Lost in time: rethinking duration estimation outside the brain.

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Summary

Most of what animals and humans must accomplish requires adapting to the temporality of events relevant to their survival. While internal clocks help living organisms to anticipate the daily transition between light and darkness, the mechanisms allowing them to handle much shorter and variable time intervals are still debated. A long-standing paradigm in cognitive neuroscience considers time as information and assumes that humans and animals directly estimate the duration of intervals in the sub and supra second ranges internally, through the activity of distributed neuronal ensembles serving the function of population clocks. In this framework, time and space are similar dimensions of behavior (both can be segmented into repetitive units) and changes in the dynamics of population clocks explain why the perception of time can suffer significant distortions. In this essay, I start by challenging this paradigm from the angle of Bergson's proposal that the perception of time is unlike space because it is ever-changing and indivisible (2 successive seconds are not experienced equivalently). Consequently, measuring such an heterogeneous perception can not be achieved directly or purely internally but requires taking advantage of concurrent objective changes in the environment (e.g., an observed or self-generated movement; the variation of a sensory stimuli) whose magnitude will be read *out* when a time interval ends. In a second step, I provide behavioral and neurophysiological evidence in support of such a mechanistic proposal. Indeed, a cross-species review of behavioral studies reveals that, in a variety of timing tasks, humans and animals performance heavily depends on movements and interactions with their environment. Moreover, the neural underpinnings of duration estimates strikingly overlap those of sensorimotor control and spatial cognition. Thus, both philosophical and empirical arguments question the notion of a direct measurement of time through a purely internal mechanism. I propose that the puzzle of time perception and its

volatility resolve itself by considering time as a force rather than an information. In such a framework, living beings, although they are sensitive to time, cannot directly measure its passage internally, which they compensate through interactions with regularities afforded by the world and representation drawn from movements in space.

Keywords

Basal Ganglia, Hippocampus, Internal Clocks, Space, Time, Interval Timing, Duration

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“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 telescoping of time”

Oliver Sacks. “The River of Consciousness”.

Introduction

A self-proclaimed goal of cognitive neuroscience is to understand how the brain *processes* a variety of interoceptive and exteroceptive information to guide behavior. Recently, the sense and neural representation of the passage of time (duration) have attracted a lot of attention, possibly because of the intriguing relationship between time and behavior (humans and many other animals feel time but are seemingly devoid of peripheral time sensors), or, most likely, the ever-increasing importance and presence of measured time in modern societies. Behavioral experiments across species have shown that the accuracy of time interval estimates in a variety of tasks can be captured by a simple psychophysical law (Weber's law; Gibbon, 1977). This led to the development of computational models accounting for the

processing of temporal information, that ultimately rely on the activity of ensembles of neurons working as internal clocks or timers (Gibbon et al., 1984; Killeen and Fetterman, 1988; Gallistel and Gibbon, 2000; Buhusi and Meck, 2005; Karmarkar and Buonomano, 2007; Grondin, 2010; Wittmann, 2013; Paton and Buonomano, 2018; see also Machado, 1997; Staddon and Higa, 1999).

A conceptual cornerstone of this information processing framework is that our experiences of time and space¹ share similarities. This is explicitly stated in most of the articles' introductions about the sense of time and its neuronal underpinnings. For instance, a recent study, led by one of the earliest proponents of the neuronal clock-based duration estimation theory, started with the following sentence: "*Similar to the need for the brain to orient itself in space in order to understand its surroundings, temporal orientation and tracking is an essential component of cognition as well.*" (Aryana Yousefzadeh et al. 2021). Issa et al. (2020) in their review entitled "*Navigating through time, a spatial navigation perspective on how the brain may encode time*", proposed "*that a productive approach is to draw parallels between interval timing and spatial navigation*". In the same vein, Paton and Buonomano (2018) wrote in their influential review on the neural bases of timing that "*How the brain processes information about space provides a useful analogy for the intrinsic timing perspective*". It is interesting to note that the authors used spatial metaphors to describe the importance of time in behavior (temporal orientation, navigating through time). Moreover, adjectives related to spatial measurements are used to express judgements about the duration of events. In perceptual timing experiments, subjects must report whether the duration of an auditory stimulus was *short* or *long*. Even the ideas of passage or flow of time, or expressions such as "time flies" or "drags" only make sense because we have been exposed to movement in space. The importance of spatial metaphors when speaking about time (and numbers) has been noted before by cognitive (neuro)scientists and linguists (Boroditsky 2000; Buonomano 2018; Buzsáki 2019; Buzsáki and Llinás 2017; Lakoff and Johnson 1980; Núñez and Cooperrider 2013; Walsh 2003) and the subject of psychophysical experiments in humans showing that individuals cannot avoid borrowing from the spatial domain when making judgment about duration, even in tasks that do not require linguistic

¹ Throughout this paper, I focus on time and space experienced (or perceived) by humans and animals, not the time and space of physics, the reality of which is still debated since Einstein's discovery of relativity (Smolin 2013).

representations (Casasanto and Boroditsky 2008). Importantly, this seems to hold across a wide range of cultures (Núñez et al. 2012) and the converse (time being needed for spatial judgment) is not true (Bottini and Casasanto 2010; Casasanto and Boroditsky 2008).

The reliance on spatial metaphors when expressing duration judgments and the insistence that the experience of time can be understood by analogy to our relation to space are puzzling. For instance, the proposal of Issa et al. (2020) that the encoding of time by the brain should be understood through the perspective of spatial navigation seems to contradict their other statement that because "*there is no sensory organ dedicated to the detection of time, our percept and concept of time are internally generated, maintained and understood*". Indeed, how time perception could on one hand be internal and, on the other hand, be understood through spatial navigation which makes only sense for organisms that have interacted with the outside world? More generally, if time and space were different kinds of information processed by the brain, why would our relation with space and time be similar or why should duration estimates be systematically expressed using spatial metaphors? In fact, the experience of time, as we live it rather than as we reason or talk about it, appears to be strikingly different from the experience of space. For instance, as I am writing these lines, my perception of the screen in front of me is stable while I am still aware of the passage of time. In addition, I can revisit twice the same environment but never re-experience *de novo* the same moment of my life. Thus, the analogy between time and space typically proposed by neuroscientists may be a deceptive advice derived from the fact that spatial metaphors are unavoidable to communicate about the duration of past events (Bergson 1889) although they mask the fundamental difference between the live experiences of time and space.

In this paper, I will provide both philosophical arguments and behavioral and neurophysiological evidence that question the notion of neuronal representations of time and rather support the possibility that estimating the passage of time requires transforming duration into distance (or any spatial representation) through movements (or through any regular changes in the environment co-occurring with the passage of time). I will first briefly introduce Bergson's proposal of why time is unlike space, why movements are key to measuring time and why we tend to confuse the internal feeling of time (which he believes is real) with its measurement (Bergson, 1889; see [supplementary section 9](#) for a longer

step-by-step introduction to Bergson thesis and a demonstration of why counting time is a spatial process). In the second section of this article, a critical cross-species review of behavioral and neurophysiological experiments on duration estimation and behavioral timing will be confronted with two related predictions derived from Bergson's proposal. The first one is that *estimating* the duration of intervals should depend on the ability to derive distance-like measurements at the end of intervals from movements (or any regular changes observed in the environment) that unfolded during the intervals. Consequently, the second prediction is that the neuronal mechanisms underlying duration estimation should largely overlap those required for spatial perception, the detection of changes in the environment and motor control. In the third section, the two main arguments typically advanced to claim that animals and humans have an internal knowledge of duration will be challenged: i) anticipatory behaviors in animals (section [3.1](#)) and ii) the belief that feeling time is equivalent to measuring it (section [3.2](#)). These sections and the conclusion (section [4](#)) aim at showing how the bergsonian concept of pure duration, (the ever-changing and indivisible experience of the passage of time freed from any idea of space), can i) provide new directions to better understand striking temporal features of behavior, ii) be related to an alternative computational framework than the one of information processing (the cost of time theory) and iii) provide a new angle to distinguish natural from artificial intelligence and deepen the understanding of cognition.

1. Bergson's overlooked breakthrough: time is unlike space

1.1. Bergson's distinction between qualitative and quantitative duration

Bergson's reflections on time and space can be found in his Ph.D. dissertation (Bergson 1889), published in English under the name *Time and Free Will, Essay on the immediate data of consciousness*². For Bergson, there are two forms of experience of duration. One that is quantitative and one that is qualitative. There is the duration that we measure or think/talk about and which is nothing but space. And there is the duration experienced by conscious beings freed of any spatial content, what Bergson calls *durée*: "*a succession of qualitative changes, which melt into and permeate one another, without precise outlines, without any tendency to externalize themselves in relation to one another, without any affiliation with*

² Essai sur les données immédiates de la conscience.

number" [p77/p104]³. Such a sharp distinction is derived from Bergson's consideration that our mental life is ever-changing and indivisible as it evolves in time. While I wait for a traffic light to turn green, my thoughts or feelings constantly evolve and permeate into one another. It might seem that I grow *progressively* impatient but each new moment of waiting changes entirely the quality of this experience as it unfolds itself. I cannot pinpoint the exact moment at which I become impatient or I could suddenly take an irrational decision not even envisioned a few seconds earlier (e.g., honk or scream desperately, go through the red light). In that sense, my mental life is qualitative as it unfolds when I wait in front of a traffic light. Later on, I could try to remember the order of the main feelings or thoughts that I went through while waiting and estimate their *duration*. Such a quantitative activity is applied to my past feelings/thoughts which, by definition, are not unfolding themselves anymore and it requires their *separation* and *juxtaposition*. As the words indicate such a quantification must occur in space (see Supplementary sections [9.1](#) and [9.2](#)). For Bergson, measuring how *long* I waited, as this spatial adjective indicates again, does only make sense through a spatialization of that experience after it occurred. We tend to ignore such spatialization because we have taken the habit to think that our experience of time is similar to our experience of space: we believe that our internal mental life can be divisible into equivalent temporal units. Bergson remarks that such temporal units do not exist from the viewpoint of a conscious being. They are an illusion that comes from the intrusion of regularities we observed in the world into our inner mental life. While I am waiting in front of a traffic light on a rainy day, I am watching the back and forth movements of the windscreen wipers. They create distinct coincidences with my ever-changing mental life and, so to speak, slice it into equal units. It is therefore easy to confuse my experience of the passage of time for the regularity of this movement. But, as mentioned earlier, a new moment of my waiting does not equate to a previous one but changes the quality of the entire ensemble, something that does not happen when I consider the repetitive movements of the wipers (they appear perfectly identical). The reason why we naturally attribute to our heterogeneous inner life the homogeneity of the regular movements we witness around us is that many people can relate to these external movements. While I am

³ 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)

waiting, the large numbers of back-and-forth movements of the wipers (which must be all alike to be counted), or the distance traveled by the secondhand of my watch, will serve as a common reference to communicate that, for instance, it took a *very long* time for the light to turn green.

Bergson, therefore, proposes that our experience of duration can only be quantified through its externalization in objects or events that continuously move or change while time passes by. This can be understood by considering the case of a person that wants to compare the speed of two clocks (the duration of one discrete movement of their secondhands). Of course, this person can notice whether the two secondhands move at different speeds. But this will be a *qualitative* distinction that is similar to the ability to perceive that the tempo of a melody has changed or when the duration of two events is different because of their different sensorimotor content. Indeed, it is critical to remember that Bergson does not deny that we perceive changes that occur in time, on the contrary. His concept of *durée* explains why we can be emotionally touched by a crescendo (the first notes endured and melted in the final one to create a sensation that the final note alone could not have generated) or simply perceived all kinds of changes that occurs in a certain timescale, while those developing over very short and long times are simply imperceptible to our sense, as elegantly described by Oliver Sacks at the beginning of this paper (Sacks 2017). But being sensitive to internal or external changes in time does not equate to measuring their duration, which is well illustrated by the observation that the movements of a plant can be quantified although we can't directly experience these movements. To measure the change in size of a plant, it is enough to compare two snapshots of the plant taken at the extremities of a much longer interval that our nervous system can contract in a single perceptual experience. Coming back to the example of the two clocks, *quantifying* their speeds will require the regular movements of an additional object (e.g. a pendulum that beats the time every 5 seconds or a movement that I can generate myself in a relatively stereotyped manner, such as counting on my finger until 5): I will note the positions of the two secondhands when I start counting on my fingers. Once I arrive at the 5th finger, their new positions will be noted again. Knowing each clock's speed involves measuring the distances each secondhand has covered *when I finished counting*. What happens while I was counting (the movements of the secondhands) is irrelevant to obtain the final measure, exactly as

described by Sacks when he measured the growth of the hollyhocks at several hours of interval. Those movements were perceived qualitatively through what Bergson refers to as a “mental synthesis”, a compression of sensations over a certain chunk of time and which depends on the uniqueness of my nervous system dynamics while I watched the secondhands. Indeed, the secondhands movements might have appeared qualitatively different (“faster” or “slower”) depending on my internal state (was I relaxed or in a hurry?) or the type of movements of the secondhand (they could have been smooth instead of saltatory). And they might have not even been perceivable by another species or a newborn. Conversely, our nervous system limits our perception of very slow and very fast movements as noted by O. Sacks in the introductory quote. Ultimately, Bergson proposes that feeling or perceiving is not the same than measuring and that it is only through regular movements occurring in the outside world (those of a chronometer, of my fingers or the apparent one of the sun in the sky), simultaneities (cf. *“when I finished counting”*, *“when I came back in the garden the next day”*), and ultimately distance that our experience of changes that unfolded during an interval and which originally was qualitative, can be in a second step quantified.

1.2. When Bergson's metaphysics meet the neuroscience of time

Bergson's distinction between our qualitative mental experience of time as it unfolds, and its quantitative spatial and immobile shadow when we retrospectively measure its length predates the rise of psychophysical experiments on time perception by almost 50 years (for a historical perspective see: Creelman, 1960). Still, in his PhD thesis, Bergson was in conversation with the psychological researches of his epoch (including the earliest results of psychophysics by Fechner, 1860) and throughout its entire work he insisted that philosophy could only be productive if connected to science (Bergson 1934). Can there be experimental predictions derived from Bergson's proposal that the quantitative estimation of the passage of time must depend on its transformation into a form of spatial representation through movements (or any regular changes that can be observed by the subject)? And how such predictions would differ from those derived from the neuroscientific framework in which time is seen as an information processed by the brain and directly measured by population clocks (the brain tells time)?

First, a major difference between those two views is expected at the behavioral level when animals and subjects are estimating the duration of time intervals. Indeed the

neuroscientific view implies that animals and humans should be able to measure the duration of an interval independently of other behavioral variables, such as the subject's movements or positions in space. On the contrary, Bergson's proposal predicts that animals and humans cannot perceive time directly under a quantitative form (as some of the units of time). Of course, they can sense time, experience various levels of urgency and will notice when two events have distinct durations, but measuring them requires transforming these experienced durations into a spatial representation. For that, animals would need to rely on movements (observed or self-generated), or a regular change in the environment (light intensity decaying), to estimate duration through the distance traveled (or the level of darkness) at the end of the interval. Consequently, in tasks in which temporal constraints are imposed rather than cued by progressive changes in the environment, Bergson's proposal predict that animals should struggle to precisely adapt their behavior to such abstract rules and their timing accuracy will depend on their ability to take advantage of regularities in the sensorimotor content of their experience during the intervals. In the next subsections, we will critically review behavioral studies in animals and humans performing timing tasks and examine whether they support the idea of primarily internal or embodied/externalized mechanisms of duration estimation. Second, at the neuronal level, a consequence of Bergson's proposal is that brain regions or neuronal activity implicated in the control of movements, sensory perception, spatial representation and memory should be engaged during time estimation tasks. Conversely perturbation of these brain regions, through neurophysiological or behavioral manipulations, should impact duration estimation with a magnitude that correlates with impairment of movements or spatial representations.

2. Bergson's mechanistic predictions about time estimation: a reality check.

Experimental psychologists have recognized that a major difficulty in setting up a test in which subjects must estimate the duration of time intervals is that humans can't avoid counting (see Rattat and Droit-Volet, 2012 and reference therein). Because of this, early behavioral studies using other (i.e., non-verbal) animals as subjects have played a critical role in the study and theoretical framing of time perception. Indeed, it was assumed that because animals cannot count verbally, their ability to adapt to temporal constraints in a variety of tasks should rely on their capacity to estimate time internally.

2.1. Do rodents and pigeons estimate duration internally?

Figure 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)

Two pioneering studies on pigeons (Stubbs 1968) and rats (Church and Deluty 1977) played a critical role in establishing that animals can quantify the passage of time. Food-restricted animals were challenged in the so-called bisection task which requires them to select one of two actions (press a left or right lever, or peck in one out of two feeders), following presentation of a short or long visual or auditory stimulus, to obtain a reward (Figure 1A). After training, animals responded correctly (90-100% correct responses) and performed closer to chance level for stimuli of intermediate durations. Plotting the percentage of responses for a given action ("long" response) versus a range of stimulus duration generates a typical psychophysical curve (Figure 1B). This result was naturally interpreted as evidence for an internal form of duration estimation (as there were no temporal cues available). Still, it remains possible that during the intervals, animals used their movements, somewhat like humans do when they count on their fingers. At the time of those two landmark studies, videos were not routinely recorded. Stubbs nevertheless did report that pigeons could exhibit superstitious routines during stimulus presentation. The reason why he mentioned such behaviors is most likely related to the earlier observation by Skinner (1948) that, in a task in which a food hopper was presented at a fixed-interval (FI) of 15 s., pigeons developed during the interval idiosyncratic stereotyped chains of actions such as wing flapping, head movements, pecking or circling (Figure 2).

Figure 2. Illustration of the type of circling behavior that could be displayed by a pigeon during FI reinforcement schedule.

Similar "superstitious" behaviors have been observed in a variety of timing tasks across species (Richelle and Lejeune 1980; Staddon and Simmelhag 1971; Timberlake and Lucas 1985). A first interpretation derived from Skinner's experiments is that such behaviors could eliminate the need for animals to internally estimate duration. This view has been contested because the behavioral content of these chains of actions could easily change, leaving open the possibility that they were ultimately driven by an internal clock (Richelle and Lejeune 1980). Still, stereotyped routines could help animals to associate a certain action (flapping the wings, circling in the cage) with reward delivery. Transforming the time interval into regular movements could reduce the temporal uncertainty inherent to the animals' inability to perceive duration quantitatively.

2.2. Turning bodies into clocks to detect coincidences and measure relative distances

Gouvea et al. (2014) were the first to continuously videotape rats performing a modified version of the bisection task. In this study, 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. After poking in the center port to trigger the first sound, the animals did not remain immobile but performed a stereotyped sequence of movements. Thus, they could decide whether the interval was short or long by detecting *where* in space the second sound appeared. This is exactly what was described for one of the animals, which systematically started by moving toward the left port upon presentation of the first tone ([Figure 3A-B](#)). In striking agreement with Bergson's prediction, this animal took advantage of the coincidence between the second tone and its head's position to judge the interval duration (now transformed in the distance traveled by the animal relative to the central port, that is a specific position in space). A 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

in this study 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 activity than if based on the passage of time*".

Figure 3.

Figure 3. A, Series of video frames taken from a single animal during presentations of a near boundary interval (1.38s) 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 Mello 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.

The development of idiosyncratic motor sequences is not limited to bisection tasks and has been elegantly captured in a task in which rats were required to increase the interval between two lever presses from ~300 ms to 700 ms to obtain a reward (Kawai et al. 2015). All the animals developed, through a slow trial-and-error process, a unique stereotyped ritual composed of a succession of movements (such as rearing, paw movements including wall touching, brief tongue protrusion, and head movements, see [Movie S1](#)) that filled the interval between the two presses. After extensive training (more than 20, 000 trials), animals still performed their second press slightly too early in more than 50% of the trials. This observation shows that animals are eager to obtain rewards and constantly anticipate the end of the interval (Shadmehr and Ahmed 2020). For rodents, a sense of urgency may thus coexist with a fundamental inability to perceive duration quantitatively, a problem that may be partially reduced through the usage of motor sequences (see section [3.1](#)).

The possibility that animals use stereotyped sequences of movements to successfully perform tasks with temporal constraints would be more strongly supported if the perturbation of such clock-like behaviors affected timing accuracy. There have been previous attempts to do this but with mixed success (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 by studying how the performance of a conserved stereotyped routine developed by rats in a waiting task was critical to timing accuracy (Rueda-Orozco and Robbe 2015). 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 slowly away from the reward area. By trial and error, about 80% of the rats trained in this set-up developed the following routine: during intertrials, they positioned themselves in the reward area. When the trial started, they remained relatively immobile while the treadmill dragged them away from the reward area. When they reached the end of the treadmill, they started running such as entering the reward area at about 7 s after trial onset (Safaie et al., 2020, see [Movie S2](#) compared to S1). By manipulating the duration of the waiting time and the speed of the treadmill (its magnitude and reliability across trials) or interfering with their 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. Interestingly, if rats were trained while the treadmill remained immobile, the animals that displayed the highest timing accuracy were those that developed a back-and-forth routine (they ran toward the back after trial onset, nibbled for a while there, and then ran again toward the reward area, see [Movie S3](#)). This study provides additional evidence that accurate timing requires stereotyped motor routines in rats, of their difficulty to measure time itself and it also illustrates the contribution of external features of the environment that afford temporal cues.

2.3. Estimating duration independently of movements

An important question is whether rats could perform duration discrimination without relying on motor routines. This has been recently investigated in a study that ingeniously incorporated a motorized treadmill in a temporal bisection task (Shimbo, Izawa, and Fujisawa 2021). Rats were forced to run on a treadmill for either a short or long duration (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 run duration ([Figure 4](#)). If the run duration was short (long), the animal could obtain a reward by entering the

right (left) arm of the Y-maze.

Figure 4. Schematic of the treadmill-based bisection task. Drawing from Shimbo et al. (2021) with permission. Video recorded during training: [here](#).

Critically, for each trial, the treadmill speed was randomly set at two values to avoid the animals using the distance they ran as a cue to discriminate run durations. The authors focused their investigations on the neuronal dynamics recorded in the hippocampus after learning the task. Still, 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 ([Link here](#); note that this video was taken during training and thus was not part of the published dataset), during the run, the rat kept biting the reward port located in the front of the treadmill stereotypically. This is highly similar to the mouth-to-tail contacts observed by Laties et al. (1965) in their waiting task. Although this hypothesis needs to be explicitly tested, animals may have developed a running-independent biting sequence that forms a stereotyped trajectory in the local space of the reward port and used the position of their head or mouth *at the time of treadmill offset* to discriminate between short and long runs.

2.4. Trace conditioning and one-shot temporal learning

In the aforementioned studies, rats and pigeons developed, across multiple trials and daily sessions, idiosyncratic motor routines to become proficient in tasks requiring them to behave according to abstract and fixed temporal rules. In experiments such as delayed or trace conditioning, it is believed that animals learn quickly to estimate the duration of intervals between a conditioned stimulus (CS) and unconditioned stimulus (US, food or

shock delivery; Balsam, Drew, and Gallistel 2010). Moreover, the first time an animal experienced a CS-US interval, it is not clear how its duration could be inferred from the random movements the animals performed during the interval. Before exploring how animals learn the duration of intervals in conditioning experiments, one should first verify whether the temporal profile of conditioned responses displayed by the animals after several exposures to the CS-US interval is consistent with the claim that they do acquire a knowledge of its duration. In their seminal review on time and associative learning, Balsam, Drew, and Gallistel (2010) described an experiment in which two groups of rats were exposed to a 6 second-long auditory tone (CS) paired with food delivery (US) after either a short (6 s) or a long (18 s) delay (trace interval). Strikingly, 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 not available until 6 s. after the CS offset (i.e., they started responding 12 s before the US presentation). 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 during almost 12 s if the reward was never available during this period of time? Such a pattern of response seems rather to argue for the possibility that they had literally no clue about when the reward would start becoming available and for that reason, they continuously responded since CS presentation. In section [3.1](#), I will provide an alternative explanation to that of temporal encoding and *knowledge*, based on optimal control and the cost of time theory (Shadmehr et al. 2019) to account for the different slopes and peaks of responding in the short and long trace groups. In brief, the long and short trace groups may simply display different sensitivities to the passage of time (they are more or less impatient), which is distinct from claiming that they know time.

Results obtained in delayed fear conditioning experiments also pounder the claim that temporal intervals are learned instantaneously. For instance, Bertolus et al. (2015) examined how delayed fear conditioning interfered with reward-oriented bar presses. In this type of

experiments, rats responded (i.e., inhibited their lever presses rate) as soon as a CS started to be played, despite the fact that the electrical shock was delivered 30 s after CS onset. After several weeks of training, the rats never managed to delay their initial response although they did increase its duration such as to largely exceed the time of the US delivery. Surprisingly, the temporal profile of the conditioned response was distinct depending on the nature of CS (e.g. 1 kHz vs 11 kHz prolonged auditory tone) suggesting that animals do not abstract away time but rather that their behavior is biased by the content of their sensory (and most likely motor) experiences during the interval. Similarly, it takes several days for animals to appropriately adapt the timing of their behavioral responses when the interval between CS onset and footshock delivery is changed from 30 s to 10 s (Dallérac et al. 2017), which argues against the idea that time intervals are instantaneously learned (see also Figure 2D in Rueda-Orozco and Robbe 2015).

In an elegant study, mice learned to press a lever to obtain a reward that was delivered after a delay randomly drawn from a Gaussian probability density function whose standard deviation varied in blocks of ~200 trials (it was selected from a set of three values: 50, 750, or 2,000 ms) while its mean remained fixed (3 s; Li and Dudman 2013). The authors examined how long mice waited in probe trials in which the reward was never delivered and found that the mice waiting time was proportional to the standard deviation of the delays (during high standard deviation blocks, mice waited more and thus correctly expected that the delay could be long). Still, as expected with rodents, mice were not immobile while waiting around the reward port (Dudman, personal communication). Thus, even if it is parsimonious to conclude that the mice infer probabilistic models of the delay, it is possible that such knowledge was derived from a sensorimotor-related term that co-varied with time while the mice waited.

That animals use the sensorimotor content of their actions (or their associated effort) and/or the sensory stimuli they perceived between the CS and US onsets to derive a notion of proximity between those events has not been directly investigated as virtually no study in delayed or trace conditioning provides trial-by-trial and animal-by-animal video tracking and analyses across CS-US exposures. Still, (Holland 1980) reported that short-duration (1, 5, and 10 s) auditory CSs evoked high frequencies of startle and head-jerk responses in rats, while long-duration (30 and 60 s) auditory CSs produced intermittent checking of the feeder.

During long intervals, animals do not stay put, as could be expected if they relied on internal representation of time, but rather their behavior display regularities according to the relative temporal *proximity* of the reinforcer: animals tend to explore away from the feeder at the beginning of the interval and progressively increase their approaches and contact with the feeder (Silva and Timberlake 1997).

The possibility that animals measure the duration of a learned interval indirectly through the sensorimotor content of their action, rather than directly through internal representation of time, has been demonstrated 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 and such probe trials lasted 100 s after self-initiation and were concluded by lever retraction without any pellet being delivered. At first, 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 took the form of inverted U shape with a peak aligned to 30 s relative to the initial press, suggesting that animals had formed an internal knowledge of when the reward was supposed to be delivered. Through a series of elegant experiments, the authors found that mice had learned to associate the characteristic sound made by the lever pressed at increasing frequency 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: they constantly pressed the lever until the pellet delivery. 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 duration. Rather, it is congruent with the possibility that mice, aware that a reward will be delivered at some point in the future, become impatient/frustrated while lever-pressing for the reward. This impatience leads them to press faster and faster and the repetitive association between auditory cues derived from fast lever presses and reward delivery lead them to derive an external proxy of when the reward should be delivered. In probe trials, mice infer that no reward will be delivered (and give up on pressing) when the characteristic sound of fast pressing does not trigger pellet delivery. Altogether, this study is congruent with the provocative idea that mice, despite being sensitive to the passage of time (they become more and more frustrated/impatient when an action supposed to trigger reward delivery does not), have no internal knowledge of when a reward should be delivered.

One could argue that eye-blinking delayed or trace conditioning experiments demonstrate the existence of internal representation of time. However, in these experiments, the interval between CS and US is short (below 800 ms) and the nature of the behavioral anticipatory responses displayed by animals is reflexive rather than resulting from a conscious estimation of time. Interestingly enough, in eye-blinking delayed and trace conditioning experiments performed on immobilized rabbits with short (0.35 s) or long (1 s) interval, the weakest nictitating membrane responses were observed in the long trace groups, while that same conditioning protocol induced the strongest increase in heart-rate (Meredith and Schneiderman 1967). It is therefore tempting to speculate that the lack of temporal knowledge or temporal uncertainty in the long-trace group may be conducive to a stressful state of uncertainty.

2.5. Timing without moving.

An alternative approach to random manipulations of the environment using treadmills (see [section 2.3](#)) to decouple duration estimation from movements is to force animals to remain immobile during the presentation of time intervals and to use a certain duration of immobility as a proxy for the expression of duration estimates. Such an experimental design is probably the best one to challenge Bergson's view that animals cannot perceive time or duration quantitatively independently of space or movements.

2.5.1 Can rodents estimate duration while being immobile?

Whether animals can estimate time while being immobile is a challenging question. In the interval categorization task of Gouvea et al., (2014), 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*". The same group has recently used a modified version of this task in which rats were forced to maintain their nose in the center hole during interval presentation (Monteiro et al. 2020). Thus, video recordings with different angles (allowing to track what happens inside the reward port) would be required to demonstrate the lack of contribution of movements in this task version or other timing task in which animals are trained to remain immobile while estimating the passage of time.

In an attempt to isolate movement-independent mechanisms of time estimation, Heys and Dombeck (2018) and Heys et al. (2020) have trained head-fixed mice to wait for a fixed amount of time (6 or 4 s) before crossing an invisible door to obtain a reward. First, it is important to note that what might appear as a simple rule for us may not be for rodents, as confirmed by the very progressive habituation protocol necessary to train the mice. Second, before training in the final version of the task, mice were already capable of waiting for a wide range of durations, with a marked preference for short waits (see Fig. 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. Thus, the timing accuracy of the mice was weak and the animals seemed to be eager to wait as little as possible (see also Schreiner et al. 2022, for a similar trend in a task in which mice must hold down a lever for a fixed duration). Moreover, there was no detailed video quantification of the animals' behavior during the waiting period. Given the prominence of facial and postural fidgetings in head-restrained mice (Musall et al. 2019; Stringer et al. 2019) and their massive impact on neuronal activity, the limited reduction in the incidence of short waiting times during learning may have been achieved by increased fidgeting during the waiting period and the neuronal correlates of waiting found in the medial entorhinal cortex (Heys and Dombeck 2018) may be related to fidgeting dynamics in time rather than duration estimation itself (Tsao et al. 2018).

2.4.2 Pure duration estimation in the head of non-human primates

Figure 5. A, Time discrimination task. B, Behavioral results from one experimental session. Figures from Leon and Shadlen (2003) with permission.

Leon and Shadlen (2003) developed a temporal discrimination task for non-human primates (NHPs) designed to minimize the contribution of movements to the quantitative perception of duration. In their study, monkeys 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, [Figure 5A](#)). 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 ([Figure 5B](#)). There are four points to consider regarding whether this result demonstrates that monkey internally estimated duration, as seems to indicate the drawing of a clock above the head of the schematized animal ([Figure 5A](#)). First, there is always some tolerance in terms of spatial eye fixation (typically a square of 1-degree side-length but with some variations during learning). Eyes are rarely entirely still and micro-saccades may occur inside the fixation point. Their contribution to the discrimination of duration cannot be ruled out, especially as saccades affect duration estimation (see [section 2.5](#)). Second, it is not because the animals' movements are strongly constrained that they cannot use other parts of their body to generate a motor representation of the intervals. For instance, in humans, the perception of short intervals was perfectly correlated

with muscle activity from the face (Fernandes and Garcia-Marques 2019). Third, there is an inherent contradiction to asking animals to estimate the duration of very short stimuli. Indeed, the shorter the duration, the less quantitative estimation of duration there is to be performed and the stimulus can be perceived as a single event. Animals may thus be able to distinguish the test and standard stimuli qualitatively. To take an analogy, we are capable of telling if the duration of a note inside a short melody has been modified without quantifying its duration. Such a qualitative assessment will only be possible for events of short durations. The deterioration of the animals' accuracy when judging intervals around 800 ms vs 300 ms is typically proposed to be compatible with the functioning of an internal clock that would accumulate time in a noisy manner (Gibbon et al. 1984). However, motor accuracy also decreases with movement length (Fitts and Peterson 1964). The decreased accuracy of long interval estimates could also be compatible with a movement-based mechanism whose precision degrades as the length of the movement increases. A fourth additional point that seems to argue against the fact that monkeys can perceive duration in a quantitative form is the very long time required to train them in such tasks (typically weeks or months) and their difficulty to generalize across task conditions. Rather, this could be compatible with NHPs relying on subtle stereotyped motor sequences whose length and content need to be adjusted by trial-and-error to allow discrimination of duration. Indeed, it is interesting to note that the activity of neurons in the lateral region of the parietal cortex, a region critical for eye movements control and spatial attention, approximate the timing decision of the animals (Leon and Shadlen 2003).

In an elegant study also designed to minimize the role of movements during 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). 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 supported 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 the duration of this interval as measured by the repetitive (hence timeless) and impersonal movements of human-made clocks but rather they guessed it according to the context (short or long intervals block) in which they experienced it, which directly supports Bergson's distinction between measured and lived time. As in other NHP studies, the temporal estimation of the animals was 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 which is problematic as movements of the face have been shown to contribute to timing accuracy in humans (see Fernandes and Garcia-Marques, 2019). Thus, the contribution of motor routines in this type of task can not be ruled out especially as neuronal activity in the supplementary motor area (SMA) and pre-supplementary motor area (preSMA) represented the passage of time in this task. In defense of the internal representation of time hypothesis, one could argue that it is impossible to rule out that an animal makes subtle movements to time intervals. Still, the recent development of powerful markerless pose estimation methods (Labuguen et al. 2019; Mathis et al. 2018; Nath et al. 2019) provides an outstanding tool to experimentally validate the claim that animals can measure time while being entirely immobile or at least independently of their movements. With the growing awareness of the importance of movements in a variety of time estimation tasks, strong claims about the ability of animals to estimate or monitor duration directly (Kononowicz, Wassenhove, and Doyère 2022) should at least be backed-up by video recording and analyses of movements during time intervals.

It remains interesting to note that, in an attempt to isolate purely internal representation of time from other co-varying sensory signals and movements, scientists have been forced into designing experiments that bear very limited relevance to natural behavior of rodents and NHPs. Unsurprisingly such experiments require extensive training sometimes across several months (the design are so unnatural that training often requires a progression through several task versions of increasing difficulty) or generate rebellious unexpected motor rituals during intervals (Gouvea et al. 2014; Kawai et al. 2015; Laties et al. 1965; Safaie et al. 2020; Shimbo et al. 2021; Skinner 1948). This could be a hint that time experienced by birds, rodents, and NHPs has little to do with the abstract form that scientists struggle to isolate. Importantly, even if animals were capable of complying with the unnatural constraints necessary to decouple time from behavior, it is unclear whether the type of process at play in such experiments would tell anything about the normal function of the brain (see Fig. 1C in Krakauer et al., 2017). Thus, instead of isolating measured time from movements, one alternative would be to directly examine whether movements affect quantitative estimation of duration (see below).

2.6. The importance of movement and space in humans quantitative experience of time

As I am writing this paper, I can close my eyes for a few seconds and when I reopen them, I know that only a few seconds have elapsed, not thirty or two months! While this seems to suggest that we are capable of internally measuring time, it is important to remember that there is a fundamental difference between feeling and measuring time. The latter is far from innate (those readers who have young children will certainly have witnessed their difficulty to grasp time in a quantitative manner) and ultimately relies on a spatialisation of time: seconds, minutes, days or months are units of time that only make sense because we have learned 1) to immobilize time on various forms of spatial representations such as clocks, calendars or timeline draws on the walls of classrooms and 2) that elapsed time can be inferred by computing the distance traveled by a moving body (see the introductory quote by O. Sacks and [section 1.1](#)) or by detecting the amount of change derived from a sensory cue (e.g., a change in luminosity). Thus, our ability to estimate that we only closed the eyes for a couple of seconds (and not one hour) is derived from our knowledge that we performed a couple respiratory cycles whose duration are brief (see also supplementary sections [9.1](#) and [9.2](#)) and/or that when we re-opened our eyes, the environment around us

had not changed. In support of this distinction between internally feeling time and measuring it through a movement-based spatialization (hence the expression of passage of time), 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). Below, for the sake of time and space, I will mostly focus on a series of studies showing a remarkable correlation between movement-induced alteration of spatial and temporal estimates and discuss experiments that seem to argue for movement-independent representation of time (Diedrichsen, Criscimagna-Hemminger, and Shadmehr 2007; Heron et al. 2012).

In a now seminal study that investigated how visual perception remains relatively stable despite changes in gaze and 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, Morrone, and Burr 1997). 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, Ross, and Burr 2005). The distortion of temporal estimates was robust for a wide range of saccade magnitudes including small ones (3.5 degrees), which brings this phenomenon in close range with the saccades potentially performed by NHPs during the fixation phases of timing tasks. Critically, when participants were asked to both 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 ([Figure 6](#)) (Binda et al., 2009).

Figure 6. 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. 2019, with permission.

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 lead the authors of this impressive series of studies than span over 2 decades to propose that distortion of temporal estimates may be an unavoidable consequence of mechanisms controlling sensorimotor integration.

Intriguingly, an ingenious and somehow similar experiment in which human subjects learned to control the relative timing of two actions (an arm movements and a thumb press) yielded results that, on one hand, confirmed that timing can be influenced by movements and, on the other hand, concluded on the possibility to dissociate timing from motor coordination (Diedrichsen et al. 2007). Subjects were first trained to perform a point-to-point arm reaching movements at a given speed. Then, they were instructed to produce a short force pulse with their thumb at a specific time interval relative to the arm movement initiation (ΔT , the critical task variable). Participants were assigned to eight groups, each with a specific ΔT ranging from -500 ms (thumbs press before arm movement) to + 500 ms (thumb press after movements). After training, subjects were retested while asked to perform the arm movement at a slower speed (550 ms instead 350 ms). Strikingly, in groups in which the

thumb press and arm movement overlapped, ΔT and thumb duration were altered by the slower arm movements, as expected if the subjects used the position and/or speed of their arm to time their thumb presses. In contrast, thumb press timing was not modified by the slower arm movement in subjects for which the two actions never overlapped, suggesting it was under the control of an internal representation of time. Still, the nature of this representation can be questioned as, during training, all the subjects learned to time their thumb press relative to the arm movement onset through a visual feedback in which the timing error was represented graphically with a distance measurement. Thus, it is difficult to rule out that the timing of the thumb press, when not interfered by the arm movement, was in fact dependent on a representation of space. And because the only way that distance can provide a temporal information is through an underlying regular movement (the regularly spaced ticks on the dial of a watch only make sense to tell time because the hour, minutes and second hands are moving at constant speeds), one could speculate that the timing of the thumb press was under a more covert movement-related representations that remained stable unless another movement interfered with it.

In contrast with the possibility that the estimation of time is derived from space and movements, psychophysical experiments using sensory adaptation protocols (Heron et al. 2012) combined with the description of neurons whose activity is modulated by the duration of sensory stimuli (Duysens, Schaafsma, and Orban 1996), have yielded to the proposal that "duration channels" mediate time perception in the brain. Such studies allow to clarify a potential confusion with the central claim of this paper. Indeed, there is no doubt that the repetition of prolonged stimuli might lead to adaptation in the way they are perceived and that such adaptations find their cause in alterations of stimulus-evoked neuronal activity. The key question is whether subjects infer duration directly from their spiking activity or indirectly through space and movements. Noticeably, in Figure 1 of Heron et al. (2012), which represents schematically the behavioral task, it is virtually impossible to know if subjects had to measure the length or the duration of visual stimuli. More direct evidence from the fact that duration must be measured through movements in space can also be drawn from experiments showing that temporal adaptation is affected by movements (Tomassini et al. 2012) and that motor adaptation affects similarly temporal and spatial perception (Anobile et al. 2020; Petrizzo et al. 2022).

2.7. Overlapping neural underpinnings of spatial representation, motor control and duration estimation.

2.7.1. Duration estimation and motor control share common cortical and subcortical neural implementations

We already mentioned ([section 2.4.2](#)) that cortical regions involved in the control and planning of movements are also activated in tasks in which subjects are asked to estimate durations without moving (for an in-depth review, see Merchant and Yarrow, 2016). In addition to the aforementioned representation of time in movement-related brain regions, it has been reported that neuronal activity in the supplementary motor area (SMA) of the cortex (a region critical for planning and execution of hand movements; Coull et al., 2016) correlates with time in tasks in which temporal estimates must be reported through arm movements (Mita et al. 2009). 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). Thus, neuronal activity in movement-related brain regions may not be a temporal representation per se but simply reflects the control of covert/subtle movements that are used by animals to discriminate time intervals.

Subcortical regions strongly connected with movements have also been implicated in time estimation. First, the cerebellum is often cited as being critical for the estimation of very short intervals (Buhusi and Meck 2005; Ivry and Spencer 2004) even if it is difficult to disentangle whether such a function is derived from the role of this brain region in the coordination and planning of movements according to external task constraints and sensory feedback (e.g., Diedrichsen et al. 2007 and [section 2.6](#)). It is also remarkable that a recent study suggested that the cerebellum may be critical for cognitive tasks requiring movement-like mental operations (McDougle et al. 2022). Second, the basal ganglia, and especially the dorsal striatum and its dopaminergic modulation, have long been proposed to play the role of an internal clock, especially in tasks requiring to estimate intervals of several seconds (Buhusi and Meck 2005). Strikingly, there is ample evidence for a contribution of the dorsal striatum and sensorimotor regions of the globus pallidus in controlling the speed of reward-oriented movements and decision making (Dudman and Krakauer 2016; Robbe and

Dudman 2020; Shadmehr et al. 2019; Thura and Cisek 2017; Turner and Desmurget 2010) potentially through regulation of effort and cost of time sensitivities (Jurado-Parras et al. 2020; Shadmehr et al. 2019; Shadmehr and Ahmed 2020). This motivation function depends on dopamine neuromodulation (Berke 2018) (among other neuromodulators).

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 (reviewed in Buhusi and Meck, 2005; see also Soares et al., 2016) which has been typically interpreted as causing changes in the speed of emergent or dedicated internal clocks in the dorsal striatum. However, due to the motor motivation function of the dorsal striatum, striatal activity may not represent time but primarily modulates the speed of movements serving as a workaround for duration estimation. For instance, in a study examining the ability of PD patients to estimate time intervals while verbally counting, the underestimation of elapsed time is caused by the slowness of the movements associated with counting (Pastor et al. 1992), slowness that could reflect an increased effort sensitivity (Mazzoni, Hristova, and Krakauer 2007). In rodents, an increase in dopamine tone with methamphetamine caused the animals to judge short intervals as long ones. This result was assumed to reflect an increase in the speed of the inner striatal clock (Maricq and Church 1983). But methamphetamine could increase the speed of movements performed during intervals which would lead to a greater distance traveled at the end of the interval and to judge short intervals longer than they were. Soares et al. (2016) found that transient activation or inhibition of dopamine neurons was sufficient to slow down or speed up time estimation, which the authors interpreted as a direct control of dopaminergic activity on the judgment of time. Still, it cannot be ruled that this effect was mainly indirect and reflected motivational alteration that affected a movement-based mechanism of time estimation. Critically, because motivation affects the way animals move while waiting and that striatal neurons can continuously represent the sensorimotor states of animals (Peters et al. 2021; Robbe 2018; Sales-Carbonell et al. 2018), it may not be surprising that time can be decoded from the population activity of neurons (Gouvêa et al. 2015; Zhou, Masmanidis, and Buonomano 2020). However, as pointed out by Gomez-Marin (2019) *“That the experimenter’s model can decode the signal does not mean that the brain can or does.”* The proposal that duration judgments are inferred from the activity of dorsolateral striatal neurons has been recently directly challenged (Toso et al. 2021), also the matter is most

likely not settled. Indeed, on the one hand, this study confirmed that duration estimation in rats is biased by the intensity of the stimulus (tactile stimuli of higher intensity were perceived longer), in agreement with the idea that temporal inferences are not purely internal but may depend on attending to sensory changes observed in the environment (Sherman et al. 2021). On the other hand, there has been converging reports that the modulation of dorsolateral striatal activity by sensory stimuli self-generated by the animals' movements during time intervals is critical for accurate timing in various tasks (Cook et al. 2022; Hidalgo-Balbuena et al. 2019; Pimentel-Farfan et al. 2022). One parsimonious explanation could be that the sensorimotor regions of the basal ganglia, by integrating sensory stimuli that covary with time and dopaminergic modulation, output an urgency signal that implicitly controls the speed of decisions and movements (Carland, Thura, and Cisek 2019).

2.7.2. Space, time, memory and the hippocampus. Overlapping function and representation.

A final prediction derived from Bergson's proposal that the quantification of duration can only be reached through the projection of time in space is that brain regions involved in spatial navigation/cognition should contribute to time estimation. 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 and representation (O'Keefe and Dostrovsky 1971; O'Keefe and Nadel 1978). In humans, Kesner and Hopkins (2001) showed that subjects with hippocampal damage displayed strong impairment to retain 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 affected how we retrospectively estimate the duration of past events and reported that temporal distortions induced by manipulating memory accessibility were associated with changes in hippocampal

activity measured with fMRI (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, in this last study, an involvement of the hippocampus. These works are therefore congruent with the idea that the duration of a time interval is not directly measured by the brain but reconstructed based on the changes observed and remembered during the interval, a function that may be dependant on the hippocampus when changes develop over relatively long time scales (see below and Maurer and Nadel 2021). Finally, even if this is more of an anecdotal story than a well-described neurological report, the case of Diane Van Dere 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 epileptical seizures but also drastically reduced her ability to read maps and made her susceptible to spatial disorientation (she would get lost very easily). But 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.

In rodents, hippocampal lesions impair the acquisition of trace conditioning but only for the longest intervals capable of inducing conditioning (i.e. 500 ms; Solomon et al. 1986). This result is in agreement with the hypothesis that the hippocampus could link events separated in time but occurring in the same context (Nadel and Willner 1980). In one of the rare studies investigating directly the contribution of the hippocampus in a temporal discrimination (bisection) 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. Importantly, fimbria-fornix lesions induce hyperactivity (Cassel et al. 1998), which may have affected the speed of execution of a motor routine or shortened reaction time. Thus, the overestimation of the stimuli of intermediate duration might primarily result from an increased distance traveled during the stimuli presentation rather than a change in the perception of time. 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 exactly were doing while waiting in the delay area and of how lesions affected this behavior, such results are difficult to interpret.

Nevertheless, 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 integrate behavioral/contextual changes over time.

The role of the hippocampus 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 (O'Keefe and Dostrovsky, 1971; Skaggs et al., 1996). An interesting observation is that a similar sequential activation of hippocampal neurons has also been observed when rats are running while remaining still in space (eg., while running on a wheel or a motorized treadmill; Pastalkova et al., 2008; MacDonald et al., 2011; Kraus et al., 2013). The neurons forming these sequences have been called "time cells" although they were not recorded during time estimation tasks but developed while animals needed to maintain contextual knowledge over relatively long periods of time. In humans, time cells have been recorded in the temporal lobe of subjects performing an episodic memory task, suggesting their role in representing temporal information necessary for this type of memory (Umbach et al. 2020). It is interesting to note that although their underlying mechanisms may be distinct (Wang et al., 2015; Sabariego et al., 2019), 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. It has been originally proposed that time cells could provide an accurate representation of duration (Eichenbaum 2014). But 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). This study did not examine whether this activity was necessary for estimating duration. 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.

The recent study of Shimbo et al. (2021) discussed earlier (section 2.3), is the first one 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, [Figure 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 ([Figure 7A](#)). This result is reminiscent of the rescaling of place cells firing profiles when rats ran in a corridor whose length was changed ([Figure 7B](#); Huxter et al., 2003).

Figure 7. Similar scalable representation 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 (10s vs 5s) followed by a long block (20s vs 10s) 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. (2013), modified with permission.

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 representation, 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 position of the animals in a local spatial trajectory that can be rescaled depending on the duration of the runs (short vs long blocks). Interestingly, it has been recently proposed that the hippocampus is a structure whose 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). Because animals are naturally moving or exploring while time passes by, it is therefore possible that they can infer whether two events are more or less contiguous in time indirectly through their spatial or behavioral contiguity. Hence it would be much easier for animals to solve time estimation tasks by developing motor or navigational routines (Gouvea et al. 2014; Laties et al. 1965; Safaie et al. 2020; Shimbo et al. 2021) such as to simplify the function of the hippocampus to reliably detect changes over the course of an interval.

2.8. Summary

In the above subsections, I have confronted Bergson's subversive claim _ duration cannot be directly perceived in a quantitative form _ to a large corpus of behavioral and neurophysiological experiments. Most of those studies assumed that humans or animals measure duration directly through emergent or dedicated neuronal clocks that specifically encode time. A compelling series of observations challenge such framework and support, at the behavioral and neuronal levels, Bergson's view that duration is indirectly quantified through a movement-based projection in space:

1. There is evidence that rodents use movements and distance traveled during time intervals (or the position reached at the end of the interval) to judge their durations. In trace conditioning experiments, the excess of anticipation does not argue for the animals having knowledge of time but rather for their variable urgency to obtain rewards.

2. The ability of non-human primates to estimate duration is limited to very short intervals and thus may be qualitative. Moreover, the contribution of micro-saccades and other subtle movements has not been thoroughly examined. Brain regions activated in duration estimation tasks in immobilized monkeys are the same that contribute to the execution and planning of movements.
3. In humans, all sorts of stereotyped movements significantly improve the ability to accurately estimate duration. In addition, temporal and spatial perceptual distortions are strikingly correlated.
4. Brain regions regularly engaged in duration estimation tasks are involved in motor control, motivational aspects of reward-oriented actions, and episodic memory. In the hippocampus, place cells and time cells are strikingly similar.

3. Rethinking time

3.1. Time as a force rather than an information

The belief that animals have an internal representation time or a knowledge of the duration of intervals is largely based on their well-documented anticipatory behaviors toward potential reward opportunities or to avoid threats (Balsam et al. 2010; p257 in Buzsáki 2019; p687 in Paton and Buonomano 2018). Still, if animals were aware of how much time is missing until the next reward opportunity, shouldn't they use this knowledge to avoid anticipatory responses that are at best a waste of energy (i.e., what is the point of frantically pressing a lever before the end of a learned interval if only a single well timed action is sufficient to obtain a reward?), or at worst, increase the chance for further delaying rewards (which occurs in a large fraction of trials in tasks in which early responses are penalized ; see for instance Heys et al. 2020; Hodos, Ross, and Brady 1962; Kawai et al. 2015; Safaie et al. 2020)? Alternatively, that animals lack an abstract knowledge of the duration of time interval, which would be expected if time cannot be directly quantified by the nervous system, could explain why humans and animals behave with impatience, develop superstitious routines while waiting (or hoping) for a positive event or start responding immediately when a cue predicting a delayed reward/threat is presented (see [section 2.4](#)). The idea that anticipatory responses may reflect a lack of temporal knowledge might gain some traction by considering the fact they can also be expressed in space (i.e., and not just

in time). For instance, some individuals displayed difficulties in maintaining social distancing while waiting in line at a cashier during the pandemic. Similarly, it is not uncommon that a driver in a hurry will follow the car preceding him without maintaining a safe distance, even on a road on which passing is physically impossible. If anticipatory responses during fixed interval reinforcement schedules or trace conditioning experiments are believed to provide evidence that animals are aware of time, should a person respecting social or safety distances be considered as being unaware of space? Rather, such impulsive behaviors may reflect the urgency to reach a goal independently of spatial perception. Similarly, anticipatory responses and impatience might primarily be driven by urgency but may not provide evidence for an abstract knowledge of time.

One could legitimately wonder what causes the urgency to act in anticipation of an expected reward, if it does not reflect a knowledge of time? A key aspect to consider is that, for a living organism, a given moment in time never repeats itself. As Bergson puts it: "*the same never remains the same but reinforces itself and grows from its past*". "*A sensation, by the simple fact that it lasts, modifies itself to the point of becoming unbearable*" [p115/p153]. The fact that we can become more and more impatient and that some of our most personal decisions take up to several years to mature into concrete actions made Bergson think of time as "*a concrete reality, a force of its own*". The parallel between Bergson's view of time as a force and the theory of the cost of time is striking. Indeed, for Shadmehr and Ahmed (2020), as time passes, a cost accumulates and will make animals act sooner (faster) than later (slower) to obtain a reward in a minimum of time. Importantly, the cost of time increases proportionally with the expected magnitude of the reward and its proximity in space. For instance, the reaction time of reward-oriented movements is typically shorter when the rewarded target is close (in space) than when it is distant (Shadmehr et al. 2019). In an ever-changing world, uncertainty increases with time and the opportunity of getting big and easily reachable rewards should be prioritized. Humans and animals must therefore be sensitive to the passage of time due to the potential risk of missing high-reward/low effort opportunities. In nature, rewards and threats that are more distant in space are likely to impact animals later in time (i.e., temporal proximity covaries with spatial proximity). Consequently, they can be treated with less urgency than nearby rewards/threats. The various magnitudes of anticipatory responses could therefore be explained by the distinct

sensitivity to time which is driven by the animals' awareness of reward/threat proximity in space rather than their knowledge of abstract duration. Interestingly, it has been recently proposed that, compared to humans, animals may overestimate the passage of time in bisection tasks (short intervals are judged longer than they really are) due to their tendency to discount more than humans delayed reward-oriented motor responses (Kopec and Brody 2018). This is in agreement with the idea presented in this article that animals ignore abstract human-made temporal rules but rather solve time estimation tasks through reward-oriented motor sequences. Kopec and Brody (2018) proposed that humans and other animals may process similarly temporal information while animals are more sensitive to temporal discounting. Alternatively, one could consider the possibility that neither rats nor humans process temporal information. Rather they are both sensitive to time, with the distinction that humans may have the unique ability to represent its passage through its abstract/geometric transposition in space while rodents struggle to disengage from their reward-oriented movements and can only access time through actions and the correlation between duration and distance.

In summary, anticipatory responses do not necessarily equate with abstract or disembodied knowledge of interval durations. They can be well explained if one considers that animals are sensitive to an opportunity cost associated with the passage of time. Differential sensitivities to this cost of time can emerge by inferring the imminence of a reward (or a threat) implicitly from its distance, as temporal and spatial proximities typically correlate outside experimental settings. Indeed, prey escapes predators when they are getting too close to them. They do not initiate escape responses unless an external cue gives them a hint of the imminent threat. Laboratory settings used to study interval timing create an artificial situation in which time and space are decorrelated :the lever press is present but reward is not available; in waiting tasks or trace conditioning studies, space remains stable while time passes and the reward/threat appears abruptly without progressive cueing from the environment. In such settings, anticipatory responses (Balsam et al. 2010) and motor rituals (Gouvea et al. 2014; Kawai et al. 2015; Laties et al. 1965; Safaie et al. 2020; Shimbo et al. 2021) may be considered respectively as a maladaptive behavior (again why pressing on a lever press 30 s before it become active) and attempts to recreate a correlation between time and space through behavioral sequences.

3.2. Feeling time is not measuring it.

Bergson's proposal that we cannot directly measure time is counterintuitive because we, neuroscientists, tend to assimilate *feeling* and *measuring*. For Bergson, such a confusion finds its root in our difficulty to realize that the metaphors we routinely use to describe our inner mental life are drawn from the outside world. When we say that time passes more or less quickly, we assume that this statement is primarily derived from our internal experience of time, exactly like when we say that we feel more or less warm or that a sound is more or less loud. Bergson recognized the practical value of such statements, but he challenged their accuracy and provided arguments to show that they reflect a confusion between the qualitative nature of our internal mental life as it unfolds and quantitative aspects of the world (sound frequency, temperature), the latter simply influencing the former (Bergson, 1889, chapter I). This confusion can be illustrated by considering the expression "time flies" that only makes sense because we are used to perceiving external objects or fluids moving more or less quickly (the flow of a river, the movements of the sun, or those of the secondhand of a clock, see also the introductory quote of O. Sacks). Thus, with such an expression, a personal and dynamic experience of time is transformed into a communicable static metric borrowed from the outside world. The dissociation between feeling and measuring is actually more obvious when we don't feel or perceive anything. Indeed as noted by Oliver Sacks, it is not because we don't feel the movements or growth of a plant that they cannot be measured.

Why do we tend to confuse our internal feelings with their fundamentally external labels?

"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. In the same way as the fleeting duration of our ego is fixed by its projection in homogeneous space, our constantly changing impressions, wrapping themselves around the external object which is their cause, take on its definite outlines and

its immobility" [p97/130]. Bergson thus proposes that the confusion between exteriority and interiority makes us oblivious to the fact that we, as individuals, are in a perpetual state of becoming. The fixed representations provided by language and our inability to merge into a single perceptual experience the successive events developing over long time intervals (see again the slowly growing hollyhocks of Oliver Sacks) make us blind to the fact that we are becoming older, our kids are growing, more generally that the world around us is continuously 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 *durée* has the potential to help us realize that living beings and the world around them are truly in a perpetual state of becoming and that the solutions to the societal challenges we are facing may also be found in radical creativity rather than in complex algorithms based on an already obsolete past (Vogelstein et al. 2022).

4. Concluding remarks: time to inject *durée* in Neuroscience?

The confusion between quality vs quantity and interiority vs exteriority has been an overlooked determinant of neuroscientific approaches to the question of the brain-mind relation and the neural bases of cognition. Once it is accepted that our mental life at a given moment can be reduced to a measurable physical (i.e., external) process, the next logical step is to characterize this process and figure out how it results from complex interactions occurring at different levels in the brain (molecules, cells, circuits). An example of this mechanistic approach is offered by the recent proposal that an understanding of our cognitive abilities could be more effectively reached by an inside toward outside investigation of the relationship between brain and behavior (Buzsáki 2019). Buzsaki challenges the classical method of looking for neuronal correlates of ill-defined psychological terms (see also Pessoa, Medina, and Desfilis 2022) and because brain processes are in the realm of objectivity (their externality makes them observable), he proposed to start by examining how they can be mapped on quantitative aspects of behavior. Still, the question remains of why the psychological vocabulary (memory, attention, perception,

decision-making) are unsatisfactory and whether there could be new terms coming from the inside-out approach that would be better suited to describe behavior and our most advanced cognitive abilities? To this latter question, Bergson would most likely say no, and this can be understood by restating his answer to the first question: psychological terms are useful for social purposes but added to quantitative statements (more or less pain, fear, or motivation), they remain an approximative attempt to share our inner mental life that is fundamentally unique and constantly changing. Communicating about brain circuit dynamics will require externalizing them in immobile images such that people can have a common object of discussion and link them to events observed in the world. But this would lead to the same approximations that make an expression valid during the 19th century meaningless in our current westernized society in which manners, values and mentalities have entirely changed and keep evolving. Attempts to replace psychological words with brain-derived vocabulary to explain behavior or cognition (Buzsáki 2019; Pessoa et al. 2022) seem to reflect a confusion between different levels of descriptions of the living (behavior and neuronal processes) that can not be reduced to each other (Poeppel and Adolphi 2020). The originality of Bergson is to have not stopped his reflection at this stage (i.e, why the description of our inner life with words is inevitably approximate) but further wonder *"whether the most obvious states of the ego itself, which we believe that we grasp directly, are not mostly perceived through the medium of certain forms borrowed from the external world"* [p167/223]. When we say that time passes by more or less quickly, we forget that we have *in mind* the flow of a river or the movements of a wind turbine, movements that are objectively observable in the world and thus quantifiable. Similarly, when a subject is asked to rate her level of confidence on a *scale* from 1 to 10 after making a choice, the question only makes sense because a scale is an external object many people can relate to. Here, and against Bergson's warning, psychophysics use forms taken from the external world to describe an internal psychophysical state (confidence, which is in fact ever changing in the life of human subjects). Such external images are needed to ground communication but problems start arising when (cognitive) neuroscientists forget this origin. One of the major achievements of Bergson is to have realized 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 question of the neuronal mechanisms of time estimation:

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. Because anyone can feel time internally, they assigned time estimation to the only internal process available for objectification: neuronal activity. It is only ironic that, to explain how fast or slow time seems to pass by, which is nothing else than an image borrowed from the external 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. It requires a tremendous effort (what Bergson calls intuition) to re-apprehend the live experience of time, free from images drawn from space. Starting from the inner workings or anatomy of the brain, as proposed by Buzsaki or Pessoa and colleagues, is thus unlikely to solve the issue of the deceptivity of language when it comes to understanding our inner mental life. It misses the point of why psychological terms or psychophysical quantitative statements (e.g., I am 100% 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. Bergson proposed that for psychology to move forward, it is critical to acknowledge this untold and inevitable invasion of metaphors or vocabulary drawn from observing external events in the world. Otherwise we run the risk of becoming blind to a fundamental aspect of our inner mental life which is to be ever-changing and by consequent always new and imperfectly predictable from the past (see chapter III in Bergson, 1889).

That the inner or mental experience of the passage of time is fundamentally unquantifiable may appear contradicted by the observation that animals and humans adapt very well to temporal regularities occurring in the world and the possibility to decode time from neuronal activity in the brain. First, the point of this paper is not that our experience of the passage of time is not quantifiable but rather that this quantification is not direct and requires its spatialization/externalization: adaptive behavior depends on the ability of humans and animals to interact with temporal cues in the external world (e.g., regular movements of objects such as the sun or those we can easily produce with our body such as finger tapping; see also Gibson 1979 on the concept of affordance). Indeed, people do lose track of the passage of long intervals when they are isolated inside caves for several days

even if, obviously, they can still count on their fingers. Alterations of time perception have also been reported during the pandemic, which is to be expected when daily routines imposed by the world are suddenly disturbed for a long period of time. Second, the spatialization of time for measurement purpose requires a nervous system and a body to interact with the world, and thus it is not surprising that any alteration of the brain functioning (with drugs, sensory deprivation, during sleep vs wake or at different stages of life) will necessarily be associated with distortion of our experience of time and duration estimates (see also Cook et al. 2022 for recent example). Nevertheless, such a contribution of the nervous system to our experience of time is merely that of the part to the whole (Bergson 1919). Ascribing to the brain activity the power to tell time (Buonomano 2018) is therefore reductionist at two levels. First, it is mistaken to think that the behavior or cognitive abilities of a living organism can be reduced to one of its implementation components (Gomez-Marin 2021; Krakauer et al. 2017; Poeppel and Adolphi 2020). Second, the philosophical arguments and empirical evidence presented in this paper have hopefully provided credit to the idea that the passage from feeling time, which surely depends on having a nervous system, to measuring time is not direct.

The most important realization that comes with accepting Bergson's *durée* is that our inner mental life is ever-changing and in a constant state of becoming, a statement that applies to other animals but not to robots. This 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. Indeed, because computational predictions are based on rules deduced from past correlations between internal/brain states and behavior, how can such rules apply to new inner states that have never been encountered in the past? 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 of living organisms. 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, 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 the 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 creative 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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The author declares no competing interest

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9. Supplementary section. A step-by-step introduction to Bergson's reflection on time and space

One of the main points made by Bergson in his Ph.D. dissertation (Bergson 1889), translated in English under the name *Time and Free Will, Essay on the immediate data of consciousness*⁴, is that any conscious attempt to quantify the passage of time requires a spatial operation. The second one, is that there are two forms of time-related experience. On the one hand, there is the time that we measure or think about in abstract/symbolic terms and which is nothing other than space. On the other hand, there is the time experienced by conscious beings freed of any spatial content, what Bergson calls *durée*: "*a succession of qualitative changes, which melt into and permeate one another, without precise outlines, without any tendency to externalize themselves in relation to one another, without any affiliation with number*" [p77/p104]. The aim of this section is to explain how Bergson established this distinctions.

9.1. Counting external objects

For humans, measuring the passage time is closely related to our ability to count (Rattat and Droit-Volet 2012). Interestingly, Bergson started his analysis of the perception of time and space by examining the process of counting. His claim is that "*every clear idea of number* [as a sum of units] *implies a visual image in space*" [p59/p79]. To come to this conclusion, Bergson asks us to think of a flock of sheep. To be able to count sheep, we must first forget about their individual differences and assume they are all equal. Then, and at the difference of what happens in the process of enumeration, counting requires something *to remain* such as each new sheep is added to those already counted. The idealized sheep must be *juxtaposed*. For Bergson, this juxtaposition, as the word itself indicates, happens in space not in time. Indeed, the moments of time associated with each addition are finite (or transient) and thus they cannot remain: by definition they pass. The only comprehensible way by which sheeps (or any external objects) can be separated is to fixe their trace in space (imagined or real). That the process of counting is fundamentally spatial is confirmed when one examined how kids are taught to count and the first counting tools used by humans (Figure 8).

⁴ Essai sur les données immédiates de la conscience.

Figure 8. Left, abacus ring from the Qing Dynasty (1644-1912, <http://dataphys.org>) Right, markings made on a hyena bone by a Neanderthal might have recorded numerical information. Credit F. d'Errico.

We tend to forget about the spatiality of the counting process because we learned on top of it a symbolic representation of numbers. *"What leads to misunderstanding on this point seems to be the habit we have fallen into of counting in time [using symbols] rather than in space"* [p58/p78]. Because it takes some time to count, we have the illusion that we can add identical units of time on top of each other. But fundamentally those units need to be separated in space to be counted.

9.2. Counting non-spatial events.

Next, Bergson examines whether a similar spatial process is at play when we count events that provoke a succession of sensations (i.e., events that, unlike sheep, do not appear directly under a spatially organized form but unfold in time). Bergson takes the example of hearing the successive strokes of a bell ringing in the distance. He distinguishes two cases. In the first one, *"I retain each of these successive sensations in order to combine it with the others and form a group which reminds me of a tune or rhythm which I know: in that case, I do not count the sounds, I limit myself to gathering, so to speak, the qualitative impression produced by the whole series"* [p64/p86]. Such experience is similar to what happens when we're listening to music: we may have not noticed the first two strokes but the familiar quality of the flow of sounds and silences generated by the bell makes us, at some point, realize that: "Ah, it's the church's bell". There is no counting, or quantitative perception of time, in this type of experience. Another (and radically different) type of experience that we can have when hearing the bell' strokes is the one in which we explicitly count them. To do that, as Bergson points out, *"I shall have to separate them [the strokes], and this separation must take place within some homogeneous medium in which the sounds, stripped of their*

qualities, and in a manner emptied, leave traces of their presence which are absolutely alike. The question now is, whether this medium is time or space. But a moment of time, we repeat, cannot persist in order to be added to others. If the sounds are separated, they must leave empty intervals between them. If we count them, the intervals must remain though the sounds disappear: how could these intervals remain, if they were pure duration and not space? It is in space, therefore, that the operation takes place"[p64/p87]. Once the sound and silence have been stripped of their quality and arbitrarily isolated, counting them requires storing them *separately* which must happen in space (see [Figure 7](#) and section 9.1 above). One could argue that such separation can be maintained internally through short-term memorization (stored in the brain) and for instance some form of persistent neuronal activity. There is no doubt that something is going on in the brain when we count or even remember the successive strokes of the bell. But neuronal activity and counting occur at different levels of understanding (Krakauer et al. 2017) and humans do not read their spiking activity as they count with an abacus. The fact that counting the strokes of a bell requires sustained neuronal activity does not mean that this ability is purely internal and does not exclude the possibility that counting requires a projection in space of the separated strokes and silences. For instance, if I had to count the strokes of the bell in my head and without the help of numerical symbols or my body, I would probably use an imaginary abacus and thus return to space as the fundamental form of counting. Of course, I can memorize and recall the "melody" of the bell's stroke but this does not mean that I am counting the strokes. Counting will require the additional separation of the strokes and silences in space.

9.3. Time looks like space

The above analyses led Bergson to distinguish two kinds of multiplicity: the multiplicity of objects that comes to us directly in a spatial form (the flock of sheep) and the multiplicity of our conscious or affective states, which takes the form of succession in time. It is in this context that Bergson placed himself to analyze more carefully the ideas of our perception of time. The first observation of Bergson is that when we think or speak of our experience in time, "*we generally think of a homogeneous medium in which our conscious states are ranged alongside one another as in space, to form a discrete multiplicity*" [p69/p90]. I underlined the "*as in space*" to remind the reader of the way neuroscientists describe the

perception of time (*space is a good analogy for time*) and illustrate the prescience of Bergson on identifying this tendency. Thinking that our experience of time and space are alike is derived from the impression that both objects (e.g., a ruler) and events durations (e.g., a movie) can be arbitrarily divided into portions of equal length. Bergson raises the following question: could our unconscious habit of seeing our mental life as a *discrete multiplicity* occurring along a line (a spatial representation of discrete and successive events) affect our perception of the flow of our sensations and thoughts? Bergson asks us to try to abstract ourselves from our habit to decompose and align, to verify if the way our conscious states appear to us in time, *as we live*, is a discrete multiplicity. He anticipates that this is not the case. Indeed, for Bergson, if on the one hand, we have the tendency to discretize and align our feelings and ideas as they occur in time, and if on the other hand, the process of counting successive events (here ideas and sensation) requires a form of spatialization, it is to be presumed that such view of our inner life in time is nothing but space. Bergson felt encouraged in this conclusion because if "*we are compelled to borrow from space the images by which we describe what the reflective consciousness feels about time* [e.g., this movie was too long] *and even about succession* [e.g., he left shortly after the snow started falling], it follows that pure duration must be something different [than space]". [p68/p91]

9.4. Time and space while we experience the world, the discovery of *durée* pure

Bergson proposes the following definition of pure duration which will refer to *durée* to distinguish from the duration measured by clocks: "*the form that the succession of our states of consciousness takes when our ego lets itself live, when it refrains from establishing a separation between the present state and previous states. It does not need, for that, to be absorbed entirely in the sensation or the idea which passes, because then, on the contrary, it would cease to last. Neither does he need to forget the previous states: it suffices that by remembering these states it does not juxtapose them with the current state as a point to another point, but organizes them with itself, as it happens when we remember, melted together so to speak, the notes of a melody*" [p74/p100]. So *durée* is possible because our nervous system allows merging our most recent sensation in the ongoing one. Our *durée* is therefore limited by our short-term or working memory and perceptual system. On the one hand, we can't witness the opening of a flower and hardly notice it moving in the sky. On the other hand, we can't perceive the exact movements of the hummingbird's wings. To

illustrate the idea that we can perceive successive sensations in an intermixed or overlapping manner, Bergson takes the example of what happens if the length of a single note is changed in a musical motif. It is the different quality of the motif that will be noticed immediately, not the long note in its isolation. Similarly, the same note will be perceived differently if played in isolation or at the end of a crescendo. *"We can thus conceive of succession without distinction, and think of it as a mutual penetration, an interconnexion and organization of elements, each one of which represents the whole, and cannot be distinguished or isolated from it except by abstract thought. Such is the account of durée which would be given by a being who (...) had no idea of space"* [p75/p101]. Indeed, according to Bergson, we are so familiarized with the idea of space that we can't refrain from introducing it in our conscious perception: *"we set our states of consciousness side by side in such a way as to perceive them simultaneously, no longer in one another, but alongside one another; in a word, we project time into space, and succession thus takes the form of a continuous line or a chain, the parts of which are contiguous without penetrating one another"* [p75/p101]. This view is extremely different from the one of *durée*. To take another example, if someone plays in reverse order the first 8 notes of a well-known musical motif, no one will say: "oh sure this is the beginning of the Cello Suite of Beethoven in reverse". In other words, the qualitative experience of the reverse musical motif does not provide any clue about the quality of the original order. This quality results from the overlapping or merging of the past notes into the present ones. Moreover, each time we listen to this melody, our qualitative experience will be somehow distinct, up to the point that we can become bored by a tune we've listened to too many times. On the contrary, when the melody is discretized in separate notes, the reverse order can be recovered from the original one. But for such reversion to be possible, the song had to be spatialized into a sheet of music. Thus, for Bergson, when I experience a series of sensations or ideas, either I experience them in their *durée* in which their succession is indivisible because they truly penetrate each other, or I distinguish an order. But it is important to recognize that the latter is dependent on having an idea of space and the possibility of elevating oneself above time to embrace simultaneously the moments that composed the *durée*. The observation that the musicality of a short tune cannot be retrieved by playing that tune in reversed order illustrates the famous motto of Bergson: time (*durée*) is not space.

9.5. If *durée* cannot be measured, what do clocks measure?

Time seems to be something that can be regularly divided exactly like space (aren't clock dividing time), which makes Bergson's motto counterintuitive. It is critical here to remember that for Bergson, the time that is not space is the one that is qualitatively experienced. Bergson then asked what happens when we measure the passage of time with clocks. How do we achieve a quantitative assessment of a time interval while looking at them? Bergson remarks that when I look at the running secondhand of a clock, I believe that I measure the passage of time but I am primarily experiencing discrete simultaneities, or coincidences. My first look at the clock defines a simultaneity between the position of the secondhand at that moment and my conscious state. A distinct simultaneity occurs the second time I look at the clock at the end of the interval. My perception of what happened *between* these two events (during the interval) is the result of a mental synthesis which will be different if the secondhand moves in a saltatory or continuous manner or if I was in a hurry or about to fall asleep while watching the clock. The quantitative estimation of how much time elapsed will be necessarily derived from the distance traveled by the secondhand in the space of the clock's face at the end of the interval. The observation of the discrete positions of the running hand in the clock's face might give us the impression that our internal life can be divided into equal units. From there comes the erroneous idea of time being analog to space. But the only homogenous process was the repetitive movements of the running hands in the circular *space* of the clock. Two successive moments of our inner life are never the same, in line with the fact that we can fall asleep or become impatient while watching a clock.

9.6. Duration, movements and simultaneity

Bergson then applies his discovery of the *durée* to the perception of movements, "*the living symbol of this seemingly homogeneous duration*" [p82/p110]. "*It is most often said that a movement takes place in space, and when we declare the movement homogeneous and divisible, it is the space traveled that we think of, as if it could be confused with the movement itself. Now, on thinking more about it, we will see that the successive positions of the mobile do indeed occupy space, but that the operation by which it passes from one position to another, an operation which occupies time and which has reality only for a conscious spectator, escapes space.*" [p82/p110]. When science deals with the successive

positions of a moving object, it does so by systematically leaving a gap between them, a gap that can have an infinitesimally small size but that is irreducible. Indeed, "*when the astronomer predicts an eclipse, for example, he engages in precisely an operation of this kind: he infinitely reduces the intervals of duration, which do not count for science, and thus perceives in a very short time - a few seconds at most - a succession of simultaneities which would occupy several centuries for a consciousness obliged to live the intervals.*" [p87/p116]. Consequently, during the mathematically defined interval between two discrete positions of a moving object, the qualitative perception of duration and movements requires the mental syntheses of a flow of stimuli. Such a synthesized perception should be considered as an indivisible progress rather than a thing, otherwise, it loses its fundamentally dynamical nature (see Nicholson and Dupré, 2018 for an extension of the concept of progress to all aspects of the living). To summarize this part, Bergson makes (again) the distinction between two ways of experiencing movement. One can experience a movement as an indivisible unit. This is what happens when we see a shooting star or a pole vault athlete performing a successful jump at 6.15 meters. Like for the perception of music, the qualitative aspect of such movements only emerges from experiencing them dynamically as a whole but will be lost when the movement is transformed in cartesian coordinates to be experienced quantitatively. The qualitative experience of watching Armand Duplantis establishing the new world record at 6.18 meters is not captured by the height of his jump which is an external measurement useful to compare the performance of distinct athletes.

9.7. Two forms of multiplicity, two forms of the self

So far, Bergson has established a distinction between two kinds of multiplicity of conscious states in time: i) a qualitative version that is experienced when there is no intention to measure or count, and ii) a quantitative one in which sensations or cognitive states are separated and ordered/projected in space. The problem arises from the fact that we use the latter to speak of the former, which ends up confusing the two phenomena. Language fuels this confusion by using fixed labels to describe our dynamical internal state. The idea of *internal states permeating each other* is already treacherous because it implies the existence of distinct fixed internal states. Still, Bergson recognizes that both qualitative and quantitative multiplicities go hand-in-hand and his reflection does not aim at disqualifying the latter. When we are explicitly counting the successive strokes of a bell, which is

important for obvious practical reasons, we are in parallel touched by its musicality that develops in time. Each additional stroke changes the meaning and quality of the series. *"Hence it is through the quality of quantity that we form the idea of quantity without quality"* [p92/p123].

Bergson proposed that it is the alignment of the continuous and ever-changing stream of our internal states with the homogenous movements of external objects that causes our illusion of thinking that our experience of time is homogenous and divisible. Why does this alignment cause such an illusion? This is by looking more carefully at what happens when one observes an object moving regularly (e.g., a clock, the sun) that Bergson makes an important breakthrough: *"Here we certainly have a series of identical terms, since it is always the same moving body; but, on the other hand, the synthesis carried out by our consciousness between the actual position and what our memory recalls of the former positions, causes these images to permeate, complete, and, so to speak, continue one another. Hence, it is principally by the help of motion that duration assumes the form of a homogeneous medium, and that time is projected into space. But, even if we leave out motion, any repetition of a well-marked external phenomenon would suggest to consciousness a similar mode of representation"* [92/p124]. Thus, although our successive sensations are dissolved into one another, they retain the regularity of the movements of external objects that cause them. I hear a sound progressively louder and louder and this progression gives me a feeling of continuity in time. But what is homogenous here is the movements that cause the sound. *"And thus our superficial psychic life comes to be pictured without any great effort as set out in a homogeneous medium"* [p93/p125]. Bergson therefore concludes that we can divide our conscious life into two trends. In the first one, we are paying attention to the outside world and are impressed by the regularity and homogeneity of the changes that occur there. We feel that we endure time like these objects. In the second one, we can get absorbed in our feelings, actions, or thoughts that are intimately intertwined and ever-changing. *"But because this deeper self forms one and the same person with the superficial ego, the two seem to endure in the same way. (...) That our ordinary conception of duration depends on a gradual incursion of space [through the regular movements of objects] into the domain of pure consciousness is proved by the fact that, in order to deprive the ego of the faculty of perceiving a homogeneous time, it is*

enough to take away from it this outer circle of psychic states which it uses as a regulator" [p93/p125]. This exact situation happens when we dream, as in this state our interaction with the external world is extremely limited. In such a state, our qualitative sensations are not constrained by the regularity of the world and this can lead to wild variability (hence surprise) in our perception of time. Similar variations in our sense of time happen under the influence of drugs, in extraordinary life-threatening experiences, or even in pseudo-experimental conditions in which a subject is deprived of external cues that classically mark the passage of time (prolonged stay in a cave). It is therefore essential to distinguish two types of duration. One that is qualitative and fundamentally internal, the other that is quantitative and fundamentally external.

Importantly, the dichotomy between these quantitative and qualitative views of our internal/mental life that develop as time passes by does not exclude that they can inform each other. Bergson illustrates this point using for the last time the image of the bell's strokes. *"As I write these lines, the hour strikes at a nearby clock; but my distracted ear only notices it when several blows have already been heard; I therefore did not count them. And yet, it only takes an effort of retrospective attention to sum up the four knocks already struck, and add them to those I hear. If, returning to myself, I then carefully wonder about what has just happened, I realize that the first four sounds had struck my ear and even moved my consciousness, but that the sensations produced by each of them, instead of being juxtaposed, had merged into each other so as to endow the whole with an aspect of its own, so as to make it a sort of musical phrase. To retrospectively evaluate the number of blows struck, I tried to reconstruct this sentence by thought; my imagination struck once, then two, then three, and as long as it did not arrive at the exact number four, the sensibility, consulted, replied that the total effect differed qualitatively. She had therefore observed in her own way the succession of the four strokes struck, but quite differently than by an addition, and without bringing into play the image of a juxtaposition of distinct terms. In short, the number of strokes struck was perceived as a quality, and not as a quantity; duration thus presents itself to immediate consciousness, and it retains this form as long as it does not give way to a symbolic representation, drawn from extension."* [p94/p127].

Bergson's analysis yields therefore to a dualistic view of our mental life which is separated into two trends: a superficial one that he called homogeneous duration with well-defined

and impersonal mental states and that serves as a symbolic representation of a deeper heterogeneous conscious flow or pure *durée*, in which the succession of states implies fusion and organization. While Bergson only briefly touched upon the question of the interaction of these two views of our mental life (one external and quantitative, the other internal and qualitative; see the previous quote), he warned us that his point is not to duplicate the subject. " *It is the same self which sees distinct states, and which, then fixing its attention more, will see these states melt together like snow needles in prolonged contact with the hand.*" He introduces here his method of the *intuition* that he will develop later (Bergson 1934). Our social life requires us to consider primarily our mental life as distinct well-separated states and an effort is required to get the intuition of its deeper nature, free from the practical and efficient symbols derived from the outside material world and that our intelligence is naturally prompt to grasp. It is in his next book (Matter and Memory, Essay on the relation of the body to the mind; Bergson, 1896) that Bergson will attempt to overcome the difficulties associated with this dichotomy between internal spiritual life and external material world, by considering the body as a point of junction between matter and mind allowing life to strive in a fundamentally temporal world.