additionally provide only a partial replication of a similar paradigm in rats (Meck, 1984). In that study, rats trained on two intervals were capable of using an incongruent modality to time the appropriate interval, with the only feature being a slight under-

reproduction when using an incongruent auditory modality. Notably, in that study, only one modality-duration pairing was used, in which the tone was paired with the long interval. In the present study, when the tone was paired with the long interval, we similarly found little impact of the incongruent modality. We speculate that, had the opposite pairing been used (Tone-Short), the memory-mixing pattern would have been observed. In that study, Meck suggested that the difference in modalities was driven by an attentional orienting effect, in which the incongruent auditory stimulus was more efficient at drawing attention, and so started the accumulation process earlier. Yet, this account cannot explain the present findings, in which 1) a much larger effect was observed, for both auditory and visual incongruent stimuli, and 2) no effect was observed in the Tone-Long group.

As a limitation to the present study, we note that the pattern observed in the Tone-Short group could, in principle, be explained by either a clock-speed or a memory-mixing pattern. However, we suggest that 1) the memory-mixing effect is the more parsimonious explanation, and 2) neither effect can fully explain the effect in both groups. To the first point, a true PCM clock-speed account would suggest that, with a difference in pacemaker rate between modalities, the size of the under/over-reproduction pattern should be larger for the long interval than the short one. Instead, we found that the degree of under and over-reproduction was the same between duration ranges, such that subjects over-reproduced on average by a similar amount (220ms) as they under-reproduced (201ms). To the second point, the clock-speed account would also predict a shift in the Tone-Long group, but in the opposite direction as the Tone-Short group, such that subjects should under-reproduce the short stimulus when incongruent, and over-reproduce the long stimulus when incongruent.

Overall, our findings suggest that memory for durations may be held in modal regions related to the modality duration standard. The differences in modality-specific ‘clocks’ may interfere with the memory of duration standards for different modalities, such that the clock rate of the preceding auditory stimuli with a shorter standard strongly biases the perception of later visual stimuli with a longer standard. Other researchers have observed similar differences in modality clock speeds, suggesting that different modalities specifying short and long durations may contribute to the differences in responses (Droit-Volet et al., 2007; Penney et al., 1998; Penney et al., 2000). Therefore, we propose that both modality-specific and modality-independent timing components may exist (Stauffer et al., 2012), with different modality-specific ‘clocks’ producing the initial duration representations, followed by transformation into an amodal form if these representations are identified as standards (Filippopoulos et al., 2013).

Conclusions

Based on our findings, we suggest that durations stored in reference memory retain their modal status, but that the modality additionally interacts with the duration range, such that the timed duration is differentially weighted, depending on both factors. These differences are both similar, and in contrast to earlier work by Meck (1984) on cued retrieval from reference memory, and argue against an exemplar-based retrieval from reference memory for interval timing.

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