Temporal memory averaging: 
Resolution of conflict in temporal expectations

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Abstract Animals are able to control their behavior in time so that it corresponds to the temporal relations that exist in the environment. However, what happens if temporal signals in the environment are inconsistent with one another? We have found that, when two cues that each signal a different delay to reinforcement are presented simultaneously, rats will often behave as if they are timing an average of their respective durations. We have interpreted this phenomenon as resulting from an integration process in which different temporal memories are combined into a weighted average, which is then timed in an otherwise normal manner. Here, we review the factors that moderate temporal memory averaging, and discuss implications that this averaging behavior has for theories of interval timing, as well as conflict in other domains.

Key words: Interval Timing, Rats, Memory, Integration

Interval Timing

The perception of time in the seconds-to-minutes range, interval timing, is a crucial component underlying efficient behavioral organization. For example, some have proposed that foraging organisms decide to leave a food patch when the inter-food interval becomes larger than a value related to the average rate of return for patches of that type (Brunner, Kacelnik, & Gibbon, 1992). Similarly, the interval between related events (e.g., between a neutral stimulus and a biologically relevant stimulus) moderates not only the strength, but also the temporal organization, of conditioned responding. For example, Pavlov (1927) reported that, when his dogs were trained that there was a moderate delay (e.g., 30s) between the presentation of a conditioned stimulus and an unconditioned stimulus, the conditioned response was strongest towards the end of the interval, a phenomenon that Pavlov referred to as ‘inhibition of delay’.

The peak interval procedure is frequently used to study interval timing (Roberts, 1981). In this discrete-trials task, some trials are reinforced on a fixed-interval schedule, such that the first operant response made after the passage of a set interval since trial onset (e.g., 40s after the onset of a discriminative stimulus) is reinforced. Earlier responses have no programmed consequence, and trials are separated by “black-out” periods. On other non-reinforced “probe” trials, the stimulus commences and then terminates in a response-independent manner after several times the fixed interval. Plotting the average response rate as a function of time in the trial reveals a Gaussian, or Normal, shaped curve with the mode, or “peak time”, near the duration of the fixed interval. If the

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animal had been trained with a different fixed interval, both the peak time and the spread of the response time distribution, the “peak width”, would vary in direct proportion to the duration (e.g., if the FI was doubled to 80s, rather than 40s, the peak width would also double). This relationship is known as the scalar property (Gibbon, 1977). Finally, the height of the response function (i.e., “peak rate”) is used as a measure of motivational or associative strength. Roberts (1981) showed that peak rate and peak time were dissociable.

There are numerous theories that can explain interval timing behavior, across multiple levels, from neurophysiological models (Laje & Buonomano, 2013; Matell & Meck, 2004; Simen, Balci, de Souza, Cohen, & Holmes, 2011) to behavioral theories (Killeen & Fetterman, 1988; Machado, 1997) to cognitive models (Block & Zakay, 1997; Gibbon & Church, 1984). Most of these theories can be described in information-processing terms. The “clock” is some, presumably neural, mechanism whose variation as a function of objective time maps onto subjective time. For example, Treisman (1963) proposed a pacemaker-accumulator style clock in which pulses are released from a pacemaker, and summed in an accumulator. The level or value in the accumulator maps onto time in a temporally specific, monotonic manner, growing as time passes. In relation to the peak-interval procedure described above, the value in the accumulator is reset to zero at trial onset, and then grows as time elapses. When food reinforcement is provided, the clock is stopped, and the value in the accumulator is stored in reference memory. Subsequently, at the start of a trial, a value is obtained from this temporal memory store, and the subject begins responding when the current accumulator value gets sufficiently close to this retrieved value. During probe trials, the subject stops responding when the current accumulator value gets sufficiently beyond the value drawn from temporal memory (Gibbon, Church, & Meck, 1984). Due to variance in any, or all, of these components (Gibbon, 1992), the time at which a subject starts and stops responding varies across trials (K. Cheng & Westwood, 1993; Church, Meck, & Gibbon, 1994), resulting in the Gaussian-shaped response distribution seen when the average response rate is computed across all trials.

Temporal Averaging

Perturbing the components of psychological and neural systems is a standard way to explore their composition. For example, Cheng and Roberts (1991) trained pigeons on a peak interval procedure in which two visual stimuli were associated with different FI durations. They perturbed the system by providing compound probe trials in which both of these stimuli were presented simultaneously. The compound response function was unimodal, with a peak time that fell in between the component FI durations. However, response rates were low during compound trials, causing substantial variation in peak times across subjects and also preventing an assessment of the precise shape of the response distribution. Nevertheless, these authors concluded that the pigeons were forming a vector average of the retrieved temporal memories, following from Cheng’s proposal that spatial navigation is based on an average of self-to-goal vectors derived from different landmarks (Cheng, 1989). Several years ago, we revived this approach in rats (Swanton, Gooch, & Matell, 2009). Specifically, we trained rats on a dual duration (10s and 20s) peak-interval procedure, in which two different modality cues (tone and light) were associated with the different durations. When tested during compound probe trials, the rats showed a unimodal, Gaussian-shaped peak function that fell in between the two FI durations (Figure 1A & 1B). Unlike Cheng and Roberts’ data, the peak response rate during compound trials was greater than that for either of the component cues. Most importantly, this compound peak was approximately scalar (Figure 1C), as the coefficient of variation of the compound peak function was in between that obtained for
the component peak functions. The lack of superimposition of the component cues is presumably due to the fact that the two stimuli were associated with different reinforcement probabilities (see Kaiser, 2008; Roberts, 1981). Specifically, to obtain equivalent peak rates of responding to the component cues, the short cue had twice as many probe trials as the long cue, thereby equating reinforcement density.

Because the compound peak was scalar, the simultaneous presentation of two temporal cues appeared to result in a combinatorial operation at some stage in the timing system, such that the final response output was indistinguishable from what would be expected if the animal had been trained to time a single duration at that time. Specifically, we interpreted this scalar peak as evidence that rats had integrated, or averaged, the temporal memories associated with each cue, and this average was then timed in an otherwise normal manner. This averaging phenomenon was not observed in the rate of responding, which appeared to additively summate under compounding conditions (see Weiss, 1972).

Since this initial finding, we have conducted a series of experiments to explore the rules and boundary conditions of temporal memory averaging. First, we examined whether this phenomenon was specific to the particular durations (10s and 20s) or duration ratio (1:2) used by Swanton et al. (2009). To this end, we trained rats using duration ratios of 1:3 (4s:12s and 8s:24s), 1:4 (5s:20s), and 1:6 (5s:30s) (Kurti, Swanton, & Matell, 2014; Swanton & Matell, 2011). We found that the pattern of responding was moderated by the modality-duration relationship of the trained component cues. Specifically, when an auditory stimulus signaled the short duration and a visual stimulus signaled the long duration (the tone-short, light-long group — TSLL), rats produced normally shaped, scalar response distributions that fell in between the component durations, similar to that seen in Swanton et al. (2009). However, when the visual and auditory stimuli signaled

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**Figure 1.** Average response rate functions from probe trials in the peak-interval procedure. The short and long cues (tone and houselight, counter-balanced) were reinforced on a proportion of trials at 10s and 20s, respectively. On compound trials, the tone and light were presented simultaneously, and reinforcement was not provided. Panel A shows raw response rate functions, highlighting the additive summation in response rate for the compound cue, whereas Panel B shows responding as a proportion of maximal rate to highlight the intermediate timing of compound responding. Panel C plots these response rate functions after normalizing by peak time, and shows that the compound response function largely superimposes on the component cue functions. These data show that the compound cue has scalar variability and suggests that rats are timing an averaged expectation in an otherwise normal manner. Data from Swanton, Gooch, & Matell (2009).
the short and long durations, respectively, (light-short, tone-long group — LSTL), compound responding was asymmetric in shape and broader than scalar, as the left half of the response function overlapped the left half of the short (light) response function and the right half was elongated and fell in between right tails of the component durations. One possible explanation for this unusual response form is that the rats first timed the short cue in a veridical manner, and then switched to timing an average expectation. Consistent with this, LSTL rats trained with 5s:30s durations showed bimodal compound response distributions with the first mode at the short duration, and the second mode at an intermediate time. Intriguingly, both peaks were approximately scalar. In other words, LSTL rats appear to use a sequential strategy when presented with discrepant temporal information, in which they time both an independent and integrated expectation simultaneously. Unfortunately, when the criterion durations are close together, these peaks likely merged together (see Leak & Gibbon, 1995), hindering our ability to precisely characterize the behavior. As such, we will focus on the behavior under TSLL conditions, which has shown consistent scalar temporal averaging.

Besides showing a qualitative difference in the pattern of responding as a function of the modality-duration relationship, we also found that TSLL rats’ compound peak times became progressively closer to the long duration as the durations became more discrepant (Kurti et al., 2014; Swanton & Matell, 2011). However, in order to maintain equivalent response rates for the two cues across groups/studies, we had simultaneously increased the discrepancy in their reinforcement probabilities (i.e., equated reinforcement density, as opposed to reinforcement probability). We suspected that the peak location was biased toward the duration that had the greater probability of reinforcement, which was the long duration in all cases. More specifically, we hypothesized that rats were weighting each duration by its relative reinforcement probability. Specifically:

\[ wA*A + (1-wA)*B = C \]

in which A and B are the component durations, and wA reflects the relative likelihood of a reinforced trial for that cue. If the probability of reinforcement for A=10s is 25% and the probability of reinforcement for B=20s is 50%, \( wA = 25%/(25% + 50%) = 0.33 \). Thus, the expected compound peak time = 0.33*10 + 0.67*20 = 16.7s. To assess this hypothesis, we recently plotted the predicted compound peak times (using the above equation) against the obtained compound peak times across all of these datasets (Kurti et al., 2014). Remarkably, the best fitting regression line had a slope of 0.99 (\( R^2 = 0.86 \) with the intercept set at 0), indicating that we were able to accurately account for the rats’ behavior during compound trials using nothing more than their component peak times and the programmed reinforcement probabilities.

While this relationship is very strong, it was a post-hoc characterization of the data. Holding the component durations constant and changing their relative reinforcement probabilities would be a more direct test of this hypothesis, as it would allow us to evaluate whether the compound peak times would shift in the expected manner. To this end, across two experiments, Matell and Kurti (2014) trained six groups of TSLL rats on a peak procedure in which 4 and 12 seconds served as the component FI durations and the reinforcement probabilities associated with each duration varied across groups. Consistent with our hypothesis, compound peak times largely co-varied with the component cue reinforcement probabilities, falling closer to the duration associated with the greater probability of reward. However, when the reinforcement densities were highly discrepant (e.g., in the most extreme group, the short cue’s reinforcement density was 6 times that of the long cue), the form of the compound response function became asy-
metric, with the left tail overlapping the left tail of the short cue, and the right tail declining in a shallower manner and terminating at an intermediate duration. In other words, when a cue signaled both a greater likelihood of reinforcement and a shorter delay to reinforcement, the rats changed their response strategy from solely timing a weighted average to a simultaneous timing strategy, as described above for the LSTL rats. Together, these data suggest that rats can utilize different strategies when confronted with discrepant temporal information, and that strategy selection depends upon the relative value of the cues. In fact, intrinsic differences in value may be responsible for the modality effects described above, as Weiss, Panlilio, & Schindler (1993) found visual stimuli were more readily associated with positive outcomes than auditory stimuli (for further discussion see De Corte & Matell, 2016).

Intriguingly, while the relative value of the two cues appears to moderate strategy selection, averaging behavior does not appear to be impacted by differences in the sensory-specific qualities of reinforcement. For example, Delamater and Nicolas (2015) trained a group of rats that two different cues predicted the availability of two different outcomes (i.e., equally caloric grain pellets that were either sweet or not), at two different times (5s and 20s). A control group was given equivalent training, except that both outcomes were used as reinforcement for both cues and durations. Compound testing revealed equivalent temporal averaging irrespective of whether the cues signaled differential outcomes or not. Intriguingly, selective satiation of one of the outcomes biased the compound peak away from the duration associated with that devalued outcome. These data extend the findings of Matell & Kurti (2014), by showing that the weights given to each duration are able to be altered in an online manner, suggesting that it is the cue values at the time of memory retrieval, rather than at memory storage, that bias the integration process.

In the work reviewed above, rats were trained to make the same operant response to both component cues. As such, colleagues sometimes ask whether the intermediate compound peak might simply be an artifact of the rats responding to both of the component cue durations in an independent and veridical fashion during compound trials. Overlap in the two response distributions could cause the average compound response rate to appear unimodal, with a peak falling in between the two durations. Although such a phenomenon would generate a broad, non-scalar peak, which conflicts with the scalar response form we have obtained, we sought to further explore this possibility. To this end, De Corte & Matell (2016) trained rats to associate a tone and light with different durations. However, in contrast to past studies, each cue also required a spatially specific response (e.g., tone = respond after 5s at the left nosepoke, light = 20s at the right nosepoke). The rats easily learned this discrimination, responding only on the appropriate nosepoke and time for each cue. During compound trials, we found that TSLL rats primarily responded at only one, or the other, nosepoke on each trial (i.e., rats responded on both nosepokes in a sequential manner on only 12% of compound trials). When TSLL rats responded only on the short nosepoke during compound trials, the peak time was shifted to the right by more than 50% relative to trials where the short cue was presented alone. In contrast, when rats responded only on the long nosepoke during compound trials, the peak time was shifted to the left by over 30%, relative to responding when the long cue was presented alone. In contrast, when rats responded only on the long nosepoke during compound trials, the peak time was shifted to the left by over 30%, relative to responding when the long cue was presented alone. As in our other averaging work, these compound peaks were scalar, indicating that the intermediate peaks found previously in compounding experiments were not artifacts of response summation. Surprisingly, the compound peak times at the short and long nosepokes did not overlap. Rather, the peak time at either nosepoke fell closer to its respective duration, indicating that more weight was given to the duration associated
with the aperture on which rats responded. One possible interpretation of these data is that, during each compound trial, attention was drawn toward one of the two cues, causing its respective duration to be weighted more heavily. These attentional shifts could be due to variability in the salience of the two stimuli across trials, perhaps due to habituation of a particular signal. However, during pilot studies in our lab, manipulating the volume of the auditory stimulus had no detectable effect on compound responding. Rather, following from Delamater and Nicolas’s (2015) results, the change in attention might be due to the recent (non-)reinforcement on a prior component cue trial, which may have produced a temporary increase or decrease in the value of a particular cue.

**Implications of Temporal Averaging**

While temporal averaging has provided valuable insight into how temporal expectations are formed when conflicting temporal information is present, it also has broader implications for the field of interval timing. For example, the phenomenon of temporal averaging provides constraints on the composition of interval timing theories. As mentioned previously, there are different types of timing models, with some proposing accumulation processes (Gibbon, 1977; Simen et al., 2011), and others proposing that sequences of neural network states evolve in time (Buonomano, 2000; Matell & Meck, 2000). The accumulation models represent time as a monotonically growing (or declining) variable, and therefore, within these theories, temporal memories reflect this monotonicity. In these models, the phenomenon of temporal memory averaging is relatively easy to account for by proposing that these memory values are averaged together during compound trials. For example, Scalar Expectancy Theory (Gibbon & Church, 1984) proposes that temporal memory is encoded as the number of pacemaker pulses accumulated at the time of reinforcement. Under the simplifying assumption of one pulse per second, an organism would store a memory of 10 pulses for a 10s interval and 20 pulses for a 20s interval. When the cues for both of these intervals commence, the organism could retrieve these two pulse count memories, and average them together (presumably in a weighted manner), thereby arriving at a rule to respond around 15 pulses. The resulting behavior would be scalar, as the timing system would operate in an otherwise identical manner. Alternatively, the drift diffusion model of timing (Simen et al., 2011), which is computationally related to the Behavioral Theory of Timing (Killeen & Fetterman, 1988; Simen, Rivest, Ludvig, Balcı, & Killeen, 2013) proposes that the accumulation process operates at a rate that is inversely proportional to the reinforcement delay. Responding occurs when the accumulation level reaches a fixed threshold. As temporal memory in this model is the clock rate, when multiple cues are presented, the two clock rates could be averaged together, and the timing system would then operate in an otherwise normal manner.

In contrast, the network models propose that each neural state begets the next neural state (in some ways similar to a Markov chain), but there is no requirement that there is anything monotonic about this progression (i.e., the neural activity patterns do not need to get larger in extent, rate, or complexity as time elapses). As a result, temporal memories in these models are instantiated as particular neural patterns. In other words, organisms are thought to respond when a previously reinforced network state occurs. In contrast to the accumulation models, it is difficult to account for scalar responding at an intermediate duration, because the combination or average of two non-monotonic network states is highly unlikely to be similar to the network state that corresponds to an intermediate time. An analogy will perhaps clarify this argument. One can think of the progression of neural states in these network models as the sequence of sounds produced by an orchestra, with different neurons in different neural areas represented as different
musicians playing different notes on different instruments. One could mark an important interval as the time at which the violins are playing one note, the piccolos another, and the tympani drums are struck. A later interval could be marked by the crash of the cymbals along with the bowing of a low C on the bass. The problem with accounting for temporal averaging can be seen in trying to combine these temporal representations in some manner. There is no reason to suppose that a combination of any, or all, of these instruments playing these specific notes would reflect a time point that is between these two intervals. Indeed, it is not hard to imagine that this symphonic piece was written such that between these two time points, these instruments aren’t playing at all, but rather an oboe and cello are playing a duet. Indeed, by sheer probability, it is more likely that such a combination of neural events would occur outside the interval range (given the infinite opportunity for this coincidence of elements to occur).

Temporal averaging may also provide insight into how broader theories of decision-making can be used to guide the development of future interval timing models. Specifically, studies investigating a phenomenon referred to as “cue integration” have shown that averaging behavior occurs in a variety of contexts. For example, when asked to estimate the location of an auditory and visual stimulus that are simultaneously presented in slightly different spatial positions, humans judge the two cues as originating from a single, intermediate location (i.e., they “integrate” the two cue-locations into an average). Importantly, if the appearance of the visual stimulus is corrupted, the location of this average shifts towards the position of the auditory stimulus (Alais & Burr, 2004; Battaglia, Jacobs, & Aslin, 2003). In other words, subjects appear to compute a weighted average of the two stimulus positions, with less weight being given to the cue that is more difficult to localize. Cue integration is not limited to the spatial domain, as similar reliability-based, weighted averaging occurs when subjects are presented with discrepant size (Hillis, Ernst, Banks, & Landy, 2002), shape (Johnston, Cuming, & Landy, 1994), and slant (Ernst, Banks, & Bülthoff, 2000) information. These results are often interpreted using Bayesian Decision Theory; a broad theoretical perspective geared toward explaining how judgments are made under conditions of uncertainty. Given the similarities between temporal averaging and cue integration, it would be worthwhile to examine whether temporal averaging can be explained from a Bayesian standpoint (for discussion of averaging behavior during spatial navigation in relation to cue integration see Cheng, Shettleworth, Huttenlocher, & Rieser, 2007). This has the potential to not only provide further insight into the mechanisms underlying temporal averaging but also inform recent attempts to construct Bayesian models of interval timing (For further discussion of this topic see De Corte & Matell, 2016b).

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