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Special Issue: Time in the Brain

Review

Explicit Understanding of Duration Develops Implicitly through Action

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Time is relative. Changes in cognitive state or sensory context make it appear to speed up or slow down. Our perception of time is a rather fragile mental construct derived from the way events in the world are processed and integrated in memory. Nevertheless, the slippery concept of time can be structured by draping it over more concrete functional scaffolding. Converging evidence from developmental studies of children and neuroimaging in adults indicates that we can represent time in spatial or motor terms. We hypothesise that explicit processing of time is mediated by motor structures of the brain in adulthood because we implicitly learn about time through action during childhood. Future challenges will be to harness motor or spatial representations of time to optimise behaviour, potentially for therapeutic gain.

Highlights

Perception of time is relative. Duration judgements can be biased by the sensory (e.g., spatial) context of the event to be estimated.

Explicit duration judgements depend upon attention and working memory. Because of limited cognitive capacity, children rely more upon contextual factors to build a representation of time and so are more susceptible to contextual bias than adults.

Temporal magnitude (duration) and location (order) might be preferentially represented in terms of spatial magnitude (distance) and location (position), respectively.

Temporal features of action help children implicitly construct an explicit and flexible representation of time. Neuroanatomical, neurophysiological, and neurochemical systems typically associated with action are thereby co-opted to process duration.

Action and time are mutually beneficial. Action improves timing, and temporal predictability optimises action.

The Relativity of Time Perception

Time, and especially the perception of time, is relative. When waiting for a late-running bus we focus attention on the minutes ticking by and time appears to stretch interminably. By contrast, when friends and dancing occupy our attention at a party, time flies by. A wealth of experimental evidence confirms that the perception of duration is influenced by a wide variety of factors, not only the attentional salience or relevance of the event whose duration is being estimated but also its emotional content, its size, or even its location in space [1,2]. Such malleability confirms that our perception of time is relative and, it would appear, a somewhat fragile mental construct. Our subjective ‘sense’ of time is a byproduct of the way events are represented in working and long-term memory and by manipulating the sensory, attentional, or emotional characteristics of those events, we alter our perception of time. As Gibson [3] put it, rather poetically, ‘abstract time is a ghost of the events of the world.’ Nevertheless, we are capable of perceiving and accurately judging duration. So, how do we come to acquire this ability and how is such an intangible percept represented in the brain?

Distinct lines of evidence from developmental psychology and functional neuroimaging converge to suggest that duration judgements of events lasting hundreds of millseconds to a few seconds depend upon a coordinated system of accessory cognitive processes, such as attention and working memory (WM). In childhood, these processes are relatively immature, so children rely instead on the event’s sensorimotor characteristics to inform their sense of time. This makes their duration estimates particularly susceptible to interference by, for example, the spatial characteristics (length or size) of the event. Moreover, they have difficulty abstracting an estimate of duration from the motor act with which it was learnt. Intriguingly, functional neuroimaging studies of timing in adults have identified key roles for regions traditionally implicated in motor function, such as supplementary motor area (SMA) or basal ganglia, or in spatial processing, such as right parietal cortex. We suggest that the maturation of an explicit and abstract concept of time is constructed implicitly throughout childhood by sensorimotor

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https://doi.org/10.1016/j.tics.2018.07.011

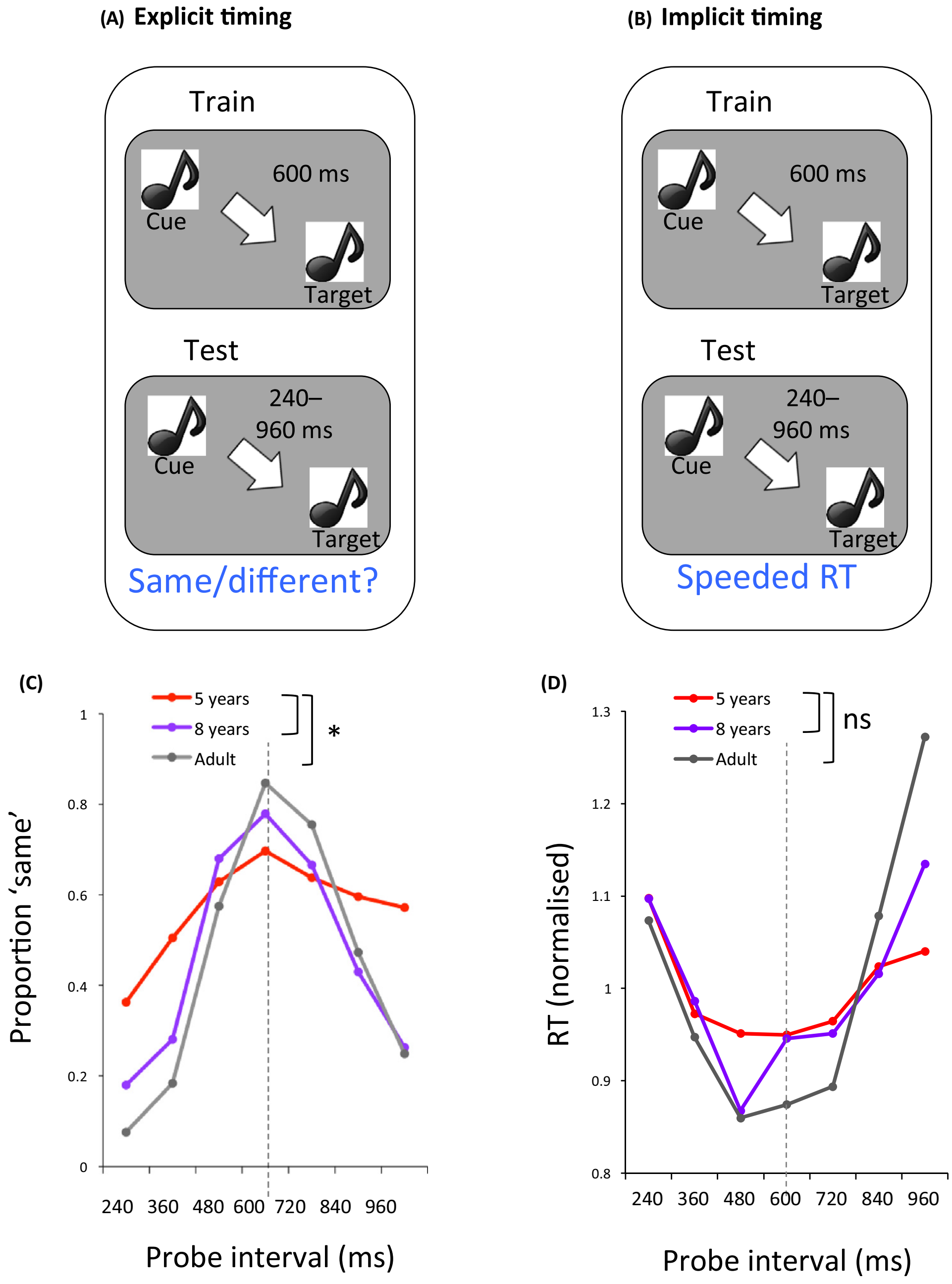
experience with the world, explaining why it has come to be neurally instantiated in spatial or motor regions of the brain in adulthood.

Explicit Timing Depends upon Attention and WM

The malleability of perceived time is likely because our perception of elapsed time depends upon a memorised representation of events in the world [4]. To estimate how long a currently elapsing event has lasted, you need to know when it started. However, the sensory information defining the onset of the event is no longer present in the external environment. Therefore, an internal representation of event onset must be accessed and compared to the sensory information available at event offset to estimate how long the event lasted. For durations in the range of milliseconds to seconds, this representation might be coded as sustained or steadily ramping neural activity from event onset to offset [5–7], as differences in transient snapshots of neural network activity at onset and offset [8–10], or as changes in the dynamics of neural firing within a population of neurons [9,11,12]. Whatever the precise neural mechanism [13], perception of duration necessitates a comparison between neural states at the onset and offset of the event being timed. Therefore, estimating duration depends upon selective attention to stimulus onset/offset and on WM, which maintains information provided at stimulus onset and integrates it with that at stimulus offset a few seconds later. Indeed, experimental data confirm the necessity of attention and WM for duration judgement. Individual differences in WM correlate with timing performance in healthy adults [14,15]. Moreover, if participants are asked to perform a WM secondary task while memorising the duration of a stimulus, they subsequently underestimate its duration [16].

In children, secondary tasks induce even greater duration underestimates than in adults, and the magnitude of the effect is directly correlated to children's attentional capacity [17]. Indeed, correlations between neuropsychological test scores of attention and WM significantly predict inter-individual differences in both the accuracy and variability of children's duration judgements [18,19]. The limited cognitive capacity of younger children might therefore explain why their duration estimates are less precise (i.e., noisy or more variable) than those of older children [20,21]. In turn, noisy temporal processing might explain why children are more prone to temporal distortion than adults. Bayesian theory states that the noisier the representation, the more participants rely on contextual information to make judgements [4]. Children are therefore more likely than adults to be influenced by temporal task context and thus experience greater distortion. For example, in Bayesian terms, perception of duration is based not only on the magnitude of the current duration (the 'likelihood') but also on the range of durations already encountered (the 'prior') [22–24]. This is exemplified by the central tendency (Vierordt's) effect in which participants overestimate the shortest duration in a range of durations and underestimate the longest duration [25]. Since children have especially noisy temporal representations, their duration estimates are heavily influenced by the prior temporal context, so the central tendency effect is even stronger in younger children [19,26]. Similarly, temporal illusions that auditory stimuli are perceived to last longer than visual stimuli [27] or that filled durations last longer than empty intervals [28] are stronger in young children than adults, and the strength of the illusion is directly related to individual differences in attentional capacity [27].

The relativity of time perception is therefore even more pronounced earlier in development. We suggest children's limited WM and attentional function prevent them from explicitly constructing precise representations of duration and, as a consequence, increase the influence that sensory, attentional, or emotional contexts have on their duration judgements. Nevertheless, when children's representation of time is measured implicitly, via reaction times to expected intervals rather than explicit judgements of interval duration (Figure 1), temporal precision is no



Trends in Cognitive Sciences

Figure 1. Young Children Can Process Duration Implicitly, But Not Explicitly. We directly compared implicit and explicit measures of duration perception in children and adults. Training in both tasks was a fixed interval reaction time (RT) task, which implicitly creates a representation of the cue-target interval. (A) In the test phase of the explicit timing task, participants judged whether or not probe intervals (240–960 ms) had the same duration as the trained reference interval (600 ms). (B) In the test phase of the implicit timing task, participants made speeded responses to targets presented after variable probe intervals (240–960 ms). The target was more likely to appear after the reference interval than the probe intervals, thereby reinforcing the representation of the reference interval (600 ms). (C) In the explicit timing task, we measured the proportion of trials in which participants judged the interval to be the 'same' as the reference interval. As expected, adults and both groups of children (5- and 8-year-olds) were more likely to respond same for the reference

(Figure legend continued on the bottom of the next page.)

Box 1. Measuring Duration Perception Implicitly with Temporally Predictable Stimuli

Reaction times (RTs) to temporally predictable stimuli provide implicit measures of timing in children [120,121]. Importantly, such implicit measures show the same 'scalar' property as more explicit measures, such that variability increases (scales) as a function of interval duration in adults [122] and infants [123]. We recently adapted a temporal prediction paradigm [122] to directly compare implicit and explicit measures of time perception in both children and adults [29]. Results in adults [122] and children [29] showed a quadratic profile of performance for both explicit (see Figure 1A in main text) and implicit (see Figure 1B in main text) versions of the task. In adults, temporal accuracy (peak of the distribution) was as good in the implicit task as it was in the explicit task [122], indicating that despite differences in task instructions, both tasks depended upon the same internal representation of time. Children's temporal accuracy was as good as that of adults for both explicit and implicit tasks, indicating that children could accurately represent duration. By contrast, children's temporal precision (spread of the distribution) was worse than that of adults in the explicit task, although it was as good as adults in the implicit task [29]. Moreover, while temporal precision in the explicit task covaried with neuropsychological scores of WM and attention, precision in the implicit task was independent of cognitive ability [29]. The implicit task therefore provides a measure of timing ability uncompromised by concurrent memory or attentional problems and thus may be particularly useful for studying timing in populations with immature (children) or dysfunctional (patients) cognitive skills.

longer correlated to WM or attention (Box 1) and, crucially, a 5-year-olds' representation of duration is as precise as that of an adult [29]. Therefore, young children may not have difficulty perceiving duration per se, they just do not have the necessary cognitive resources to turn this perception into an explicit and abstract representation of time. In line with the developmental theory of Representational Redescription [30], we suggest that the temporal information embedded implicitly within temporally predictable sequences or spatiotemporal trajectories is gradually integrated over development to eventually form an explicit, independent representation of time [31]. As cognitive and executive function develops with maturation of the prefrontal cortex, children become better able to represent time in an explicit and flexible manner and their duration judgements improve accordingly.

Indeed, the prefrontal cortex is not only implicated in WM and executive function but also in timing [32,33]. In particular, fMRI data show that timing activates the right inferior frontal cortex across a variety of temporal contexts [34]. This activation might reflect the WM processes needed to integrate information between stimulus onset and offset to obtain a duration estimate. To test this hypothesis, we directly compared discrimination of the duration (temporal condition) or distance (spatial condition) of the trajectory of a moving dot [35]. The time (or position) of stimulus onset had to be retained in memory and then integrated with the time (or position) of its offset. Integration in WM was therefore matched across tasks. A direct comparison of temporal and spatial conditions revealed activation of SMA, but not lateral prefrontal cortex, for duration estimation [35]. The ubiquitous activation of prefrontal cortex in most timing studies might therefore simply reflect the relatively higher WM demands of temporal tasks, if this parameter has not been adequately controlled for.

In the same study, we also confirmed prior fMRI findings [36,37] that SMA activity increases as a function of either objective or subjective duration. This indicates a specific role for SMA in processing the temporal magnitude of events (Figure 2). Moreover, SMA activity increased with duration only in the temporal task, not during the spatial task when duration was task irrelevant [35]. By contrast, activity in right occipital cortex varied as function of stimulus duration in both temporal and spatial tasks, that is, whether or not temporal information was task relevant [35].

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interval, indicating accurate estimation of interval duration. However, temporal judgements were significantly (*) less precise (flatter curves) in 5-year-olds than in older children or adults. (D) In the implicit timing task, we measured RTs to probe targets (normalised to account for age-related differences in motor speed). All participants responded fastest to targets appearing after the reference interval, indicating implicit processing of the reference interval. Importantly, 5-year-olds' temporal judgements were as precise (ns) as those of older children or adults. Adapted from [29].

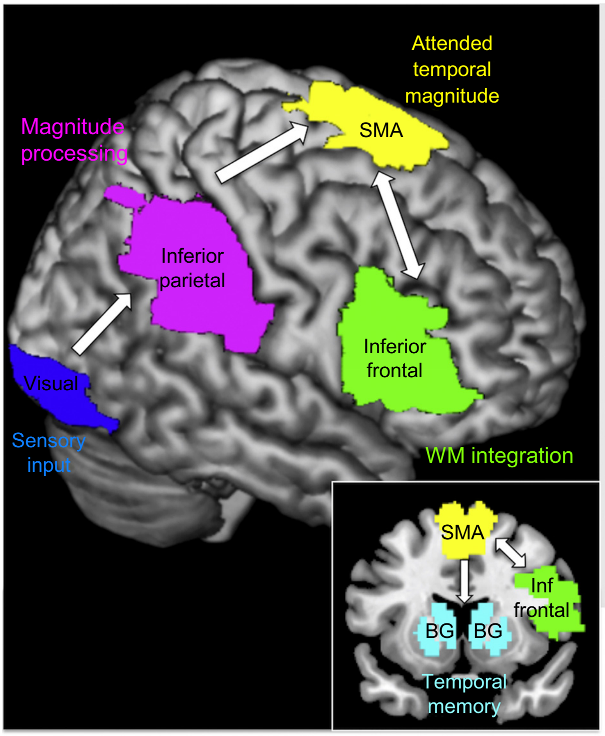


Figure 2. A Cooperative Neuroanatomical Network for Duration Judgement. Activity in sensory-specific regions, such as visual cortex, increases as a function of stimulus duration due to sustained sensory input over time. The magnitude of this sensory input is passively tracked by activity in right inferior parietal cortex. If stimulus duration is attentionally relevant, either due to temporal task goals, perceptual salience, or statistical probability, the magnitude of temporal information is actively coded by activity in supplementary motor area (SMA). A reciprocal connection between SMA and inferior frontal cortex allows the running tally of temporal information to be constantly updated and maintained in working memory (WM). This temporal tally can then be compared to that of a prior stimulus (inferior frontal cortex) or encoded into working, or long-term, memory for later use [basal ganglia (BG)]. The figure illustrates duration processing of visual stimuli. However, activity could vary as a function of stimulus duration in any stimulus-specific sensory processing region (e.g., auditory cortex, somatosensory cortex).

Trends in Cognitive Sciences

Similarly, in a separate study, neurons in right inferior parietal cortex were found to be tuned to specific stimulus durations whether participants were performing a timing task or a shape discrimination task in which duration was incidental to task demands [38]. Together, these studies suggest activity in sensory processing areas, such as right occipital or parietal cortices, passively codes the magnitude of temporal information (see also [39]), whereas SMA processes temporal information further whenever attention is directed to temporal stimulus characteristics. Importantly, SMA activity varies with temporal features whether attention is directed voluntarily to these features because they are task relevant (top-down attentional mechanism) or drawn automatically to them either because they are perceptually salient [40] or statistically probable [41] (bottom-up attentional mechanism).

In fact, right inferior parietal cortex is involved in processing magnitude generally, whether in temporal, spatial, or numerical domains [42–44]. We might therefore conceive of duration processing being mediated by a coordinated network of regions, each of which contribute a specific functional component: passive processing of magnitude in right parietal cortex, attentionally guided coding of temporal magnitude in SMA, and integration and updating of temporal information in inferior frontal cortex (Figure 2). In support of the idea that distinct nodes of this functional network are interconnected, the degree of temporal distortion induced by magnetic stimulation to right inferior parietal cortex correlates with the amplitude of electrophysiological activity recorded over frontocentral sites [45]. Moreover, a recent electrophysiological study in 9-month-old infants [46] showed that while activity in right prefrontal cortex was involved in temporal rule learning in both adults and infants, the neural signature of temporal expectation was localised to temporo-parietal cortex in infants but to the SMA in adults. This suggests that automatic processing of temporal information is restricted to context-specific brain regions early in development, but in adulthood, once sensorimotor experience has helped construct an explicit representation of time, temporal processing is mediated by activity in SMA [46].

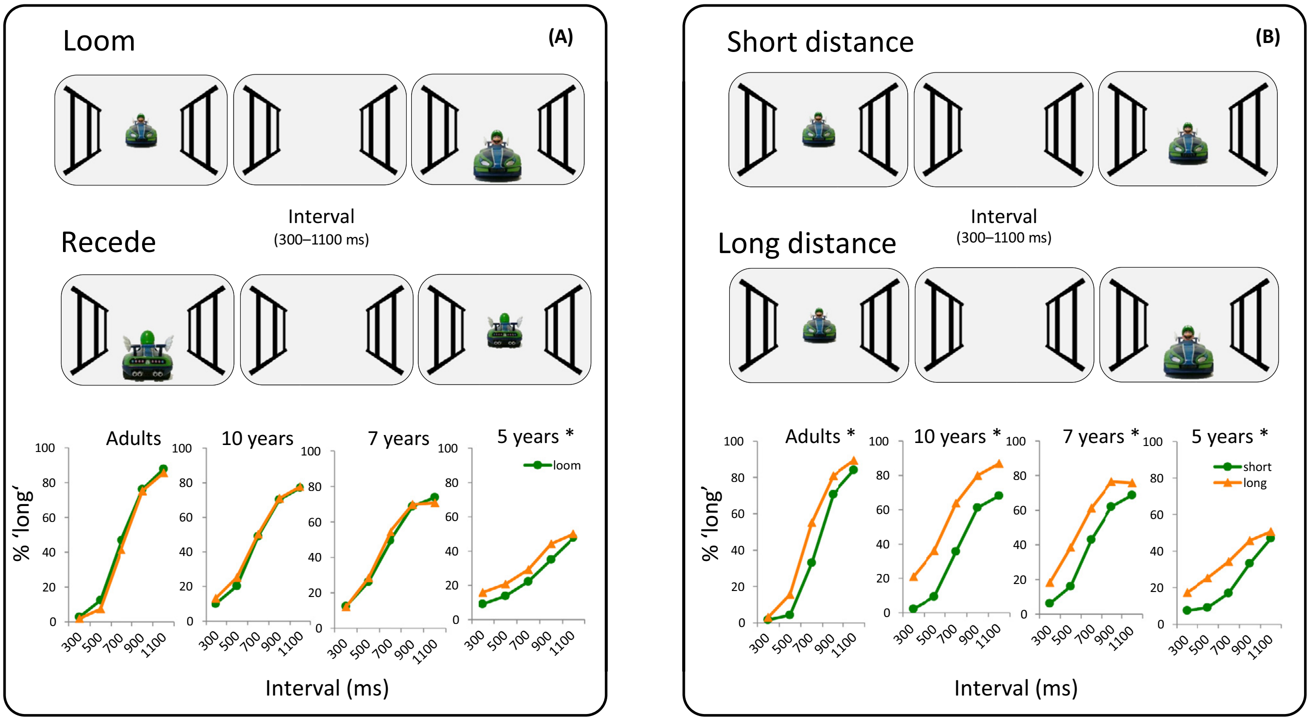
If temporal information is processed in context-specific regions in infancy and childhood, then this could explain why children's duration judgements are more susceptible to influence by contextual factors. Because they have not yet constructed an explicit representation of duration in higher-order brain areas, their representation of duration is bound to the context in which it was experienced [30]. So, for example, repeated associations between spatial and temporal magnitude (a long distance usually takes a long time) might implicitly bias the way that duration is represented in the brain (e.g., in right parietal cortex) and, ultimately, could explain why our notion of time is often couched in spatial terms [47,48].

Spatial Representation of Time

Spatial Magnitude

In a seminal set of studies, Piaget [49] demonstrated that young children have great difficulty disentangling the notions of time and space when judging the duration of moving objects. In general, long distance trajectories were judged to last longer than short distance trajectories of the same duration. As suggested earlier, one explanation is that children's immature WM function makes it difficult for them to construct an explicit representation of duration, so the more tangible spatial characteristics of the object (distance travelled) override the more abstract temporal characteristics (duration taken), thus biasing their estimates of duration [50]. As cognitive function develops with age, children become better able to focus attention on the pertinent temporal dimension and to ignore potentially conflicting information from other dimensions, resulting in more precise duration judgements. For example, the numerical magnitude of a stimulus biases duration estimates in 5-year-olds, although by 8 years old the extent of the bias is reduced [51]. We have also found that the direction of movement influences duration estimates in 5-year-olds, but not in older children or adults [52]. In this study (Figure 3), we asked children to estimate the duration of a car's journey, using a two-frame illusory motion paradigm in which the start- and endpoint of the journey were separated by an empty interval. The car could appear to travel away (recede) from the point of view of the observer or to come towards the observer (loom). Five-year-olds, but not older children or adults, judged looming trajectories to have a shorter duration than receding trajectories (Figure 3A). Consistent with a Bayesian interpretation of duration processing [4,22–24], we hypothesised that the illusion of impending collision induced by the attentionally salient endpoint image of the looming trajectory led to a retrospective shortening of the immediately preceding interval. This bias was more evident in young children because noisy temporal representations meant their duration judgements were more influenced by the sensory or attentional context [19,26].

By contrast, the influence of spatial magnitude on duration judgement was equally strong in adults and children (Figure 3B), confirming previous studies [53,54]. Adults and 10-year-olds overestimate the duration of long-distance trajectories as much as 5- and 6-year-olds, whether the object's trajectory is in the lateral (left-right) axis [53,54] or the frontal (front-back) axis [52]. We have also found that children and adults are equally susceptible to temporal distortions induced by the mere illusion of spatial length in a Ponzo illusion [52], replicating previous findings in adults [55]. The influence of spatial magnitude on duration processing is therefore a robust effect that appears early in development.



Trends in Cognitive Sciences

Figure 3. The Influence of Spatial Stimulus Characteristics on Duration Judgement across Development. The start point and endpoint of a car's virtual trajectory were separated by an empty interval (300/500/700/900/1100 ms), whose duration had to be judged as short or long. The car appeared to (A) either loom towards the observer or recede into the distance and (B) travel either a short or a long distance. Short and long trajectories were presented in both the looming and receding directions. Graphs show the percentage of trials in which the participant responded that the interval was 'long'. Data are plotted as a function of either (A) looming/receding direction or (B) short/long distance. As expected, adults and the three groups of children (5-, 7-, or 10-year-olds) were more likely to respond long as a function of increasing interval duration. This indicates all groups understood task instructions and were able to estimate duration, although temporal judgements were less precise (flatter curves) in younger children, replicating many previous findings [19]. Five-year-olds, but not older children or adults, significantly (*) underestimated interval duration during looming trajectories. By contrast, all four age groups significantly (*) overestimated the duration of long distance trajectories. Graphs are constructed from data reported in online supplemental information in [52].

The wealth of data illustrating a tight link between spatial magnitude (distance or size) and temporal magnitude (duration) inspired the influential ATOM (A Theory of Magnitude) model [42]. ATOM proposes that whatever the dimension being measured (space, time, number), stimulus magnitude is processed by the same neural mechanism, likely instantiated in right inferior parietal cortex, which is suggested to be innate [42]. Indeed, an influence of spatial magnitude on duration perception has been reported in infants [56,57], neonates [58], and monkeys [59,60]. Moreover, there is a mutual influence between space and time in babies [56] and monkeys ([59], but see [60]), with temporal features affecting spatial judgements as much as spatial features affect temporal judgements. This supports the idea of a single mechanism common to spatial and temporal dimensions, although methodological differences in paradigms used to test infants and adults preclude, as yet, a definitive conclusion that this mechanism is innate. Nevertheless, the strength of the space–time relationship might explain why we try to make the rather intangible sense of time a little more concrete by thinking about it in spatial terms. For example, the same words 'short' and 'long' are used to quantify both temporal duration and spatial distance, and we even mix metaphors when referring to events happening within 'a short space of time.' Moreover, numerous studies now show that language and/or

Box 2. Distinguishing Magnitude from Location in Space and Time

To fully comprehend the relationship between space and time, it is critical to distinguish different ways of measuring these two dimensions. In time, temporal location refers to the order of events in time (e.g., past/future or first/second), whereas temporal magnitude refers to the duration of an event (e.g., short/long). In space, spatial location refers to the position of events in space (e.g., left/right or front/back), whereas spatial magnitude refers to the distance or size of a stimulus (e.g. short/long or small/large).

A temporal interval comprises both order (first/second) and magnitude features. Therefore, when synthesising the literature on the spatial representation of time, it is critical not to conflate magnitude with location in either the spatial or temporal dimension. Indeed, it is helpful to bear in mind that distinct temporal concepts of order and duration might be more usefully represented by one or other spatial metric (location or distance) [47,48]. The notion of temporal magnitude (duration) might be more usefully conceptualised in terms of spatial magnitude (distance), while the notion of temporal location (order) might be better represented in terms of spatial location (position) [64]. Moreover, it is important to consider that location and magnitude might be differentially represented in distinct spatial planes. For example, spatial location in the frontal axis (front-back) appears to be a more useful spatial metaphor for deictic concepts of temporal order than spatial location in the lateral axis, in either the horizontal (left-right) or vertical (up-down) direction [124]. By contrast, temporal magnitude can be represented by spatial magnitude equally well in the frontal or lateral axes [52].

In this review article, we focus on the acquisition and representation of duration. Comprehensive reviews of the spatial representation of temporal order, or the way in which temporal order is acquired in childhood, can be found elsewhere [62,118].

culture build upon this fundamental space–time relationship [61,62], so that time comes to be represented not only in terms of spatial magnitude but also in terms of spatial location (Box 2).

Spatial Location

In 1890, William James drew an analogy between the perception of time and space, stating ‘date in time corresponds to position in space’ [63]. While the spatial representation of time in terms of magnitude (small/large or short/long) might be innate, the spatial representation of time in terms of spatial location (left/right or up/down) is culturally acquired [47,48,62,64,65]. The mental timeline theory (analogous to the mental numberline [47]) proposes that time is ordered along a linear spatial axis [64,65]. This is based upon evidence that short durations [66,67] or early/past moments in time [68] are associated with the left side of space in Western culture, while long duration and late/future moments are associated with the right side of space. A mental association is thought to be created between the temporal order in which words are read and the position of those words on the page. Thus, events happening first are on the left and those happening later are on the right [69]. In countries with a right-to-left reading direction this association is reversed [70], and in countries whose inhabitants read from top to bottom, it is rotated to the vertical axis [61]. These patterns demonstrate a clear cultural influence [48,62,65], as does the fact that the mental timeline can be flipped through training [71] or mirror reading [72].

Cultural habits might also influence our concept of duration, that is, temporal magnitude rather than temporal order (Box 2). As we read from left to right, time elapses, and so short duration comes to be associated with the left and long duration with the right. However, during reading, this association would have to be reset every time we moved to the next line, making it less robust and perhaps explaining why there is less experimental evidence for a mental timeline for duration than for temporal order [64]. Indeed, the use of the mental timeline for representing temporal order emerges earlier in development than its use for representing duration. While children used a left-right mental timeline to convey the meaning of words referring to relative temporal order (deictic time words, such as ‘yesterday’ or ‘next year’) by the age of 4–6 years, their understanding of the relative remoteness of these words from the present time (i.e., temporal magnitude) did not develop until the age of 7 years [73]. In fact, the influence of spatial location on temporal order might even be present from infancy [74]. By contrast, the influence of spatial location on estimates of duration develops relatively late. While 10-year-olds and adults were found to underestimate the presentation duration of leftward-facing arrows, arrow direction had no influence on perceived duration in younger children [75]. However, when location was manipulated by the physical position of the stimulus on the screen (left/right side) rather than its symbolic shape (left/right arrow), even 5-year-olds' duration estimates were influenced by spatial location [76]. Nevertheless, these developmental data collectively support the premise that the mental timeline might be more intuitive for representing the temporal order of individual events, rather than their duration.

Given its critical role in orienting attention to spatial locations, it is perhaps unsurprising that right parietal cortex is involved in representing the mental timeline. For example, patients with spatial neglect, often caused by lesions to right parietal cortex, do not have the same spatial representation of either temporal order [77] or duration [78] as healthy controls. In addition, magnetic stimulation of right inferior parietal cortex in healthy volunteers interferes with their use of a mental timeline for duration [79]. Right inferior parietal cortex is also thought to mediate common processing of spatial, temporal, and numerical magnitudes [42,80]. We suggest that while right parietal cortex (or other sensory-specific regions) mediates passive, low-level coding of temporal magnitude [35,38,39], attentionally guided integration of temporal information into a duration judgement is more likely mediated by the SMA [35,40] (Figure 2). Spatially distorting low-level processing of duration information in sensory association cortices would therefore interfere with the way it is ultimately integrated in SMA to produce a duration estimate (see also [33]).

An intriguing question then is why time should be integrated in a structure of the brain, the SMA, that is traditionally associated with motor function (see also [81,82]). This question is particularly compelling given that SMA activity varies with duration even when it is measured during mere perception of stimulus duration, independent of any motor behaviour [35,36,83]. One seductive possibility is that because limited cognitive resources in infancy and childhood preclude the formation of an explicit, abstract notion of time, temporal information is instead picked up implicitly through action (Box 1), so motor circuitry gets co-opted to process temporal features (Box 3).

Motor Representation of Time

Functional neuroimaging studies identifying a key role for SMA in duration processing [34,81,83] are complemented by single-cell recordings in rats and monkeys. Neural firing in SMA increases as a function of duration, with distinct populations of SMA cells firing to distinct stimulus durations suggestive of a duration-tuning mechanism [84,85]. Moreover, SMA firing peaks at the moment a temporal decision can be made [10], confirming results of prior electrophysiological recordings in humans [86]. Nevertheless, the whole-brain methodology of fMRI has the advantage of revealing the entire network of regions involved in processing duration (Figure 2). Other structures related to motor function, such as basal ganglia and cerebellum, are also implicated in timing [34,87]. For example, fMRI has shown that basal ganglia are activated selectively during the initial encoding of temporal magnitude into WM [88,89] (Figure 2), with higher activity correlating with better timing performance [88,90]. The amplitude of basal ganglia activity might therefore mediate the depth of encoding of stimulus duration, resulting in a more accurate representation of time. This function is not incompatible with its role in rhythmic or beat-based timing [91], since successive intervals in a sequence must be memorised to determine rhythmicity.

Box 3. Temporal Predictability Optimises Motor Behaviour

The interaction between action and time is mutual. Action helps construct and hone accurate representations of time and, reciprocally, accurate timing helps optimise motor behaviour. Being able to predict when an event will happen allows us to safely cross the street before an approaching car, or clap in time to the music. Temporally predictive information, whether provided by symbolic cues, dynamic trajectories or rhythmic sequences, improves both speed and accuracy of responding to temporally predictable targets [125,126]. Infants and young children are sensitive to the predictability of the temporal structure of events [46,120,127]. Furthermore, infants as young as 15 months old can use symbolic cues to predict the onset time of an event [128] and children younger than 10 years old can use the temporal information conveyed by symbolic cues to speed responses to predictable targets [121,129]. Nevertheless, these benefits are only seen when targets are spatially, as well as temporally, predictable. If targets are spatially unpredictable, then even children as old as 11 years fail to use temporal cues to enhance motor speed [130]. This result may reflect the benefits of a spatial scaffold for effectively making use of temporal information [126,131].

Beta-band oscillations, normally associated with motor function, align to the temporal predictability of stimuli in both adults [97–100] and young children [113,114]. Indeed, the electrophysiological dynamics of temporal prediction are similar in infants, children, and adults [46,114], suggesting that the neural mechanisms mediating temporal predictability are in place from a young age. Nevertheless, these mechanisms are instantiated in temporo-parietal cortex in infants but in SMA in adults [46]. This anatomical shift might reflect the developmental shift from an implicit, context-bound representation of duration in infancy to a more explicit and flexible representation in adulthood [30].

Electrophysiological recordings in monkeys also demonstrate changes in neural firing as a function of temporal predictability in a variety of context-specific processing regions [7,132–137]. By contrast, whole-brain recordings in humans [100,138,139] indicate a context-independent role for left inferior parietal cortex in temporal predictability, probably reflecting top-down orienting of attention to predictable moments in time. Left inferior parietal cortex is implicated in action selection, and damage to this region can lead to ideomotor apraxia (an inability to voluntarily execute skilled action) [140]. The neuroanatomical (left parietal) and neurophysiological (beta-band) overlap in the neural substrates of temporal and motor processes highlights once again the putative functional overlap between time and action.

The importance of basal ganglia for timing has been amply demonstrated in rodents [9,12,32] and monkeys [92,93], with neurophysiological data indicating that duration is encoded as dynamic changes in patterns of striatal firing. Furthermore, oscillatory neural activity in the beta frequency band, which is normally associated with motor function [94], has been found to vary as a function of duration in basal ganglia [93]. In humans, beta-band activity varies as a function of duration over fronto-central electrodes [86] and may be involved specifically in encoding temporal magnitude into WM [95]. Moreover, beta-band activity was higher during a timing task than a colour control task, even though both tasks made equivalent demands on WM [96]. Beta-band activity in SMA and cerebellum has also been found to align to the temporal predictability of a stimulus [97], even when no movement is required [98] (Box 3). In parietal cortex, beta-band activity indexes the accurate temporal prediction of stimulus onset [99,100].

In parallel, dopamine (DA), a neurotransmitter traditionally linked to motor function, has consistently been shown to modulate duration processing in animals [6,101,102] and humans [103–106]. In a combined functional neuroimaging and psychopharmacological study [104], DA-induced changes in timing performance were correlated to DA-induced changes in activity of two motor structures, SMA and basal ganglia, even though activity was measured at a purely perceptual stage of the task. Taken as a whole, the comprehensive neuroanatomical (SMA, basal ganglia), neurophysiological (beta oscillations), and neurochemical (dopamine) overlap between timing and motor function is suggestive of a corresponding functional overlap [33,81,82]. An appealing possibility is that timing shares neural circuitry with motor function because our sense of time is acquired and honed through action.

Developmental studies lend support to this hypothesis by demonstrating that young children (around 3 years old) appear to represent time in motor terms. Their duration estimates are more accurate when the duration is filled with an action than when it is empty [28] or when task instructions are given in terms of motor force ('press harder) rather than duration ('press longer') [107]. Their duration estimates are also improved by simultaneously imitating the duration of another's action, rather than simply listening to verbal instructions or watching a demonstration [108]. In addition, they find it difficult to dissociate an estimate of duration from the motor act with which it was experienced. For example, 3-year-olds could not reproduce the duration of one action with a different action (e.g., 'press the button . . . now, squeeze the bulb for the same amount of time'), although by the age of 5 years such temporal transfer was possible [31]. Even in adults, temporal information is tightly bound to the specific action with which it was learnt [109]. Nevertheless, action helps construct explicit representations of time that can be used to optimise behaviour generally. Moving in time to a rhythmic stimulus improves perceptual discrimination of non-temporal features of stimuli occurring on the beat [100] and helps participants [110], especially non-musicians [111], to find the beat in ambiguous rhythms. Bouncing infants in time to a particular beat also helped them to later disambiguate different rhythms [112], indicating that the association between action and time can be established from a very young age. The physiological mechanism linking action and timing might be neural oscillations in the beta frequency band, which vary as a function of temporal predictability not only in adults but also in children [113,114].

Rhythmic action (tapping) also improves later perceptual estimates of duration in healthy adults [115]. Even simply imagining rhythmic movement can help later timing performance [116]. In children, we recently found that rhythmic action training helped children aged 5 years to accurately reproduce a rhythmic sequence and, more interestingly, helped both 5- and 8-year-olds to discriminate the trained rhythm in a purely perceptual timing task [117]. The temporal information implicitly embedded within rhythmic action therefore helps construct an explicit, independent, and flexible representation of duration that can be used to make accurate perceptual temporal discriminations.

Concluding Remarks

Passive sensory coding of temporal information is mediated by neural activity in sensory-specific processing regions of the brain and is therefore subject to distortion by specific sensory features of the event (e.g., its spatial magnitude, location, or emotional content). However, as soon as temporal stimulus features are attended (due either to voluntary, goal-directed top-down mechanisms or automatic, stimulus-driven bottom-up capture), higher-order regions of the brain mediate the active integration of temporal information into an overt temporal judgement (Figure 2). This process of integration depends fundamentally on attentional and WM capacity, and so may be compromised in children or in patients with cognitive dysfunction. We suggest that in childhood, action may help mediate the transfer from an implicit to explicit representation of duration [30,31], co-opting motor circuitry of the brain to do so and thereby making it more resistant to interference by spatial or other contextual factors. This proposal is a neuroscientific update (see also [33,42]) of the theory that our perception of time is constructed by performing actions in space [31,49,108,118]. To validate this theory, it would now be helpful to track the relative instantiation of temporal processing in sensory-specific and motor structures of the brain across development (see Outstanding Questions).

In summary, despite the metaphorical appeal of an innate 'internal clock' specifically dedicated to temporal processing, we suggest instead that we learn to judge time and to represent it in the brain through our interaction with the world. Even though this makes our perception of time relative and susceptible to contextual bias, we can nevertheless make use of it to guide action and optimise behaviour, even from a young age (Boxes 1 and 3). It may even be used to clinical

Outstanding Questions

Can implicit measures of timing better identify selective temporal deficits in patients, over and above any concurrent attentional or WM dysfunction?

Is temporal magnitude (duration) more usefully represented by spatial magnitude (distance) than by spatial location? Reciprocally, is temporal location (order) more usefully represented by spatial location (position) than by spatial magnitude? This can be addressed by factorially manipulating these four distinct metrics of space and time.

Are there distinct developmental trajectories for the spatial representation of duration or order?

Does the spatial representation of time (in terms of either magnitude or location) depend upon underlying cognitive function? This can be addressed by correlating neuropsychological test scores to the size of the spatial influence on temporal performance.

Can we reliably distinguish regions of the brain that are common to the processing of magnitude in any dimension from those that are specific to magnitude processing in the temporal domain?

Does action benefit processing of spatial and numerical magnitude, or are its effects specific to the temporal dimension?

Can we track a progressive instantiation of temporal processing in motor structures of the brain throughout development? This could be addressed with longitudinal electrophysiological studies from infancy to childhood.

Can we harness spatial or motor representations of time to devise cognitive rehabilitation strategies that temporally structure patient's experience or behaviour? Will this temporal scaffold help them overcome non-temporal clinical symptoms of their disorder?

The idea of a dedicated, internal clock that estimates duration in the range of seconds is now widely rejected in advantage. A common therapeutic technique for alleviating the motor symptoms of Parkinson's disease is listening to temporally structured rhythms [119]. An exciting challenge for the future is to examine how effective this technique might be for other motor disorders or, indeed, for children with learning difficulties.

favour of a distributed, cooperative network for processing time. Should we now abandon the term 'internal clock', or is it still a useful shorthand for expressing any mechanism that measures the elapse of time?

Acknowledgments

J.T.C. is funded by an Agence Nationale de la Recherche grant (ANR-16-CE37-0004-02). S.D-V. is funded by a European Research Council H2020 grant (TIMETORM, H2020-FETPROACT-2014). We thank Pom Charras for providing data for Figure 3. J.T.C. thanks Erik Christensen for drawing her attention to the chapter by Gibson [3] on space and time. Finally, we're grateful to Giovanni Mento for providing very helpful comments on an earlier version of this manuscript, and to an anonymous reviewer.

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