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**Visualising time in the brain: Perceiving the present and predicting the future**

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Being able to accurately estimate the passage of time is an integral part of our everyday lives. For example, anticipating the moment at which a traffic light will turn green helps you to accelerate away more quickly. Alternatively, if the light turns amber just as you reach it, you must decide whether you have enough time to race through or whether you should hit the brakes. In these situations, time is being estimated implicitly to help guide motor behaviour. But it's also possible to make explicit perceptual judgments about duration – for instance, it's easy to judge whether a red traffic light typically lasts for a longer or shorter time than an amber one.

It might seem trivial, but it's crucial to note that to estimate how long an event lasts, we need to remember when it started. In other words, to estimate event duration we compare information at event offset with information at event onset. But the tricky thing about time is that at event offset, the information about event onset is no longer available in the environment. Therefore, in order to accurately judge event duration, we must access a memorised representation of information that is no longer physically there. As Gibson (1975) put it “Time is a ghost of the events of the world”. Our sense of time is therefore constructed both from current sensory information and representations in working memory (WM). As the French philosopher Guyau (1890) said over 100 years ago “time can only be perceived ... as representations rather than immediate sensations”. And the fact that time is a cognitive construct makes it rather fragile and susceptible to interference or influence by other factors (Matthews and Meck, 2016). For instance, we've all experienced the sensation that time flies when we're having fun or that a watched pot never boils. In other words, the less we pay attention to the passage of time the shorter time appears, whereas the more we pay attention to it the longer it appears (Macar et al, 1994; Brown, 1997). Moreover, attention is not the only factor that influences our sense of time. For example, it's often been reported that time appears to slow during stressful events like car accidents. This phenomenon has been investigated experimentally in the laboratory and the duration of emotionally charged or stressful events, like angry faces (Droit-Volet et al, 2004) or bungee jumps (Stetson et al, 2007), are typically overestimated, which would correspond to a subjective slowing of the passage of time. Physical stimulus characteristics can also influence the perception of time. The duration of bigger or longer stimuli are overestimated compared to smaller or shorter ones (Xuan et al, 2006; Casasanto & Boroditsky, 2008), and the duration of stimuli presented on the right-hand side of a screen (Vicario et al, 2008), or even of stimuli that simply draw attention to the right of the screen (Droit-Volet and Coull, 2015), are overestimated compared to those on the left.

The cognitive mechanisms underlying the rather slippery sensation of time might be elucidated by identifying where it is represented in the brain. Around 25 years' worth of functional neuroimaging studies of duration perception have identified several timing-related regions of the brain, including the inferior prefrontal cortices, a region of dorsomedial frontal cortex called the Supplementary Motor Area (SMA), the basal ganglia, and the cerebellum (Wiener et al, 2010; Coull et al, 2011; Merchant et al, 2015; Teghil et al, 2019). Among these, the SMA is the region that is the most consistently implicated in duration processing (Nani et al, 2019), independently of WM and attentional task demands (Coull et al, 2015). As its name suggests, the SMA has traditionally been implicated in motor function, specifically motor preparation. But the SMA is activated even when participants are making purely perceptual judgements about stimulus duration (Coull et al, 2004; Wiener et al, 2010; Schwartze et al, 2012). So why would a region of the brain traditionally implicated in motor preparation be involved in perceiving time?

One possibility is that we build a notion of time in childhood from the duration of certain actions. For instance, when young children question how long a particular unit of time is, you might tell them that 10 minutes is the time it takes to walk to school or that one hour is

the duration of their dance class. Indeed, experimental evidence suggests that young children represent time in terms of action. For example, Droit-Volet and Rattat (1999) asked children to press a button for however long they liked and then to squeeze a rubber ball for the same amount of time. The youngest children in the group (3-year-olds) had great difficulty with this task. Their perception of time was entirely defined by the action of the button press and did not exist independently of that action. However, by 5 years old, children were able to extract the temporal information from the button press action, transform it into an abstract mental representation of time, and then apply it to another, distinct action. In fact, action continues to improve and hone the sense of time even once an abstract representation of duration has been acquired in older children and adults. For instance, Monier et al (2019) showed children a rhythmic sequence of 33 dots that were presented consecutively at 800ms intervals. One group of children was asked to simply watch the sequence of dots while another group was asked to tap in time with the dots. They were then shown a single interval, bounded by two dots, and asked to estimate whether that interval was the same or different to the interval used in the rhythmic sequence. Children who had previously tapped in time to the dots had a more precise perception of the 800ms interval than children who had simply watched the sequence, indicating that action helped sharpen their representation of time. Action also helped relieve the memory burden of performing such timing tasks. Temporal precision in the group of children who had simply watched the sequence was strongly linked to their scores on neuropsychological tests of memory, confirming several previous findings (Droit-Volet et al, 2015; Zelanti and Droit-Volet, 2011, 2012). The better the memory capacity of the child, the better their performance on the timing task. By contrast, there was no link between timing performance and memory capacity in children who had tapped in time to the sequence, suggesting that action had provided an alternative functional framework that helped shape their representation of time.

So why do children find it so difficult to judge time? One possibility is that since performance on duration judgement tasks covaries with neuropsychological measures of memory, children's relatively poor memory function makes their judgements more variable (Droit-Volet and Hallez, 2019). However, the tight relationship between memory and duration judgement means that duration judgement tasks might not be entirely representative of children's timing ability. To test this, Droit-Volet and Coull (2016) compared children's performance on two comparable timing tasks: one that measured timing via explicit duration judgements and one that measured timing via implicit temporal learning. In the training phase of both tasks, children were trained on a standard 600ms interval by asking them to press a button upon presentation of the second of two auditory tones, which was always presented 600ms after the first. During the subsequent test phase of both tasks, the interval between the two tones was varied (from 240ms-960ms). However, the instructions for the two tasks differed. In the explicit duration judgement task, children were asked to decide whether the (variable) interval between two tones was the same, or not, as the trained (600ms) interval. In the implicit temporal learning task, we asked them simply to respond as quickly as possible to the presentation of the second tone. For the duration judgement task, confirming many previous findings (Droit-Volet, 2016), 5-year-olds were more likely to judge that an interval shorter or longer than 600ms was actually the same as the 600ms trained interval, meaning their temporal precision was significantly worse than that of older children or adults. By contrast, for the implicit temporal learning task, their temporal precision was as good as older children or adults: across all age groups, reaction times to the tone were fastest when the test interval was the expected 600ms and progressively slower when it was shorter or longer. If the 5-year-olds had failed to acquire the 600ms trained interval, their reaction times would have been no faster for 600ms test intervals than for shorter or longer ones.

Therefore, it appears that children are capable of precisely representing time: they just find it difficult to translate that into an explicit duration judgement.

The U-shaped nature of the reaction time distribution in the implicit learning data indicate that the expectation for the 600ms trained interval is not a categorical on-off mechanism. Performance isn't fastest at 600ms and equally slow at all other intervals. Instead, there is a parametric slowing in response times as the test interval gets increasingly shorter or longer than 600ms. It's as though there's a spotlight of attention on the 600ms interval, that fades with increasing temporal distance from that interval. Although the idea of a spotlight of attention is usually discussed in spatial terms, with items in the spatial spotlight being processed better than those out of the spotlight, it appears that a spotlight of attention also exists in the temporal domain. This begs the question as to whether directing attention in time can optimize behaviour in the same way as directing attention in space?

Coull and Nobre (1998) attempted to answer this question by modifying the Posner spatial orienting of attention task (Posner, 1980). In the classic spatial version of the task, an arrow cue tells the participant whether a subsequent target is likely to appear on either the left or right side of the screen. If the target appears in the location predicted by the cue (a valid trial) RTs are faster than if it appears in the location not predicted by the cue (an invalid trial). In a temporal analogue of this task, cues predicted when (rather than where) the target was going to appear. Data showed that RTs were slower for invalid versus valid trials in both the spatial and the temporal versions of the task. In other words, there were RT costs then the target did not appear either where or when expected. Moreover, functional imaging data revealed a very neat hemispheric lateralisation for these two processes: while orienting attention in space activated right inferior parietal cortex, orienting attention in time activated left inferior parietal cortex. Preferential activation of left parietal cortex for temporal orienting of attention has been replicated several times in a variety of different contexts (Bolger et al, 2014; Cotti et al, 2011; Davranche et al, 2011; Coull et al, 2016).

It's important to note that left parietal cortex activation for temporal orienting is not incompatible with the SMA activation for duration perception mentioned earlier. These neuroanatomical differences merely reflect the fact that there are many functionally distinct forms of timing. SMA and left parietal cortex activation differentially represent the ability to judge how long an event lasts (duration perception) versus the ability to predict when an event will happen (temporal orienting). The functional and anatomical dichotomy between "how long" and "when" is particularly interesting given the fact that temporal order judgement tasks also activate left-lateralized parietal cortex (Davis et al, 2009; Binder, 2015; Mizayaki et al, 2016; Moser et al, 2009). In these tasks, participants typically judge which of two events appeared first, and so requires a judgement about "when" one event appears relative to another. Left inferior parietal cortex might therefore be implicated more generally in the ability to temporally resolve and pinpoint the precise moment in time at which an event happens (Coull and Giersch, 2022).

In conclusion, action helps render the rather abstract concept of time more concrete. Children construct their notion of time through action, and action helps hone and sharpen the representation of time in adulthood. The association between time and action might therefore explain why the perception of time has come to be represented in motor structures of the brain.

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