

Tracing the shadow of time

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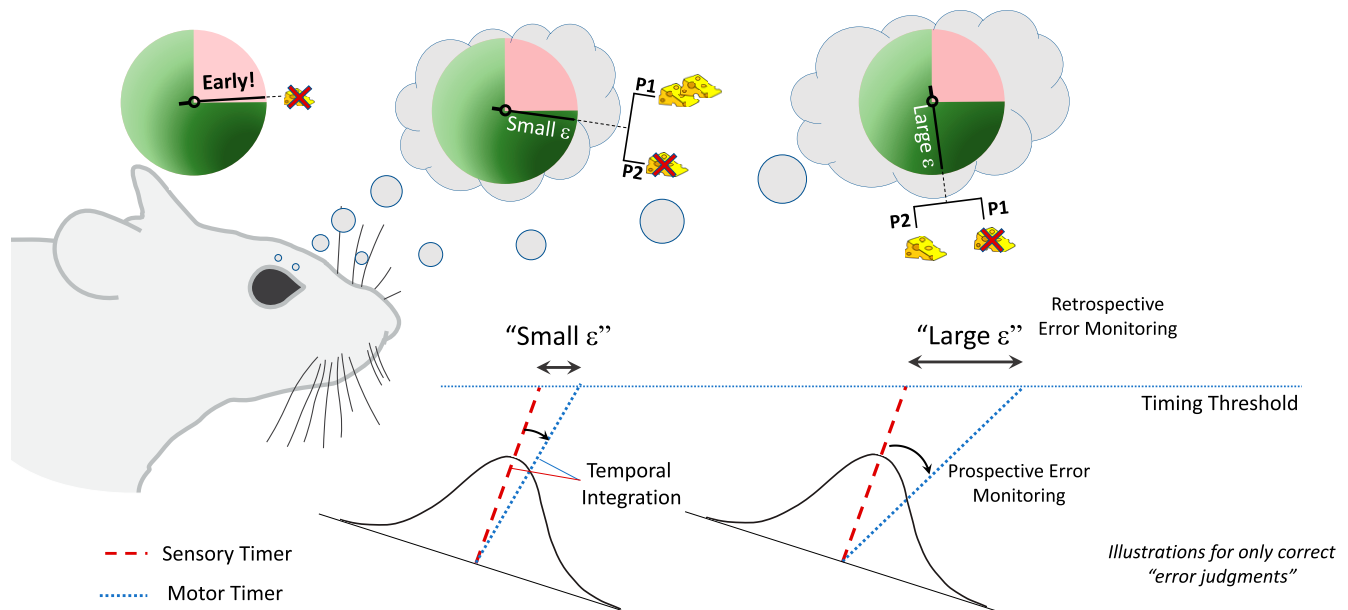


Fig. 1. Task representation of Kononowicz et al. (2) along with the illustration of how the magnitude of timing errors can be traced prospectively vs. retrospectively.

Our daily lives are deeply shaped by many contingencies of different time scales (e.g., subway schedules, test deadlines, traffic lights). Humans adapt to these relations rather well without having to rely on timekeeping devices. Other animals too can estimate and organize their behaviors adaptively around seconds- to minutes-long intervals. This ability is called “interval timing.” For instance, one can train rodents to estimate an arbitrary duration of T seconds by simply waiting for T seconds between each reward delivery, and test for the resultant temporal expectancy by occasionally omitting a scheduled reward. The average timing of anticipatory responses in these test trials would typically match the reward availability time (high temporal accuracy). But this is only part of the story, because timing behaviors also exhibit variability between trials. Theoretical accounts attribute this variability to the imperfection of the internal clock (e.g., noisy integration of “clock” inputs, fuzzy memory representation) or precision limit in the representation of time intervals (1). Whatever the source of the timing uncertainty is, it is manifested as timing errors in individual estimates. In PNAS, Kononowicz et al. (2) demonstrate that rats can estimate the magnitude of such timing errors and thereby exercise a metrically informed complex form of error monitoring.

Although timing uncertainty is a common subject of psychophysics, it has only recently become a research topic of decision science. Several of these studies emphasized the role of the level of timing uncertainty in

determining the reward rate maximizing decisions and showed that both humans and other animals can maximize reward rate by following these optimal strategies (3). A key question is how subjects adjust their behavior in a near-optimal fashion, considering their timing uncertainty. Can they cognitively access (metacognition-like) the level of their endogenous timing uncertainty and “plan” their actions accordingly? If so, may subjects rely on their trial-based timing errors to estimate their endogenous timing uncertainty, which is what leads to timing errors in the first place?

This rather unconventional account has received partial support from findings showing that humans, primates, and rats can keep track of their binary errors in their choice behavior (e.g., ref. 4). But this conclusion cannot readily apply to monitoring timing errors because, different from binary errors, timing errors have magnitude

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(small vs. large errors) and direction (early vs. late) and result solely from the information processing dynamics of the brain, without a “sensory benchmark.” To address this question, more recent studies asked human participants to reproduce a target interval and then to judge the magnitude and direction of error in their reproduction. Participants’ error judgments indeed tracked the direction and magnitude of their own timing errors, highlighting the metric character of error monitoring ability (5).

Current Study

Building on the discovery of temporal/metric error monitoring, Kononowicz et al. (2) test whether rats can keep track of the magnitude of their timing errors. They trained rats to press a lever (either by continuously depressing it or by demarcating the interval with two lever presses) for a minimum duration. Temporal productions were categorized as those longer than but close to the minimum duration (small errors) and those much longer than the minimum duration (large errors). When animals made a small error, they received two pellets by choosing one port (P1) or no pellets if they chose the other port (P2). But, if animals committed a large error, they received one pellet by choosing P2 or no pellets if they chose P1 (Fig. 1). The authors find that all rats tested in this task exhibit better than chance-level performance by choosing the correct port for the magnitude of their timing error in that trial. Interestingly, the choice behavior depended on both the errors and the history of responses in earlier trials. This study shows that nonhuman animals can keep track of the magnitude of errors and the rich informational basis of their choice behavior as part of temporal error judgments. The results of the current study also address one of the fundamental questions regarding the function of error monitoring; rats adjusted their timing behaviors based on the timing errors in previous trials, which highlights the role of temporal error monitoring in guiding subsequent performance.

The findings of this study have high theoretical relevance and importance on multiple grounds. The most obvious contribution of the current study is testing metric error monitoring (as a component of metacognition) in nonhuman animals and providing a compelling example of the complexity of the error representations of rats. Only a few earlier studies have demonstrated rats’ metacognition-like behaviors, but in nonmagnitude domains. For instance, Kirk et al. (6) trained rats to press a lever for a reward, which also resulted in signaling the arm of a T-maze that contained another reward. Even when the immediate reinforcement was omitted later on in the task, rats still continued to press the lever to seek information regarding the location of the food in the T-maze. Furthermore, the information-seeking behavior of rats increased substantially when the amount of information that could be gained by pressing the lever was increased from one bit to three bits by testing animals in the radial arm maze [eight arms; $-\log_2(1/8)$] instead of the T-maze [two arms; $-\log_2(1/2)$]. When the uncertainty regarding the food location was eliminated by presenting the reward always in the

same arm ($-\log_2(1)$, zero bits of information), rats ceased seeking information.

In another (metamemory) study (7), rats made a decision based on their memory of locations and made a temporal bet regarding whether their choice was correct (as a proxy for memory confidence). Longer bets led to larger rewards in only correct choices. The authors found that rats bet more for correct choices than incorrect choices, and temporal bets were lowest for invalid (choice of uncued locations) choices. Finally, Templar et al. (8) showed that, when their odor memory was weak, rats declined the memory test for a smaller but certain reward, while taking the test when the odor memory was strong; rats’ performance was higher in those trials in which the decline option was available but the memory test was taken vs. when the memory test was forced. Importantly, the authors also showed that, in generalization tests (controlling for potential external sources of stimulus control), rats adaptively transferred the use of decline response when no sample was presented and when the memory strength was modulated with repeated samples or changing retention intervals. The results of Kononowicz et al. (2) go beyond these studies by showing that error judgments of rats can keep track of even metric information in a domain that has no concrete counterpart (i.e., time). Although it is not possible to attribute the generative process that underlies these behaviors to metacognition in its strictest definition, they might point at a rudimentary form of metacognition without consciousness.

Building on the discovery of temporal/metric error monitoring, Kononowicz et al. test whether rats can keep track of the magnitude of their timing errors.

Another theoretical contribution of this work relates to its implications for the theories of interval timing. One way to account for temporal error monitoring performance is by assuming that the brain measures the duration of each interval simultaneously with multiple timers. As an illustrative example, assume that the sensory and motor systems have dedicated internal clocks; rats tested in the temporal reproduction task of Kononowicz et al. (2) would rely on motor timing for responding, while their sensory timer would also simultaneously keep track of the duration of the same event (e.g., lever press duration). In such a timing architecture with multiple clocks, comparing the outputs of the motor and sensory timers (Fig. 1) would predict, albeit not perfectly, the degree of disparity between the output of the motor timer and the target as well as whether the output of the motor timer is earlier or later than the target (5). This approach is similar to race models of choice behavior where the confidence depends on the difference between the noisily integrated evidence from two independent accumulators (9). In line with this view, the idea of multiple clocks has received independent support from earlier studies. For instance, rats can time multiple intervals simultaneously (e.g., ref. 10). A more recent study by Kheifets et al. (1) showed that the timing precision of rats and mice did not change or even decreased after experimentally increasing exogenous timing variability. Based on these findings, the authors argued that subjects can

distinguish between their own measurement error and exogenous timing uncertainty, which is most readily accounted for by multiple independent clocks.

An alternative mechanistic account relies on the notion that “confidence neurons” detect the rate of temporal integration prior to responding and lead to confidence judgments when compared to the average (veridical) slope estimate (11) (Fig. 1). Consistent with this account, earlier work by Kononowicz et al. (12) showed that the initial state of the beta power (e.g., denoting the initial network condition for the timing episode in a given trial) predicted the temporal error monitoring performance in humans.

Interestingly, data gathered from rats in tone-cued, simple reaction time tasks support both of these accounts. Narayanan and Laubach (13) showed that the primary dorsomedial prefrontal cortex of rats encoded errors retrospectively after the error was committed, and the posterror activity of some of the neurons was associated with subsequent behavioral adjustments. In support of the prospective coding of errors, Laubach et al. (14), showed that lateral and medial agranular areas of the motor cortex of rats prospectively encode errors by showing differential activity prior to the correct and incorrect responses. These findings suggest the need for a synthetic approach to modeling temporal error monitoring based on both prospective and retrospective computations. Future studies are needed to test the different predictions of these two different accounts of temporal error monitoring.

The results of the current study lay the foundation for other novel research questions. For instance, if metric error monitoring performance is indeed derived from the comparison of motor and sensory timers as in the illustrative example above, how manipulating uncertainty in sensory vs. motor timing affects metric error monitoring performance would provide insights into the computations that underlie this ability. One critical aspect of metric error monitoring that is missing in Kononowicz et al. (2) is error directionality judgments; future animal research targeting also this component would help elucidate temporal error monitoring in its full complexity. Furthermore, using the decline option with well-controlled generalization tests would reinforce the robustness of evidence in support of temporal error monitoring in nonhuman animals. One outstanding question is how temporal errors are represented in the brain; as the first step, the relationship between the amplitude of error-related negativity and the absolute magnitude of timing errors can be tested (but see ref. 12). Finally, error monitoring has been shown to be disrupted in different neurological conditions such as autism and obsessive-compulsive disorder, and the procedure developed in this paper provides the tools for studying the same function in animal models of these disorders.

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