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Review article

# Lost in time: Relocating the perception of duration outside the brain

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ABSTRACT

It is well-accepted in neuroscience that animals process time internally to estimate the duration of intervals lasting between one and several seconds. More than 100 years ago, Henri Bergson nevertheless remarked that, because animals have memory, their inner experience of time is ever-changing, making duration impossible to measure internally and time a source of change. Bergson proposed that quantifying the inner experience of time requires its externalization in movements (observed or self-generated), as their unfolding leaves measurable traces in space. Here, studies across species are reviewed and collectively suggest that, in line with Bergson's ideas, animals spontaneously solve time estimation tasks through a movement-based spatialization of time. Moreover, the well-known scalable anticipatory responses of animals to regularly spaced rewards can be explained by the variable pressure of time on reward-oriented actions. Finally, the brain regions linked with time perception overlap with those implicated in motor control, spatial navigation and motivation. Thus, instead of considering time as static information processed by the brain, it might be fruitful to conceptualize it as a kind of force to which animals are more or less sensitive depending on their internal state and environment.

> "*As a boy, I was fascinated by speed, the wild range of speeds in the world around me. (.). The wings of insects moved too fast to see (.). Our pet tortoise, which could take an entire day to cross the lawn, seemed to live in a different time frame altogether. But what then of the movement of plants? I would come down to the garden in the morning and find the hollyhocks a little higher, the roses more entwined around their trellis, but, however patient I was, I could never catch them moving.*
>
> *Experiences like this played a part in turning me to photography, which allowed me to alter the rate of motion, speed it up, slow it down, so I could see, adjusted to a human perceptual rate, details of movement or change otherwise beyond the power of the eye to register. Being fond of microscopes and telescopes (.), I thought of the slowing down or the speeding up of motion as a sort of temporal equivalent: slow motion as an enlargement, a microscopy of time, and speeded-up motion as a foreshortening, a telescopy of time.*"
>
> Oliver Sacks. The River of Consciousness.

## 1. Introduction

Most of what humans and other animals accomplish in their lives requires adapting to the temporality of events relevant to survival, a temporality that can span several orders of magnitude and can be either highly repetitive and regular, such as the 24-hour light/darkness cycle, or largely unpredictable, such as the sudden and unexpected approach of a predator. This essay addresses the question of the mechanisms allowing animals, including humans, to explicitly estimate the length of ongoing events or intervals in the second-to-minute range, an ability referred to as prospective time perception or interval timing. Although temporal estimates are prone to distortions (Eagleman, 2008), humans can easily distinguish between short (e.g., 1 s) and relatively longer (e.g., 3 s) time intervals. An important feature of interval timing is that it conforms to an invariant law at play during the perception of sensory stimuli referred to as the Weber-Fechner law: the accuracy of perceiving a just noticeable difference between two stimuli decreases with the intensity of the stimuli (Fechner, 1860; Weber, 1834). In the time domain, this means that the probability of correctly identifying which of two intervals is longer is high when both are relatively short (e.g., two tones lasting 1 and 3 s) and closer to chance when they are long (e.g., 31 et 33 s), despite an identical absolute difference. Critically, the variability in

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timing performance (accuracy) increases linearly with the duration of the interval to be estimated, not only in humans but also in other animals such as rodents and pigeons engaged in tasks in which rewards were delivered according to temporal contingencies (Gibbon, 1977). This led to the development of a first series of computational models establishing the so-called scalar expectancy theory (SET), in which time-based decisions depend on internal pacemakers or oscillators that generate neuronal units (or quanta) of time whose noisy linear accumulation is compared to a representation of time stored in the brain (Buhusi and Meck, 2005; Gallistel and Gibbon, 2000; Gibbon et al., 1984; Grondin, 2010; Treisman, 1963; Wittmann, 2013). In parallel, it became accepted that animals such as rodents and pigeons explicitly rely on an internal representation (knowledge) of elapsed time in a wide range of timing tasks. If there is any doubt regarding this "accusation", suffice to read the introduction of Gallistel and Gibbon (2000) in which the authors wrote that they will "*assume that the subjects in conditioning experiments do in fact store in memory the durations of interventions interval and subsequent recalls those remembered durations for use in the decisions that determine their conditioned behavior*".

At this stage, some definitions and clarifications are necessary to avoid misunderstanding. In prospective perception of time, the word perception refers to the explicit (or conscious) measurement of the duration of an ongoing event (Issa et al., 2020; Tsao et al., 2022). I will therefore use the words perception, judgment, estimation, or measurement of time indifferently. Here, such an explicit and quantitative perceptual process, will be distinguished from feeling or sensing time. Indeed one can feel time (being impatient while waiting at a red light) without measuring duration (unfortunately that is often the crux of the problem with impatience). Finally, when presenting the viewpoint of neuroscience, I will describe the perception of time as being internal or direct because both terms capture the idea that animals estimate durations in their heads thanks to neuronal representations of time, without doing anything else.

Recently, due to the difficulty to find dedicated neurobiological support for clock-based algorithms allowing time perception, and the observation that time is inherently encoded in the dynamics of neuronal activity, it has been proposed that duration could be *intrinsically* represented by ensembles of neurons distributed over multiple brain areas activated in a given timing task (Karmarkar and Buonomano, 2007; Paton and Buonomano, 2018; Tsao et al., 2022). This intrinsic framework takes advantage of the possibility to represent the evolving activity of a neuronal population as a trajectory in a low-dimensional state space. Like the dedicated-clock model, the intrinsic one is typically based on the assumption that well-timed behaviors depend on the explicit reliance on internal representations of time (e.g., Tsao et al., 2022). In dedicated-clock models, prospective time perception is conditioned by the rate of a pacemaker and the total number of neuronal pulses emitted, or accumulation height, at the end of the interval. In the intrinsic population clock model, the neuronal population trajectories are continuous and they evolve non-linearly in a state space whose units allow length or distance measurements, and the speed of this trajectory correlates with the subjects' perception of duration (see Figures 1 and 2 in Tsao et al., 2022).

The above description of the main mechanistic models underlying prospective time perception reveals that a key aspect of neuronal representations of time is their spatial form (such as accumulation "height" or the "speed" of a pacemaker or neuronal "trajectory"). Interestingly, the reliance on spatial representations or movement-related metaphors is also necessary when verbally expressing how much time has elapsed. For instance, researchers typically use the words "duration" and "length" interchangeably when asking subjects to report whether an auditory stimulus was "short" or "long". The idea of the passage or flow of time, as well as expressions such as "time flies" or "drags", only make sense because we have experienced a variety of movements in space (see the introductory quotation by Oliver Sacks). The importance of spatial/movement analogies when speaking about time (and numbers) has been noted before by cognitive (neuro)scientists and linguists (Boroditsky, 2000; Bueti and Walsh, 2009; Buonomano, 2018; Buzsáki, 2019; Buzsáki and Llinás, 2017; Lakoff and Johnson, 1980; Núñez and Cooperrider, 2013; Walsh, 2003). Experiments have shown that humans automatically rely on spatial information when making judgments about duration, while the converse (time being needed for spatial judgment) is not true (Bottini and Casasanto, 2010; Casasanto and Boroditsky, 2008), leading to the idea that humans represent time using a spatial layout, the mental timeline, whose direction reflect writing habits (e.g, left to right in western society, Bonato et al., 2012) or culture-specific landscape-related gestures (Cooperrider, Slotta, and Núñez, 2022; Núñez et al., 2012).

The difficulty to avoid spatial references when dealing quantitatively with duration, both at the neuronal and semantic levels, might explain the recent proposal "*that a productive approach is to draw parallels between interval timing and spatial navigation*" (Issa et al., 2020). In the same vein, Paton and Buonomano (2018) wrote in their review on the neural bases of timing that "*How the brain processes information about space provides a useful analogy for the intrinsic timing perspective*". To sum-up, contemporaries' mechanistic views on time perception share the following features. First, they assume that both humans and other animals explicitly use internal representations of time to estimate durations in the second to minute range. Second, these representations are based on the notions of accumulating quanta of time or evolving neural trajectory and ultimately rely on an isomorphism between time and space which is explicitly endorsed by contemporary neuroscience (time is similar to space) and seems unavoidable when time must be quantified or represented.

The straightforwardness of this general framework in which time is considered like space should not mask its conceptual difficulties. Indeed, while the discretization of regular movements in space is a powerful mechanism to quantify the passage of time (i.e., it is the basis of human-made clocks and solar/moon calendars), it is unclear how such a process could happen *internally*. Indeed, even if there are stereotyped patterns of activity in the brain, subjects do not perceive their features (increasing spike count, trajectory in neural space) like those of external observable moving bodies or stimuli. In fact, ascribing to dedicated or emergent neural networks the power to tell time, seems to constitute a confusion between separate levels of understanding (Gomez-Marin, 2021; Krakauer et al., 2017; Poeppel and Adolfi, 2020), which dispense researchers to consider the question: how *behaviorally* do humans and other animals estimate duration? If the answer is "internally", then one must verify whether the conscious experience of a time interval can be discretizable (like space) into repetitive hence summable units, as suggested by the general form of pacemaker/accumulator-based models of time perception.

More than 100 years ago, Henri Bergson challenged this assumption in his first major book, Time and Free Will (Bergson, 1889). In brief, Bergson remarked that conscious living organisms such as humans never experience discrete infinitely small snapshots of time (James, 1890; Whitehead, 1920). Thanks to their nervous system that allows them to retain past information, they inhabit, so-to-speak, a certain thickness of time in which the past is constantly contaminating the present: they endure. In other words, even if a subject remains immobile while watching a still-landscape or closing its eyes, its inner state is a continuously changing heterogenous mixture of past and present. Consequently, the present is fundamentally novel, and two consecutive moments of time that one would artificially isolate will never repeat (Bergson, 1889, 1907, 1922; Whitehead, 1920). Bergson concluded that the conscious inner experience of time can not be divided into equivalent units, which makes it *unquantifiable*. It is important to note that, for Bergson, the impossibility to quantify the inner experience of elapsing time is not due the subjectivity of time perception but rather to the inevitable spilling of the past into the present. This objective feature (the merging of the past into the present) allows humans to experience changes occurring over a certain timescale, and for instance, to be touched by events such as a melody or shooting stars and, conversely, to entirely miss very fast (e.g., the movements of a dragonfly's wings) and slow (e.g., those of a growing plant) ones. Importantly, because living organisms are in a constant state of becoming, time is now considered as a transformative force rather than as static information. Bergson named this process durée (which unfortunately translates into duration in English, but should be understood as an experience that endures and brings change, not as the fixed duration measured with clocks) to distinguish it from the time of Newton's physics, which provides an abstract spatialized layout for measuring the duration of the movements of inert (i.e., without memory) matter (Bergson, 1889, 1896; James, 1890; Whitehead, 1920). Bergson proposed a solution to the problem of quantifying the conscious experience of elapsing time by taking advantage of external changes that unfold in time, such as the trajectory of an observed or self-generated movement and comparing its starting and ending positions at the beginning and end of the interval (chapter III, in Bergson, 1922). This comparison is possible because movements can leave an immobile trace in space, unlike the experience of time (durée) which is by nature ever-changing.

Bergson's views can be summarized into two related points: 1) the inner experience of the passage of time is ever-changing and 2) its quantification cannot be achieved on a purely internal basis and requires its externalization through observed or self-generated movements unfolding in space. The second point provides a testable mechanism for explicit time estimation, *at the behavioral level*. Clearly, this mechanistic proposal appears counterintuitive if not plain wrong. Isn'it disqualified by our ability to count in our head and the repeated observations that other (i.e., non-verbal) animals solve a variety of time estimation tasks and anticipate events relevant for their survival on a wide range of timescales? Moreover, Bergson's challenge of the notion of internal representation of time seems to be contradicted by their ubiquitous presence in several brain regions. The philosophical nature of Bergson's proposal (see Appendix A in supplementary material for a step-by-step introduction to his arguments, and specifically Appendix A′ subsections 2 and 3 for a demonstration that counting is a spatial process), which he developed before the rise of psychological and neurophysiological experiments on time perception, may explain that it has been often overlooked by neuroscientists and experimental psychologists studying the perception of time (Arstila and Lloyd, 2014; Buonomano, 2018; Wearden, 2016; Wittmann, 2017).

The goal of this essay is to show that there is substantial experimental evidence, at the behavioral and neuronal levels, supporting Bergson's forgotten proposal and that time should be seen as a force to which animals are sensitive rather than as static information (like space) processed internally. In the first and main section of this essay (Section 2), a cross-species examination of behavioral studies will highlight that the proficiency of humans and other animals in a variety of time estimation tasks is facilitated by their ability to spatialize time through self-generated movements. In addition, it will be shown that the temporal structure of animal behavior in timing tasks (e.g, anticipation), which has been assumed to reflect explicit reliance on internal representation of time, can also be accounted for by time-varying motivational constraints. In the second section, I will turn toward the so-called neuronal representation of time and show that one of their main features is that they occur in brain regions implicated in sensorimotor control, spatial navigation/cognition and motivation (Section 3). In the last section, I will first highlight the originality of a bergsonian approach to time in regard to other theories, especially how it fundamentally differs from the behavioral theory of timing (Killeen and Gregor Fetterman, 1988; Section 4.1). Because an exhaustive review of the timing literature is beyond the scope of this essay, it is likely that a reader will immediately think of a particular study, not cited here, that concluded that animals perceive time internally or reported on the existence of representation of time. Thus, in Section 4.2, a general method is provided to verify whether a given study does indeed provide evidence in favor of an explicit reliance on internal and quantitative knowledge of time or leave some space for the alternative framework proposed here. Finally, this essay will be closed with an attempt to demonstrate why a conceptual confusion on the question of time was almost impossible to avoid, and how the concept of durée introduced by Bergson is intellectually fertile beyond the question of prospective time perception to tackle recently disputed problems such as the validity of so-called old fashioned psychological terms (Buzsáki, 2019), the difference between natural and artificial intelligences or to explain our difficulty to conceptualize and take action against global warming (Section 4.3).

## 2. Internal explicit estimation of time intervals in the second range: a reality check

### 2.1. Do rats and pigeons perceive time in temporal categorization tasks?

The idea that animals internally measure the duration of time intervals has started to be tested in pioneering experiments on pigeons (Stubbs, 1968) and rats (Church and Deluty, 1977) engaged in bisection tasks. In this paradigm, to obtain a reward, food-restricted animals were first trained to select one of two actions (press a left or right lever, or peck in one out of two feeders) in response to a short or a long visual or auditory stimulus. After extensive training, stimuli with short, intermediate and long durations were presented and the proportion of "long"responses reported (Fig. 1A). Rats and pigeons displayed high levels of accuracy in response to the longest and shortest stimuli while performing closer to chance level for stimuli of intermediate durations, a performance profile that is well captured by sigmoid psychophysical curves (Fig. 1B). This type of result was interpreted (and still is) as supporting the idea that animals explicitly estimate the length of a time interval in the supra-second range. But what were the animals actually doing while listening or watching the stimuli in this type of task? If they were estimating time internally, one would expect them to stay immobile or to behave relatively randomly during the interval. At the time of those two landmark studies, videos were not routinely recorded and the authors did not provide a detailed description of the behavior of their animals during task performance. Gouvea et al. (2014) were the first to continuously videotape rats performing a modified version of the bisection task. In this study, thirsty rats had to poke in a central port to trigger the delivery of two brief sounds separated by an interval that could take one out of seven values between 0.6 and 2.4 s. If the interval was longer(shorter) than 1.5 s, animals had to poke in the left(right) port to obtain a reward. Similarly to what was observed in the aforementioned bisection tasks (Church and Deluty, 1977; Stubbs, 1968), rats categorized almost perfectly the longest and shortest intervals while performing close to chance level for those near the stimulus boundary. But against the anthropomorphic view in which animals count time in their head before deciding whether the interval was short or long, the video recordings and movements quantification revealed that the rats developed idiosyncratic stereotyped motor sequences that were initiated by the presentation of the 1st tone. The authors provide a video showing the behavior of a rat during all the trials of a given session in which the longest interval was presented (see Supplementary Movie 1 in Gouvea et al., 2014). As soon as the first tone was played, the rat systematically exited the central port and moved toward the right (short) side with very little variability. After 1.5 s, i.e. before the second tone was even played, the animal moved in the opposite direction and reached the right (long) port. Two interpretations are possible. The animal used an internal knowledge of time to decide when to leave the right port and reach the left one. Alternatively, the animal may have developed a motor routine in which he learned that if it had not received any reward after moving toward and licking in the short port, the reward will be delivered in the opposite port. The authors provide compelling evidence for such an action-based strategy by examining the movements of the rats when a near-boundary interval was repetitively presented, a condition in which rats' categorization accuracy was near chance level. They observed that in two out of three animals, the trajectory of their heads during the

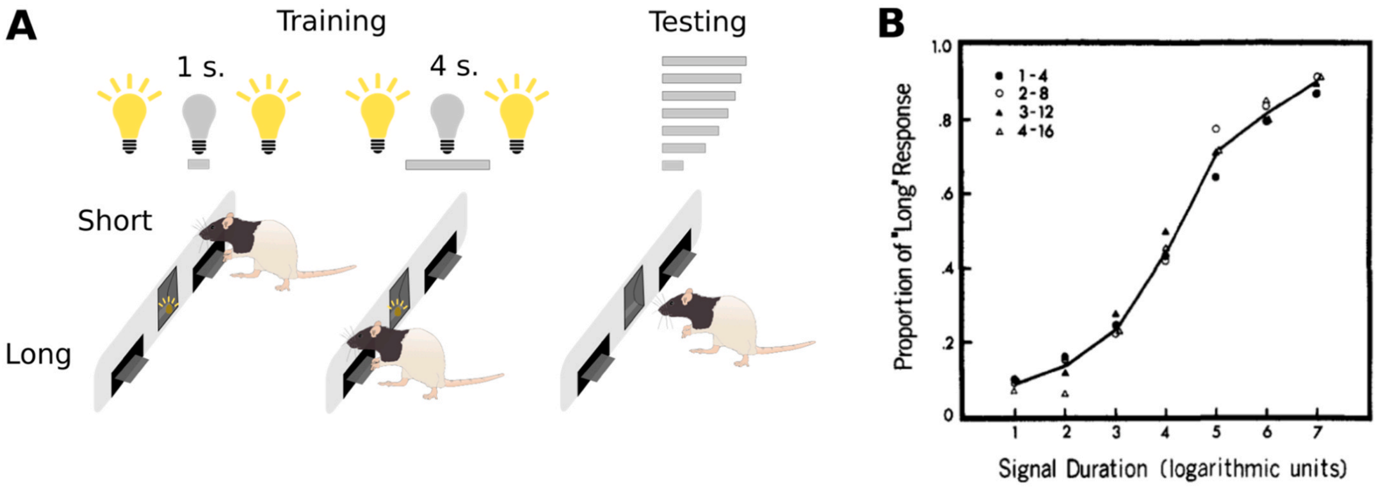

**Fig. 1.** Bisection task. A, In the training phase, a light is turned off transiently for either a short (1 s) or long (4 s) duration and rats must press the correct lever to obtain a reward (Left lever press response for long duration). In the testing phase, in 50% of the trials, intermediate durations are presented. B) Proportion of long response as a function of light-off duration, for 4 ranges of duration (see inset, duration range in seconds). Data from Church and Deluty (1977).

interval accurately predicted the animals' choice. The authors provide a compelling video showing an animal which, contrary to the previous one, moved toward the left (long) port following the presentation of the first tone (see Supplementary Movie 2 in Gouvea et al., 2014). Critically, at the exact time at which the second tone was played, the animal changed direction toward the right (short) port only in trials in which it had not yet reached the left port. Thus, in striking agreement with Bergson's proposal, thanks to the development of stereotyped movements that unfolded following the presentation of the first tone, this animal used its position in space when the second tone was played as a proxy of the length of the interval (i.e., long choice co-occurred with longer distance traveled during the interval, despite fixed interval presentation; Fig. 2A-B). This study clearly challenges the commonly assumed vision of rats perceiving duration directly to judge the length of time intervals. Importantly, a qualitatively similar result had been reported using the classical bisection task in which pigeons and rats were required to discriminate between a 6 s and a 12 s long interval (Fetterman, Killeen, and Hall, 1998). There was no video recording but the authors reported the development of stereotyped motor routines during the stimulus presentation and that "*prediction of their temporal judgments was always better if based on collateral* [motor] *activity than if based on the passage of time*". Finally, the fact that animals do not abstract duration during discrimination choice tasks is supported by the early observation that changing the nature of the stimulus that provides duration indication (e.g., switching from light to sound), induced a profound drop in performance and a slow relearning process over the course of ten days, effects that are easier to explain if animals relearned a new sensory-delimited motor ritual than relied on abstract representations of time (see Figure 2 in Roberts, 1982).

Proponents of the view in which animals explicitly use neuronal representations of time will argue that the above study (Gouvea et al., 2014) does not rule out that the rats were internally estimating time while moving. For them, the short and long choices observed for near-boundary stimuli would be explained by different speeds of their internal clock (dedicated or intrinsic) that would "artificially" contaminate their movements. This possibility should be addressed experimentally (see below) but one can nevertheless notice that it does not explain why the animals developed such stereotyped behavior in the first place. In contrast, if animals were using their position in space at a given time (or the distance they moved between the two tones) as a proxy for interval duration it would make sense that they develop stereotyped motor sequences (i.e., if the movements varied too much the animals could not rely on them). In addition, arguing that rats may have internally counted is unfalsifiable (no one can ask the rats) and could find its root into an deceptive anthropomorphisation of animals' inner life common in experimental psychology (Despret, 2015).

There are several experimental predictions one can make if animals do perceive duration indirectly using their sensorimotor state at a given time rather than internally. The first one is that sensorimotor-based strategy relying on stereotyped motor sequences should be the norm in timing tasks across species. The second prediction is that interfering from the outside with the sensorimotor state of the animals/subjects should alter their timing accuracy. The third one, which directly follows from the second one, is that providing experimental conditions that favor movements or the usage of external sensory cues should improve timing accuracy. The last one is that in experiments in which animals can't develop stereotyped motor sequence or in which temporal inaccuracy is not strongly penalized, the animals/subjects should not display accurate behavior. We will see below that all those predictions are largely verified.

### 2.2. *When animals do as they please, or the ubiquity of motor stereotypies during timing tasks*

That animals develop stereotyped motor behaviors when rewards are delivered according to temporal contingencies is not limited to bisection tasks but in fact has been repetitively observed since the earliest interval timing studies. Notoriously, Skinner (1948) reported that pigeons developed idiosyncratic stereotyped chains of actions such as wing flapping, head movements, pecking or circling during a task in which a food hopper was presented at a fixed-interval (FI) of 15 s (Fig. 3). In tasks with FI schedules of reinforcement (the first lever-press performed after a given interval following the previous reward triggers a new delivery), rats display stereotyped cascades or chains of actions during the interval (Killeen and Gregor Fetterman, 1988). The unexpected and often idiosyncratic nature of these behaviors that are not instrumental for the obtention of reward (i.e., only a given lever press was), lead researchers to defined them as collateral, adjunctive or even "superstitious" (Skinner, 1948; Staddon and Simmelhag, 1971; Timberlake and Lucas, 1985).

In this type of task (e.g. FI reinforcement schedules), it is important to emphasize that timing accuracy is not required to obtain rewards, as early presses during the interval are not penalized. This can explain why rats display prominent and temporally variable anticipatory presses, sometimes several seconds before the end of the interval (Church et al., 1994; see also Cook et al., 2022), but also why collateral behaviors can

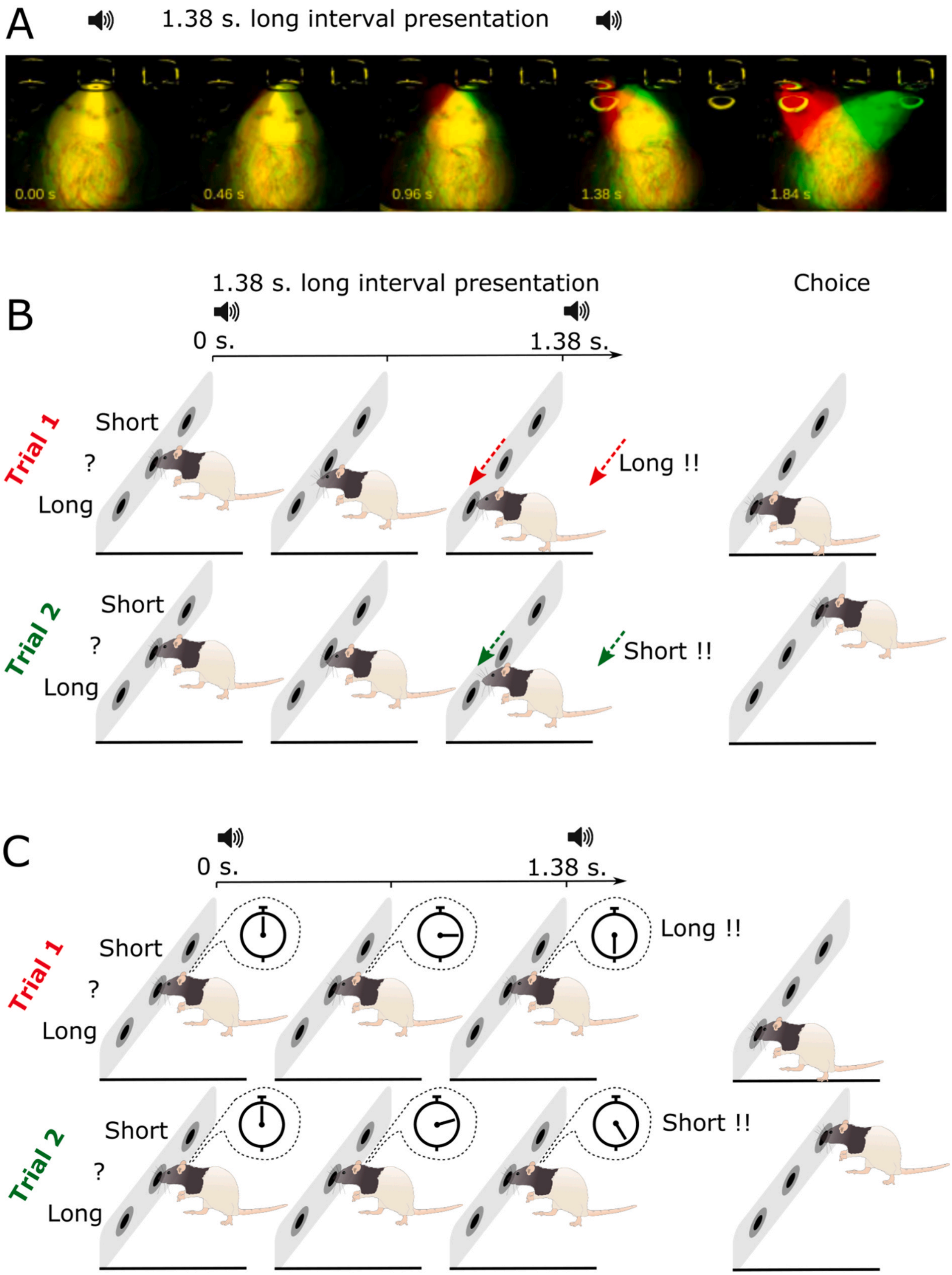

**Fig. 2.** A, Series of video frames taken from a single animal during presentations of a near boundary interval (1.38 s) in a single session and overlapped. Frames from trials in which the animal judges the interval short(long) were colored in green(red). Note that when the second tone was played (t = 1.38 s), trials in which the animal had already(not yet) reached the left port were classified as long(short). Data from Gouvea et al. (2014), with permission. B, Schematic representation of a rat using its position at the end of the time interval to decide between the left and right reward port. C, Same as B but according to the neuronal clock hypothesis.

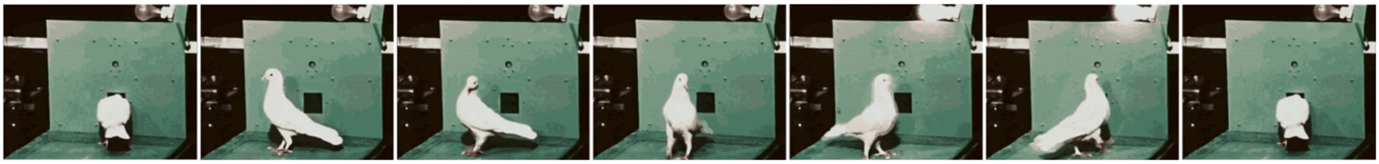

**Fig. 3.** Illustration of the type of circling behavior that could be displayed by a pigeon during FI reinforcement schedule.

drift quite substantially during the course of a given testing session (reviewed in Richelle and Lejeune, 1980). Added to the observation that the different actions composing a superstitious sequence were not randomly distributed during the intervals, this led researchers to think that collateral behaviors did not emerge because they were necessary to estimate time but rather that they were themselves driven or controlled by some sort of internal clock-like mechanism (Killeen and Gregor Fetterman, 1988; Richelle and Lejeune, 1980). Nevertheless, it is striking that robust collateral behaviors were reported in tasks in which time accuracy was critical to obtain rewards. For instance, in differential reinforcement of low rates (DRL) schedules, a lever-press delivers reward if, and only if, it follows the preceding press by a given interval (i.e., an early anticipatory response would further delay reward delivery). Strong and stereotyped collateral behaviors such as tail neebling, cage biting, climbing, grooming or exploratory runs aways from the feeder, were observed in those experiments (Laties et al., 1965; Wilson and Keller, 1953). Importantly, such behaviors were not restricted to pigeons and rats but were also observed in monkeys (Hodos et al., 1962) and humans (Richelle and Lejeune, 1980), which raises the issue that, they could be hidden from the experimenters (e.g., mouth/-tong mumbling). Recently, the high-speed video recording of rats challenged in an interval reproduction task requiring them to press twice a lever with a 700 ms delay demonstrated the prominence of stereotyped movements during tasks with strong temporal contingencies (Kawai et al., 2015). In this study, all the animals developed, through a slow trial-and-error process, idiosyncratic rituals composed of a succession of movements (such as rearing, paw movements including wall touching, brief tongue protrusion, and head movements, see Movie S1 in Kawai et al., 2015) that filled up the interval between the two presses. This study challenges an anthropomorphic view of timing tasks in which rodents would press, wait, and then press again after internally estimating the length of rewarded delay in their head. In addition, it showed that, when accurate timing is required to obtain rewards, the level of stereotypy was near perfection across trials. This observation is important because drift in the content of collateral behaviors has been one of the main arguments to reject their causal contribution to timing (Killeen and Gregor Fetterman, 1988; Richelle and Lejeune, 1980).

Even if the development of stereotyped motor sequences has been reliably observed in a wide range of timing tasks (DLR, motor reproduction, temporal bisection) and is now well-documented thanks to video recordings, it does not rule out that animals perceive duration in a disembodied manner when experimental conditions hampered the usage of motor sequences. To understand the neural bases of time perception devoid of motor confound, we attempted to train rats in a timing task while forcing the animals to continuously run on a motorized treadmill. In our task, rats needed to wait for 7 s after trial onset before entering a reward area located at the front of a long motorized treadmill. Trial onset coincided with turning on the treadmill at a constant speed in a direction that pushed the animals away from the reward area. While we originally expected the animals to run in front of the reward area while estimating the delay durations, we observed that a large majority of the animals developed by trial-and-error a conserved “front-back-front” trajectory inside the treadmill which seemed to be required to enter the reward area near the waiting time. Specifically, during intertrials, the rats positioned themselves in the reward area. After trial onset, they remained relatively immobile while the treadmill dragged them away from the reward area until they reached the rear wall of the treadmill at which point they started running forward and crossed the treadmill in one go, leading to a reward area entrance time of about 7 s (Rueda-Orozco and Robbe, 2015; Safaie et al., 2020; see Movie S2 compared to S1 in Safaie et al., 2020). Thus, animals seemed to rebel against our attempt to “clamp” them in a running state to study the neural bases of time estimation. In addition, we used theoretical simulations to verify that the strategy used by the animals was not the one we could have expected if animals relied on disembodied representations of time (see Figure 6 in Safaie et al., 2020). Critics will argue that the task parameters (velocity of the treadmill, rear wall position, waiting time) did favor this embodied and situated strategy. However, we found that other rats trained in a version of the same task in which the treadmill remained immobile became proficient by sequentially running toward the rear wall (instead of being passively dragged there after treadmill onset), performing idiosyncratic motor rituals in the rear section of the treadmill (rearing, biting of the belt or walls) and running back in the reward area just on time (see Movie S3 in Safaie et al., 2020). Interestingly, the animals that displayed the highest timing accuracy were those that developed such an active front-back-front routine. Moreover, similar behavioral results were observed in a study which was designed to investigate the neural basis of time estimation freed from any motor confound (Shimbo et al., 2021). In this work, rats were forced to run on a treadmill for either a short or long interval (e.g., 5 s vs 10 s). When the treadmill was turned off, a lateral door opened and the animals could enter the central stem of a Y-Maze to express their judgment of the run duration (Fig. 4). If it was short (long), the animal could obtain a reward by entering the right (left) arm of the Y-maze. Critically, the treadmill speed could take two values according to the trial duration (it was twice slower for long duration trials) to avoid the animals using run distance as a proxy for duration. Again, and despite such precautions, it appears that most of the rats progressively developed stereotyped routines while the treadmill was on (Fujisawa’s personal communication). In a video shared by the authors (Supplementary Video S1; note that this video was taken during training and thus was not part of the published dataset), the rat kept biting the reward port located in the front of the treadmill and its head movements and body posture were stereotyped across successive presentation of the time intervals to discriminate. This behavior is strikingly reminiscent of the mouth-to-tail adjunctive behavior observed by Laties et al. (1965) and that was instrumental for performance of the DRL task (see below). Thus, and even if this hypothesis needs to be explicitly tested, animals may have developed a running-independent orofacial action sequence to differentiate short and long intervals *at the time of treadmill offset*. Importantly, this behavior occurred despite the fact that time intervals to discriminate were strikingly different.

### 2.3. Movements and time estimation beyond correlations

Even if highly stereotyped motor behaviors have been reliably observed in “freely” behaving animals performing timing tasks with strong temporal constraints, correlation does not establish causation. Previous attempts examining whether their direct alterations impaired timing proficiency met mixed successes (Richelle and Lejeune, 1980). For instance, in a waiting task in which a rat made several mouth-to-tail contacts to delay its reward-oriented response, covering the animal’s tail with a bitter solution, only partially altered the ability of the animal to wait (Laties et al., 1965). One possible explanation proposed by the authors is that once the animal could not bite its tail "*other behavior emerged to mediate successful pauses, perhaps a collateral chain that had been learned previously but had been supplanted by the more efficient chain*". We recently addressed this issue in our treadmill-based waiting task, taking advantage that most rats converged on the same front-back-front motor routine. By manipulating the speed of the treadmill (its magnitude and reliability across trials) or interfering with the animals initial position at trial onset, we created conditions that prevented the development or optimal usage of this motor routine. The timing accuracy of the animals was systematically reduced in such conditions (Safaie et al., 2020). Even if this task did not require animals to compare the length of different time intervals, this study provides evidence that accurate timing does require stereotyped motor routines in rats. It also illustrates the contribution of external features of the environment that afford temporal cues.

A limitation of behavioral experiments in rodents is that there is no way to instruct them to explicitly estimate duration in their heads. While this does not explain their systematic reliance on situated motor sequences to obtain rewards in various forms of timing tasks, it leaves open the possibility that they could estimate time internally if they understood what was required from them. Such a limitation should not apply when studying how humans perform time estimation tasks. Still, there is ample experimental evidence showing that our ability to measure duration is built upon sensorimotor interaction with the world during childhood (Coull and Droit-Volet, 2018). In a task in which children were watching movies depicting snails moving on a screen with a balanced combination of distance and duration, spatial information influenced temporal judgments more than temporal information influenced spatial judgments (Bottini and Casasanto, 2013; Casasanto and Boroditsky, 2008). In adults, a large number of human studies using diverse timing paradigms have reported that the accuracy of time estimation is improved or distorted by movements (see De Kock et al., 2021 for a recent and exhaustive review on this topic). For instance, when humans categorized supra-second intervals as short or long using a joystick that they could freely move during interval presentation, they spontaneously moved it first toward the short target and then gradually moved it toward the long one. Critically, externally slowing down the joystick' speed by increasing its viscosity lead to shorter distances traveled during interval presentations and shorter perceived durations (De Kock, Zhou et al., 2021). One could obviously object that such a study only shows that time perception is biased by movement speed and does not rule out a fundamental internal process responsible for time estimation. Nevertheless, there is additional evidence showing the fundamentally intricacy between movements on the one hand and spatial and temporal estimates on the other hand. In a series of studies relying on saccadic eye movements, participants were asked to locate a visual stimulus briefly flashed on a screen. At different times around the presentation of the stimulus, the subjects were required to perform a saccade. Spatial localization was accurate when the saccade was performed much before or after the presentation of the visual stimuli but a mislocalization was observed (a shift toward the target of the saccade) when the saccade occurred just before the visual stimuli (Ross et al., 1997). Critically, in a follow-up study, it was observed that a similar mislocalization was observed in the time domain when participants were asked to report on the duration of an interval between two visual stimuli (Morrone et al., 2005). The distortion of temporal estimates was robust for a wide range of saccade magnitudes including small ones (3.5 degrees) and when participants were asked to localize the visual stimuli *and* estimate its timing relative to two auditory tones played before and after stimuli presentation, the magnitudes of the spatial and temporal distortions induced by the saccades were highly correlated (Fig. 5) (Binda et al., 2009).

Importantly, similar distortions were also induced by full arm movements (Tomassini et al., 2014; Tomassini and Morrone, 2016) or rhythmic finger tapping (Tomassini et al., 2018), which led the authors to propose that distortion of temporal estimates may be an unavoidable consequence of timing mechanisms that ultimately require sensorimotor integration.

### 2.4. *Measuring time while being immobile: an impossible quest?*

Collectively, the studies presented so far revealed the intricacy between time estimation and movements in primates, rodents and birds. A surprising but reliable observation is that when rewards are delivered according to strong temporal contingencies (i.e., not respecting them significantly delays the next reward opportunity) such as in bisection or temporal reproduction tasks, freely behaving rodents spontaneously develop stereotyped motor sequences during the behaviorally relevant intervals (e.g., Gouvea et al., 2014; Kawai et al., 2015), even when the testing apparatus were a priori designed to limit such motor confounds (Safaie et al., 2020; Shimbo et al., 2021). An obvious objection to such an intrinsically embodied and situated view of prospective timing is that humans can estimate time by counting in their head while being immobile and animals might be able to perform a similar operation (but see Bergson's dissection of the processes at play when counting time; subsections 2 and 3 in Supplementary Appendix A). To eliminate potential motor confounds, researchers studying prospective time perception have also developed protocols in which rodents are forced to maintain their head in a nosepoke during the presentation of intervals (Gouvêa et al., 2015) or have their head completely immobilized using a restraining device (Heys and Dombeck, 2018). They have also taken advantage of the possibility to perform well-controlled psychophysical

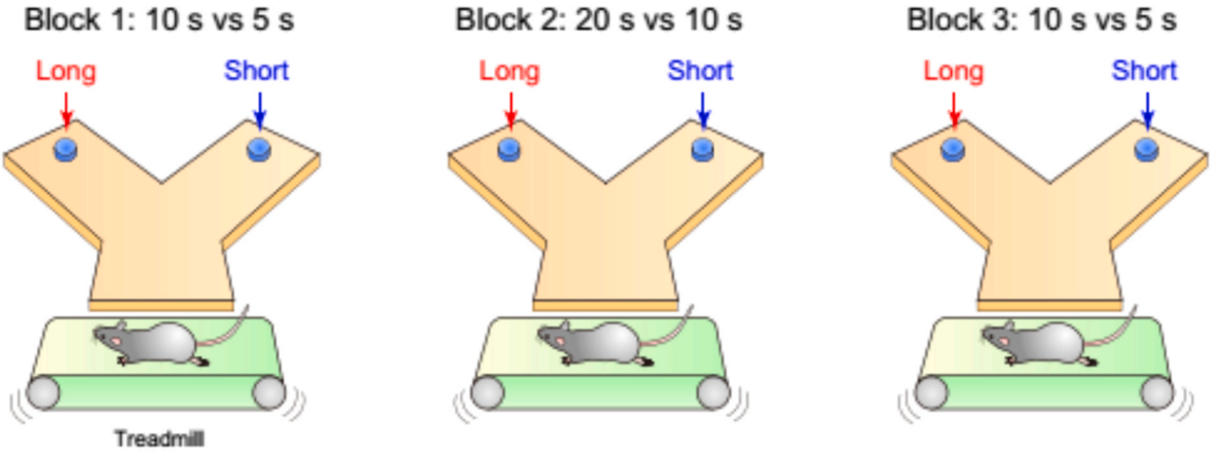

**Fig. 4.** Schematic of the treadmill-based bisection task. Drawing from Shimbo et al. (2021) with permission. See supplementary video S1 recorded during training.

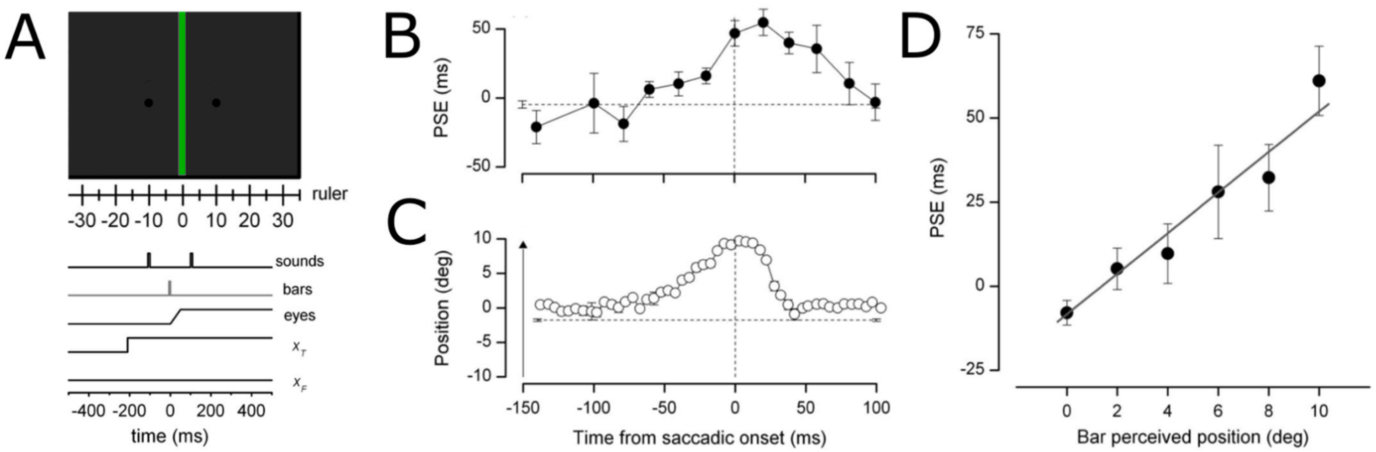

**Fig. 5.** Saccades induced temporal and spatial misperceptions of visual stimuli whose magnitudes are correlated. A) Experimental design. A green vertical bar is presented at different positions on the screen and between two sounds. Subjects must localize the position of the bar relative to a remembered ruler and estimate whether it was played closer (in time) from the first or second tone (bisection). The subjects are also asked to saccade from the left to right targets (black circles) at different times around the bar presentation. B) Average temporal mislocalization of the bar (point of subjective equality, PSE) in function of the stimulus presentation time relative to the saccadic onset. C) Spatial mislocalization of the bar in function of the stimulus presentation time relative to the saccadic onset. D) Correlation between the spatial and temporal distortions. Data from Binda et al. (2009), with permission.

and electrophysiological experiments in non-human primates immobilized in restraining chairs. Before discussing studies using such a strategy, it is necessary to lay out their associated experimental challenges. First, requiring animals to remain immobile even for a short amount of time while waiting to have an opportunity to obtain a reward can only be achieved through long and progressive training procedures. In some cases, a significant fraction of animals fail to go through such procedures. For a task as simple as holding a button for more than 2.5 s, NHPs need to be first trained on very short intervals (more than 0.2 s) which will be gradually increased during 1–2 months of daily training (Lebedev et al., 2008). This already suggests that the idea of estimating time while being immobile, derived from human introspection, is unnatural for other animals. The fact that most tasks requiring animals to wait before doing reward-oriented actions require to start by very short intervals, shows that animals naturally value immediate reward. This will raise a potential confound between motivation (or urgency), which will increase as the animals wait to perform an action and time estimation. Second, even when the training procedure is successful, it will be hard to exclude that animals have not developed motor sequence to assist time estimation, using less-constrained parts of their body. For instance, Gouvea et al. (2014) reported that in their temporal categorization task, one of the animals "*did not display overt head trajectories during the interval period, staying at the initiation port throughout presentation of the stimulus interval instead. However, close inspection of individual videos suggested that this rat may have produced smaller scale movements around the initiation port in the axis normal to the image plane*". In fact, one could argue that the reason why it takes so long for animals to become proficient is congruent with a slow trial-and-error process necessary to create and fine-tune a motor sequence that will be useful to discriminate whether a given duration is shorter or longer than a reference one. Because distinguishing intervals of one versus two seconds seems rather easy, one would also expect that performance curves displayed a sharp positive inflection once animals understand the rule, which to the best of our knowledge has never been reported. More generally, it has been more recently reported that even after extensive training, head-restrained mice display prominent facial and postural fidgetings during decision-making tasks with brain-wide impact on neuronal activity (Musall et al., 2019; Stringer et al., 2019). During 1 s trace conditioning learning, mice spontaneously display a wide range of orofacial movements including whisking and eye movements between the CS offset and US onset, thus never remaining immobile (Coddington et al., 2023). While the role of fidgeting in timing tasks has not been explored in rodents and non-human primates (NHPs), its potential functional relevance is supported by the observation that the perception of short intervals by human subjects was perfectly correlated with muscle activity from the face (Fernandes and Garcia-Marques, 2019). Moreover, as described above (section 2.3), even small eye movements can have a strong effect on time perception. With these potential caveats in mind, let's describe the results obtained in representative studies investigating prospective time perception in extensively trained non-freely moving animals.

Using a virtual reality environment, Heys and Dombeck (2018) and Heys et al. (2020) trained head-restrained mice to wait for a defined amount of time (6 or 4 s) before crossing an invisible door and running for a reward. Importantly, before being trained in the final version of the task, mice already displayed a wide range of waiting durations, with a marked preference for short waits (see Figure 1C top, in Heys et al., 2020). After training, the mice performed fewer short waits (< 3 s, see Fig. 1C bottom) but the distribution of the waiting times was strongly skewed toward times shorter than 4 s. While the authors interpret their findings in the framework of internal representations of time perception, one could wonder why it was so difficult for mice to wait for only a few seconds if they were able to perceive duration (see also Schreiner et al., 2022, for a similar difficulty in a task in which mice must hold down a lever for a short durations). There was no video quantification of the animals' behavior during the waiting period, leaving open the possibility that mice used postural or orofacial fidgeting to increase the proportion of long wait times. Thus, the results obtained in this study could also be interpreted as illustrating their impossibility to perceive time (hence their difficulty to perform this simple task) and sensitivity to the cost of time (to optimize capture rate, mice attempt to obtain reward as early as possible (see section 2.5 below).

Leon and Shadlen (2003) developed a temporal discrimination task for NHPs in which the subjects had to estimate whether the duration of "test" visual stimulus (a fixation point that turned transiently white for a duration that could take one out of 12 values between 130 and 1600 ms) was shorter than a "standard" visual stimulus (the same fixation point that turned blue for either 300 or 800 ms) presented just before the test stimulus. The animals had to saccade toward one of two colored targets to indicate their choice (long or short, Fig. 6A). They discriminated accurately the duration of very short versus very long test stimuli, performing closer to chance when the test stimulus duration was close to the standard one (Fig. 6B). While those results are congruent with an internal perception of time, the contribution of facial movement

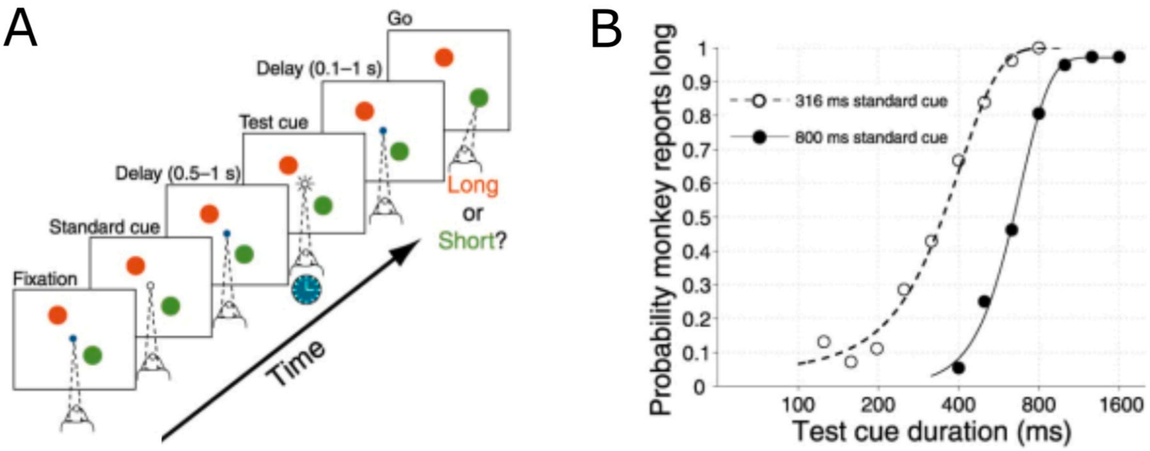

**Fig. 6.** A, Time discrimination task. B, Behavioral results from one experimental session. Figures from Leon and Shadlen (2003) with permission.

(including saccade) was not investigated. Moreover, the authors focused on very short intervals (the two reference intervals smaller than 1s). This is somehow contradictory with the idea of prospective time perception (which is really relevant for supra-second intervals) but might relate to the difficulty in having NHP holding fixation for long intervals, as observed in mice. Moreover, the authors' underlying assumption that monkeys explicitly estimated the duration of the intervals (they speak of the *monkey's uncertainty about its temporal judgment*) is somehow in contradiction with the fact that the interval durations could be extremely short, often below 300 ms. It is unclear how one can explicitly perceive a time interval of 150 ms. Finally, the authors themselves discuss an alternative mechanism in which the monkey would attend "first to the short-choice target and then gradually shift attention to the long-choice target". It will be discussed later that this "movement" based mechanism makes sense from a neurophysiological perspective (Section 3.1).

In a study explicitly designed to minimize the contribution of movements to temporal perception, NHPs were trained to reproduce a short or long interval between two visual stimuli before acting with one of two effectors (button press with the hand or visual saccade to a screen target). The interval to be reproduced and motor effector to express duration estimates (eyes or hand) changed on a trial-by-trial basis and was cued by the color and shape of the fixation point (Wang et al., 2018). The contribution of eye movement, although not explicitly investigated, is compatible by the higher temporal precision displayed by the animals when the effector was the eye compared to the hand. Moreover, activity profiles in regions of the cortex that are important for motor control and inhibition scaled accordingly for short and long intervals. The same group developed a refined version of this task by training two monkeys to reproduce a range of intervals (Sohn et al., 2019). The experiments were performed in blocks of short (ranging from 480 to 800 ms) or long (from 800 to 1200) intervals, allowing to compare how animals estimated the same interval (800 ms) depending on whether it was presented inside a short or long block. Animals perceived this 800 ms-long interval shorter (longer) when it was presented in the context of short (long) intervals. Thus, NHPs do not seem to estimate time in an abstract manner. While it is not directly obvious why such a contextual-dependency for very similar time ranges would occur if NHPs used disembodied time estimation, this would easily be explained if those animals used different sensorimotor-based strategy for the two types of intervals. Moreover this later interpretation is also congruent with the fact that duration estimates were well predicted from neuronal activity recorded in brain regions implicated in the control of saccadic eye movements (Supplementary Eye Field) and action planning (Supplementary Motor Area).

An earlier study examined the ability of NHPs to estimate duration over much longer intervals (2, 4, and 8 s) according to the color of an instruction cue (Mita et al., 2009). The authors used electromyography to record the activity of several limb and trunk muscles and mentioned they did not observe any consistent changes in activity during the hold time of three different duration. However, the activity of facial muscles was not recorded.

Altogether, the above studies provided evidence for internal estimation of time interval in the second and supra second ranges although they do not rule out (and are sometimes congruent with) a contribution of covert movements.

### 2.5. *Response timing in fixed interval, peak procedures and trace conditioning. Evidence for internal time estimation or reward rate sensitivity?*

Until now, the focus of this essay has been to illustrate the importance of movements in a variety of time estimation tasks (e.g., bisection or reproduction/waiting procedures) and to challenge the view that animals are proficient in such tasks thanks to explicit internal representations of time. However, the concept of internal (i.e., movement-independent) representation of time guiding behavior is also derived from observing rats and pigeons responses in FI schedules of reinforcements, peak procedures (FI with probe trials lacking reward delivery) or trace conditioning experiments, that do not require accurate timing (Church, 1984; Church et al., 1994; Gallistel and Gibbon, 2000; Gibbon et al., 1984). Indeed, in FI schedules of reinforcement, the first response after a fixed interval triggers the delivery of a reward, independently of whether the animal had already pressed the lever several times during that interval (i.e., anticipation). Similarly, in trace conditioning experiments, in which the presentation of the conditioned stimulus (CS) and the unconditioned stimulus (US) is separated by an interstimulus interval, animals are free to initiate their conditioned response (e.g., lever pressing, licking, freezing) before the actual reward (or punishment) is delivered. When averaging the timing of the instrumental/conditioned responses over multiple trials, those studies have revealed two trends. First, the average response rate of a trained animal starts increasing way before the end of the interval to be estimated and, if no reward is delivered (i.e, probe trial of peak procedure), it reaches its maximal around the time interval to be estimated before decaying toward baseline level. Second, such bell-shaped average response curves scale linearly with the duration of the interval to estimate (i.e., distinct curves obtained for different intervals overlap once normalized along the time axis). These two observations have been assumed to be congruent with the idea that animals explicitly time their rate of responses according to an internal perception of duration. Critically, in regard to the mechanisms underlying interval perception, even if collateral behaviors have been reported during FI or peak procedures, they can be quite variable (Richelle and Lejeune, 1980) and do not explain why animals, in average, press faster around the expected time of reward delivery, or why they start lever-pressing earlier for short FI compared to long FI. In addition, in trace conditioning, it is unclear how the animals could infer the interstimulus interval length from the relatively random behavior they produce across trials. Thus, the behavioral results obtained in this type of tasks seem to challenge the main hypothesis of this essay. Below, I will highlight that the several features of the learned responses observed in FI tasks, peak procedures and trace conditioning are not compatible with an explicit reliance on an internal representation of time. Rather they appear to reflect the ability of animals to detect changes in reward rate, which will in turn control response vigor (Niv et al., 2007; Shadmehr et al., 2019). In other words, the timing of animals's lever presses in a FI task may reflect primarily their ability to learn and update utility functions.

In their seminal review on time and associative learning, Balsam et al. (2010) described an experiment in which two groups of rats were exposed to a 6 s-long auditory tone (CS) paired with food delivery (US) after either a short (6 s) or a long (18 s) delay (trace interval). On average, rats in the short trace group immediately increased their number of head entries into the reward magazine upon CS presentation, despite the fact that the US was only available 12 s later. In the long trace group, the increase in the rate of response was slower compared to the short trace group, and it reached a lower peak value about 12 s before the food became available (see Figure 3 in Balsam et al., 2010). The authors concluded that "*the lower level of responding [of the long trace group] would appear to reflect an accurate knowledge of when the reinforcer will be delivered*". But such an interpretation seems to be contradicted by the fact that the short trace group can't even wait before the end of the CS to start responding. Why do animals respond in a sustained manner 12 s too early while having an internal knowledge of when the reinforcer will be delivered? Such a pattern of response seems rather to argue for the possibility that they had literally no explicit accurate knowledge about when the reward would start becoming available and for that reason, they continuously responded since CS presentation to obtain it as early as possible. A second issue with the "classical" interpretation of FI and peak procedures' behavioral data, is that, also the mean response rate appears to increase progressively and reach a peak around the time to be estimated, animals typically abruptly change their rate of responses over the course of individual trials (Church et al., 1994; Cook et al., 2022). Thus, the smooth increase in response rate does not reflect the fact that animals press faster and faster as they internally know that they are closer to the expected rewarded time but rather the large trial-by-trial variability at which animals start pressing at a steady rate, variability that seems to argue against their explicit reliance on internal representation of time.

Still, if animals are not explicitly aware of the interval length in FI or peak procedures, why, on average, animals in the long trace group increased more slowly their response rate following CS onset compared to rats trained with the shorter delay? An important aspect to consider is that those two groups did not only differ by the length of the interval between the CS and US but also by the average reward rate they received during the course of an experiment. Critically, it has been shown that if one makes the assumption that animals balance the energetic cost of acting quickly against the benefit to obtain reward sooner than later, the long run average reward rate will dictate the delay and speed of reward-oriented actions (Niv et al., 2007). The average reward rate, which correlates with the interval length, can therefore be considered as an opportunity cost: when it is high, delaying reward-oriented actions would lead to missing some potential benefits. Time is therefore valuable in high-reward rate conditions. On the contrary, when the reward rate is low, it is useless to spend energy and generate costly reward-oriented actions that are unlikely to bring any benefit. This normative theory predicts that the latency to start pressing for rewards should be inversely proportional to the intervals in FI reinforcements schedules, peak procedures or trace conditioning experiment, as these intervals directly influence the long-run average reward rate (Niv et al., 2007) and therefore it provides an alternative explanatory framework to understand the temporal structure of behavioral responses of rats in such tasks. Critically, this framework does not necessarily require animals to explicitly estimate time but rather to integrate benefits and costs on a moment-to-moment basis to generate utility functions (see also Shadmehr et al., 2019). It is also in agreement with experiments showing that the rate of reinforcement biases the timing of behavioral response in modified versions of the peak procedures (Bizo and Geoffrey White, 1994; Sanabria, Thrailkill, and Killeen, 2009).

In addition to potentially explaining behavior in FI tasks or peak procedures, an economic normative view in which animals minimize both the energetic cost of action and the time to collect rewards, is powerful to understand why rodents struggle in tasks requiring them to wait for short time intervals (Heys and Dombeck, 2018; Kawai et al., 2015; Safaie et al., 2020; Schreiner et al., 2022). Indeed, in all those studies, and despite considerable training, hungry or thirsty animals tended to not wait enough (either by acting too soon or by moving too quickly), which makes sense if by doing so they were attempting to save time and increase their reward rate. Similarly, compared to humans, animals tend to overestimate the passage of time in bisection tasks (short intervals are judged longer than they really are; Kopec and Brody, 2018). It was proposed that this difference stems from the fact that rodents are more sensitive to temporal discounting which would make sense considering that, unlike humans, they are typically water or food-restricted when performing this type of task. Importantly, it is unclear why rodents would predominantly make this type of impulsive errors if they were estimating time, as unbiased error in time estimations should lead to both shorter and longer estimates. Thus, for rodents, a sense of urgency, related to motivation constraints, may thus coexist with a fundamental inability to perceive duration quantitatively, a problem that may be partially reduced through the usage of motor sequences.

While sensitivity to the long-run reward rate may be sufficient to explain why in FI or peak procedure animals start pressing earlier for rewards when intervals are short, it is unclear how such a mechanism could help rodents to know when to check for the presence of reward in the food magazine. Strong evidence against internal knowledge of time was recently provided in mice trained in a new self-paced fixed interval task (Cook et al., 2022). In this study, food-restricted mice could self-initiate a timer by pressing a lever after its extension in the testing cage. Like in classical fixed interval instrumental tasks, the first press performed 30 s after the timer was initiated by the animals triggered the delivery of a pellet in a food tray. Critically, in one third of the trials, no pellet was delivered. At first, naive mice pressed at a low and constant rate throughout the probe trials. But after a couple of days, the mice progressively increased their rate of lever-press, which, in average, took the form of inverted U shape with a peak aligned to 30 s relative to the initial press. Critically, the authors found that mice had learned to associate the characteristic sound made by the lever when pressed at fast speed and the noise of the pellet falling in the reward tray. Indeed, the inverted U-shape lever press rate profile was strongly altered when the ears of the mice were sealed. In addition, when the noisy pellet was replaced by a silent delivery of diluted milk, the behavior of the animals totally changed: after timer initiation, the mice repetitively checked for reward delivery by going back and forth between the lever and reward magazine suggesting that mice were unsure of whether the reward had been delivered. Their lever press rate profile peaked at about 10 s and was still altered following ear sealing. Importantly, mice trained 20 days without probe trials did not display an inverted U-Shape lever press profile when submitted to a session containing one third of probe trials. Rather, they constantly pressed the lever showing that they did not spontaneously form a knowledge of the 30 s long interval. Thus, and contrary to an ambiguous claim made by the authors, the behavior of the animals does not appear to be driven by an internally monitored sense of the interval length. Rather, it is congruent with the possibility that mice were, on the one hand, sensitive to the average reward rate they can obtain and adapt their vigor accordingly (latency to start pressing). On the other hand, they inferred the interval length through sensorimotor information derived from their movements and the sound generated by the reward delivery. Importantly, a similar sensorimotor-based mechanism for accurate timing is at play in a rhythmic tapping task, suggesting that its relevance is not limited to mice and long time intervals but is also at play in human who received explicit instruction to time accurately their movements in the subsecond range (Morillon et al., 2014).

### 2.6. *Conclusion and future directions*

Because timing is an important feature of all adaptive behaviors and that animals are not equipped with time sensors, it has been assumed that animals explicitly estimate internally the length of behaviorally-relevant events or intervals in the range of one to several seconds, a process referred to as prospective time perception. Here, a reappraisal of a wide range of interval timing studies across species suggests that this view reflects more an anthropomorphisation of animals cognition (because we, humans, count time and abstract it in our head, we assume others animals do so) than an unbiased interpretation of the available experimental results (Despret, 2015).

On the one hand, in tasks requiring accurate estimation or reproduction of time intervals, freely moving animals systematically develop stereotyped motor sequences instead of remaining immobile and timing in their head. Importantly, the development of motor rituals in freely behaving animals occurs even when the experiences were designed to avoid this kind of strategy. Although, it is not clear how such a systematic development of motor rituals was expected if animals were explicitly estimating duration in their heads, one could argue that those results only establish a correlative link between timing and movement or arised from the inability of researchers to instruct the animals to pay attention to time. Nevertheless, experimental evidence, across species and tasks, demonstrates that timing accuracy depends on movements. In addition, in several timing studies in humans in which movements were manipulated, the effects on time estimation were congruent with a movements based mechanism. Finally, forcing animals to remain immobile during intervals requires extensive and unnatural training procedures against which they struggle at two levels: they often display impulsive responses and can’t resist to develop complex movements (postural fidgeting and orofacial twitches) whose timing functions are difficult to rule out. Altogether, the majority of the available data (see also Section 4.2) is congruent with animals not perceiving internally time for itself (i.e., in a quantitative manner independently of their movements or timing cues afforded in their environments) which incidentally would explain why in early studies their proficiency was often poor despite the apparent ease of the timing challenges they were facing (see chapter 2.1 in Richelle and Lejeune, 1980) or why, we human, are easily lost in time especially when we can’t rely on movements or external temporal cues.

On the other hand, the temporal structure of behavioral responses that emerge in temporal conditioning experiments (trace conditioning) and reinforcements schedules (FI and peak procedures) that do not require accurate estimation of duration has been assumed to reflect the animals’ reliance on internal representation of time. It is unlikely that motor rituals explain why rats start lever-pressing for rewards earlier when intervals are short than when they are long. Nevertheless, the limited temporal accuracy displayed by animals in those tasks (excessive anticipation that varies from one trial to another) argues against an explicit internal knowledge of interval duration. Critically, in such experiments, the fact that animals anticipate differently for distinct intervals can be explained by their ability to approximate reward rates which systematically co-vary with the duration of intervals. The timing of reward-oriented actions may therefore primarily reflect motivational factors and be congruent with a theoretical framework in which time is seen as an opportunity cost (Niv et al., 2007; Shadmehr et al., 2019) rather than an abstract information to be processed by the brain and internally represented.

Still, some key experiments are needed to demonstrate the fundamental intricacy between time estimation and movements, or to rule it out, and, on the other hand, to push forward a framework in which time would be considered as a source of motivation (almost like a force) rather than a static information like space. For instance, a better quantification of orofacial and postural movements and their external manipulation are still lacking during temporal categorisation tasks in rodents relying on head-fixation paradigms. So far in NHPs, most of the experiments have attempted to limit movements while their potential positive contribution has rarely been investigated (e.g., including different types of movements during interval estimation). Similarly, the importance of motivational factors (urgency, effort, reward rate) has been overlooked in tasks requiring accurate estimation of time intervals and could be manipulated to assess their contribution. More generally, most of the daily life examples of well-timed behavior (driving a car, foraging, or even playing music or practicing sports such as tennis) do not actually require to estimate time for the sake of it and one can display well-timed behavior while being oblivious to time (Taatgen et al., 2007). Taking inspiration from the variety and ever-changing nature of time intervals outside laboratories, it could be fruitful to invest in experimental designs in which organisms adapt to realistic (i.e., variable rather than fixed) temporal constraints rather than the artificial ones derived from a view in which time is considered like an abstract and fixed information that subjects can estimate with a stopwatch (van Rijn, 2018; Salet et al., 2022).

## 3. What function(s) for the neural representations of time ?

Here I will review a selected set of neurophysiological experiments (electrophysiological recordings of so-called representations of time, perturbation studies) in animals performing timing tasks and examined whether they provide strong evidence for internal explicit estimation of time (prospective time perception) or, alternatively, are congruent with well-timed behavior resulting from movement-based spatialization of duration, detection of contextual changes, or motivational processes, as shown in the previous section.

### 3.1. *Neocortical representations of time in cortical “motor” regions*

As mentioned earlier, in an attempt to isolate purely internal representation of time, one approach has been to perform electrophysiological recordings in non-human primates trained to estimate time while remaining immobile (section 2.4). An exhaustive review of all these studies is beyond the scope of this essay and I will first discuss a limited but influential series of experiments that reported time representations in neocortical regions. In a task relying on eye fixation, short time interval betweens visual cues ranging from 200 to 1600 ms, and visual saccades toward two targets to express duration judgment, Leon and Shadlen (2003) reported that neurons in the LIP areas represented elapsed time and, at the population level, firing variability explained the animals’ uncertainty about time. From these results, the authors suggested that “*the monkey could base its judgment of time on the discharge pattern of [such] neurons*”. First, as mentioned in the introduction of this essay, it is unclear how a time-based decision can be made based on firing patterns as those are not observable like a stop-watch. This interpretation seems to reflect a conflation between implementation and algorithmic levels of understanding of time-based decisions (Gomez-Marin, 2019; Krakauer et al., 2017; Poeppel and Adolfi, 2020). Importantly, the authors themselves discuss an alternative mechanism in which the monkey would attend “*first to the short-choice target and then gradually shift attention to the long-choice target*”. Because LIP neurons are thought to represent the locus of spatial attention (Bisley and Goldberg, 2003) and contribute to high-level control of eye movements, such an interpretation is at least equally plausible than the mysterious access to internal neuronal activity, and has the advantage of providing a testable mechanism at the behavioral level. Following this landmark study, other studies using time-estimation tasks based on reaching action have reported representations of time in the firing pattern of neurons recorded in the control and planning of reaching (reviews in Coull et al., 2016; Merchant et al., 2013; Merchant and Yarrow, 2016). For instance, neuronal activity in the pre-SMA and SMA correlated with time in tasks in which supra-second long temporal estimates must be reported through arm movements (Mita et al., 2009). Moreover, when NHPs perform categorization of intervals (short or long) over three ranges of intervals, a significant number of neurons in the pre-SMA displayed a pattern of activity that scaled with the categorization boundary (Mendoza et al., 2018). Finally, in a temporal reproduction task in which NHPs had to hold down a touch button between 2.5 and 4.5 s, encoding of time through ramping signals was observed in motor and premotor cortical areas (Lebedev et al., 2008). In regard to the potential role of movements as a necessary mechanism for time estimation, the engagement of such movement-related cortical regions in timing tasks, even when animals are apparently immobile is striking.

### *3.2. Subcortical representations of duration*

Beyond movement-related cortical regions, two other important contributors to motor control, the cerebellum and the basal ganglia, have been implicated in time estimation. I will only briefly touch upon the timing function of the cerebellum, as it mainly concerns the subsecond range, which is not the main scope of this essay. Indeed, it is unlikely that humans and other animals engaged in fast sensorimotor activities (such as hunting/fleeing behaviors or playing sport such as tennis) explicitly estimate how long they must wait before initiating a particular action nor the duration of their movements. If professional tennis players were relying on explicit time estimation to return their opponent serve (which at 200 km/h takes about 400 ms to cross the court), they would probably never catch a single one. The production of such well-timed behaviors is most likely emerging from the continuous interaction of the nervous system with muscle properties and sensory cues and feedback, without the need for an internal explicit representation of duration (Erlhagen and Schöner, 2002). While the cerebellum is implicated in various tasks requiring precise timing, there is no evidence that it works as a task-independent dedicated system for explicit estimation of short interval duration (Ivry and Spencer, 2004). Its role in fast sensorimotor timing may simply reflect a more generic function related to the adaptive prediction of sensory outcome of motor commands (Shadmehr and Krakauer, 2008).

The case of the basal ganglia, and especially the dorsal striatum and its dopaminergic modulation is directly relevant to this essay. Indeed, on the one hand, they have long been proposed to play the role of a dedicated internal clock for prospective time perception (for a landmark review and introduction to the striatal beat frequency model, see Buhusi and Meck, 2005). On the other hand, they are well-known to control the speed and duration of reward-oriented movements and decision making, (i.e., vigor; Carland et al., 2019; Dudman and Krakauer, 2016; Robbe and Dudman, 2020; Turner and Desmurget, 2010) potentially through regulation of motivational factors (Jurado-Parras et al., 2020; Niv et al., 2007; Shadmehr et al., 2019; Shadmehr and Ahmed, 2020; Shadmehr and Krakauer, 2008). Moreover, lesions of the sensorimotor region of the dorsal striatum have been shown to strongly alter the kinematics of the motor rituals that contribute to the accurate reproduction of short time intervals (Dhawale et al., 2021; see section 2.2). Thus, while there is a large consensus that the striatum contributes to timing, it is unclear whether such function is related to the generation of disembodied internal representations that inform subjects of how much time has elapsed (i.e.,time processing through internal dedicated or population clocks), the control of movements that are necessary for timing, or motivational aspects in timing tasks incorporating rewards (e.g., urgency as in Thura and Cisek, 2017).

There are mainly two lines of results that have suggested a role of the basal ganglia and its dopaminergic modulation in prospective time perception. The first one is that dopaminergic alterations (experimentally-induced or arising from neurodegeneration in Parkinson disease, PD) have been reported to affect the performance of humans and animals in a variety of timing tasks, a result assumed to reflect changes in the speed of an internal clock in the dorsal striatum (reviewed in Buhusi and Meck, 2005). The second one is based on electrophysiological recordings of striatal activity reporting changes in neuronal activity that track and predict the passage of time. For instance, in rodents, an increase in dopamine tone with methamphetamine caused the animals to judge short intervals as long ones in the aforementioned bisection task (Maricq and Church, 1983). This result was assumed to reflect an increase in the speed of the inner striatal clock (for an extensive review of dopaminergic modulations of timing, see Buhusi and Meck, 2005). But considering, on the hand, that freely moving rats engaged in bisection tasks develop stereotyped motor routines to become proficient (sections 2.1 and 2.2), and on the other hand the well-known pro-locomotor effects of methamphetamine (Shoblock et al., 2003), performance changes (short intervals are perceived longer than they were) may reflect a greater distance traveled at the end of the interval under drug influence rather than a change of time perception. Dopamine could affect the movements necessary for task proficiency while the animals may well be oblivious of the abstract temporal rule imposed by the experimenters (i.e., they would not process time). Another aspect to take into account is that in bisection tasks, animals aim at maximizing rewards during behavioral sessions whose length are typically fixed. Thus methamphetamine may also interfere primarily with motivation not time per se, which may impact their choice of short versus long responses. In agreement with such a possibility, it has been proposed that in peak procedures, the effect of dopaminergic manipulation on lever-press initiation time might be related to increased motivation for rewards (Balci et al., 2010) which could explain the leftward shift in peak responses following methamphetamine injections (Matell et al., 2006; Meck et al., 2012).

A classical argument given to sustain the claim that the basal ganglia and dopamine directly contribute to time estimation is that patients suffering from Parkinson and Huntington disease display "*an impaired ability to process time*" (Buhusi and Meck, 2005). For instance, in an early study examining the ability of PD patients to estimate time intervals while verbally counting, an underestimation of elapsed time was reported (Pastor et al., 1992). A similar result (a long interval was perceived shorter than it was) was reported in a study that also showed a deficit in motor reproduction (Malapani et al., 1998). Critically, this study showed the magnitude of error correlated with reaction and movement time. Thus, rather than a deficit in time processing per se, the underestimation of time may reflect slower vigor of a movements-based mechanism contributing to time estimation and thus reflect the engagement of the basal ganglia in motor control rather than time itself. In line with this alternative interpretation, bradykinesia in PD has been proposed to reflect an increased effort sensitivity (Mazzoni et al., 2007), raising the possibility that timing impairment following dopaminergic dysfunction reflect motivational alteration, which would make sense based on well-known contribution to dopamine to such a function (Berke, 2018). Recently, Soares et al. (2016) found that transient activation or inhibition of dopamine neurons was sufficient to bidirectionally change the categorization of time intervals, which the authors interpreted as a direct control of dopaminergic activity on the "judgment of time". However, it is likely that mice used a similar embodied strategy than rats in this unrestrained behavioral test (Gouvea et al., 2014) and the manipulation of dopaminergic neurons by altering motivation, may have impaired a movement-based mechanism of time estimation rather than the judgment of time itself.

The second line of research that supports the view that the dorsal striatum generates temporal representations used to estimate the duration of intervals is derived from studies using electrophysiological recordings of the striatum in rodents engaged in a variety of timing tasks (e.g., Matell et al., 2003; Mello, Soares, and Paton, 2015; Zhou et al., 2020). Such studies demonstrate striking and flexible representations of time but an issue to consider is that, as discussed earlier, even head-fixed animals continuously move in a structured manner during time intervals (Coddington et al., 2023) and that movement dynamics change depending on the length of intervals. For instance, in Mello et al. (2015), not only the pattern of collateral movements and lever-press will be distinct for a short (12 s long) and a much longer (60 s) time interval, but the motivational dynamics will also differ, raising the question of whether striatal activity at the cellular or population levels, track time itself or changes in motivation and/or movements that correlate with time. This later alternative would be congruent with the repetitive observation that striatal neurons can continuously represent the sensorimotor states of animals (Peters et al., 2021; Sales-Carbonell et al., 2018; for review see Robbe, 2018). So far, one of the most convincing studies supporting a role of the striatum in time estimation took advantage rats performing a modified version of the duration categorisation task described earlier (Fig. 2, Gouvea et al., 2014) in which animals were forced to maintain their head in the central port of the apparatus during interval presentation (Gouvêa et al., 2015). The authors reported that during presentation of near boundary stimuli, the activity of a significant fraction of the recorded neurons could predict long or short judgments. While this result is correlative (but see indirect causal evidence in Monteiro et al., 2022), it is nevertheless perfectly in agreement with the internal perception of time model. At the behavioral level, what remains unclear is whether animals use subtle orofacial or postural movements during head-fixation and were in fact oblivious to the abstract time rule. This is not unlikely as the same group reported such potential confound in one of the recorded rats while it maintained its head in the nosepoke device and the second set of recording was performed in an animal from which judgment could be predicted based on its movements in a no-fixation version of the task (Gouvea et al., 2014), raising the possibility that this subject simply adapted its movement-based strategy to the fixation task version. Finally, it is also possible that the difference in neuronal activity reflected differential motivation (e.g., urgency) which could bias the preferences of the animal for the short or long choice. At the cellular level, striatal projections neurons are largely silent during immobility, and their spiking activity is driven by sensorimotor input from the cortex and thalamus. Several studies have recently reported that neuronal activity in the dorsal striatum was strongly modulated by sensory stimuli generated by the animals movements during intervals, which appear critical for accurate timing in various tasks (Cook et al., 2022; Hidalgo-Balbuena et al., 2019; Pimentel-Farfan et al., 2022). This raises questions regarding the ability of this brain region to generate disembodied clock-like signals. While such type of intrinsic activity of striatal projection neurons has been shown to be possible at the theoretical level (Ponzi and Wickens, 2022), future neurophysiological experiments will most likely be necessary to settle this difficult question.

### 3.3. *The entorhinal-hippocampal system and time: a question of space?*

In addition to regions involved in high-level aspects of motor control and motivation, another set of areas that has been proposed to represent the passage of time and underlie prospective timing are the hippocampus and entorhinal cortex. Again, an exhaustive review of studies addressing timing functions and time representations in the entorhinal-hippocampal system is beyond the scope of this essay. I will try to demonstrate that a role of these regions as generators of pure time representations explicitly used to estimate time is yet to be demonstrated. Rather, the available experimental data argue in favor of their involvement in tracking contextual changes (in either an allocentric or egocentric framework) and inferring duration indirectly through distance measurement.

In one of the rare studies investigating directly the contribution of the hippocampus in a temporal discrimination task, Meck et al. (1984) reported that lesions of its main output (fimbria/fornix) did not altered the discrimination of the longest and shortest stimuli (2 and 8 s), but intermediate intervals were overestimated. Because the assumption of the researchers was that rats estimated time internally, the potential contribution of motor routines during the presentation of the intervals was not considered. However, if one considers, on the one hand, that routine were most likely present as the animals were freely moving, and on the other hand, that fimbria-fornix lesions induce hyperactivity (Cassel et al., 1998), which may have affected routine execution, the overestimation of the intermediate interval duration might primarily result from an increased distance traveled during stimuli presentation rather than a change in processing of time. Similarly, in a task in which rats learned to take a right or left turn after being held in a delay location for 10 or 20 s, lesions of the hippocampus and the medial entorhinal cortex made the animals increase their proportion of short duration choice (Sabariego et al., 2020; Vo et al., 2021). Because there was no quantification of what the animals were doing while waiting in the delay area and of how lesions affected this behavior, such results are difficult to interpret. The fact that the lesions did not result in a random choice between short and long duration responses could be accounted for by an inability of the lesioned animals to accumulate how much movements they have performed during those intervals.

In humans, Kesner and Hopkins (2001) showed that subjects with hippocampal damage displayed strong impairment to retain both duration and spatial information beyond 8 s. Moreover, hippocampal lesions affect the ability of subjects to estimate time over relatively long (minutes) timescales (see Palombo et al., 2016 and reference therein). fMRI studies in which subjects performed mental time and spatial travel tasks suggest that both activities depend on egocentric remapping and distance computation although they engage different subregions of the medial temporal lobes (Gauthier et al., 2020; Gauthier and Wassenhove, 2016). Very recently, a study suggested that the content of memories shaped the judgment events' duration in the second range, an effect associated with an activation of the hippocampus (B. E. Sherman et al., 2021). Moreover, the judgment of duration appears to be biased by the number of events contained inside a recently experienced interval (Faber and Gennari, 2015) or its contextual dissimilarity (Ezzyat and Davachi, 2014), with again an involvement of the hippocampus. These works are congruent with the idea that the duration of a time interval is reconstructed based on changes observed and remembered during the interval, a function that may be dependent on the hippocampus. Several studies have also highlighted the correlation between time and distance estimates in a variety of prospective and retrospective timing tasks (Brunec et al., 2017; Deuker et al., 2016; Riemer et al., 2018). Finally, the case of Diane Van Dere, even if it lacks well-controlled assessments at the behavioral and neural level, is a powerful example of the relationship between spatial representation, duration estimation and memory. Indeed, the surgical ablation of a small region of Ms. Van Dere's temporal lobe not only freed her from recurrent epileptic seizures but also drastically reduced her ability to read maps and made her susceptible to spatial disorientation (she would get lost very easily). Surprisingly, this supposedly negative side-effect helped her to become one of the best ultra-runners in the world: she could remain focused on her running rhythm without forming any quantitative idea of how long she had been running.

A potential interpretation of this set of functional data is that the hippocampus is a system that detects contextual changes (Maurer and Nadel, 2021; Nadel, 2021). Because the speed of displacement of animals is constrained (i.e, an animal can not travel between two distant points in a very short amount of time), the amount of contextual changes covaries with time and can therefore be used as a proxy for duration. The entorhinal-hippocampal system, through its ability to detect high-level changes in context by integrating allocentric and idiothetic information, could help animals to spatialize time. Interestingly, the hippocampus is well known to be implicated in both the formation of episodic memory (Scoville and Milner, 1957), which has been defined as the ability to travel back and forth along a mental timeline to *locate* and relate the timing of events (Tulving, 1983), and in spatial navigation (OKeefe and Dostrovsky, 1971; Okeefe and Nadel, 1978). While a link between episodic memory and spatial navigation has been attempted at the neuronal level (Buzsáki and Moser, 2013), it may also be made directly at the behavior level by postulating that any explicit representation of time, be it to estimate the duration of an event (for how long have I been walking on this trail) or remember when differents events in our life occurred (i.e., episodic memory) required a spatialization of time.

A counterargument to the above proposal is that there are both place and time cells in the hippocampus that could perform separate functions in navigation and prospective time perception. Indeed, on the hand, the hippocampal contribution in spatial navigation is well-supported at the cellular level by the existence of place cells: pyramidal neurons that fire always in the same order and location when a rat explores their environment (OKeefe and Dostrovsky, 1971; Skaggs et al., 1996). On the other hand, a similar sequential activation of hippocampal neurons has also been observed when rats are running while remaining still in space (eg., on wheels or treadmills; (Kraus et al., 2013; MacDonald et al., 2011; Pastalkova et al., 2008; Villette et al., 2015). The neurons forming these sequences have been called “time cells” and have been proposed to provide an accurate representation of duration (Eichenbaum, 2014). However, it is critical to remember that time cells were not recorded during time estimation tasks but while animals needed to maintain contextual knowledge over relatively long (typically several seconds) periods of time. The fact that the reliability of hippocampal sequences deteriorates as time passes by in behaving rats is also congruent with such an activity reflecting bodily derived information (idiothetic cues) related to the distance traveled by the animals (Pastalkova et al., 2008; MacDonald et al., 2011; Kraus et al., 2013). Interestingly, neuronal activity in the lateral entorhinal cortex (the major cortical source of inputs to the hippocampus) of rats exploring repetitively two environments changed progressively in time through the moment-to-moment encoding of their sensorimotor experience rather than in a clock-like manner (Tsao et al., 2018). Again, in this study, no explicit estimation of time was required from the animals. It is nevertheless striking that a region of the temporal lobe is “representing” the passage of time in a way that depends on the behavioral variability exhibited by animals in time. Because in the aforementioned studies time representations in the entorhinal-hippocampal system occurred even while no time estimation was required, it is possible that such neuronal process play a much more broader function such as the tracking of changes, rather than an abstract time perception the animals did not need to be aware of.

The recent study of Shimbo et al. (2021) discussed earlier (section 2.2), is the only one so far to have examined the firing pattern of hippocampal neurons in a task in which rats had to discriminate durations. Hippocampal recordings were performed while animals underwent successively three blocks of trials with different ranges of duration to discriminate (short: 10 s vs 5 s; long: 20 s vs 10 s; and short again, Fig. 4). During the forced running period, hippocampal neurons fired sequentially and displayed a pattern of activity similar to both time and place cells. The firing rate profile of these “duration” cells rescaled between the short and long blocks (Fig. 7A). This result is strikingly reminiscent of the rescaling of place cells firing profiles when rats ran in a corridor whose length was changed (Fig. 7B; Huxter et al., 2003).

Thus, in a task in which rats were challenged to discriminate short vs long durations, animals appeared to develop stereotyped motor routines and the firing activity in their hippocampus, a brain region well-known for its contribution to spatial representations, changed similarly as if duration was space. A possible explanation would be that in this task, the firing pattern of hippocampal neurons does not relate to duration itself but to the movements of the animals in a limited space, movements that can be rescaled depending on the duration of the runs (short vs long blocks). Such a view would be in line with the proposal that the hippocampus’ main function is to track changes occurring on a moment-to-moment basis (Maurer and Nadel, 2021) and to link together events that were separate in time and space (Nadel, 2021). In this framework, time cells and place cells could in fact perform a similar function, that is, the detection of changes in different behavioral contexts (i.e, not necessarily limited to navigation (see Jiang et al., 2022). And indeed, although their underlying mechanisms may be distinct (Wang et al., 2015; Sabariego et al., 2019), which make sense as they are not generated in similar behavioral contexts, time cells’ firing patterns strikingly resemble those of place cells: both fire for a similar amount of time/distance and display the same type of modulation by the hippocampal theta rhythm.

### 3.4. *Conclusions and future directions*

An overview of neurophysiological studies points to a set of brain regions recurrently involved in prospective time perception, namely neocortical areas involved in high-level control of movements (LIP and SMA), the basal ganglia and the entorhinal/hippocampal system. This list does not pretend to be exhaustive, and many other brain regions have been involved in interval timing, either because their perturbation alter the temporal organization of behavior (e.g. the secondary auditory cortex in Cook et al., 2022) or because their neuronal activity encodes the passage of time (e.g., the prefrontal cortex in Zhou et al., 2020). How to make sense of such a plethora of brain areas involved in timing tasks? It has been argued that the ability to tell time could depend on the intrinsically changing activity of brain regions specifically involved in a given timing task (Karmarkar and Buonomano, 2007; Paton and Buonomano, 2018), in line with a view that high-level cognitive function emerged from the interaction between many brain regions (Pessoa, 2022). Still, the possibility that brain areas could switch functions across tasks has been recently questioned both conceptually and due to the lack of firm experimental evidence (Krakauer, 2023). For instance, in the case of LIP or hippocampal contribution to time perception, how can their downstream brain regions “know” when the signal received carries temporal vs spatial attention information or temporal vs spatial information?

One way to resolve this challenge, which is at the core of this essay, could be to consider that there is no such thing as *pure* temporal representations in the brain used to explicitly tell time, or that temporal representations can only emerge from subjects capable of interacting in their surroundings. Bergson’s proposal that we don’t measure duration internally but estimate it from observable changes that unfold with time is counterintuitive because we, humans, can count time in our heads apparently without moving. However this ability to internalize the counting process does not mean that it is not spatial by nature (See subsection 2 and 3 in Supplementary Appendix A for Bergson’s detailed analysis of the process of counting time), as illustrated by the fact that we often invoke imaginary movements, such as those of sheeps, to count in our head. Noticeably, similar patterns of neuronal activity are engaged during imagined and executed movements (Berthoz, 1996). In addition, it has been proposed that the dynamics of complex events can be perceived and predicted through internal simulations based on sensorimotor representations (Schubotz, 2007). Considering that the same motor regions were activated in non-human primates performing time estimation tasks while being largely immobile, this raises the question of whether those so-called neuronal representations of time reflect a cross-species mechanism for time estimation based on sensorimotor simulations. Freely moving animals would thus spontaneously spatialize time with their situated body but when this is not possible, may internalize this process by imagining movements, sketching them in covert actions or simulating sensory changes. This possibility could be experimentally investigated thanks to new approaches allowing to manipulate how humans and other animals interact with their environment such as virtual-reality setups and brain-machine interfaces.

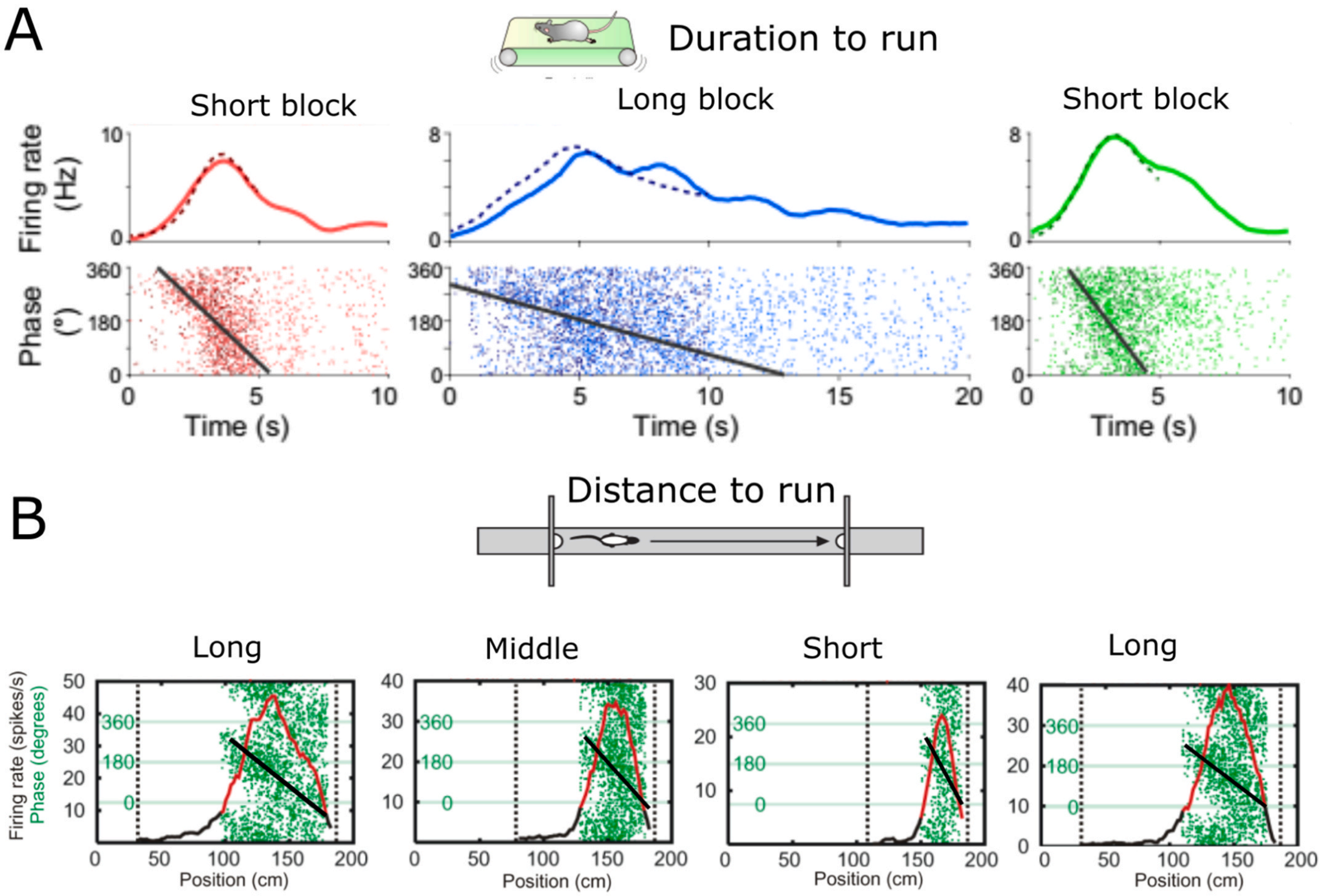

**Fig. 7.** Similar scalable representations of distance and duration by hippocampal principal neurons. A) Example of a "time" cell recorded while a rat performs the bisection task in a short duration block (10 s vs 5 s) followed by a long block (20 s vs 10 s) and back to short. Data from Shimbo et al. (2021) with permission. B) Example of a place cell recorded while a rat ran back-and-forth on a corridor whose length was successively shortened and back to normal. Lines representing phase precession slope were drawn by hand for illustration purposes. Data from Huxter et al. (2003), modified with permission.

## 4. Conclusion: time to rethink time?

### 4.1. Summary and relation with other timing theories

In this essay, I presented behavioral and neurophysiological evidence that don't fit the framework in which time is considered as an information processed by the brain nor the idea of a purely internal perception of the duration of time intervals. First, unlike humans that can count time covertly while remaining immobile or randomly moving around, other animals such as rodents and birds spontaneously developed motor routines and use their position in space (or kinematics parameters of their movements) as a proxy for duration in a variety of timing tasks. In behavioral tests designed to limit the usage of motor routines, animals manage to create unexpected ones and forcing animals to estimate time while remaining imobile requires extensive and unnatural training procedures with debatable results. In addition, there are many studies in humans showing that movements improve the accuracy of timing and the intricacy between spatial and temporal perceptions. Second, the patterns of responses in peak procedures and fixed interval schedules of reinforcement (e.g., scalable anticipation) can be explained by motivational constraints rather than an internal knowledge of time. Third, the quest for neuronal representations of time in a variety of interval timing tasks has failed to reveal the existence of dedicated internal clocks predicted by SET but rather has highlighted the recurrent implication of brain regions involved in motor control/decision, motivation and spatial navigation. Added to the fact that both humans and other animals often appear unaware of how much time has elapsed in a given interval, these observations are in agreement with Bergson's early ideas on time and space (Bergson, 1889) and support a view in which 1) duration estimation depends on the ability to externalize time either through movements in space or the observation of regular changes spontaneously occurring in the subject's surrounding 2) time is considered as an opportunity cost, a source of motivation. To put it boldly I propose that although animals are sensitive to time (like us they feel time), there is no such a thing as an internal perception of time, at least if the expression "internal perception" is taken in the sense of an explicit and quantitative process independent of space.

The present proposal is obviously challenging theories assuming that the ability of animals to estimate duration is based on internal representations of time generated by neuronal clocks as in the SET (Church, 1984; Gibbon, 1977) or derived from memory decay (e.g., as in the multiple-time-scale timing model; Staddon and Higa, 1999). However, it may at first appear similar to the behavioral theory of time (BET), which attempted to integrate collateral behaviors in a model accounting for the performance of rats or pigeons in bisection and fixed-interval tasks (Killeen and Gregor Fetterman, 1988). Indeed, in a somewhat contradictory manner, the authors proposed that "*choice responses constituted the end of the chain of behaviors*" although they did not believe "*that the collateral behaviors emerge because they are instrumental in aiding timing*" (Killeen and Gregor Fetterman, 1988). This latter statement can be understood if one realizes that, in BET, collateral behaviors occurring during an interval (such as running in wheel or nibbling with its tail between two reinforcers) are considered as states that repeat themselves at a rate controlled by a pacemaker and the transition between different states is probabilistic. In other words, how long rats will run in a wheel before lever pressing is still under the control of an internal clock or pacemaker. Our proposal is therefore different from BET in at least three ways. First, it is devoid of an internal pacemaker. Second, it does not assume that the inner life of animals can be discretized into sensorimotor states that repeat themselves. On the contrary, it is the fact that such temporal units are lacking that make animals incapable to estimate time internally. Third, time is considered here as an opportunity cost, which accounts for changes in behavior according to the animals sensitivity to reinforcers rate without invoking a reward rate modulation of an hypothetical neuronal pacemaker.

Two other significant theoretical attempts have been made to understand how animals such as rodents or birds develop chains of collateral behavior during interval timing tasks. First, the learning-to-time model (LET, Machado, 1997) is a dynamical and determinist instantiation of BET. As such, it still requires a discretisation of time and an internal parameter that will account for when the animal leaves a given state and transitions to the next one. While our proposal does not share such assumptions, Machado nevertheless stated that "*at the heart of the model is the belief that animals do not passively tell time by using central, all-purpose internal clocks; rather, they act on and interact with their environment, and in the process their behavior changes*" (see discussion in Machado, 1997) a view that is similar to the one presented in this essay but that is not fully captured in the LET model. A distanciation from the concepts of pacemakers and comparison between ongoing and learned representations of time is also at the core of a second type of model in which well-timed sequences of behaviors do not require a discretization of time and emerge from a competition between variable actions: those produced during an interval (collateral behavior) and the "terminal" response (e.g., lever-press to obtain the reward; Dragoi et al., 2003). Our proposal is clearly in line with such a model that questions the need for explicit internal representations of time. However, similarly to the aforementioned "behavioral" models (BET and LET), the emerging learning property model of Dragoi et al. (2003) leaves untouched the fundamental question of why, in the first place, animals develop collateral behaviors during timing tasks. The originality of the present proposal is to consider, following Bergson's work, that the inner life of animals (including humans) is not discretizable in repetitive units and that, consequently, the estimation of duration *requires* its spatialization through movements (observed or self-generated) in space. Indeed in most daily life situations, time is given with space. For instance, a gazelle is safe as long as the lion is far away. It has time (space) to escape. As the lion gets too close, the prey will (hopefully) choose the right time (space) to run away without estimating duration explicitly. It is only in laboratory settings that time is decoupled from space. Animals can be right in front of the reward magazine but the food will drop in there randomly, all of a sudden. "Superstitious" motor routines may therefore reflect an attempt of animals to recreate the link between space and time that is broken in laboratory settings. Because this proposal accounts for why animals develop stereotyped chains of actions in timing tasks, one could be tempted to consider it as a form of behaviorism. This is in fact quite the opposite as our proposal is based on Bergson's concept of durée: the moment-to-moment inner life of animals is constantly contaminated by its past experiences, with the consequence that their present is fundamentally new. Thus, animals can be seen as undetermined creative beings, a view that can't be more distant from reducing animals to machines conditioned by reinforcement or processing information. Combined with the notion that animals have agency (Gomez-Marin and Ghazanfar, 2019) and are not passively processing stimuli to compute then act, our proposal accounts for why animals will develop idiosyncratic and original routines in timing tasks (Gouvea et al., 2014; Kawai et al., 2015; Safaie et al., 2020) and why such routines drift over time (reviewed in Richelle and Lejeune, 1980).

Finally, this proposal is distinct from the current framework in which brains are telling time thanks to the changing activity of distributed ensembles of neurons that function as population clocks (Paton and Buonomano, 2018). This view requires some mysterious homunculus to read such population clocks and seems to confuse different levels of understanding of behavior. In addition, the concept of emergence at the network level would require brain regions, who have been linked to action planning/execution, navigation or motivation, to switch function, a concept for which there is yet to come substantial evidence (Krakauer, 2023). This is obviously not to say that population dynamics are not a good predictor of the speed and timing of decision and actions. But taking in account that the nervous system is intrinsically connected with the body and its surroundings (Gomez-Marin and Ghazanfar, 2019) and that there is no clear reason why the variable of interest should be limited to neurons (aside from trying to impose a reductionist and materialist philosophy that assumes that the brain generates behavior), extending it to the body interacting with its environment would make this distributed framework compatible with our proposal, with the following key distinction: it is primarily thanks to movements or the perception of salient sensory dynamics (Roseboom et al., 2022; Sherman et al., 2021) that one could tell time, not through the mysterious reading of internal clocks.

### *4.2. Does the brain really tell time (to its owner)?*

Over the last 50 years, the psychology and neuroscience of time interval perception has emphasized its neuronal underpinning and considered it as an explicit process occurring in the head of animals, a view popularized by the idea that the brain tells time (Buonomano, 2018). The influence of this framework is attested by the fact that there is hardly a week that goes by without the publication of a study reporting a new form of time representation in the brain. It would be a daunting task to critically assess the hundreds of old and new articles whose titles or abstracts appear to contradict this essay. Rather, I will list a series of checkpoints one should verify before concluding that humans and other animals estimate duration using internal representations of time and dismissing the alternative direction proposed here.

First, in many studies, neuronal representations of time were derived from recordings performed while human and other animals did not have to estimate time (e.g., Harvey et al., 2020; Kraus et al., 2013; Omer et al., 2022; Tsao et al., 2018; Villette et al., 2015). This does not mean that such patterns of neuronal activity are not behaviorally relevant nor that we cast doubt that scientists can use them to decode time. But assigning them the function of representing time may reflect a natural, but possibly misleading, tendency to anthropomorphize the inner life of animals (Gomez-Marin, 2019) and to subjectively interpret neuronal activity against abstract constructions derived from human-made instruments (Buzsáki and Llinás, 2017; Buzsáki and Tingley, 2018). In addition, studies reporting representations of time in human subjects engaged in timing tasks often fall short to demonstrate a specific and causal link between these patterns of neural activity and timing performance (Heron et al., 2012; Protopapa et al., 2019).

Second, animals engaged in timing tasks are typically water or food restricted. In these conditions, they will attempt to obtain rewards as soon as possible. This has forced researchers to use progressive learning protocols in which animals are first trained to wait for very short intervals (e.g., Heys and Dombeck, 2018; Kawai et al., 2015; Lebedev et al., 2008). This raises the question of whether neuronal recordings performed in such experiments are truly representations of time used by the animals to estimate ongoing duration or simply reflect a growing urgency to obtain rewards, which can only be resolved by manipulating motivationals constraints.

Third, many studies claim that the well-timed behavior of their animals reflect internal knowledge of time but only quantifies the instrumental responses of animals (e.g., the time of lever-presses) without reporting their movements during the interval to measure. For instance, in a recent publication in which rats were trained to reproduce a time interval by either holding a lever or pressing it twice briefly, the authors concluded that their accurate timing reflected the reliance on “*explicit representation of time intervals together with their uncertainty around the internal target duration*” (Kononowicz et al., 2022). Based on a previous study (Kawai et al., 2015), using a similar time reproduction task and reporting a systematic usage of idiosyncratic motor routines during the interval, it is hard to imagine why animals would not use such an embodied strategy. In agreement with this possibility, in the press condition, which leaves more freedom to the animals to move, the accuracy was significantly higher than in the hold condition. Surprisingly, the authors acknowledge that the difference in accuracy could be related to different motor sequences required to reproduce the timing (Kononowicz et al., 2022). If rats are using motor routines to reproduce the interval, questions arise as to whether there is an internal target duration. Recent advancements in software technology have allowed for detailed quantification of movements, including orofacial and eye movements (Labuguen et al., 2019; Mathis et al., 2018; Nath et al., 2019). Critically, detailed movement analysis should not be limited to tasks in which animals are freely moving, but should also be performed when animals are forced to maintain nose-poking during intervals or while head-restrained. Subtle postural and orofacial movements are well-known to be produced in these conditions, and should thus not be overlooked (Fernandes and Garcia-Marques, 2019; Gouvea et al., 2014; Musall et al., 2019). A recent study by Hughes et al. (2020) has shown that even when no overt behavior is observed, force sensors can detect continuous movements in head-restrained mice. Finally, temporal adaptation (a form of time perception) in human subjects has been assumed to require “duration channels” in the brain (Duysens et al., 1996; Heron et al., 2012) but has been shown to be affected by movements (Anobile et al., 2020; Petrizzo et al., 2022; Tomassini et al., 2012). Thus, as proposed earlier, future timing studies, including those performed with human subjects, should manipulate movement requirements rather than attempt to eliminate them and combine such an approach with detailed movements quantification.

Forth, in trace or delay conditioning experiments in which simple motor activity (licking, blinking, swimming, freezing) is measured, it is often assumed that its timing reflects animals’ knowledge of duration. It has been discussed earlier how conditioned responses lack temporal accuracy (section 2.5). Indeed, that fishes start swimming frantically or rats freeze for 10th of seconds after a US (Drew et al., 2005; Tallot et al., 2020) does not necessarily guarantee that animals were explicitly estimating time. All these behavioral modulations can be explained by reinforcement-driven changes in the dynamics of sensorimotor coupling without the animals being aware of time itself (whatever this could mean for a fish). Similarly, the fact that drosophila mate for a precise duration (Thornquist et al., 2020) does not mean that they were counting time, like when we automatically wake up at the same time of the day due to the circadian regulation of our nervous system.

Lastly, many early (and sometimes contemporary) studies assuming that animals explicitly estimate intervals’ durations through internal processing are based on tasks such as FI or peak procedures, which do not require accurate time estimation as early responses were not penalized. Without re-entering into the debated contribution of collateral behaviors (Richelle and Lejeune, 1980), which anyway were poorly quantified and would gain of a quantitative reappraisal, there is recent evidence that self-generated sensorimotor information contribute to the response patterns observed in the peak procedure (Cook et al., 2022) raising additional questions about their dependence on explicit internal representation of time. Still, one may argue that variation of the FI and peak procedures (e.g., multiple intervals, introduction of gaps, intervals signaled by different sensory modalities) can not be solved through motor routines. First, even if the task is unlikely to be solved by motor routine, a continuous description of the full sensorimotor dynamics could provide mechanistic insights into the temporal organization of the lever presses. Second, as discussed earlier, even though the behavioral responses are under temporal control they can also be explained by dynamical motivational factors and by considering the passage of time as an opportunity cost (Niv et al., 2007; Sanabria et al., 2009; Shadmehr et al., 2019). For instance, the temporal shift of responses when gaps/distractors are introduced in a peak procedure can be explained by a resetting of context-dependent motivational signals or of collateral behaviors that influence the lever-press timing of the animals (Buhusi and Meck, 2006). The double “scallop” pattern of responding in experiments in which a long interval signaled by a light is divided in shorter intervals using brief sounds (Meck and Church, 1984) could be explained by the multiplication of two motivational signals that arise from the animals integrating the probabilistic coincidence between sensory stimuli and reward delivery, and the average reward rate. The fact that rats’ peak response profile may reflect their sensitivity to the average reward rate in tasks with multiple intervals is also in perfect agreement with experiments in which animals were trained on two sensory-cued (stimulus A or B) fixed intervals of different duration (e.g, tone A: 10 s, light B, 20 s) and display a peak response midway between the two times on compound trials (A and B presented simultaneously; Swanton et al., 2009). Thus, before concluding that the timing displayed by animals reflects an internal processing of temporal information with one or several internal clocks, it could be interesting to examine whether the pattern of responses observed could be explained in the opportunity cost framework of Niv et al. (2007), by manipulation of motivational constraints, and reporting quantitatively what exactly the animals are doing during time intervals.

### 4.3. Time to inject durée in Neuroscience?

In this closing section, I will turn back to Bergson who, more than 100 years ago, not only anticipated the potential conceptual confusion that could arise from a psychophysic of time perception but also explained why this confusion is almost inevitable. It appears that his explanations provide insights to understand the nature of time in the context of animal behavior and to tackle recently disputed questions such as the validity of so-called old fashioned psychological terms, the difference between natural and artificial intelligences and to explain our difficulty to conceptualize and take action against global warming.

Bergson’s proposal that experience of time cannot be measured is counterintuitive because we obviously feel the passage of time and are also very good at measuring the length of time interval (using clocks or our fingers), even with our eyes closed (e.g., we count in your head). Moreover, as these two phenomena (feeling and measuring) happen almost simultaneously, we tend to confuse them. Still, the case of the imperceptible growth of plants, captured by Olivier Sacks’s quote at the start of this essay, illustrates, if necessary, that feeling and measuring are distinct. For Bergson, their confusion finds its root in language. When we say that time passes more or less quickly, we assume that this statement is primarily reflecting our internal experience of time. We nevertheless forget that those words are derived from observable (i.e., external) movements, such as the flow of a river or the speed of wind turbines, that provide a quantifiable metric many people can simulataneously agree on. Why do we confuse our ever-changing internal feelings for their fundamentally fixed and external semantic or metaphorical representations? “*The reason is that our outer and, so to speak, social life is more practically important to us than our inner and individual existence. We instinctively tend to solidify our impressions in order to express them in language. Hence we confuse the feeling itself, which is in a perpetual state of becoming, with its permanent external object, and especially with the word which expresses this object.*” [p97/130].[1] Thus, for Bergson, expressions

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[1] Page numbers inside brackets refer to the French’s edition of Bergson first book on time and space (Essai sur les données immédiates de la conscience, édition Quadrige, PUF) followed by the comparable section in the english translation (Time and Free Will: An Essay on the Immediate Data of Consciousness, trans. F. L. Pogson, New York: Dover Publications, 2001)

such as “I felt that I did not see the time *passing*” are just fine because there is no way to describe perfectly an inner mental life that is constantly changing. They allow us to communicate approximately even if sometimes we simply have no words or misunderstand each other. Still Bergson warned us that “*by using these [external] forms to gain a knowledge of our own person, we run the risk of mistaking [our internal life for] the reflection of the frame in which we place it,* i.e. *the external world*” [p168/223]. This is exactly what happened with the perception of time: neuroscientists, abused by language, forgot that the concept of measured duration is derived from space and thus fundamentally dependent on an interaction with the external world. It is both ironic and instructive that, to explain how fast or slow time seems to pass by, which is nothing else than an image borrowed from movements in the world, neuroscience and cognitive sciences have come back full circle by postulating the existence *in the brain* of clocks, which are also devices borrowed from the world.

When trying to understand cognition (beyond time estimation) and solve the issue of the aforementioned deceptivity of language, one could be tempted to focus on the brain, especially when one considers that “after all, the brain gives rise to behavior and cognition” (Buzsáki, 2019). Indeed, in his latest book, György Buzsaki challenged the classical method of looking for neuronal correlates of ill-defined psychological terms (see also Pessoa et al., 2022). He proposed focusing on how brain processes relate to each other in a reader-centric framework and how they can be mapped onto quantitative aspects of behavior (i.e., actions) to acquire meaning. Even if one can only applaud Buzsaki’s call of caution when interpreting the functional relevance of neural processes that are oblivious to cognitive labels (a brain region does not know what time or space is), some kind of vocabulary or abstract representations will be necessary to describe behavior, at least for the practical purpose of scientific communication. These representations will nevertheless remain poor in relation to the ever-changing and unique inner life of its subject. By starting from the brain, Buzsaki only displaced the problem he tried to solve, oblivious to the fundamental differences between the inner mental state of subjects and its neural implementation and the irreducibility of behavior to the sole nervous system. The brain can not generate a quantitative estimate of duration on its own, as measuring the length of a time interval only makes sense for a subject interacting in a world in which regular changes can be observed. Buzsaki’s inside-out approach misses the point of why psychological terms or psychophysical quantitative statements (e.g., I am “highly” confident) *must* be inaccurate. If they were accurate (i.e., reflecting the complexity and uniqueness of our ever-changing inner mental life), no one would understand each other.

The main insight gained from comprehending Bergson’s concept of durée is that humans, as well as other living creatures, are in a perpetual state of becoming. Living organisms should thus be thought of as interactive processes rather than isolate things (Nicholson and Dupré, 2018). Still, the fixed representations provided by language and our inability to *feel* changes over long time intervals (see the slowly growing hollyhocks of Oliver Sacks in the introduction quote) make us blind to the fact that we are constantly becoming older, our kids are growing, that the world around us is changing and that the present is radically new. The ongoing global warming and recent pandemic, on the one hand, and the difficulty of our society to modify its policies to efficiently adapt to these changes, on the other hand, provide illustrations of our deeply rooted illusion that the state of the world is stable or even reversible. Thus, Bergson’s concept of *durée* has the potential to help us realize that the solutions to the challenges we are facing may also be found in radical creativity rather than in algorithms based on an already obsolete past. Nothing is entirely played in advance.

Bergson’s durée constitutes a challenge for the neuro-computational approaches in which a subject’s inner state at a given time can be simplified as a mathematical object and its future predicted on a moment-to-moment basis (Vogelstein et al., 2022). Indeed, because computational predictions are based on rules deduced from past experiences, how can such rules apply to new inner states that have never been encountered? Bergson does not deny that science captures an important aspect of the reality of living and non-living systems through mathematical formalism. But for him, there is a distinction between explaining (or understanding) the past and predicting the future. Thus, the concept of *durée* provides an interesting angle to understand why, despite the wealth of (neuro)scientific knowledge, human and animal behavior can be, under certain circumstances (in fact those that matters the most), largely unpredictable. The ever-changing and indivisible nature of the inner state of animals distinguishes them from machines whose ongoing state does not endure (one could transiently pause AlphaZero without affecting its ability to finish a game started much earlier) and can be entirely predicted from the previous states. This realization should remove some burden from cognitive neuroscience, AI, physics, and mathematics, as the most legitimate alliance to provide a complete understanding of human behavior. Rather, it calls for a much more inclusive (and humbler) approach in which humanities and arts should not be confined to secondary roles. This might prove to be a powerful strategy against the multiple pressing challenges that our globalized society faces (mental disorders, global warming, reduction of biodiversity) while getting rid of the pervasive confusing (and potentially dangerous) idea, also drawn from the outside world, that the brains of humans and animals functions literally like computers (Richards and Lillicrap, 2022).

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## Conflicts of interest statement

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2023.105312.

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