Published in final edited form as:

Behav Processes. 2014 January ; 101: 72–80. doi:10.1016/j.beproc.2013.09.003.

Effect of distracter preexposure on the reset of an internal clock

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Abstract

Interruptions and unfamiliar events (distracters) during a timed signal disrupt (delay) timing in humans and other animals. We hypothesized that repeated exposure to a stimulus may reduce its subsequent time-disrupting properties. To test this hypothesis rats were trained in a reversed peak-interval (RPI) procedure, in which dark timing trials were separated by illuminated inter-trial intervals. Rats were then repeatedly exposed to an auditory stimulus (noise) in either dark (DARK group), or illuminated chambers (LIGHT group); control rats were not exposed to the noise (NOVEL group). Afterwards, the time-resetting properties of the noise were tested by presenting it unexpectedly during the (dark) RPI trials. The noise reset timing in NOVEL rats, but stopped timing in DARK rats, suggesting that preexposure reduces the time-resetting effects of distracters. However, in LIGHT rats, the noise stopped timing when the presented early in the RPI trial, but reset when presented late, suggesting that exposure to noise was only partly effective in overriding other relevant variables, such as distracter location. These results suggest that the effect of distracter preexposure on the reset of an internal clock depends on complex associative and temporal interactions which require further investigations.

Keywords

distracter; habituation; preexposure effect; rat; reversed peak-interval procedure; salience; time-sharing

Introduction

Associative and temporal learning are fundamental for behavioral control. Animals learn to predict appetitive and aversive environmental stimuli using information from both domains. They learn that some events are good predictors of particular outcomes, and that reward prediction is reliable within a particular time window. Flexibility in using associative and temporal landmarks is critical for adaptive response and survival (Buhusi & Meck, 2005; Gallistel, 1990; Gallistel & Gibbon, 2000; Kirkpatrick & Church, 1998). Also adaptive is the capability to filter out inconsequential stimuli (Lubow, 1989). Should such events not be filtered out, they would impact on both associative and temporal processing. For example, presentation of novel events during a to-be-timed signal reset timing. On the other hand, novel events increase arousal (Sokolov, 1960) and associability (Lubow, 1989), and produce disinhibition (Thompson & Spencer, 1966). Therefore, the capacity to filter out

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inconsequential distracters is critical for both proper associative and temporal processing. Here we investigate the interplay between associative and temporal properties of novel and familiar events in resetting an internal clock. Previous studies investigated the role of intensity and discriminability of novel distracters (Buhusi, 2012), and the effect of unexpected presentation of reinforcement (Matell & Meck, 1999) on the reset of an internal clock. Here we examine the role of stimulus familiarity on the reset on an internal clock, by evaluating the effect of stimulus preexposure on its subsequent time-disrupting properties.

To investigate the interactions between associative and temporal variables on regulation of timed behavior, one could examine the effect of interruptions (gaps) and distracters (unfamiliar events) in a discrete-trial peak-interval (PI) procedure (Buhusi & Meck, 2000; Catania, 1970; Church, 1978). For example, during fixed-interval (FI) trials, the to-be-timed signal is turned on and the subjects' first response after the criterion interval is reinforced and turns the to-be-timed signal off. During peak-interval (PI) trials, the to-be-timed signal is presented for a much longer duration than the criterion, but subjects' responses are not reinforced. Trained subjects typically wait at the beginning of PI trials, then start responding and continue to respond throughout the trial, and quit responding towards the end of the trial: Therefore, in PI trials, the average rate of response gradually increases and peaks at the expected time of reward, then gradually decreases toward the end of the trial. In the PI procedure, the effect of interruptions can be evaluated by presenting gaps (interruptions in the to-be-timed signal, retention intervals) during an PI trial, or by presenting distracters (novel, unfamiliar events) during the uninterrupted to-be-timed signal (Buhusi & Meck, 2000, 2006a, 2006b), and evaluating the delay in responding produced by these distracters.

The fact that distracters delay timing in a manner undistinguishable from gaps despite the presence of the timed stimulus (Buhusi & Meck, 2006a, 2006b), and the fact that the response may be delayed anywhere on a continuum (Buhusi & Meck, 2006b; Buhusi, Paskalis, & Cerutti, 2006; Swearingen & Buhusi, 2010) between no delay (ignoring the distracter) (Buhusi, et al., 2006), and a large delay (indicative of restarting the entire timing process after the gap) (Aum, Brown, & Hemmes, 2004; Bateson & Kacelnik, 1998; Brodbeck, Hampton, & Cheng, 1998; Buhusi & Meck, 2006a; Buhusi, et al., 2006; Buhusi, Sasaki, & Meck, 2002; Cabeza de Vaca, Brown, & Hemmes, 1994; W. A. Roberts, Cheng, & Cohen, 1989) provides strong support for a time-sharing hypothesis (Buhusi, 2003; Buhusi & Meck, 2009), which can be applied in the framework of the Scalar Expectancy Theory (Gibbon, 1977; Gibbon, Church, & Meck, 1984) as follows (Figure 1A): Pulses regularly emitted by a pacemaker accumulate and are temporarily stored in working memory. During each FI trial, reinforcement is provided for the first response after the criterion interval, and the number of pulses currently in working memory is stored in the reference memory. During PI trials, subjects use a ratio rule to compare currently accumulated time (stored in working memory) and the learned number of pulses associated with the time of reinforcement (stored in reference memory), so that the average response rate reaches a peak when the two values are equal, i.e., at the expected time of reinforcement. According to the time-sharing hypothesis, during an interrupting event (gap and/or distracter), working memory for the interval preceding the interrupting event decays at a rate proportional to the salience of the interrupting event, due to memory and/or attentional resources being diverted toward processing the interrupting event (Buhusi, 2003; Buhusi & Meck, 2009). This view is consistent with the resource-sharing hypothesis from the human interval-timing literature (Fortin, 2003; Lejeune, 1998; Thomas & Weaver, 1975; Zakay, 1989, 2000) (Figure 1A).

Further investigations of this phenomenon indicated that, both in pigeons and rats (Buhusi, et al., 2002), the delaying effect of an intruder is proportional to its perceived salience (Buhusi, 2012). The role of salience in time-sharing is supported by studies in pigeons

(Buhusi, et al., 2002) and rats (Buhusi, Perera, & Meck, 2005) showing that despite gap duration and position being kept fixed, manipulations of the contrast in brightness between the gap and the timed signal shift the response functions in a great dynamic range. According to the time-sharing hypothesis, the higher the distracter salience (e.g., novel or salient distracter), the more resources would be diverted towards it, the fewer working memory resources would be available for timing, and the faster the accumulated time would decay during the distracter, resulting in a considerable delaying effect (Figure 1A). In contrast, the lower the distracter discriminability, the fewer resources would be diverted to its processing, the more resources would be available to timing (Figure 1B). For example, at 40% gap-signal contrast pigeons are minimally interrupted in their timing, while at 100% contrast they delay their timing after the gap (Buhusi, et al., 2002). A similar phenomenon has been observed in rats (Buhusi, 2012).

We hypothesized that the salience of a distracter, and the timing delay, may decrease with familiarity of the distracter, possibly due to habituation (Thompson & Spencer, 1966), a decrement in the investigatory reflex (Pavlov, 1927) or orienting response (Sokolov, 1960), or a decrement in conditioned attention (Lubow, 1989; Lubow, Schnur, & Rifkin, 1976). Therefore we manipulated the ability of stimuli to engage time sharing, by extensively exposing rats to an auditory stimulus (white noise), prior to presenting the noise as a distracter during a “reversed” PI paradigm, in which the to-be-timed signal is the absence of the house light (dark), as opposed to the “standard” procedure, in which rats time the presence of the house light. In previous studies, rats delayed much longer after interruptions (gaps) in a “reversed” paradigm than in a “standard” paradigm (Buhusi & Meck, 2000, 2006a; Buhusi, et al., 2006; Buhusi, et al., 2002). Because we investigated the possible decrease in the delaying effect by extensive exposure to the distracter, we thought to make it harder for the exposure to show effects by using the reversed PI paradigm, in which rats would be more inclined to delay. It was thought that should any effects be seen, it would clearly indicate that distracter preexposure alters its ability to disrupt timing.

Because the above phenomena are context dependent (Lubow, Rifkin, & Alek, 1976; Wagner, 1979), changes between the preexposure and the test phases were expected to elicit disinhibition (or to impair attention), and to increase the salience of the distracter, thus delaying timing after the noise. Therefore, in the current experiment, we also manipulated the conditions under which the subjects were preexposed to the noise relative to the test conditions. A group of rats was exposed to the noise in the dark, while another group was exposed to the noise in the illuminated chamber; control rats were not exposed to the noise. The effect of noise preexposure was subsequently tested by presenting it in dark (reversed) PI trials. We expected that in rats preexposed and tested in the dark, the noise would be less salient, and would have little delaying effect, while in rats preexposed in the light, as well as in non preexposed rats, the presentation of the salient noise in the dark would delay timing. These predictions were only partly confirmed experimentally.

Materials and methods

Subjects

Twenty-four naïve Sprague-Dawley male rats (3 months old at the beginning of the experiment) were housed in a temperature-controlled room, under a 12/12-h light-dark cycle, with water given ad libitum. Rats were maintained at 85% of their ad libitum weight by restricting access to food (Rodent Diet 5001, PMI Nutrition International, Inc., Brentwood, MO). All experimental procedures followed ethical standards for use of laboratory animals (2011).

Apparatus

The apparatus consisted of 8 standard rat chambers (MED Associates, St. Albans, VT) housed in sound attenuating cubicles. Each chamber was equipped with two response levers situated on the front wall of the chamber. All experimental procedures used only the left lever. According to the schedule, 45-mg precision food pellets (PMI Nutrition International, Inc., Brentwood, MO) were delivered in a food cup situated on the center of the front wall, 1 cm above the grid floor, by a pellet dispenser. The to-be-timed visual stimulus was a house light mounted at the center-top of the back wall. The auditory distracter was an 8-s 70dB white noise produced by a white-noise programmable generator (MED Associates, St. Albans, VT) mounted on the front wall, above the right lever. The intensity of the distracter was measured with a sound-level meter (Realistic Radio Shack, Model 33-2050) from the center of the box.

Phase 1: Reversed fixed-interval (RFI) training

Rats were shaped to lever press, then trained in a reversed fixed-interval (RFI) 40s procedure as described in Buhusi & Meck (2000) (Figure 2). The first lever press 40s after the offset of the visual signal was reinforced by the delivery of a food pellet and turned on the house light for the duration of a random 90 ± 30 s inter-trial interval (ITI).

Phase 2: Reversed Peak-Interval (RPI) training

Afterwards, rats were trained in a reversed peak-interval (RPI) procedure, as described in Buhusi & Meck (2000), during which RFI trials were randomly intermixed with non-reinforced RPI trials in which the visual signal (dark) was presented for a duration three times longer than the RFI, before being terminated irrespective of responding for the random 90 ± 30 s illuminated ITI. At the end of the training phase, two rats failed to acquire the timing task (their timing was about 50% off the 40s criterion) and were eliminated from the study.

Phase 3: Noise preexposure

Rats were randomly assigned to three groups: DARK, LIGHT and NOVEL control. Rats received 12 RPI training sessions, randomly intermixed with 11 noise sessions, except for rats in the NOVEL group, which were not exposed to the noise in this phase (Figure 2). RPI sessions consisted in 24 RFI trials randomly intermixed with 24 RPI trials, separated by a 90 ± 30 s random (illuminated) ITI. Noise sessions were 1.5hrs long, and consisted of about 96 inconsequential 8-s noise presentations with a random 62 ± 17 s inter-stimulus interval. During noise sessions, the chamber was dark (similar to the timed signal) in DARK rats, and illuminated (similar to the ITI) in the LIGHT rats. In all, during the 11 noise sessions, rats in the DARK and LIGHT groups received over 1,000 noise presentations.

Phase 4: RPI+N Test

The delaying effect of the noise was examined by presenting it during one RPI+N test session, during which rats received 48 RFI trials randomly intermixed with 32 RPI trials, and 16 RPI+N trials (8 early, 8 late) as follows: RPI+N trials were similar to RPI trials except that the 8-s noise was presented either early (8s from trial onset) or late (24s from trial onset) during the uninterrupted to-be-timed dark signal. Trials were separated by a 90 ± 30 s random (illuminated) ITI.

Data collection and analysis

The experimental procedures were controlled through a MED Associates interface connected to an IBM-PC compatible computer running a MED-PC software system (MED-Associates, 1999). Lever presses were recorded in real time. Lever presses recorded during

RPI and RPI+N trials were used to estimate the peak time, peak rate, and precision of timing (width of the response functions) for each rat using four methods: curve fitting (Buhusi & Meck, 2000), iterative median (S. Roberts, 1981), inter-quartile range, and individual-trial (single-trial) analysis (Church, Meck, & Gibbon, 1994). For each subject, all four analyses were conducted on the data from a 80-s interval of interest (IOI), starting at signal onset for RPI trials, and starting at noise offset for RPI+N trials.

For the curve fitting method (FIT) (Buhusi & Meck, 2000), the number of responses (in 4-s bins) was averaged daily over trials, to obtain a mean response rate function for each rat. The mean response rate in the IOI was fit using the Marquardt-Levenberg iterative algorithm (Marquardt, 1963) to find the coefficients (parameters) of a Gaussian+linear equation that gave the “best fit” (least squares minimization) to the data as described in (Buhusi & Meck, 2000). The fitting algorithm provided the following parameters of the response curve: the accuracy of timing (estimated response peak time), precision of timing (estimated width of response function), and peak rate of response. For two rats (one in group LIGHT and one in group NOVEL) the fitting algorithm failed to provide reliable estimated parameters for at least one of the RPI+N test trials; these two rats were eliminated from statistical analyses. For the remaining rats, the goodness of fit R^2 was 0.81 ± 0.02 in the DARK group ($n=7$), 0.82 ± 0.03 in the LIGHT group ($n=8$), and 0.72 ± 0.04 in the NOVEL group ($n=5$).

In the inter-quartile range (IQR) method, for the average distribution of responses in the IOI we estimated the lower quartile (first 25% responses), and high quartile (last 25% responses). The middle of this interval was taken as an estimate of peak time. The median method (MED) followed (S. Roberts, 1981). Briefly, we started by estimating the median of the IOI, and continued computing the median iteratively by shrinking the IOI until the IOI became one bin; this time bin was taken as the estimated peak time. In the individual-trials (single trials) analysis (ITA) (Church, et al., 1994), individual trials were analyzed to estimate the change from a lower rate of response to a high rate of response (start time, S1), and the change from a high rate of response to a low rate of response (stop time, S2). The average midpoint between S1 and S2 was taken as an estimate of the peak time, and was submitted to statistical analyses. The estimated peak time was submitted to repeated measures ANOVAs with group (DARK, LIGHT, NOVEL) as between-subject variable, and method (FIT, IQR, MED, ITA) and trial (RPI, Early N, Late N) as within-subject variables. All statistical tests were evaluated at a significance level of 0.05 (two tailed).

Computer simulations with the time-sharing model

Experimental results were simulated with the time-sharing model as detailed in (Buhusi, 2012), using model parameters matching our lab settings. The model assumes that working memory for time is given by the balance of two concurrent processes: time accumulation and working memory decay (due to intruder presentation). As in Buhusi (2012) we assumed that time accumulates with a rate of 5 pulses/s, equivalent to 200 pulses for the 40s criterion duration. The rate of decay was assumed to be proportional to the perceived salience (intensity) of the noise. Using experimental data collected in our lab, we derived the relationship between perceived salience (intensity) and rate of decay in our lab settings, as follows: decay rate = $0.006 \cdot 10^{\text{perceived intensity}/38}$, where perceived intensity is the perceived intensity in dB (see Buhusi 2012 for details). Current simulations were carried out under the assumption that noise exposure diminishes the salience (perceived intensity) of the noise, thus affecting the rate of working memory decay. For each condition we determined the best perceived intensity that would fit the experimental results (least square minimization). The purpose of the simulation was to estimate whether changes in perceived salience alone can address all results observed in the current experiment.

Results

RPI trials without noise

The average percent maximum response rate in RPI trials (without noise) is shown in the top panel of Figure 3, which indicates that rats in all groups acquired the timing task. ANOVAs with group (DARK, LIGHT, NOVEL) as between-subject variable failed to reveal reliable main effects of group on either peak time or precision ($F_{(2,17)} < 3.06$). In all groups, the response functions peaked about the criterion time, 40s ($t_s < 1.01$).

RPI trials with noise

The average percent maximum response rate in RPI trials with early and late noise are shown in Figure 3. The middle panel of Figure 3 shows that in early RPI+N trials the DARK and LIGHT rats delayed minimally, while NOVEL rats delayed considerably more. The bottom panel of Figure 3 shows that in late RPI+N trials only rats in the DARK group delayed minimally, while rats in the LIGHT and NOVEL groups delayed considerably more. Finally, response functions seem to have similar widths; this latter suggestion was supported by a repeated measures ANOVA of the estimated width (estimated by the curve fitting method) with group (DARK, LIGHT, NOVEL) as between-subject variable and trial (RPI, Late N, Early N) as within-subject variable, which failed to indicate any reliable main effects ($F_{(2,17)} < 2.22$) on response width, suggesting that response functions were simply delayed by the presentation of the noise.

To further analyze the differential effect of the noise on response timing in the three groups, an estimate of the peak time was computed for each trial type using four different methods: curve fitting (Buhusi & Meck, 2000), iterative median (S. Roberts, 1981), inter-quartile range, and individual-trial (single-trial) analysis (Church, et al., 1994) (see methods). Afterwards, a delay in peak time in RPI+N trials relative to PRI trials was computed by subtracting the estimated peak time in RPI trials from the estimated peak time in RPI+N trials, as shown in Figure 4. A repeated measures ANOVA of the delay with group (DARK, LIGHT, NOVEL) as between-subject variable and method (FIT, IQR, MED, ITA) and noise (Early N, Late N) as within-subject variables indicated a reliable group $\times$ noise interaction ($F_{(2,17)} = 5.33$), but no main effect of group ($F_{(2,17)} = 2.69$), noise ($F_{(1,17)} = 1.86$), or method ($F_{(3,51)} = 0.92$). Results were consistent irrespective of the estimation method (see Buhusi & Meck 2006b for another example of comparing various estimation methods): For the Early noise (Figure 4, left panel), planned comparisons revealed that NOVEL rats delayed reliably more than both DARK and LIGHT rats ($F_{(1,17)} = 5.64$); no difference was found between the DARK and LIGHT groups ($F_{(1,17)} = 0.29$). On the other hand, for the Late noise (Figure 4, right panel), analyses indicated that DARK rats delayed reliably less than LIGHT and NOVEL rats ($F_{(1,17)} = 7.29$); no difference was found between the DARK and NOVEL groups ($F_{(1,17)} = 0.19$). These results suggest that the rats were differentially affected by the noise preexposure: Rats in the NOVEL group, for which the noise was an unfamiliar event, were maximally affected (large delay). In contrast, rats in the DARK and LIGHT groups, for which the noise was familiar, were less affected by the noise: Rats in the DARK group were minimally affected (small delay), while rats in the LIGHT group stopped for the early distracter and reset for the late distracter, suggesting that besides simple familiarity (number of noise presentations), other differences between these latter two groups affect distractibility. Non-parametric statistical analyses of the delay (estimated by FIT method) further supported this interpretation: A Wilcoxon matched pairs test indicated reliable differences between the early and late noise conditions in the LIGHT group ($z = 2.19$). Moreover, a Mann-Whitney U test indicated reliable differences between DARK and LIGHT rats in the late noise trials ($z = 2.08$), suggesting that noise exposure was effective in

the DARK group above and beyond the effect of noise location, while in LIGHT group, rats continued to be sensitive to the location of noise, despite extensive noise preexposure.

Estimated start times

To further investigate possible differences between groups, we analyzed the pattern of response in the three groups, by estimating whether the noise was presented before or after rats started responding. The estimated start time (S1, ITA method) and stop time (S2) in RPI trials were submitted to one-way ANOVAs with factor (DARK, LIGHT, NOVEL), which failed to indicate reliable main effects of group, ($F(2,17)=1.18$), for the start time, and ($F(2,17)=0.99$), for the stop time. This suggests that the pattern of response was similar in all groups, and thus the (learned) pattern of response cannot in itself be responsible for differences between groups in regard to responding when the noise was presented. The estimated start time was 24.26 ± 0.89 s, and the estimated stop time was 60.29 ± 1.25 s. Thus, in early trials the noise was presented (from 8 to 16s) before rats started responding, while in late trials the noise was presented (from 24 to 32s) after or about the time rats started responding. While this may explain differences between early and late trials, it cannot address differences between groups. In turn, this supports the suggestion that differences between groups are due to noise preexposure.

Response rate

Figure 5 shows the response rate before the test (phase 3), and during the RPI, Early N, and Late N trials (test phase). The response rate decreased in all groups during the test, even in the NOVEL group, and even in RPI trials without the noise, and further decreased in noise test trials. A repeated measures ANOVA of the response rate with group (DARK, LIGHT, NOVEL) as between-subject variable and trial (RPI phase 3, RPI phase 4, Early N, Late N) as within-subject variable indicated a reliable effect of trial ($F(3,48)=50.23$), but no main effect of group ($F(2,16)=0.05$) or interaction ($F(6,48)=0.74$). Planned comparisons revealed reliable differences between RPI phase 3 and RPI phase 4, and between RPI phase 4 and early and late trials ($F_s(1,16)>5.13$), suggesting that during testing the response rate decreased in all trials and in all groups, irrespective of whether the noise was familiar or not.

Because rats in the LIGHT group delayed considerably for late trials, when rats had the lowest response rate, but not for early trials, when rats had a higher response rate, or for RPI trials without a noise, with an even higher response rate, we also investigated the possible relationship between the delay in responding and the rate of response. Presumably, responding may be easier to disrupt in rats with a low response rate, such that they may reset, while rats with a higher rate of response may not be disrupted as easy. Such a possibility is partly supported by studies investigating the effect of distracter intensity (Buhusi, 2012), which suggested that noise distracters delay timing but also decreases the response rate (Buhusi, 2012, Figure 3A). However, no reliable correlations were found at the alpha level 0.05, (two tailed test) in either group or condition ($R^2<0.47$), failing to support this hypothesis. Over all subjects, the R^2 was 0.03 for the early noise condition, and 0.02 for the late noise condition, thus failing to support a relationship between response rate and timing delay in our setting.

Finally, to further evaluate whether distractibility (indexed by the delay in responding) varied with the rats' response rate, for each rat, in each condition, we estimated response suppression by the noise as the ratio between the number of responses during the 8-s noise, and the sum of responses during the 8-s noise and the 8-s pre-noise interval. Presumably, the more the noise may suppress responding (relative to the pre-noise interval) the more the rat may delay responding after the noise. Analyses failed to indicate reliable correlations between the delay in responding and the response suppression ratio, for either the early (R^2

= 0.01) or late trials ($R^2 = 0.09$), suggesting that response patterns, or response suppression do not account for the differences between groups, further supporting noise preexposure as the most likely variable addressing results.

Computer simulations with the time-sharing model

For each condition we determined the best perceived intensity that would fit the experimental results (least square minimization). The purpose of the simulation was to estimate whether changes in perceived salience alone can address all results observed in the current experiment. We found that rats in the NOVEL group behave as if perceiving a sound intensity of 70dB (above and beyond the background noise provided by the fan), while rats in the DARK group behave as if perceiving a drastically attenuated intensity of noise, 30dB, possibly due to extensive exposure. For LIGHT rats we found that data are accounted for by only a moderate decrease in perceived intensity, 60dB, possibly due to context change.

The left panels of Figure 6 show the simulated accumulated time (in working memory) throughout the RPI+N trials. The time when working memory reaches the number of pulses equivalent to the timed criterion (200 pulses) is the predicted peak time, noted and contrasted with the experimental value in the right panels of Figure 6. The left panels of Figure 6 indicates that for rats in the NOVEL group, for both early and late noise presentations, working memory decays during the distracter considerably, but accumulation continues after the distracter such that rats' response is maximally delayed (reset). On the other hand, for rats in the DARK group, in which the noise was preexposed and tested in the dark context, for both early and late noise presentations, working memory is least affected by the noise. The model predicts that rats should run for early noise (Figure 6, upper-right panel), and should stop for late noise (Figure 6, lower-right panel). In contrast, present experiment results indicate that rats in both conditions stopped timing, suggesting that preexposure, although extensive (over 1,000 presentations) was not fully effective, as predicted by the model.

Most interestingly, for rats in the LIGHT group, in which the noise was preexposed in the light and tested in the dark, we expected considerable disinhibition due to the change of context: Under these conditions, the left panels of Figure 5 indicate that working memory decays little during the early noise (stop) but decays considerably during the late noise. In other words, changes in perceived salience alone (due to noise preexposure) was ineffective in overriding other relevant variables of the model, such as the currently accumulated time (in working memory) at the moment of distracter presentation (Early, Late). Indeed, the currently accumulated time varies with the location (Early, Late) of the distracter, which is known to affect the response to interruptions and distracters (Buhusi & Meck, 2000, 2006a, 2006b; Buhusi, et al., 2006).

Discussion

The results from this experiment can be interpreted within the framework of associative learning theories and/or timing theories. For example, within an information-processing model of timing (Gibbon, et al., 1984) (Figure 1A, left), the effect of distracters was previously addressed by assuming an internal clock incorporating a switch mechanism that connects the pacemaker with the accumulator (Gibbon, et al., 1984), or by assuming that the memory for the pre-distracter interval decays passively during the distracter (Cabeza de Vaca, et al., 1994). Both assumptions predict that the effects of distracters depend solely on the temporal parameters of the paradigm. Clearly, these assumptions do not fully address present results, as the preexposure conditions were found effective in modulating the disruptive properties of the noise in spite of the three groups having identical temporal parameters during the test.

Considerable differences in responding to interrupting and distracting events were reported in both rodents and birds, depending on the experimental conditions: The response may be delayed anywhere on a continuum (Buhusi & Meck, 2006b; Buhusi, et al., 2006; Swearingen & Buhusi, 2010) between running (no delay, ignoring the distracter) (Buhusi, et al., 2006), and resetting (a large delay indicative of restarting the entire timing process after the gap) (Aum, et al., 2004; Bateson & Kacelnik, 1998; Brodbeck, et al., 1998; Buhusi & Meck, 2006a; Buhusi, et al., 2006; Buhusi, et al., 2002; Cabeza de Vaca, et al., 1994; W. A. Roberts, et al., 1989). On the run - reset continuum, a delay equal to the length of the gap is sometimes referred to as stopping (no timing during the gap) (Buhusi & Meck, 2006b; Church, 1978; Meck, Church, & Olton, 1984; S. Roberts, 1981; S. Roberts & Church, 1978). As in previous studies in our lab, results cannot be accommodated by discrete run/stop/reset response rules (Buhusi & Meck, 2006b; Buhusi, et al., 2006; Swearingen & Buhusi, 2010), as they seem to vary with temporal or associative variables, e.g., perceived salience of the distracter, likely affected by distracter preexposure.

A quite different, associative-like, account of the effect of distracters is provided by Zentall's instructional ambiguity hypothesis, which proposes that distracters (e.g., gaps) elicit resetting of an internal clock based on a similarity gradient with the ITI: The more similar to the ITI, the more the distracter would instruct the internal clock to reset; the less similar from the ITI, the less the effect on timing (Kaiser, Zentall, & Neiman, 2002; Sherburne, Zentall, & Kaiser, 1998; see also Staddon & Cerutti, 2003). Therefore, the noise should stop timing in NOVEL rats, as the unfamiliar noise is clearly not similar to the silent, illuminated ITI. However, in both the DARK and LIGHT rats, the noise should have signaled the lack of reinforcement, and as such should have been instructionally similar to the ITI, thus predicting a reset of timing. These predictions do not match the observed results, thus failing to provide support for an instructional effect of distracters in this study.

The most comprehensive explanation for effect of gaps and distracters on timing (reviewed in Buhusi & Meck, 2009) seems to be offered by the time-sharing hypothesis (Buhusi, 2003, 2012), which builds and extends upon the memory decay hypothesis (Cabeza de Vaca, et al., 1994). The time-sharing hypothesis assumes that (a) memory decay is a process concurrent with timing, i.e., is not limited to gaps in the timed signal, but occurs throughout the trial, and (b) the rate of decay is dependent on salience-related features, rather than being fixed (see Buhusi 2012 for an example of implementation). We hypothesized that noise preexposure should decrease the salience of the distracter, either due to habituation (Thompson & Spencer, 1966), a decrement in the investigatory reflex (Pavlov, 1927) or orienting response (Sokolov, 1960), or a decrement in conditioned attention (Lubow, 1989; Lubow, Schnur, et al., 1976), and should minimize its time-resetting effect. However, as these phenomena are context dependent (Lubow, Rifkin, et al., 1976; Wagner, 1979), we expected preexposure to be effective in the DARK group, but not in the LIGHT group, preexposed in the light context and tested in the dark context. Taken together, the predicted results based on salience-dependent time-sharing model were as follows: Rats in the DARK group, in which the noise was preexposed and tested in the dark context, should be minimally affected by the noise. Rats in the NOVEL group, in which the noise was unfamiliar, should be maximally delayed after the noise. Rats in the LIGHT group, in which the noise was preexposed in the light but tested in the dark, should show an intermediary effect, as noise preexposure should not be effective due to the context change.

While strongly supporting a role for distracter salience in the delaying effect of distracter presentation, simulations presented in Figure 5 indicate that the time-sharing model addresses most but not all the results. The most interesting finding is that the time-sharing model easily accounts for the LIGHT rats stopping for early noise but resetting for the late noise, simply based on the location of the distracter (Early v. Late) in conjunction with a

minimal decrease in perceived intensity (due to preexposure). However, should extensive exposure be effective, the model predicts that the rats in the DARK groups should ignore the noise; instead they were (minimally) delayed by it, suggesting that preexposure, although partly effective in decreasing its salience, did not allow rats to ignore the distracter.

Why was the extensive noise exposure ineffective in making DARK rats ignore the noise? This result cannot be explained by a floor effect, as previous results in our lab indicate that decreasing the intensity of a noise distracter can make rats ignore an auditory distracter (Buhusi, 2012). Therefore, the relative lack of effectiveness of noise preexposure must be due to some procedural detail which might have generated some disinhibition. For example, because the noise and light were not presented in the same session before testing, the presentation of the illuminated ITI (non-target) closely followed by noise (target) might have generated some disinhibition of resetting to the target noise (Thompson & Spencer, 1966). This interpretation is supported by the disruption of conditioned attention to a target (pre-exposed) stimulus by presentation of a second (non-target) stimulus (Lubow, Schnur, et al., 1976).

Alternatively, the disinhibition may have been due to randomly intermixing RPI and noise exposure sessions. For example, Mackintosh (1973), Mercier and Baker (Mercier & Baker, 1985), and Reed (Reed, 1995) found that latent inhibition is disrupted if a non-target stimulus is preexposed simultaneously with the target stimulus. Moreover, our own simulations (Buhusi, Gray, & Schmajuk, 1998) with the SLG model of latent inhibition (Schmajuk, Gray, & Lam, 1996) suggest that preexposure to alternating events increases Novelty, increases the attention paid to the target, and leads to disinhibition. Thus, the random mix of RPI and noise sessions could be the reason that extensive noise exposure, albeit effective in reducing the attention paid to the noise, did not allow the DARK rats to fully ignore the noise.

On the other hand, the results are difficult to explain based on associative notions alone. For example, LIGHT rats should have been maximally delayed, because they experienced a change in contextual cues: The noise was preexposed in the light, but was tested in the dark. Due to this contextual change, LIGHT rats should have disinhibited, and should have delayed timing considerably even for the early trials; yet, they were minimally delayed in early noise trials, suggesting a need to nuance this associative interpretation using temporal parameters.

The role of associative factors may be revealed by examining response rates. For example, the effect of the noise may depend on the response state (low responding / high responding) of the subject, which in turn may be an index of the associations established during learning. This associative explanation is highly unlikely to address the current results. First, no differences in start and stop times were found between groups, suggesting they are all in the same state (either high or low) when the noise is presented, thus failing to address group differences. Second, while rats with a lower response rate (low state) may be more easily disrupted than rats with higher response rates (higher states), no reliable correlations were found between response rates and response delay. Finally, the presentation of the noise may switch rats back from a high to a low response state, thus further delaying responding, no reliable correlations were found between response suppression in the presence of the noise and the delay after the noise. Therefore, the pattern of responding, the (low/high response) state, and response reactivity to noise are unlikely to explain current results, particularly the differences between groups.

Therefore, the present data suggest that phenomena like the one reported here are difficult to account for by timing theories alone (e.g., that distracters reset timing) or associative

theories alone (e.g., that preexposure should reduce the salience of distracters). A more nuanced, or possibly, a more integrated view is necessary to explain current results. Such an integrated view may be provided by real-time associative models of timing (e.g., Buhusi & Schmajuk, 1996, 1998, 1999), which incorporate associations (updated continuously, each time unit) as well as temporal predictions (which compete for associations with the reward.) For example, a more complex, associative version of the Spectral Timing Model (Grossberg & Schmajuk, 1989) was shown to address associative phenomena such as cue competition and occasion setting, as well as their temporal properties (Buhusi & Schmajuk, 1999). Moreover, Hopson (2003) explained the effect of gaps within the Spectral Timing Model (Grossberg & Schmajuk, 1989), as being due to decaying timing traces, an interpretation in accord with the time-sharing model (Buhusi, 2003, 2012), which also assumes a form of working memory decay. Together with other models (e.g., Machado, 1997), real-time associative models could provide a “missing link” between the associative and temporal learning fields (Buhusi & Schmajuk, 1996).

In summary, the current body of evidence suggests that the notion of simple behavioral run / stop / reset rules -- a notion consistent with timing theories -- needs to be replaced by a more general notion of a continuous delay in the response function, varying with both associative and temporal parameters of the procedure. The latter is consistent with a modulatory role of associative features of events over properties (e.g., salience) that may affect the temporal features of events (the reset of an internal clock based on salience-controlled rate of working memory decay). The results reported here support an integrative approach to the data patterns in interval timing tasks. Irrespective of the theoretical underpinnings, the present results suggest that further work is necessary to integrate associative learning and timing theories, now, when more than ever the researchers in the two fields are identifying experimental paradigms that require notions from both fields.

Acknowledgments

This work was supported by grants MH65561 and MH73057 from the National Institute of Mental Health to CVB. The authors would like to thank Bret Guercio, Kevin Lawanto, J. Daniel Obray, and Benjamin White for excellent assistance with data collection and analysis.

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- We hypothesized that cue preexposure reduces its subsequent time-disrupting abilities
- We hypothesized that context changes impair this preexposure effect
- Non-preexposed rats, showed maximal disruption (delay) by distracter
- Rats preexposed and tested in the dark showed minimal disruption by distracter
- Rats preexposed in the light and tested in the dark were affected by distracter location

Figure 1.

Effect of preexposure in a model of time-sharing controlled by the discriminability (salience) of distracters. The time-sharing model assumes limited attentional or working memory resources: Timing (left) and other processes (right) share the access to these resources (center). Working memory for time is updated by two concurrent processes: time accumulation and active decay due to sharing of resources. The rate of memory decay is assumed to depend on the discriminability (salience) of the novel distracter. (A) A novel distracter will engage resources taken away from timing, which will determine a reset of an internal clock. (B) We hypothesize that familiarity with the intruding event would decrease its salience, and its disrupting effect on timing, by engaging fewer resources.

Figure 2.

Experimental design. **Phase 1:** Rats were trained to time in a reversed fixed-interval (RFI) 40s procedure, in which timing trials signaled by turning off the house light (dark) were separated by illuminated inter-trial intervals. **Phase 2:** RFI trials were then intermixed with non-reinforced reversed peak-interval trials (RPI), in which the timed signal was presented 3-4 times longer than the 40s criterion. **Phase 3:** After timing was established, rats received RPI sessions randomly intermixed with noise sessions, during which they were exposed to an auditory stimulus (white noise) presented repeatedly and without consequences. For DARK rats, the chamber was dark during the noise sessions; for LIGHT rats, the chamber was illuminated during the noise sessions; rats in the NOVEL group did not receive noise sessions. **Phase 4:** Rats were tested by presenting the noise unexpectedly, early or late, during the RPI trials. The delay in peak time between RPI trials with noise (RPI+N) and RPI trials without noise (RPI) was submitted to statistical analyses.

Figure 3.

Response functions during testing. Average normalized response functions during probe trials without noise (RPI, upper panel), trials with early noise distracter (Early N, middle panel), and trials with late noise distracter (Late N, bottom panel) in the three groups of rats. The black rectangle indicates the presentation of the noise. The “run”, “stop”, and “reset” markers are provided for comparison purposes and do not represent “options”.

Figure 4.

Average delay during testing. Average delay ($\pm$ SEM) in trials with early noise distracter (early N, left) and late noise distracter (Late N, right) relative to RPI trials without noise, as estimated by four analysis methods: curve fitting (FIT), inter-quartile range (IQR), iterative median (MED), and individual-trial (ITA). The “run”, “stop”, and “reset” markers are provided for comparison purposes and do not represent “options”.

Figure 5. Average rate of response before and during testing. Average rate of response ($\pm$ SEM) before testing (phase 3), and during testing, in RPI trials without noise, and in trials with early and late noise.

Figure 6.

Simulations with the time-sharing model. (Left) Simulated accumulated time in RPI+N trials. (Right) Average observed peak time $\pm$ SEM (DATA) and simulated peak time (MODEL) in RPI+N trials. (Upper panel) Early noise trials. (Lower panel) Late noise trials. Simulations were conducted with parameters matching our lab settings (Buhusi, 2012) assuming a rate of accumulation of 5 pulses/s, with a decay rate equal to $0.006 \cdot 10^{\text{perceived intensity}/38}$, please see Buhusi 2012 for an experimental derivation of the relationship between perceived intensity and rate of decay. To match the observed results, we selected values of “perceived intensity” which provide a good fit to the data in each condition: 70dB for the NOVEL group, 30dB for the DARK group, and 60dB for the LIGHT group. The “run”, “stop”, and “reset” markers are provided for comparison purposes and do not represent “options”.