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Temporal memory averaging and post-encoding alterations in temporal expectation

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Abstract

Recent work in our lab has demonstrated that rats trained to associate two different reinforcement delays with two different cues will generate a scalar temporal expectation at a time between these delays when presented with the cue compound. This work demonstrates that rats will integrate distinct temporal memories at retrieval, revealing that temporal expectation need not be a veridical representation of experience. Following from this recognition that processes occurring at or after memory retrieval may transform or bias temporal expectations, we suggest that previous pharmacological work that had been interpreted as resulting from sensorial, or clock-speed, changes, may be alternatively interpreted as resulting from mnemonic alterations. We end with a brief review of the impact of post-encoding alterations of memory on behavior other than timing.

Keywords

Interval Timing; Time Perception; Integration; Retrieval

The temporal control of behavior in the range of seconds to minutes is an important capacity enabling organisms to efficiently interact with the temporal regularities of the world. For example, a foraging hummingbird visiting a patch of replenishing nectar needs to return to the patch after a sufficient amount of time has elapsed since the source was depleted, while limiting the revisit interval to prevent competitors from cashing in on a full source. Different nectar sources have different replenish durations (McDade & Weeks, 2004), and hummingbirds can identify the correct durations to use for each patch (Gonzalez-Gomez, Vasquez, & Bozinovic, 2011; Henderson, Hurly, Bateson, & Healy, 2006). Such data clearly demonstrate that different temporal memories can be selectively encoded and retrieved to guide behavior, and imply that errors associated with these memory processes will have profound effects on behavior. Nevertheless, work in the field has tended to focus on the sensational side of the coin (i.e., the operation of an “internal clock”), rather than the mnemonic side. For instance, after training subjects to time a 7s interval, Maricq, Roberts, & Church (1981) administered methamphetamine in an acute manner and found a leftward shift in the time of peak responding. These data, like many others, have been interpreted as resulting from an increase in the speed of an internal clock process. In some respects, this clock-focused approach seems apropos; certain psychophysical methods, such as a reproduction task in which a subject reproduces a duration that varies on every trial, can be utilized without reference memory processes (though see Jazayeri & Shadlen, 2010). However, in the foraging situation described above, and presumably in the majority of

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circumstances in which temporal control is utilized outside the lab, temporal reference memory processes are critical for temporal perception. Indeed, recent work in our lab showing that rats will integrate multiple temporal memories to generate a singular expectation has emphasized the importance of reference memory processes in timing. This work has caused us to begin re-evaluating and re-interpreting patterns of data that have traditionally been explained as reflecting the role of internal clock processes in the temporal control of behavior.

It has been argued that all models of timing are composed of three information processing components: a clock process that provides a sensation of time passing, a memory store that holds the clock readings associated with biologically relevant events, and a comparison process that evaluates the similarity between the current clock reading and the appropriate memory (Church, 1997). A number of different instantiations of this generalized information processing model exist, with nearly all of them varying in the processes underlying the clock. For instance, in perhaps the most influential model of timing, Scalar Expectancy Theory (SET), the clock is composed of a pacemaker-accumulator process that grows in a linear manner as a function of time (Gibbon, 1977; Gibbon & Church, 1984; Gibbon, Church, & Meck, 1984). The accumulator is reset at the beginning of each “trial”, and the magnitude of the accumulator (i.e., the number of pulses) at the time of a biologically significant event is a measure of the amount of subjectively elapsed time, and is stored in reference memory. Due to variability in either clock speed and/or a multiplicative memory storage process, the value stored on each trial may differ despite equivalent objective times of reinforcement. As such, a distribution of temporal memories is postulated to exist for a single duration event. Upon subsequent opportunities to time, a sample from this distribution of memories is retrieved and is compared in an online manner to the developing accumulator value. To generate scalar variability in temporal behavior given the linear accumulation process, the comparison process is a proportional one (i.e., a computation of the relative discrepancy between current accumulator value and sampled memory). Interestingly, because of the potential for a scalar transform during the transfer to reference memory, the original model assumes that either there is no bias in this transfer or there is an opposite transform during the retrieval process.

In contrast, in the Striatal Beat Frequency (SBF) Model, a network state model, the clock is instantiated by the dynamic spatial-temporal pattern of cortical activity, such that a monotonic progression of subjective time does not exist (Matell & Meck, 2000, 2004). Temporal memories are encoded as cortico-striatal synaptic weights that are potentiated or attenuated based on the activity of these synapses coupled with the activity of the striatal neuron and the presence or absence of reinforcement, and thus reflect a composite of all past memories. Responding occurs whenever cortical activity, filtered through these synaptic weights, reaches the threshold for firing an action potential.

Finally, while harder to fit into an information processing framework, the Learning to Time (LET) theory (Machado, 1997), which is a dynamic offshoot of the Behavioral Theory of Timing (Killeen & Fetterman, 1988), construes the clock as a sequential activation of overt or covert behavioral “states”, with the rate of state transition inversely proportional to the reinforcement delay. In BET, a pacemaker pulse drives the transition to the next state in sequence, while in LET, the spread of activation relates to the “synaptic” strength between states, or as Machado (1997) suggested, the size of the hole in a chain of leaky buckets. In any case, while the pacemaker rate in BET, or spread rate in LET, is analogous to temporal memory, it is assumed to reflect a composite of past reinforcement rates, and is not a discrete distribution that can be sampled as in SET.

While there have been legitimate criticisms of all of these models, SET has nevertheless proved to be a particularly useful framework for interpreting the effects of pharmacological manipulations, and we review the effects and interpretations here. The most intriguing findings are those of Meck (1983). In this work using a bisection procedure, he demonstrated that drugs that increase synaptic dopamine levels, such as methamphetamine, cause a leftward shift in the point of subjective equality (PSE) when given acutely, but not when given chronically. In contrast, drugs that increase cholinergic activity, such as physostigmine, cause a leftward shift in the PSE when given chronically, but not when given acutely. These data were interpreted as resulting from changes in the clock speed and the memory storage transform bias parameters, respectively. Specifically, the argument was presented that when trained on saline, and then given methamphetamine, the speed of clock processes increased, thereby leading to more rapid accumulation, and a leftward shift in the PSE. In contrast, when trained on methamphetamine, the faster clock leads to a different accumulated pulse count at reinforcement, but all behaviors during testing are based on these “fast” clock memories, so temporal control is veridical. In other words, if you learn to time an event that objectively lasts 10s with a fast stopwatch, the stopwatch may read 15s at the end of the 10s period, but you will simply use the stopwatch mark of 15s as your basis for controlling behavior to match the appropriate, 10s, duration. In contrast, as the cholinergic agonist, physostigmine, did not cause a shift in the PSE when given acutely, but did produce a shift when given chronically, the effect was interpreted as being due to a diminishment in the memory storage bias parameter such that a smaller than veridical accumulated value was stored in reference memory. In other words, imagine that you read 10s on your stopwatch after a 10s interval has elapsed, and then tell your partner to record 10s in the memory log, but your partner records 8s instead. As such, all subsequent attempts to time the duration will be short, because your partner tells you to stop at 8s, rather than 10s. Intriguingly, this finding of a chronic underestimation implies that the reverse memory transform is not equivalently impacted by cholinergic drugs. In summary, these pharmacological effects are well accounted for by an information processing model with the potential for variation in clock speed and memory encoding.

Temporal Memory Averaging

Several years ago, in the context of conducting an electrophysiological recording experiment for use with behaving rats (Matell, Shea-Brown, Gooch, Wilson, & Rinzel, 2011), we trained subjects using a multiple-duration peak-interval procedure to time 10s when presented with one modality cue (e.g., a tone), and to time 20s when presented with a different modality cue (e.g., a houselight). To eliminate differences in reinforcement density between the cues, the probability of reinforcement was twice as large for the 20s signal (50%) than the 10s signal (25%). As expected, the rats had response functions that peaked around 10s when presented with the short cue, and peaked around 20s when presented with the long cue. Anticipating that we would see different neurons selectively active for the two durations, and wanting to rule out the explanation that this differential activity was simply due to the different modalities of cues, we also presented the two stimuli in compound during non-reinforced probe trials. We anticipated that responding would simply begin at an early time appropriate for the short stimulus, and terminate at a late time appropriate for the long stimulus. Remarkably, we found that the rats responded in a normal peak-shaped manner at a time in between the two trained durations. Out of concern that this effect might have resulted from the potentially disruptive effects of the electrode cable or the electrode implantation surgery, we re-ran this experiment in naïve, intact, rats (Swanton, Gooch, & Matell, 2009). Our results are shown in Figure 1A. Importantly, normalizing the peak functions by the obtained peak time and response rate revealed that the compound peak superimposed on the component cue peaks, thereby demonstrating scalar timing (Figure 1B).

Because of the peak location and scalar response form, we interpreted these data (under the framework of SET) as resulting from the following set of processes. First, during training, two different memory distributions were formed, centered at the respective criterion durations, each associated with a distinct stimulus. Second, during testing, the simultaneous presentation of both cues induced the retrieval of both a short memory sample and a long memory sample. Third, the detection of multiple and/or discrepant memories led to a combinatorial process being exerted on these memories (i.e., temporal memory averaging). Finally, normal temporal behavior was generated based on this averaged expectation. On the other hand, the peak rate associated with the compound stimulus was significantly greater than the peak rate of the component stimuli, in line with past work showing partial summation of response strength under stimulus compounds (Weiss, 1972). As response rates are not predicted by SET (i.e., motivational factors cancel out in the model), this latter result is neither consistent nor inconsistent with SET, thereby indicating its limits in explaining data in temporal production procedures.

In contrast, the scalar compound response function is inconsistent with a network state model such as SBF, as the temporal memories in this model are instantiated by a broad spectrum of cortical-striatal synaptic weights. First, it is unclear how one would abruptly average different synaptic strengths in response to a compound stimulus. More importantly, as different cortical inputs are not systematically related to the durations being timed, it is highly improbable that an “average” of these synaptic inputs would produce maximal activity at an intermediate time. In other words, because the network state does not grow or decline as a function of time, but just changes in a repeatable, but non-systematic manner, there is no reason to expect an intermediate network state to occur at a time in between the component durations. The model could potentially produce maximal responding at a time in between the component durations if each duration was encoded by different neurons (which is the basic form of the model), and the temporally controlled output of these neurons was integrated by a downstream process. However, such integration would be expected to be similar to a summation process, and even with an appropriately chosen threshold, would not produce scalar responding.

Whether the basic finding of scalar compound responding at a time in between the component durations could be accounted for by LET depends on certain assumptions. The first question is whether the transition rate between states depends solely on the delay until reinforcement on food trials, or on the reinforcement density of the stimuli, thereby incorporating the ratio of food trials to probe trials (and perhaps length of the probe trials). In the latter scenario, because of the different probabilities of reinforcement used in the described experiment, the reinforcement density of each stimulus is either equal (when probe lengths that extend past the reinforcement time are ignored), or actually slightly larger for the long cue (when probe lengths are considered). As a consequence, transition rates would be either equal or faster for the long duration cue than the short duration cue, and therefore temporally controlled responding to the long cue could only result from later states being associated with responding than for the short cue. To achieve normal temporal control with the component cues (i.e., to avoid continuous responding at both early and late states), independent sets of states would need to be activated for the two cues. Under this scenario, compound responding would presumably result from both sets of states being activated, and responding would reflect a summation of the response rates generated from both states, thereby producing a broader than scalar, potentially bimodal, response function (in a manner similar to SBF above).

In contrast, if the state transition rate is based solely on the delay until food (i.e., without considering reinforcement probability or probe lengths), it would be half the speed on long 20s trials than short 10s trials, and would thereby account for the scalar response functions

of the component cues. In this case, the same set of states could be used for both durations, as they would be activated at different rates, and therefore different times, on short and long trials. In this case, if the compound stimulus drove the rate of the state transition process at a rate that was in between the rates associated with the component stimuli (perhaps via processes akin to lateral inhibition), scalar responding at an intermediate time would emerge. However, as described above, there was a greater level of responding to the compound stimulus compared to the component stimuli. Since responding is driven by the strength of the associative links of each state, this scenario would simply generate compound responding at the same rate as seen for the component stimuli. As such, it is necessary to conclude that an independent set of behavioral states is activated for each stimulus, and compound responding is the result of both sets of behavioral states being activated simultaneously, each driven by the same, intermediate, transition rate process, and each driving the operant behavior independently (so that there is summation in response vigor). We note here that while transition rate (or clock speed) is the process being “averaged” in LET, clock speed serves the role of temporal memory in this model, and thus under both SET and LET, intermediate, scalar compound responding would result from an integration of temporal memories.

These results of Swanton et al. (2009) were not the first data to suggest that animals would integrate temporal memories in response to stimulus compounds. Cheng and Roberts (1991) trained pigeons using a single modality design in which one visual cue signaled probabilistic reinforcement at a short duration (9s), and a different visual cue signaled probabilistic reinforcement at a long duration (30s). Responding on compound probe trials tended to occur at a time in between the two criterion durations. In keeping with the vector averaging model developed previously by Cheng (1989) in regards to spatial searching, the authors suggested that the birds were computing a weighted vector average of the criterion durations, and using this average to guide their behavior. However, the response rate on compound trials was extremely low, and responding extinguished very rapidly, leading to difficulties drawing firm conclusions regarding both the expected time of reinforcement and the form of responding (i.e., whether it was a single, scalar, peak or had a multi-modal form). In contrast, the rats in Swanton et al. (2009) had peak rates on compound trials that were greater than their peak rates on the component cue trials, and the response form was clearly scalar, thereby suggesting that their behavior was based on a single, average, expectation.

An averaging of expectations was also seen by Matell & Meck (1999) who examined the temporal control of behavior in rats on a multiple duration peak procedure, in which reinforcement was sometimes available at 10, 30 and 90 sec after tone onset on three different response levers. In contrast to other similar procedures with multiple reinforced durations (Fetterman & Killeen, 1995; Gallistel, King, & McDonald, 2004; Leak & Gibbon, 1995; Matell, King, & Meck, 2004), reinforcement at the shorter durations (i.e., 10 sec and 30 sec) did not terminate the stimulus, and reinforcement could be earned again on the same trial at a later duration (i.e., 30 sec and 90 sec). Analysis of peak responding on the 30-sec lever showed that the peak occurred at 25 sec when no reinforcement occurred at 10 sec, but at 35 sec when reinforcement was provided at 10 sec. Similar results were found for responding on the 90-sec lever, as a function of 30 sec reinforcement. These data were interpreted as indicating that the rats reset their temporal accumulation processes upon reinforcement, and therefore learned that reinforcement was available on the 30-sec lever after 30 sec (when no reinforcement-induced resetting occurred) or after 20 sec (when 10 sec reinforcement led to accumulation reset). It was further suggested that as a result of these incongruent pieces of temporal information, the two durations associated with the 30-sec lever (20 and 30 sec) were averaged to produce an expected reinforcement time of 25 sec.

Indirect evidence of temporal memory averaging can also be seen in Meck, Komeily Zadeh, and Church (1984) who trained rats on a peak procedure in which reinforcement was available either 10 sec or 20 sec after trial onset (duration counter-balanced between groups). After achieving steady state performance, the interval was switched (i.e., 10 sec rats were now reinforced after 20 sec or vice-versa), and the median time of responding on individual trials was tracked until the rats were correctly timing the new duration. These investigators found that the time of responding did not abruptly jump from one criterion time to the other, nor move in a smooth and gradual manner, but jumped first to an intermediate duration for a brief run of trials, and then jumped again to the new reinforced duration (although see Lejeune, Ferrara, Soffie, Bronchart, & Wearden, 1998). The peak time of the intermediate duration occurred at approximately 14 sec, the geometric mean of the reinforced durations, and this time was not modulated by the direction of the shift. The authors interpreted these data as suggesting that when confronted with uncertainty regarding the time at which reinforcement could be earned, the rats computed the geometric average of the previously reinforced and most recently reinforced times, and responded at that average time.

These averaging findings are also reminiscent of the “migration effect” shown by Malapani et al. (1998) in which Parkinson’s patients were found to blend multiple duration memories when trained and tested off their dopamine replacement medication. Specifically, patients were initially trained and tested with an 8s duration and a 21s duration in separate blocks using a peak-interval procedure. They tended to reproduce the 8s duration at a time longer than 8s, but they reproduced the 21s duration at a time earlier than 21s. In contrast, when trained and tested with a 21s duration alone, a small rightward shift was found. Together, these data suggested a problem in memory encoding or retrieval when multiple durations were learned. To determine whether encoding or retrieval processes were responsible for the migration effect, Malapani, Deweer, and Gibbon (2002) conducted a train-test medication removal paradigm, in which patients were trained and/or tested without their dopamine replacement medications. Migration effects were seen when tested without medication, irrespective of medication status during training. In contrast, when tested on medication, migration patterns were not found, irrespective of medication status during training. These data suggest that diminished dopaminergic activity disrupts a selective retrieval process in which only the appropriate temporal memory is utilized for behavioral control, thereby leading to both duration memories influencing responding for a single duration. Intriguingly, this effect may simply be an exaggeration of normal timing behavior, as the interaction of multiple temporal memories on one another appears to be a general phenomenon. Specifically, Veirordt’s Law, the observation that when tested with multiple durations, reproductions of the shorter durations tend to be longer than their objective duration while reproductions of longer durations tend to be shorter than their objective duration, has been seen in numerous experiments in both healthy human and non-human animals (see Lejeune & Wearden, 2009 for review). In other words, Veirordt’s law suggests that some degree of temporal memory integration occurs whenever multiple temporal intervals are processed.

To evaluate the boundary conditions associated with temporal memory averaging using stimulus compounds, we conducted a second, similarly designed, set of studies in which the absolute durations and duration ratios were varied (4s:12s, 8s:24s, 5s:20s, & 5s:30s Kurti, Swanton, and Matell (in press); Swanton and Matell (2011)). A representative example of these findings using the 4s and 12s durations is shown in Figure 2. Several unexpected findings were obtained. Both the form and placement of the compound peak function differed as a function of the modality-duration relationship. In rats with the tone-short/light-long relationship, compound responding peaked at a mean time of 10.8s, which was in between the short (5.2s) and long (12.8s) peak times. Importantly, the compound peak function was scalar, as demonstrated by its superimposition with the component peak

functions. In contrast, in rats with the light-short/tone-long relationship, while the compound peak function (peaking at 9.2s) also fell between the component cue peaks (peaking at 5.4s and 14.6s), the response function was obviously skewed, with a long right tail, and was significantly broader than scalar.

As before, the scalar compound peak in the tone-short/light-long rats indicates normal timing of a singular temporal expectation resulting from integrating the temporal memories associated with the tone and light cues. However, the finding that the compound peak was considerably closer to the long duration than the short duration did not mesh well with a simple average of the temporal memories. To explain this finding, we suggested that the rats behaved as though they were computing a weighted average, with the relative likelihood of reinforcement of the component durations serving as weights. In other words, the time at which the rats expected reinforcement during a compound cue reflected a combination of the expected times of reinforcement for the component cues, biased by the probabilities that food was available at each of those times. As shown in Figure 3, the actual compound peak times across 5 different experiments were well predicted by a relative reinforcement probability weighted geometric average of the component peak times, whereas the non-weighted averages were systematically earlier than the actual compound peak times, and grew more discrepant as the relative likelihood of reinforcement favored the longer duration. In contrast, a reinforcement probability weighted average of the transition rates in LET predicts a compound peak time that is approximately 10% earlier than the obtained compound peak time (± 0.07).

Such weighted averaging is not wholly surprising, as a similar phenomenon has also been observed in spatial navigation behavior. It has been repeatedly shown that animals will integrate the spatial information provided by external landmarks that specify the location of reinforcement (Cheng, 1989). Specifically, after learning that multiple, simultaneously available cues provide consistent information regarding the location of food, the manipulation of these cues (i.e., altering their relationship to one another) leads to spatial search at an “average” of the locations predicted by each of these cues. However, this integration of spatial information is biased by the usefulness of the landmarks (Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006). Specifically, when rats were trained with multiple landmarks in a Morris water maze, if one frequently presented landmark provided highly accurate information (i.e., when it was close to the target), the less reliable landmarks were not well learned. However, when the frequently presented landmark provided less accurate information (i.e., when it was far from the target), then other low accuracy landmarks were learned. In other words, the extent to which multiple cues are utilized to guide behavior reflects their relative reliability. Similarly, in the compounding studies described above, the reinforcement probability of the component cues reflects their reliability in predicting when food is available, and therefore influences the integration process so that one cue is utilized to a greater extent. Intriguingly, such information integration appears to extend beyond a single dimension. For example, it has been shown that temporal duration can be averaged with spatial position to produce a time-place expectation of reward (Cheng, Spetch, & Miceli, 1996). Additionally, multisensory cues are thought to be combined to create an integrated understanding of the environment. More specifically, combining disparate stimuli that potentially originate from the same source, such as sudden movements seen in the periphery and animal vocalizations, helps in interpreting and adapting to the environment (Körding et al., 2007). In concert with seminal work by Georgopoulos, Schwartz, and Kettner (1986) showing vector averaging of cortical motor neuron activity to generate movement directions, these findings suggest that information integration occurs across a range of levels of the sensory-motor processing network, and reflects a general mechanism for dealing with discrepancy in the brain. As such, it is worth reiterating the fact that the

scalar nature of the compound responding described here demands that it is temporal memories, rather than motor outputs, that are being integrated.

In marked contrast to the scalar compound responding seen in tone-short/light-long rats, the behavior of the rats trained under light-short/tone-long conditions was not consistent with normal timing behavior operating on a single temporal expectation, as responding was highly rightward skewed and broader than scalar. Single trial analyses suggested that during a compound cue trial the rats typically appeared to initiate responding at nearly the same time as they initiated responding for the short duration. However, termination of compound responding tended to occur at a time between the termination times for the short and long cues. However, the compound cue stop times were more variable than those of the tone-short/light-long rats, and relatively more variable than their responses to the component cues. As such, these data may suggest that the rats generated different stop time decisions on different trials (i.e., some short, some long, and some at an average duration). In any case, these data indicate that different rules and/or factors are utilized for initiating versus terminating responding. Such a discrepancy is generally inconsistent with SET, as although it allows different thresholds to be utilized for starting and stopping (Church, Meck, & Gibbon, 1994; Gibbon & Church, 1990, 1992), these thresholds are presumed to be tied to the same memory sample. In contrast, it appears that wholly different memories are used to guide starting and stopping in the compounding experiments. However, there is no obvious reason why the model could not be revised so that start and stop decisions are applied using different memory samples. For the same reason, these effects are also inconsistent with LET, as the “start” transition and “stop” transition should depend on the same underlying state transition process. One possible way in which different start and stop patterns could be accounted for by LET would be to allow the integration of “short” and “long” transitions rates to fluctuate over the trial. Perhaps a lateral inhibition type process, which would take into account the relative activity levels from the short versus long states, could generate this asymmetric outcome.

Like integration processes, selection strategies have also been seen in spatial navigation. For example, when navigating back to the nest site after a foraging run, both landmark-based cues and dead reckoning information is available, and these two sources of information are usually redundant. However, when these information sources are put into conflict, rats will selectively utilize the landmark based cues, until those cues deviate substantially from internally provided dead-reckoning information, at which point this internal information source takes precedence (Whishaw & Tomie, 1997). Based on these data, Cheng, Shettleworth, Huttenlocher, and Rieser (2007) argued that the degree of overlap in the distributions of spatial mappings moderates the selection/integration processes. It is well understood that sensorial and mnemonic information is noisy, and as such, a single snapshot of the environment or a single sample from memory provides only a possible instance of the true location. In situations where multiple noisy cues point to similar locations, the true location is most likely to fall at the point at which the location distributions are maximally overlapping, thereby generating behavior consistent with integration. In contrast, if the cued distributions do not overlap (i.e., the information provided by the cues is highly divergent), then responding at a point in between the locations is unlikely to be correct. Instead, responding at the mode of the more valuable or more reliable distribution makes better sense. As applied to temporal processing, if the discrepancy in the temporal memories, coupled with their variability and reliability, generated insufficient overlap at an intermediate duration, then the animal would presumably select one or the other temporal memory to guide behavior, rather than integrating them.

Nevertheless, it remains unclear why the modality-duration relationship should moderate this integration versus selection dichotomy. One possibility that follows from the

distribution overlap hypothesis is that there is a greater discrepancy in subjective durations when lights indicate a short duration and tones indicate a long duration, than in the reverse condition. Given work suggesting that auditory cues drive the clock faster than visual cues (Droit-Volet, Meck, & Penney, 2007; Penney, Gibbon, & Meck, 2000; Wearden, Edwards, Fakhri, & Percival, 1998), a 4s tone will seem longer than a 4s light, and a 12s light will seem shorter than a 12s tone. As such, a 4s tone will have a subjective duration that is more similar to a 12s light than the reverse, which is consistent with a discrepancy explanation. However, we found temporal averaging under tone-short/light-long conditions with the highly discrepant durations of 5s/30s (a 1:6 ratio), while we have not found temporal averaging with light-short/tone-long conditions with durations of 4s/12s (a 1:3 ratio). Given the relatively small differences in perceived duration between auditory and visual modalities (on the order of 10%), it is highly unlikely that a 1:6 tone:light ratio is perceived as being more similar than a 1:3 light:tone ratio. As such, it may be the case that it is the subjective value of the cues, which reflects a combination (Ho, Mobini, Chiang, Bradshaw, & Szabadi, 1999) of reinforcement magnitude, probability, and delay, that modulates the integration/selection decision. However, it is unknown whether there are modality dependent differences in delay, probability, or magnitude discounting or their integration, and if there are, whether they would be in the right direction and size to account for the effects described here.

Retrieval-Related Modulation of Temporal Expectations

Our findings suggest that post-encoding mnemonic processing is an important variable in the temporal control of behavior. The remainder of this paper considers whether alterations in post-encoding memory processing, specifically memory retrieval processes, might be usefully invoked to explain disruptions in temporal control resulting from drug administration. As stated earlier, the acute administration of a dopaminergic agonist, such as methamphetamine, leads to a proportional leftward shift in peak time, an effect that has been classically interpreted as resulting from an increase in the speed of an internal clock process (Buhusi & Meck, 2002; Maricq et al., 1981; Matell, Bateson, & Meck, 2006; Meck, 1983). However, this effect could also reflect an alteration in the reference memory value used to guide behavior (note that in LET, state transition or clock speed and reference memory are one and the same thing, so the following discussion only applies to models in which sensation and memory are construed as different processes). One possibility is that the retrieved memory is multiplicatively transformed, leading to an earlier expectation that is then timed in an otherwise normal manner (i.e., with a normal clock speed). A different possibility (at least for models that allow a distribution of memories to exist for each duration), is that the sampling process is biased. In such a scenario, the sampling process would selectively retrieve memories from the early side of the distribution. In both cases, the transform or bias would influence temporal control immediately, thereby appearing in acute experiments, which had previously been considered to be evidence of a clock speed effect. Indeed, following from the notion that start and stop responses can be based on independent memory samples (Church et al., 1994; Gibbon & Church, 1990), recent work by Taylor, Horvitz, and Balsam (2007), showing that amphetamine shifts the initiation, but not the termination, of responding is consistent with a memory bias operating on the start decision, whereas it is inconsistent with an increase in clock speed, which should produce equivalent results on both start and stop times.

One potential argument against this notion comes from the results with chronic administration of DA agonists (Meck, 1983, 1996). Meck (1996) trained rats on a peak procedure without drug and then administered methamphetamine in a chronic manner. In these rats, peak times shifted to an earlier time on the first drug session, but over repeated sessions, the shift diminished and rats returned to peaking at the criterion time. At this point,

saline was administered, and the rats shifted to a later peak time (i.e., rebound), with subsequent training leading to another renormalization. Meck explained these dynamic effects as resulting from the rats learning the new faster clock count reward relationship, and this new knowledge progressively dominating the memory distribution. One possible explanation for these effects within the framework of a sampling process disruption can be developed by reference to recent work showing that memories are not simply encoded and consolidated, but are reconsolidated following retrieval (Duvarci & Nader, 2004; Nader, Schafe, & Le Doux, 2000). Specifically, it has long been known that administration of a protein synthesis inhibitor immediately after fear conditioning training will prevent memory consolidation (Davis & Squire, 1984), thereby causing rats exposed to a tone-shock contingency on day 1 to fail to freeze when tested on day 2. Remarkably, administration of a protein synthesis inhibitor after testing on day 2, following normal learning on day 1, will cause rats that showed fear on day 2 to show no fear on day 3. These results have been interpreted as demonstrating that consolidated memories become labile following retrieval and need to be re-consolidated. Applied to the present situation, we propose that the biased sampling of a short memory will lead to a discrepancy between expected and obtained reinforcement. As a result of this discrepancy, the sampled memory's strength will be weakened. Continued early biased sampling will therefore cause the distribution to shift to the right, until the biased sample time and the criterion duration overlap. Upon removal of drug, unbiased sampling will result in selection of memories that are later than the criterion duration (as the distribution is now rightward skewed) and the reverse course of events will follow. It should also be noted that renormalization was not seen by Matell et al. (2004) following chronic cocaine administration, nor was it found by Kim and Matell (2012), following chronic amphetamine administration. In both cases, an immediate leftward shift was seen that remained similar in magnitude across the 10–14 sessions of testing.

The same basic approach can also be used to explain the performance of rats trained on a bisection task while they were being chronically administered methamphetamine (Meck, 1983). At test, their performance was veridical, whereas administration of saline resulted in a rightward shift in the point of subjective equality. However, one additional assumption must be made, that retrieval of the short and long memories for comparison occurs at signal onset, rather than signal offset (as is necessarily the case in the peak procedure). As such, when trained on methamphetamine, the rats would show a bias and sample from the left side of the short and long memory distributions. These memory samples would lead to an expectation of signal termination at these “early” times, and since the signal in fact would terminate at the (later) criterion durations, extinction processes would lead to the left side of the distribution being cut off. As such, at test, a leftward biased retrieval process would sample the appropriately veridical durations, and performance equivalent to saline trained rats would result. Subsequent administration of saline would eliminate the sampling bias, thereby leading to retrieval of later durations. As a result, the rats would deem intermediate durations to be more similar to the short sample, thereby leading to a rightward shift in the psychophysical function.

Post-Encoding Memory Dysfunctions in other Domains

The above experiments illustrate how reference to mnemonic rather than sensorial processes can be used to explain the temporal control of behavior. We argue here that an enhanced consideration of memory retrieval processes when designing and interpreting timing studies will facilitate our understanding of this important behavioral system. Additionally, mnemonic processes may be able to account for results traditionally explained using sensorial mechanisms, such as changes in clock speed. To drive this point home, we will briefly review the influence that altered mnemonic mechanisms, such as selection biases and

transforms occurring at memory retrieval, have in a variety of other domains (see Schacter, 2001 for a more thorough overview of human memory malfunctions).

A substantial body of research explores the potential fallacy of memories. For example, there have been a number of cases in which therapeutic techniques have led patients to “remember” past traumatic experiences, such as childhood abuse, the authenticity of which is later disputed (Loftus, 1997). In laboratory investigations of this phenomenon, when false events are presented among a number of true events (i.e. events that actually occurred during the participant’s childhood), the percentage of participants claiming to recall said false events increased in subsequent interviews (Hyman, Husband, & Billings, 1995). Similarly, the integrity of memories described by courtroom witnesses has also come under scrutiny because of possible retroactive modifications. Indeed, imagination exercises and leading questions have been found to influence both confidence in and the content of memories (Garry, Manning, Loftus, & Sherman, 1996). Source confusion could also lead to the retrieval of multiple memories with similar content, such as witnessing a crime and being questioned about it later, that are then mixed together to produce partially incorrect memories (Mitchell & Johnson, 2000). While this mixing is not the same as the “temporal averaging” described above because the memories are considerably more complicated and do not consist solely of variations of a single dimension, it is conceivable that these phenomena share common processes. In any case, the demonstration of false memories in humans reveals clear distortions of retrieved memory as a consequence of post-encoding processes.

The retrieval of memories can also show both positive and negative biases that are thought to be affected by internal factors, such as goal motivation and mood. Older adults tend to exhibit the positivity effect in which their attention and memory focus on positive over negative or neutral material (Carstensen, Mikels, & Mather, 2006). For example, when asked to recall past autobiographical events, older adults tend to recall a higher ratio of positive to negative events than younger adults. In one study, participants were asked to answer a questionnaire about past experiences for a second time identically to the way they had 14 years prior (Kennedy, Mather, & Carstensen, 2004). When they were asked periodically during the session to focus on their emotional states, they remembered the past more positively than they had first reported. On the other hand, when they were told to focus on informational accuracy of responses, they remembered the past more negatively than they had first reported. This suggests that current motivation and emotional regulation can bias memory retrieval. Indeed, depressed individuals exhibit a phenomenon that is essentially opposite to the positivity bias shown by older adults. This population shows a negative memory bias in which they recall more negative and less positive information than control participants that are not depressed for both autobiographical memories and in laboratory tasks (Pyszczynski, Hamilton, Herring, & Greenberg, 1989). Similarly, depressed people sometimes report diurnal variations in mood, and retrieval of unhappy experiences occurs more often during the more depressed parts of their day (Clark & Teasdale, 1982).

In addition to affecting past recollections and interpretations, biases in memory retrieval can also influence future expectations. Previous experience is often the best predictor of the future. However, if the experience retrieved from memory is systematically biased, it follows that expectation will also be biased. In depressed individuals, this may be particularly relevant since they exhibit unrealistically negative future expectations, or extreme pessimism or hopelessness, which correlates with suicidal intent (Beck, Weissman, Lester, & Trexler, 1974). A positive memory bias, on the other hand, could lead to unrealistically optimistic future expectations. For example, the incentive salience model of drug addiction suggests that drug-seeking behavior is elicited because of an increase in “wanting” rather than “liking” of the substance (Robinson & Berridge, 1993). Specifically,

rather than the drug generating an increase in experienced hedonic value, resulting in desensitization of this system, withdrawal symptoms and drug taking to alleviate these negative symptoms (Koob, 1996), the incentive salience model proposes that drug abuse results in a sensitization of the system generating incentive motivation toward the drug, thereby increasing drug-seeking behaviors. While this model does not reflect a transform or bias in hedonic memory, per se, it does reflect a change in a motivational system that is directly downstream from hedonic memory. Thus, the incentive salience model of drug addiction provides an example of how mechanisms associated with memory, in this case increasing the incentive salience associated with drug related stimuli, rather than those involved in sensation, or hedonics itself, can influence behavior.

To summarize, there are numerous examples of memory alteration and retrieval biases in a variety of domains. In the temporal domain, averaging of temporal memories appears to occur through mechanisms operating at memory retrieval. Additionally, temporal disruptions previously explained via reference to sensorial changes, could alternatively be explained as resulting from a memory retrieval bias. As such, we believe both mnemonic and sensorial mechanisms need to be considered equally when developing experimental designs and interpreting data.

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Highlights

- Rats show maximal temporal expectation at the average of previously trained component times when presented with a stimulus compound.
- The compound peak function is scalar thereby suggesting that rats average temporal memories and time the expectation in a normal manner.
- The compound peak time is well predicted by a reinforcement probability weighted average of the component cue peak times.
- Computations and biases during memory retrieval may impact temporal expectations.
- Retrieval based modulations of memory should be considered more strongly when interpreting timing experiments.

Figure 1.

Temporal memory averaging results from compounding two discriminative stimuli in a mixed-duration peak-interval procedure. Panel A shows the average peak response functions on probe trials from a peak-interval procedure in rats who were trained that one cue (tone or houselight, counterbalanced) predicted food availability after 10s, while a different cue (the cue not used for the 10s duration) predicted food availability after 20s. To equilibrate peak rates associated with these cues, the 10s cue was associated with 25% FI trials, and 75% probe trials, whereas the 20s cue was associated with 50% FI trials and 50% probe trials. In addition, the peak response function resulting from presentation of a tone-light compound is displayed. Rats were never reinforced on compound trials, yet showed a single, robust peak of activity at the midpoint between the two component cue peaks. Panel B shows superimposition of the peak functions after being normalized by peak time and response rate, thereby demonstrating that the compound peak was scalar. These data show that on compound trials, the rats are behaving as though they have retrieved two discrepant

temporal memories associated with the two component cues, averaged them to generate a singular expectation, and then timed this single expectation in an otherwise normal manner. Figure from Swanton, D. N., Gooch, C. M., & Matell, M. S., Averaging of temporal memories by rats, *Journal of Experimental Psychology: Animal Behavior Processes*, 35(3), 434–439, 2009, APA.

Figure 2.

The form and placement of responding to stimulus compounds in the peak-interval procedure varies as a function of the modality-duration relationship of the component cues. The top panels show average peak response functions on probe trials from a peak-interval procedure in rats who were trained that one cue (tone or houselight, counter-balanced) predicted food availability after 4s, while the other cue predicted food availability after 12s. Reinforcement probabilities for each cue were adjusted to equate mean response rates. The peak response function resulting from presentation of a tone-light compound is also displayed. Rats were never reinforced on compound trials, yet showed a single, robust peak of activity at the midpoint between the two component cue peaks. Those subjects in which the tone signalled the 4s criterion duration and the light signalled the 12s criterion duration are displayed on the left, whereas subjects with the reverse relationship (light = 4s, tone = 12s) are displayed on the right. Notice that the compound peak function is symmetrical, and closer to the 12s duration in tone-short/light-long rats, whereas it is rightward skewed, broad, and closer to the 4s duration in light-short/tone-long rats. The lower panels demonstrate scalar compound responding in the tone-short/light long rats, but not in the light-short/tone-long rats. Figure from Swanton, D. N. & Matell, M. S., Stimulus compounding in interval timing: the modality-duration relationship of the anchor durations results in qualitatively different response patterns to the compound cue. *Journal of Experimental Psychology: Animal Behavior Processes*, 37(1), 94–107, 2011, APA, adapted with permission.

Figure 3.

The compound peak time is best predicted by a geometric average of the component peak times when weighted by the relative reinforcement probability of the component cues. The data for this figure comes from tone-short/light-long rats, as subjects in this group showed scalar compound peak functions. On the ordinate, accuracy is computed as predicted compound peak time (based on averages of the obtained component peak times) divided by obtained compound peak time. The programmed component durations used for each experiment and the percentage of FI trials for each cue (with the remaining trials for that cue being probe trials) are displayed on the abscissa. The weights used for the weighted averages correspond to the relative probability of reinforcement. For example, in the 10s/20s group, the relative probability of reinforcement for the short cue is $33.33\% = 25\% / (25\% + 50\%)$, with a corresponding 66.66% relative likelihood for the long cue.