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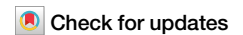
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Towards a neurodevelopmental cognitive perspective of temporal processing

Giulia Buzi¹, Francis Eustache¹, Sylvie Droit-Volet², Pierre Desautay^{1,3} & Thomas Hinault¹ ✉

The ability to organize and memorize the unfolding of events over time is a fundamental feature of cognition, which develops concurrently with the maturation of the brain. Nonetheless, how temporal processing evolves across the lifetime as well as the links with the underlying neural substrates remains unclear. Here, we intend to retrace the main developmental stages of brain structure, function, and cognition linked to the emergence of timing abilities. This neurodevelopmental perspective aims to untangle the puzzling trajectory of temporal processing aspects across the lifetime, paving the way to novel neuropsychological assessments and cognitive rehabilitation strategies.

The ability to keep track of events unfolding over time is a fundamental and instinctive feature of humans and animals' perception and cognition, essential for adaptation to complex and challenging environments¹. Indeed, predicting the events to come, interacting with others, crossing the road, remembering a planned appointment, or catching the train on time are all activity of everyday life supported by temporal processing, without which, autonomous behaviors would not be possible. Temporal processing encloses a wide range of timescales (i.e., from milliseconds to decades), across multiple sensory modalities. Nevertheless, the temporal experience could be considered as formed from four main dimensions: temporal order and simultaneity, the processing of durations, the feeling of the passage of time and mental time travel². These dimensions are usually investigated in laboratory using various temporal tasks and questionnaires (detailed in Box 1). They call on partially shared brain underpinnings and have close links with most cognitive processes^{3,4}. Nevertheless, the debate upon which neural mechanisms underlies the processing of time is still open (Box 2).

Evidence agrees that temporal sensitivity⁵⁻⁷ and semantic temporal concepts develop until adulthood^{8,9} and then become more variable and less precise with advancing age¹⁰. Yet, there is no consensus about which biological and psychological processes evolve and support this development. While some data suggest changes of the speed of the internal clock¹¹⁻¹⁴, others show that the evolution of timing abilities, duration processing in particular, would be supported by the development of working memory¹⁵⁻¹⁹, executive functioning²⁰⁻²³ and attention²⁴⁻²⁶. However, the involvement of cognitive processes depends on the temporal tasks used and whether they are more or less cognitively demanding^{27,28}. In addition, although several compelling works reviewing evidence of temporal abilities in new-borns²⁹, infants³⁰, children^{6,7,9,31}, and older adults^{10,32,33} exist, a unified trajectory addressing the development of the underpinnings of the ability to perceive and organize the time from the intra-uterine life to older age is lacking.

The present neurodevelopmental perspective claims that our ability to perceive and prospectively process durations and time passing emerge thanks to the interaction between various endogenous (e.g., brain maturation) and exogenous factors that we are exposed to, depending on the different stages of life. According to this perspective, the temporal processing, among other factors⁷, evolves and refines itself step by step at each life stage, as a function of the gradual shaping of the structural and functional architecture of the brain (Fig. 1). This approach could help to specify the maturation of the regions associated to temporal processing (Box 2) throughout lifetime while highlighting its evolutionary contribution. What is more, retracing the stages of a physiological course of timing abilities will add important bricks in the building of a neurodevelopmental model of human time processing, which will be proposed in the end part of the review (Fig. 2).

Far to conduct an exhaustive review of the entire cerebral and cognitive development, we will provide an overview of the emergence of the ability to perceive and process time, in parallel to the development of the brain structural and functional milestones considered to support prospective judgments in explicit temporal processing tasks. Furthermore, we will also focus on the rise of the cognitive functions most related to these temporal skills. For each life stage, we will highlight the adaptive advantages provided by the temporal dimension which unfolds. Lastly, we will show that deviations from the healthy neurodevelopmental trajectory could result in an impaired ability to keep trace of time (Boxes 3 and 4).

The intrauterine life (15 Post Conceptional Weeks (PCW) – 0 years old)

Starting from the second trimester, the formation of neural tube (*neurulation*) as well as the generation of neurons (*neurogenesis*) are for the most part completed. Since the 15th Post Conceptional Week (PCW), the brain

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Box 1 | Different measures for different temporal aspects

A wide array of tasks and questionnaires assessing different aspects of the subjective experience of time passing have been accumulated over the last 50 years. Overall, it could be measured in laboratory settings through **retrospective** (in which the participant is unaware that a temporal estimation must be made) or **prospective** paradigms (in which the participant knows that a temporal estimation is required)^{299,300}. These two types of paradigms are respectively implemented in **implicit** (in which a temporal estimation is made, but the participant does not track the time unintentionally) or **explicit** timing tasks (in which the participant is consciously involved in the temporal estimation)²⁸. However, a precise taxonomy of these paradigms is lacking. We will provide here some examples of the most used ones (for an extensive review, see)³⁰¹.

Order and simultaneity could be assessed through (A) Sensorimotor Synchronization Tasks (SMS) to measure the coordination of physical actions in time with a rhythmic sequence²⁷² in which participants are asked to tap in synchrony with an external rhythm (i.e., an isochronous metronome) or with an internal periodic rhythm marking the beat of a specific sequence³⁰² and/or by (B) Simultaneity Judgment Tasks, through the Stimulus Onset Asynchrony (SOA) at which two consecutive stimuli are subjectively perceived as simultaneous³⁰³.

Durations Processing concerns the production, reproduction, and comparison of intervals between two stimuli or of the duration of a stimulus on the range of hundreds of milliseconds to several tens of

seconds - also known as *Interval Timing*^{304,305}. Few studies have examined duration judgment over several minutes.

Temporal production tasks consist in marking the beginning and the end of a specific interval and temporal reproduction tasks in pushing a button for the duration judged to correspond to the target interval³⁰⁶. The tasks based on comparison judgments are for example: temporal generalization and temporal bisection. In temporal generalization tasks, participants are required to establish whether the probe stimuli are equal or not to a standard reference that was initially presented; Temporal bisection tasks (^{307,308}) involve the training to recognize a short and a long duration standard interval. Then, participants are asked to judge if the probe duration is more like the short or the long standard duration.

The **Passage of Time Judgments (POTJ)**³⁰⁹ are based on the subjective feeling of the speed of time passing, and spans on short (present POTJ) and longer timescales (from minutes and hours to days and months; retrospective POTJ). An overview of the felt passage of time could be obtained by Visual Analog Scales (VAS) and questionnaires (i.e., Metacognitive Questionnaire on Time (MQT) by Lamotte and colleagues, 2014.

Mental Time Travel is the ability to mentally reexperience past events (episodic autobiographical memory) and to imagine the future ones (episodic future thinking) of the order of weeks, months, and years¹⁸⁴ and it is often assessed by autobiographical interviews (i.e., Autobiographical Recollection Test³¹⁰).

Box 2 | Neural Bases of temporal processing: a ground of debate

The processing of temporal information in the brain elicits a core of regions which vary according to the task paradigm, the duration intervals, and the sensory modality³¹¹.

Overall, fMRI studies probing the perception of rhythms found activity in the supplementary (**SMA**) and pre-supplementary motor area (**pre-SMA**), **cerebellum**^{312,313} and **basal ganglia**, bilaterally³¹⁴. Also, the processing of both short (<500 ms) and longer durations (>1500 ms), has been, in addition, associated to the activity in the **insula**, the **precentral** and **cingulate gyri** and **superior temporal gyrus**³¹⁵⁻³¹⁸. The **inferior frontal gyrus (IFG)**¹⁴⁴ and the **dorso-lateral prefrontal cortex**^{319,320} were also seen to be active during short duration tasks. Conversely, the passage of time and the mental time travel, are observed to be linked to the activity higher-order **parietal medial temporal cortices**^{321,322}, the **hippocampal formation** and the **amygdala**³²³.

Although neuroimaging evidence provide crucial insights on cerebral activations patterns associated to temporal processing, the neural timekeeping mechanisms remain mostly unknown. After the very first information processing models based on pace-maker accumulators of pulses in the brain (namely, *Scalar Expectancy Theory*^{11,12}), connectionist models based on multiple oscillators processing several durations from a

few seconds to several minutes^{324,325} started to be conceived³²⁶. Altogether, this evidence led to the conception of the *Striatal Beat Frequency Model*¹⁶⁷ where the striatal spiny neurons would serve as a coincidence detector of the phase synchronization of the cortical oscillatory neurons which are triggered by a dopaminergic discharge from the substantia nigra, at the onset of a temporal stimulus to be estimated¹⁶⁶. Other intrinsic and distributed models instead, claim that time, being an intrinsic property of neural networks, would be encoded by the instantaneous changing of its state, resulting in real-time trajectories of the networks embodying durations (namely, *State Dependent Networks*^{327,328}).

Nevertheless, none of the above-mentioned models could explain the processing of durations longer than a few minutes (but see ref. 329 for a tentative to extend to minute range the internal clock model) making a unified model of several aspects of temporal processing still hard to imagine. Furthermore, these models lack a neurodevelopmental perspective, leaving modeling of temporal perception incomplete, mostly focused on brain functioning in healthy young individuals rather than conceiving a neuroanatomic circuitry that develops as brain mechanisms development progresses too.

structure starts to assume its human-specific configuration, with the ganglio-thalamic formation connecting the telencephalic proliferative zone to the major thalamic regions³⁴⁻³⁶. The formation of the thalamus-based relay of information from the 24th PCW has a pivotal role in the setting up of cortical networks, as it allows to sensory inputs to reach the developing cortex³⁷, laying the groundwork for the formation of sensorimotor, visual, and auditory circuits. Since the womb life, fetuses are exposed to several internal biological rhythms, originated by the mother's cardio-vascular system, breathing, walking, but also some stimuli of the external environment as sounds or the mother's voice.

The setting up of the cortico-striatal pathways at this stage, as a result of the increased fractional anisotropy (FA) of the basal ganglia^{38,39}, would set the ground for the emergence of an elementary form of sensorimotor synchronization. Near term fetuses indeed are able to perceive rhythmic sequences like maternal rhythmic movements, walking, rocking, or breathing and to coordinate with them accordingly. Evidence from studies using Heart Rate (HR) demonstrated that fetuses changed their own HR depending on the mother's rhythmic movements⁴⁰, and differentiated their breathing pace in response to rhythmical rocking or sinusoidal oscillations²⁹. Also, fetuses react to auditory stimuli, such as variation in music and speech, with a prevalence of

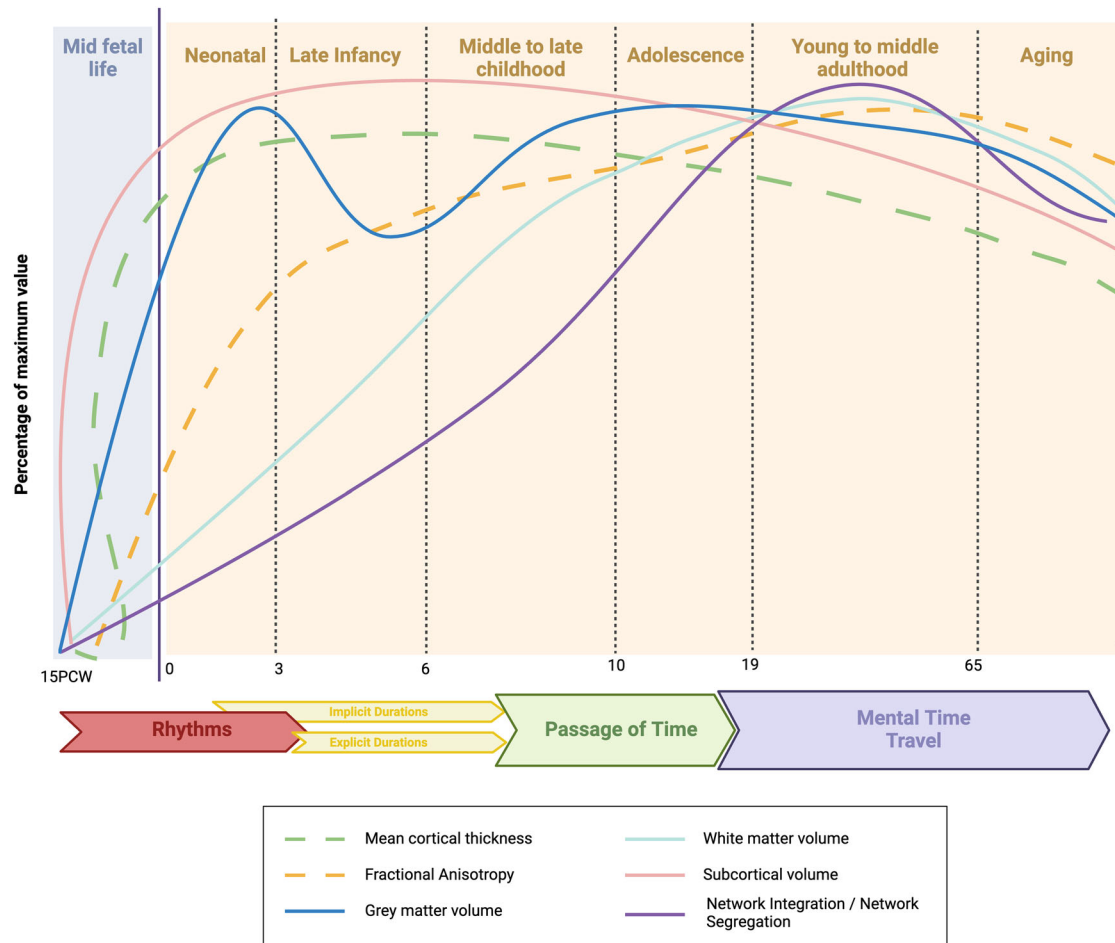


Fig. 1 | Lifetime lines. Life-span trajectories of structural and functional development of the human brain paralleling the emergence of each of the four aspects of temporal processing. Created with Biorender.com.

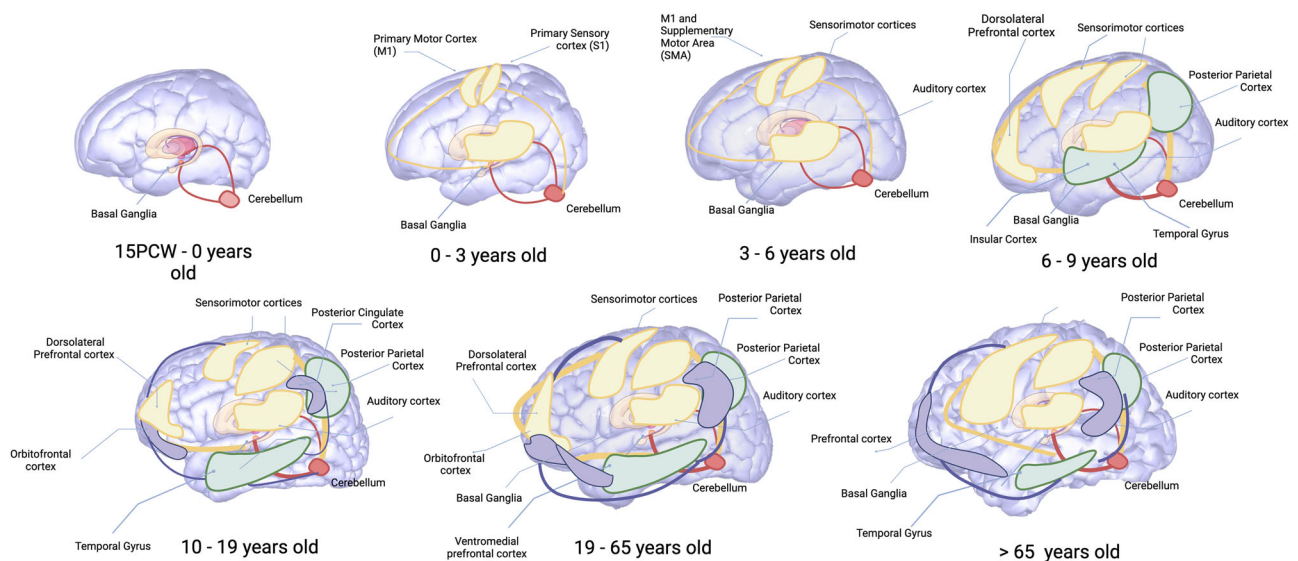


Fig. 2 | The neuroanatomical development of the temporal processing circuit. The proposed additive maturation model of RDPM, according to the functional specialization of the temporal processing circuit, for each of his aspect. Red: Rhythms; Yellow: Durations; Green: Passage of Time; Purple: Mental Time Travel.

Created with Biorender.com. Brain templates have been reconstructed with Brainstorm software by Tadel et al. (2011)²⁹⁴ leveraging on Li et al. (2015)²⁹⁵; Shi et al. (2011)²⁹⁶; Fonov et al. (2009)²⁹⁷; Dong et al. (2020)²⁹⁸.

Box 3 | Deviations from the neurotypical development

The evidence that temporal processing is an emerging function of the brain, is reflected by the presence of abnormal temporal performances in neurodevelopmental disorders. Among the different neurodevelopmental conditions, we can present as examples the **autism spectrum disorder (ASD)**, **dyslexia**, and the **Attention Deficit/Hyperactivity Disorder (ADHD)**.

Interestingly, the first hallmarks of the **ASD**, are represented by avoiding eye contact, a lack of joint attention and shared gaze with others³³⁰, with an absence of facial expressions between 3 and 9 months³³¹. Among others, an interrupted flow of the dyadic interaction with the caregiver³³² has been associated with deficits in order and rhythmicity processing³³³ which could involve the lack of synchronization between brain regions in processing multisensory stimuli^{334,335}. In this framework, the difficulty in temporally coordinating their own actions and intentions with the other, could affect their feeling of interrelatedness later in adult life, making ASD a proper social timing deficit^{336,337}. Distortions in duration processing have also been observed in high functioning ASD children which showed a shift toward more long responses to a temporal bisection task and gradual less precision in estimating durations longer than 5s³³⁸⁻³⁴⁰ implicating working memory and attention deficits (for a review³⁴¹). Nevertheless, children with ASD reached similar performances to a temporal bisection task with a similar duration range compared to typically developing children when controlling for intelligence scores³⁴².

Also, the impaired Theory Of Mind (ToM) and language skills likely explaining the lack of temporal knowledge³⁴³ could partly determine the deficits of mental time travel (MTT)³⁴⁴.

Time processing disruptions have also demonstrated to be the earliest and specific signs of **ADHD**^{345,346}, which occurs later in infancy. Children with ADHD indeed show overall higher thresholds in duration discrimination tasks on seconds to milliseconds range and tend to overestimate durations³⁴⁷ also resulting in less accuracy and more variability in temporal production and reproduction³⁴⁸. Functional neuroimaging studies reported deactivations in most regions of the fronto-striato-cerebellar and frontal-parietal networks supporting timing functions, therefore explaining alterations of temporal performances. What is more, ADHD treatments based on Methylphenidate - a dopamine agonist and psychostimulant - resulted to mitigate timing dysfunctions³⁴⁹.

Abnormal temporal estimations have also been reported in **dyslexia**: children with specific troubles in reading and learning indeed demonstrated to segregate spatiotemporal perceptual units of information at a slower rate than the control group³⁵⁰, likely due to an inefficient phase-locking at one or more temporal rates in processing speech stream³⁵¹, (but see ref. 352 for a review). Nevertheless, a greater variability of performances in children with dyslexia could even be observed both in explicit and implicit temporal bisection task with non-speech stimuli³⁵³.

Box 4 | Deviations from healthy aging

Neuropathological aging is marked by degeneration processes of the large-scale brain networks and the underlying structure affecting cognition, behavior, and motion. Among these symptoms, alterations of the subjective experience of time have been observed in several neurodegenerative syndromes (for a review^{354,355}).

Although no difference has been reported on implicit duration processing between patients at the prodromal stage of **Alzheimer's Disease (Mild Cognitive Impairment)** and healthy older adults³⁵⁶, several disruptions have been reported in the ability to mentally travel in the past and in the future, with less vividness of details reported³⁵⁷. The MTT impairments toward past events could reflect the initial episodic memory degeneration of the middle temporal lobe, hippocampi, and entorhinal cortices. As the neurodegenerative process unfolds, extending to parietal and then prefrontal areas, deficits in - mostly explicit - duration processing tasks became more evident, as they demonstrate higher error rates and less accuracy³⁵⁸. Increased variability in temporal bisection tasks (i.e., milliseconds)³⁵⁹ and decreased precision in duration estimation^{360,361}, temporal production tasks spanning from seconds to few minutes³⁶² have also extensively been observed in AD patients³⁶³.

Patients affected by **Frontotemporal Dementia (FTD)**, and its behavioral variant (**bvFTD**), may show impairments in both self-paced than externally paced tapping³⁶⁴, under-productions and over-

estimations of duration intervals³⁶⁵. In **semantic dementia (SD)**, the progressive deficit affecting primarily comprehension of words and then the related semantic processing³⁶⁶ disruptions of the ability to imagine future events, have been frequently reported, albeit they show a relative preservation of recent memories³⁵⁷. The loss of words serving as temporal connectors characterizing these patients, would have broken the links connecting temporal events.

More findings come from **Parkinson's Disease (PD)**, as its principal neuropathological hallmark affects the nigrostriatal and meso-cortical dopaminergic pathways, notably deemed to be involved in rhythm³⁶⁷ and interval timing³⁴⁹. PD patients indeed struggle to processing beat based rhythms³⁶⁸ and a lower temporal sensitivity and temporal under estimations³⁶⁹ for long temporal intervals (1–5 s)³⁷⁰, in explicit temporal tasks^{371,372}.

Since clear clinical hallmarks of alterations of timing abilities are far to be established, due to differences in task design, paradigms implemented and inter-individual variability, a deeper understanding of neural mechanisms underlying temporal dysfunctions in neurodegenerative disease is necessary to help clinicians to make early diagnosis and develop new treatments, therefore ameliorating the quality of life of patients.

left temporal activation⁴¹. Studies have shown that fetuses preferentially react to the sound of mother's heartbeat⁴² and voice^{43,44}. Therefore, fetuses are already able to memorize and recognize the temporal harmonic structure of the prosody of the mother's speech⁴⁵.

Fetuses also produce rhythmic activities (kicking, sucking). Although they are fairly stereotyped and inflexible, some changes in rhythm production in response to the exogenous factors during fetal life have been noted by studies on finger sucking, which are observable by the 15th PCW

and rhythmic mouth movements, from the 20th PCW²⁹. The ability to adapt their own rhythm to an external one is crucial for the newborn to comprehend the temporal organization of interpersonal interactions, setting the stage for speech and communication^{46,47}. Furthermore, biobehavioral synchrony plays a crucial role in mother-infant attachments, providing a constant safety link, and contributing to the development of the sense of self and relatedness⁴⁸. The prenatal temporal competencies are therefore orchestrated by spatiotemporal synchronization, and appear in the abilities

of fetuses to perceive, predict, and adjust behavior to external rhythmic structures.

Infancy (0-3 years old) – kindergarten years

The exponential formation of new synapses occurring at birth is followed by an extended period of *synaptic pruning*⁴⁹. The myelination in the basal ganglia (caudate, putamen, globus pallidus) is paralleled with a rapid gray matter thickening^{50,51} in primary sensory and motor cortices. On the other hand, the *proliferation* and widespread *migration* of the new, mostly inhibitory, interneurons, to the cingulate cortex and superior frontal gyrus (SFG) are responsible of the gray matter growth in frontal areas⁵² occurring at around two years old⁵³. Resting state functional connectivity studies showed that the primary sensorimotor and auditory networks are already formed at the time of birth^{54,55}. Conversely, the connectivity of the visual network steeply increases during the next three months while fronto-parietal attentional (FPN) and default mode network (DMN) regions mature later⁵⁶.

Neurophysiological footprints of speech perception are detectable as early as the 4th day of life, as shown by a greater activity of left auditory association cortices to dichotically presented syllables^{57,58}. This increased left-ward activation has been demonstrated to be responsible of fast rhythms processing⁵⁹, characterizing the phonemic rate of the speech^{60–62}. Duration processing abilities have also been observed in the first months of life. As early as 4 months old, **Provasi and colleagues (2011)**⁶³ observed that babies exhibited an adult-like psychophysical response to an adapted temporal bisection task, during which they were trained to look to the left after the long standard (1500 ms) and to right after the short standard duration (500 ms). The proportion of long responses, measured as the duration of the gaze, increased with the target duration, already demonstrating a relative sensitivity to time.

Successful duration discrimination to an auditory oddball-timing of milliseconds to seconds range intervals that differed by 1:2 ratio between the inter-stimulus interval standard (1500 ms) and the deviant stimuli (i.e., 370, 500, 750, 1000 ms) was observed in six months old babies⁶⁴. Precision in interval discrimination to milliseconds to seconds range has also been demonstrated to increase from six to ten months, as shown by the larger amplitude of the Mismatch Negativity (MMN) and the increased ratio between the standard and the deviant interval⁶⁵. Also, precursors of the P1–N1–P2–N2 complex sensitive to differences in tone durations have been observed in the left temporal and the premotor cortices in six to eight months old infants⁶⁶.

Later, cortical thickness increases rapidly in superior temporal gyrus, parietal, and pre-motor cortices, and in the insula⁶⁷. This cortical expansion, the refinement of primary sensory networks, together with the increased FA of commissural fibers could set the stage for temporal production, temporal comparison, and temporal discrimination abilities on short duration range (i.e., up to two seconds) across multiple perceptual modalities^{68,69}.

The intrinsic connectivity reported by fMRI studies between regions of the dorsal attention, the salience, executive control network, in nine to twelve months old babies⁷⁰, likely supports the development of cognitive abilities such as attention⁷¹ and visual-spatial skills⁷². This may explain the higher sensitivity to duration in the auditory modality than in the visual modality^{19,73,74}.

For methodological reasons there are few studies on children aged between one and three years old concerning both the perception and production of duration and rhythm. The most basic motor actions following a rhythmical pattern such as pace tapping, stepping, and dancing are also followed by more complex activities like singing or playing music. As it will be mentioned in the following section, there is still an improvement of these abilities between three and six years based on the development of motor skills and motor inhibition. The ability to detect temporal regularities of prosodic cues help to grasp acoustic statistical dependencies between words^{75,76} fundamental for language acquisition⁷⁷.

Late Infancy (3–6 years old) – Pre-school years

During early childhood, the myelination of the cortico-cortical association tracts is coupled with cortical thickness decreases within medial and polar occipital regions, and to a greater extent in prefrontal and parietal cortex⁷⁸. In parallel, VBM studies conducted in toddlers showed gray matter volume increases of some prefrontal and cerebellar regions, which decreases consistently in volume thereafter^{79,80}. From a functional perspective, hubs of the DMN are already present but in an immature form⁸¹, failing to synchronize into a coherent network⁸². Yet, a significant coupling of dorsal mediofrontal cortex and posterior regions was observed as early as age four at rest⁸³. Also, throughout early childhood, the bilateral precentral gyrus is pivotal for functional network development, showing the major nodal efficiency increase in the development of structural networks⁸⁴. The increasing network organization emerging by this stage, could explain the differences in temporal perception between sensory modalities. The learning of new durations at this stage is better in motor learning (imitation, motor synchronization) than in perceptual learning condition^{85–87}. The three-year-old can remember a specific duration associated with an action six months after it was learned⁸⁷, and already have a good knowledge of the duration of familiar activities⁸⁸. This leads authors to state that at this age time is still linked to the experience (“experienced time”⁸⁵) and to the events (“event time”⁸⁹), and not yet an abstract concept enabling them to voluntarily focus their attention on the time flow. This could also result in an improvement of time estimations from three years of age onward, especially in the temporal generalization tasks that require a comparison between a current duration and a standard duration stored in memory^{6,89–91} (Box 1).

A primary configuration of the core hubs of the DMN, notably medial prefrontal and medial temporal cortices^{92–95}, together with the lengthening of coherence in an anterior-posterior gradient between four and six years, could support the improvement of interval timing of five⁸⁹ up to eight seconds⁹⁰ observed from three to five years old. On the other hand, the incomplete maturation of parietal association cortices and the still-to-be defined boundaries between resting state and task-positive networks, result in limited working memory and attentional abilities, likely linked to the more variable temporal estimates compared to late childhood^{7,18,27,96,97}. This would account for their more variable, fuzzier internal representation of time in memory^{90,98,99}, and their greater time distortion in dual-task and attention distraction paradigms^{25,100}.

During infancy, children are fascinated by the world around them, starting to integrate different aspects of the reality¹⁰¹. However, the cross-modal comparison of speed and time is still difficult to afford. The passage of time feeling thus remains extremely context-dependent, with, for example, the feeling that time passes faster with the increase in the feeling of happiness or when the durations lengthen¹⁰² and with ore events meaning more time elapsed¹⁰³. Indeed, Stojić et al., (2023)¹⁰⁴ observed that pre-kindergarteners retrospectively judged one minute of an eventful video lasting longer than an uneventful one of the same length. What is more, when asked to place the silhouettes of three human shapes along a horizontal timeline, three-year-old infants placed the larger silhouettes in the future, while the smaller figures were placed long ago in the past¹⁰⁵, reflecting a magnitude effect^{106,107}.

Language development, notably since entering kindergarten, also helps establishing connections between objects and events¹⁰⁸, allowing children aged five years old to be able to locate events in the past or in the future^{9,109}. Furthermore, the acquisition of duration words in the development, make four years old children able to comprehend a difference in magnitude between seconds, minutes, hours, weeks, months, and years, even without any knowledge about the precise duration corresponding to these words¹¹⁰. Learning of duration words allowing to denote different moments of the day indeed would make children at this stage already able to understand and to actively be part of their daily routine.

The development of the ability to infer other people’s internal states (Theory of Mind)^{111–113} would enable four years old toddlers to better embody other’s time observed in various situations, thus improving their temporal sensitivity in social contexts¹¹⁴, but also to interact and cooperate with others. From an embodied cognition perspective^{115,116}, the subjective

experience of time is *grounded* to our own mental, emotional, and motor states^{117–119}. As an example, from the age of three, children show distortions of time when an angry face is presented^{120–122}.

Furthermore, the specialization of the motor pathways, led children to further improve their motor rhythm (e.g., dance, walk and run smoothly). Despite the varying results across studies, the overall of results is that the spontaneous motor tempo is faster (at about 300–400 ms)¹²³ and especially more variable at this age^{124,125}. Also, the ability to synchronize movements to external rhythms (e.g., group dance, singing)^{126,127} is reflected by a better control in slowing down their pace and a greater tapping regularity from eight years old⁸⁶. The perception of rhythms and short intervals is fundamental for children at this stage for the beginning of sport activities, as they involve waiting, movements coordination and manipulating moving objects. (e.g., football, baseball, or tennis). Furthermore, time discrimination and number processing is proved to underpin advanced numerical and temporal concepts, as well as aspects of higher order cognition¹²⁸.

Middle and Late Childhood (6–10 years old) – school years

From a morphological point of view, cortical gray matter volume increase until ten years old, and it is then followed by a linear cortical thinning increasing with age, primarily in parieto-temporal areas¹²⁹ likely reflecting the *synaptic pruning*¹³⁰. At the same time, frontal gray matter was observed to grow with increasing age¹³¹. These changes are mirrored at a micro-structural level, both by global and regional white matter volume expansion^{132,133}, and increased myelination rate. This augmented speed in axonal conductivity supports an improved information transmission between structurally connected and jointly activated regions, resulting in an enhanced communication between functional networks^{71,134}. At a functional level, EEG studies in healthy five to eight years old children showed that RSNs, such as the DMN, dorso-attentional, cingulo-opercular, ventral and FPN are well formed, but still show an indistinct pattern of activity compared to adolescents¹³⁵. In late childhood (that is, from six years old to the onset of puberty), the network topology of the brain is reshaped to be more efficient and stronger, with an increase in both local and global efficiency with a specific decrease of connections between adjacent regions (segregation)¹³⁶. Indeed, although still not completely efficient, there is an improved working memory¹³⁷, executive control of attention^{138–140} and processing speed¹⁴¹.

The increasing myelination of frontal areas and the white matter volume increase in left precentral gyrus and in left insular cortex¹⁴² seen around the age of ten¹⁴³ and the increasing activation with age of the fronto-striatal and fronto-parietal areas could be pivotal for the improvement of interval timing at this stage¹⁴⁴, as a sharp enhanced precision in temporal generalization was reported in eight years old compared to three- and five-years old children⁹⁰. Improved duration processing abilities were associated to an increased capacity of storage of a reference duration and the comparisons with the probe stimuli^{18,21,27,97}. Moreover, a better duration processing was associated to increased capacities to direct attention to temporal information and to maintain it throughout the entire duration¹⁴⁵. The development of these cognitive capacities allows children to better detect the precise start and end of the duration, to better follow and retain the time flow in working memory and to better update it^{25,100,146}. All this, results in better time encoding with less noisy memory representation of time⁹⁸. Enhanced inhibitory abilities with development also results in lower impulsivity and fewer tendency to press too early in temporal reproduction task and to endure the temporal wait¹⁴⁷. Despite a clear improvement compared to toddlers, it is only by nine years of age that children achieve adult-like performances in supra-second duration estimations¹⁴⁸. Although time sensitivity is close to the adults' one¹⁸ at 8 to 10 years old with short (<1 s) and longer intervals (>8 s), for example, does not mean that there is no improvement from this stage onward. Also, some age differences are still observable between 8-years old children and adults in bisection tasks when a smaller ratio (5:6) is used between two anchor durations (<1 s and >3 s)⁹⁷, with a higher variability of performances in time discrimination⁶. This lower

sensitivity has been related to lower selective attentional capacities, or slower processing speed rather than decisional processes, with age being the best predictor of variance of the Weber Ratio in short than long anchor durations. Differences are still evident in temporal generalization paradigms involving short-term memory as suggested by the flattening of the generalization gradient in younger children after the introduction of a retention delay (500 ms, 5 s, 10 s), which was not observed in their adult counterpart¹⁴⁹.

These dynamic maturational changes on the structural and functional substrates of temporal processing, concurrently with the wide variety of stimuli and instructions with which the child benefit from during the first school's years, would boost the development of fluid cognitive skills and expand the vocabulary^{150,151}. Around nine years old indeed, the acquisition of the concept of time allows the child to think about it in several contexts¹⁵² and to begin to appropriately use the spatial metaphors of time^{9,153,154} (e.g., to say that the shorter the duration, the faster time passes)¹⁰². One can also use time counting strategies to ensure its accurate measurement¹⁵⁵ or being to reason about the complex relationship between time, space, and speed¹⁵⁶.

In addition, the higher precision in timing abilities reached at this stage is not only crucial for mastering many gross and fine motor skills, but also for estimating the time elapsed since the last event, and the time ahead until the next event. The development of a temporal organization of the events is pivotal to establish connections between past, present and future, therefore structuring our temporal reasoning and logic links, for instance, the concept that physical causes precede effects⁸. Moreover, the acquisition of calendar's landmarks, which requires a good representation of the sequence of months over the whole year and a constant update in memory¹⁵⁷ contribute to orientate in time and to project themselves into the future, therefore helping the construction of a coherent narration of the self¹⁵⁸.

Adolescence (10–19 years old) – high school - college

Adolescent's brain structure shows higher white matter and lower gray matter volume in the frontal and parietal cortices compared to younger children (i.e., nine years old)¹⁵⁹. In prefrontal and parietal cortices, gray matter volume peaks around at age 12¹⁶⁰ whereas the one of the temporal lobes continue to expand until 17 years old¹⁶¹. Of note, a steep acceleration in gray matter loss and a considerable white matter increase have been observed in the dorsal prefrontal and orbitofrontal cortex, back over to the posterior parietal regions¹⁶². In parallel, the increase of myelination¹⁶³ is considered to support the improvement of speed of processing documented throughout adolescence¹⁶⁴.

At a functional level, the systems projecting from basal ganglia show increased participation of the striatum and precuneus¹⁶⁵. Notably, the dorsal striatum, as a part of the thalamo-cortico-striatal circuit deemed to be central in timing^{166,167} (Box 3) reaches its mature functional connectivity¹⁶⁸, starting to establish long-range connections between pre-frontal and the posterior cingulate gyrus, which continue to develop during adulthood^{169,170}. In addition, increasing segregation between control networks, such as the CON, FPN and DMN, has been observed to increase in early adolescence (i.e., 13 years old)^{171–173}. The strengthening of communications between basal ganglia and prefrontal cortices may contribute to the improvement of working memory, response inhibition and attentional set shifting^{174,175}, therefore improving cognitive control processes¹⁷⁶. Although many of the executive control networks are still in place, the very limited number of studies linking interval timing and brain functional connectivity in adolescence does not allow us to discern which of the executive control processes would benefit the most to temporal precision.

These maturational changes in gray matter within the frontal, parietal¹⁷⁷, and striatal¹⁵⁹ cortex could support a refinement of the ability to discriminate intervals ranging from 400 to 1100 ms and reproduce durations lasting from two¹⁷⁸ to eight seconds⁵. Indeed, progressive age-related increases in activation in left dorsolateral/inferior prefrontal cortex, and in right hemispheric striato-thalamic and superior parietal regions during the duration discrimination of 500-to-300 ms of difference from a 1000 ms reference interval was observed from 8- to 14-years old children¹⁷⁹. Also, by

using a temporal bisection task, **Li and colleagues (2021)**¹⁸⁰ distinguished two developmental stages (7–11 and 12–17 years old), suggesting a steady improvement in time sensitivity from the childhood.

However, there is a gap in studies on time perception between nine years and adolescence, probably because duration discrimination abilities at that stage are already close to those of adults¹⁴⁸, although differences remain in certain difficult temporal tasks such as the complex kinetic time judgment tasks, fundamental for motor imagery ability¹⁸¹.

Findings of passage of time in adolescent are scarce too^{31,182}, and further longitudinal studies are needed to outline a neurodevelopmental trajectory of this temporal aspect. Awareness of time and its passage, awareness of being subject to time distortions, self-construction, and uncertainty about the future¹⁸³ should also impact time judgments and the imagination of future scenarios (i.e., mental time travel)^{184–186}. Indeed, the imbalance between the development of limbic structures involved in reward and the still immature prefrontal cortical top-down control system¹⁸⁷ would lead adolescents to assume more risky behaviors¹⁸⁸, therefore underestimating future consequences. On the other hand, the maturation of long-range connections between posterior and anterior parts of the DMN^{176,189} supports, among other functions¹⁹⁰ the ability of “mind-wandering”^{191,192}. The ability to decouple from the present, allows to mentally travel in time, which involves the integration of multiple timescales¹⁹³. Hence, the mental time travel could be pivotal in this period for the exploration of several identities in order to develop a coherent sense of self.

The adolescence could be considered as a sensitive period during which endogenous (i.e., the brain development) and exogenous factors interact dynamically. Indeed, alcohol and drugs abuse, the exposure to negative life experiences, substance abuse and/or low parental education, increase the vulnerability from adolescents aged 11 to 16 years old onward, to unfold neuropsychiatric conditions, like mood^{194,195}, personality and/or psychotic disorders^{143,196} which are known to alter the subjective experience of time (for a review²).

Adulthood (19–60 years old)

The maturation during adult age is characterized by a significant acceleration of frontal and striatal gray matter loss^{188,197–199}. The caudate and putamen reach 90% of their development after 25 years of age²⁰⁰. The pallidum and the cerebellum instead show an inverted U-shape, starting their gray matter volume shrinking after 25 years old²⁰¹. On the contrary, myelination of most prefrontal-striatal pathways^{202,203}, notably cortico-spinal tracts, continue later throughout adulthood (i.e., 28 years old)²⁰⁴. Although less markedly, the myelination of thalamus nuclei, caudate and putamen, has been ascertained to increase between 18 and 41 years old²⁰⁵, and to remain stable until sixty years old²⁰⁶.

From a functional standpoint, task positive (comprising dorsolateral prefrontal, precentral, and inferior parietal cortices) and task negative networks (whose hubs lie in posterior cingulate cortex, lateral parietal areas, parts of the medial frontal gyrus and the ventral anterior cingulate cortex)²⁰⁷ become more and more defined by their specific roles, showing the strongest anti-correlations between the right anterior insula, bilateral infero-parietal lobule and the CON at rest¹⁷⁶. The increasing anti-correlation between these regions into adulthood, could be an important hallmark of mature executive functions²⁰⁸, linked to sustained attention, working memory and inhibitory capacities²⁰⁹. The gradual development of task-specific fronto-striatal and fronto-parietal networks in the transition from adolescence to young-adulthood was identified as a proper hallmark of brain maturation^{210–212}.

Therefore, the enhanced performance to duration tasks both with sub-second^{98,213–215} and supra-second standard intervals^{126,73,216} observed between eight/nine-years-old children and adults might be associated with the improved connectivity between inferior fronto-striatal-parietal pathways¹⁸⁰. Also, the strengthening of the links between right Fronto-Insular Cortex and other hubs of the salience, and executive control network, could be pivotal for integrating information of internal timing signals and external temporal cues, improving timing performances.

Furthermore, improved processing speed, a larger working memory storage and enhanced decision-making abilities in adulthood²¹⁷ have also been associated with better performances across temporal production, reproduction, and bisection tasks^{27,218}. In temporal generalization task, the asymmetric gradient observed in adults compared to the symmetric gradient observed in children (and also in rats)^{98,215} has been attributed to changes in decision rules linked to an increase in subjects' confidence in the precision of their temporal estimation and time knowledge^{99,219}. Moreover, the temporal precision for processing short durations, together with a well-structured temporal cognition organizing days, weeks and months reached during adulthood, make time management optimal at this stage of life.

Further longitudinal studies on every aspect of temporal processing from late childhood throughout adulthood remain necessary to outline the characteristics of knowledge about time and metacognition of time, and their impact at different levels of temporal information processing (e.g., attention, memory, decision)^{114,219}, and the interweaving with several timescales (i.e., minutes and days).

Towards aging (>60 years old)

After the fifth decade of life, the earliest macrostructural changes consist in gray matter atrophy of prefrontal²²⁰ superior frontal and insular cortices^{221–224}. Although non-linearly, gray matter volume changes also occur in subcortical structures, such as hippocampus²²⁵ cerebellum²²⁶ and striatum²²⁷. On the other hand, white matter total volume declines steadily after 60 years old²²⁸ and alterations of white matter microstructure follow a posterior to anterior gradient in tracts traversing motor and sensory cortices²²⁹ mirroring the rate of demyelination^{230,231}. This has been associated with the slow-down of processing speed of information usually observed in healthy aging^{232,233}. The degradation of structural pathways is deemed to involve a reorganization of the functional connectivity^{234,235}, which becomes more random and less complex²³⁶. Indeed, brain networks in aging shows more functional integration and less segregation²³⁷, notably between FPN and DMN, leading to less efficiency²³⁸. Altogether, these structural and functional changes occurring in healthy aging^{239,240}, notably affecting the fronto-striatal pathways^{241,242}, lead to the impairment of executive control functions²⁴³, although differently across individuals^{244,245}.

The observed decrease in functional connectivity between the right fronto-insular cortex and control executive network²⁴⁶ could impact the efficient duration processing on the range of few milliseconds. Increased variability in temporal estimations has indeed been observed in production and reproduction of intervals ranging from 450 to 1750 ms¹⁵ and from 480 to 1920 ms²⁴⁷, as well as in bisection tasks^{248,249}, highlighting an even stronger modality effect compared to younger adults²⁵⁰. The disruption of the prefrontal-striatal pathways²⁵¹ could explain a reduced precision in reproduction of rhythmic sequences of 2 to 3 s interval range²⁵² therefore impacting the sense of *nowness*^{253,254}, defined as “the amount of temporal stimulation that could be perceived at a time”²⁵⁵. Moreover, underestimations in aging have also been observed while producing and reproducing longer intervals, ranging from 4 to 14 s and up to 38 s in presence of working memory deficits, slowdown of processing speed^{1256–260} and attentional capacities decreases^{248,249,261}. Furthermore, the error rate of the older adult's performance increased at the increasing of the complexity of the task²⁶².

On the other hand, changes in episodic memory and future thinking in aging²⁶³ could impair the ability to mentally explore other temporal dimensions, and the vividness of the mental time travel reports^{264,265}. In addition, a reduced subjective feeling of temporal distance both for weeks and months has been reported with increasing age²⁶⁶. Although the study of the developmental trajectory of temporal perspectives goes beyond the scopes of this review, subjective temporal distance could be affected by the perceived shortening of their future time perspective²⁶⁷, bearing in mind the idea that time would pass faster now than before the last 5–10 years, or as we get older^{31,182,268}. This finding could be in line with the underestimation of an event duration by representing a smaller time window related to an event duration of several seconds to minutes range in a horizontal timeline²⁶⁹.

Box 5 | Outstanding question

1. Which aspects of time processing are innate, and which are acquired?
2. Which are the neural correlates of temporal processing?
3. What is or is not supported by cognitive functions in temporal judgments?
4. Which is the cognitive model that better explain the processing of time?

Altogether, these changes could reflect the hippocampal volume shrinkage²⁷⁰, and disconnections between posterior cingulate and prefrontal cortices²⁷¹.

In contrast, sensorimotor synchronization abilities, which are considered to rely on primary sensory and motor cortices, supplementary motor area, anterior cerebellum, and basal ganglia, are generally spared with advancing age^{124,272–274}. A slower spontaneous motor tempo is nevertheless found in older compared to young adults²⁷⁵. Temporal order judgments were demonstrated to change in aging in both visual²⁷⁶ and auditory²⁷⁷ modalities, this latter being more evident in centenarians²⁷⁸.

The contrasted findings reported by the few studies conducted on the passage of time^{31,279} make reconstructing a neurodevelopmental framework of this aspect quite challenging. Further longitudinal neuroimaging studies on timing abilities, involving more complex temporal judgments, with changing contexts, are needed to explain how the neural mechanisms supporting several aspects of temporal processing evolve with advancing age. Although in a heterogeneous manner, internal and external factors (e. g., factors contributing to cognitive reserve, social stress, social isolation, cognitive load) could contribute to the different trajectories of age-related neurophysiological changes in temporal perception and cognition. This interplay could explain the larger variability observed in duration processing compared to adults. Distortions of temporal skills could impact on older individuals' ability to respect a scheduled appointment or treatments, by forgetting to take the medications at a planned hour. Timing difficulties could not only affect the quality of life of seniors, but also, for example, the ability to manage weekly appointments or to cross the street, thus restricting their autonomy in the daily life. In addition, aging at work, the feeling of not being able to manage one's own time, for example, can increase stress, which in turn, impact judgments of time²⁸⁰. Numerous studies have also shown the role of emotions and their regulation on time judgments²⁸¹. Conversely, having a whole and rich collection of personal memories forming our own autobiographical memory, help to maintain a stable self-identity, avoiding disorientation in aging. Deficits of time processing performances in aging might also serve as behavioral marker for pre-clinical stages of dementia²⁸² (Box 4).

Concluding remarks

Throughout the lifespan, we face the constant challenge of providing adapted behaviors in complex and changing environments. Such adaptation requires temporally specific representations and actions across time scales and temporal judgments¹. This ability is constrained by neurobiological maturation and evolution, in response to specific environmental challenges. Here, we reviewed the milestones of the maturation of neural and cognitive underpinnings of time processing from gestational period to senescence in the attempt to conceive a neurodevelopmental model of the emergence of each aspect of time processing (order and rhythmicity, duration processing, passage of time and mental time travel; for a review see ref. 2). The efficient integration of these aspects in every day's life supports a wide array of survival functions, such as motor control²⁸², action coordination²⁸³ and language^{284,285}. An integer sense of time support consciousness' mechanisms²⁸⁶, fundamental for one's own grounding in the *moment*²⁸² as well as for temporal anticipation of future events^{285,287}.

Current models of time perception, being based on central or distributed timing mechanisms, only took in account timing mechanisms underlying the processing of short durations (from milliseconds to few minutes) in healthy young subjects (Box 2), ignoring their developmental trajectory. We encourage future investigations to specify how the current models can account for data acquired across age groups. Here we propose an additive maturational model (Fig. 2), based on functional specialization, that could be named **RDP** as **Rhythm** (Simultaneity and Temporal Order) – **Durations** - **Passage Of Time** - **Mental time travel**. That is, these four temporal aspects would emerge following this order. The emergence of each aspect will add to the previous one, enriching temporal cognition, due to the interaction between “internal factors” (i.e., structural and functional specialization of targeted brain areas, neurotransmission and neuroendocrine regulation) in the attempt to cope with the environmental challenges, namely “external factors”. According to this framework, the first sub-cortical structures to set up, such as basal ganglia, cerebellum and primary sensory cortex promote the development of rhythmicity already before birth, in the attempt to synchronize with mother's movements to establish a sort of interaction (**R**). Then, newborns and infants began to handle short durations (**D**) by the mean of myelination increase and cortical volume growth of frontal areas. Nevertheless, it is only from middle to late childhood that the processing of longer durations became akin to the adult one, thanks to the maturation and specialization of higher-order cortices and the myelination of frontal-striatal pathway promoting top-down attention regulation and working memory. Growing up, the feeling of the passage of time (**P**) appears and refines itself concurrently with the development of parietal and inferior and medial temporal cortices, by the need to integrate speed, space and duration. At last, Mental time travel (**M**) ability would only appear thanks to the refinement of prefrontal cortices and the flourishing of connections between temporal and pre-frontal lobes in adolescence, to support abstract reasoning since adolescence. The neuroanatomy of a temporal circuitry would set up progressively, involving at first only sub-cortical areas, to then extend itself to higher-order cortices (Fig. 2).

Overall, the evolution of temporal abilities throughout lifespan seem to follow the “*last in, first out*” hypothesis, according to which the most recent brain areas to be developed are the first to be affected in aging^{287,288}. Therefore, the most primitive and the first timing capacities to be developed such as rhythmic processing^{289–291} are the ones that last longer, while the most sophisticated and the last to appear mental time travel is the first to change in aging.

Nevertheless, further longitudinal neuroimaging studies are needed to elucidate the neurodevelopment of the passage of time judgments and their relationships to duration judgments throughout the life span to reconstruct a complete neurodevelopmental progression of the temporal processing (Box 5). Specifying a healthy trajectory of the development of brain and cognitive substrates supporting timing abilities, could expand our understanding of neural mechanisms and cognitive models of temporal processing, shedding light on the intricate debate among distributed and centralized models (Box 2).

To conclude this lifespan approach could clarify the evolution of temporal mechanisms underlying the **Rhythm (Simultaneity and Temporal Order) (R)**, **Durations processing (D)**, **Passage of Time (P)** and **Mental time travel (M)**. Also, this perspective would foster future longitudinal works to assess the neural bases and cognitive functions linked to each of these temporal aspects. Furthermore, we encourage to consider alterations of temporal cognition and its interweaving with neuropsychiatric conditions which may unfold throughout the life-course in clinical settings^{292,293}. In this way, it would be possible to promote the design and the clinical use of cognitive batteries assessing temporal performances across temporal mechanisms. Evaluating temporal perception and cognition could therefore be useful for the detection of neuropsychiatric disorders of the development and neurodegenerative disorders early in the latest stages of life, improving the development of new treatments and disease management (Box 3).

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Author contributions

G.B. conducted the literature search and wrote the paper; F.E. and P.D. helped the reflection and reviewed the manuscript; S.D. wrote and reviewed the paper, contributed to the research; T.H. designed and supervised the work, helped write the paper and reviewed the manuscript.

Competing interests

The authors declare no competing interests.

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