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## Time Perception: Space–Time in the Brain

Accurate timing over the sub-second scale is essential for a range of human perceptual and motor activities, but the mechanisms for encoding this time scale are poorly understood. Recent work is suggesting that timing does not involve a centralised clock, but patterning within a distributed network.

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Time perception over fine scales is fundamental to many aspects of our lives, including speech recognition and production, motion perception, sound localisation and fine motor coordination. Many of these tasks do not require explicit encoding of time: perception of visual motion, for example, relies on the output of spatio-temporally tuned neurons rather than on independent estimates of space and time. However, the conscious awareness of the passage of time and judgement of duration do require an explicit representation of time. Although we now have a quite firm understanding of the mechanisms of many processes that involve temporal encoding — such as binaural sound localisation and motion perception — the mechanisms that allow us to estimate the duration of events are far more elusive.

The prevailing model for event timing has involved a centralised internal clock or pacemaker feeding into an accumulator (for example, see [1,2]). More recent models, however, consider distributed timing networks, with different mechanisms timing different interval lengths [3,4]. While there is good evidence for different clocks for different interval lengths, most evidence to

date suggests that clocks transcend sensory modalities. For example, performance in rhythmic tapping is well correlated with the ability to judge the length of auditory intervals of similar periodicity [5], implying a common mechanism. Similarly, training in somatosensory interval discrimination — which can cause a 2-fold improvement in performance — generalises across skin locations and also across modalities to improve auditory discrimination of similar intervals [6], and learning a visual discrimination of stimuli presented to the left visual hemifield transfers completely to stimuli in the right hemifield [7].

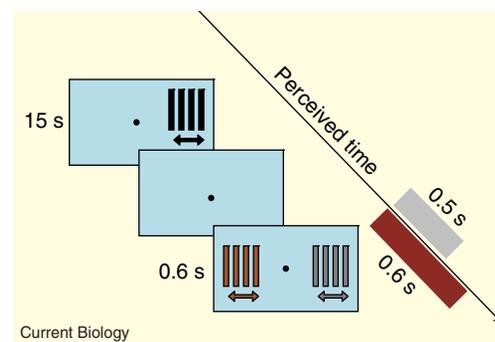
A new study, reported in this issue of *Current Biology*, questions the notion of centralised cross-modal clocks. Johnston *et al.* [8] have shown

Figure 1. The main experiment of Johnston *et al.* [8].

Subjects fixated at centre while observing a spatially localised grating move rapidly, alternately leftwards and rightwards, for 15 s. After a brief pause a 'standard' grating was presented for 600 ms on the unadapted side (brown symbols) followed (or preceded) by a probe of variable duration on the adapted side (grey symbols), and subjects asked to judge which appeared longer (in the actual experiment they were sequential, not simultaneous). In order to appear the same duration as the standard (brown bar), the probe presented to the adapted retina had to be about 100 ms (17%) shorter (grey bar).

that adaptation to a fast-moving (20 Hz) spatially localised grating decreases the apparent duration of subsequently presented gratings by about 17% (Figure 1). The adaptation does not affect the apparent duration of auditory tones, nor of visual stimuli displayed to spatially different positions, whether in the same or different hemifield. Various control experiments excluded the possibility that apparent temporal frequency, reduced via adaptation, was responsible for the diminution in apparent duration. Interestingly, the adaptation did not affect the perceived onset or offset of the visual stimuli (measured by auditory matching), only the apparent duration between them.

The results suggest that the timing of visual events is more complicated than counting the pulses of a centralised pacemaker: not only were auditory events unaltered, but the adaptation was spatially specific. Johnston *et al.* [8] argue that their results show that duration is governed by a spatially localised temporal rate signal that is subject to adaptation; this would be consistent with classical and recent work showing that moving



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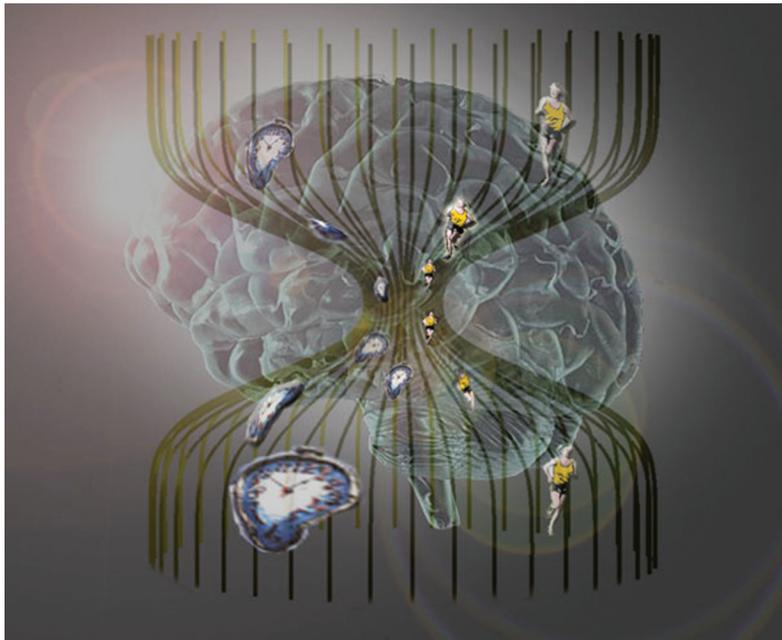


Figure 2. An artist's impression of the intrinsic connections of space and time, and how relativistic-like effects could compress perceptual space and time.

targets appear to last longer than stationary targets [9,10]. They further speculate that the purpose of the adaptation might be to maintain temporal calibration over space: as the temporal statistics of natural scenes tend to be spatially invariant, local adaptation provides an effective calibration strategy.

While the results certainly point to decentralised timing control, it is hard to imagine how the adaptation might serve a functionally useful role in 'calibrating' time across space. The temporal statistics of our retinæ are in fact rarely homogeneous: simply walking through the environment creates a complex optic-flow pattern, with the point of heading essentially stationary while the scenery either side of the heading point streams rapidly by. Indeed local adaptation could be a potential problem, were the effects not so small, around 17%, below the limit of temporal discrimination for these intervals (usually about 20% [7,8]).

A possible mechanism for the adaptation, briefly entertained by Johnston *et al.* [8], is that several systems are involved with event timing, such as the parvocellular and magnocellular systems that

are believed to carry different types of visual information, and that adaptation of one of these disrupts the balance between them. Certainly this is a testable prediction, as various techniques exist to isolate magnocellular and parvocellular function.

It is tempting to compare this new study with our own group's recent work, which also argues against centralised clocks. We have recently shown that saccadic eye movements cause a dramatic, 2-fold reduction in apparent duration of visual, but not auditory events [11] (paralleling the spatial compression that also occurs during saccades [12]). As the magnocellular system is selectively suppressed during saccades [13], it is possible that the two sets of results could reflect some common cause. But there are some major differences between the results. The effects of saccades on duration that we observed were much larger than those reported by Johnston *et al.* [8] and, under some conditions, they resulted in a reversal of perceived order. Furthermore, saccades not only reduced apparent duration, but also increased the precision of interval judgement commensurably,

preserving the Weber law relationship that characterises interval judgements [2,7]; whereas in Johnston *et al.*'s study [8] precision remained constant despite the 17% reduction in perceived duration. While it remains to be seen how much common ground may explain the two experiments, both point clearly to the existence of visually based timing mechanisms.

It would be interesting to ask whether the spatial specificity is retinotopic or spatiotopic: that is, if the observer's gaze changes between the adaptation and test stimuli, is the reduction in apparent duration specific to the part of the retina that was adapted or to the region of external space? The answer to this question could help to locate the locus of the effect [14]. If the specificity were retinotopic — if it follows the eyes — it would point to a fairly early stage of visual processing where receptive fields are locked to the retina, for example, the magnocellular system of the thalamus and its targets in V1 and V2. On the other hand, if the adaptation were spatiotopic — fixed in external coordinates — it would implicate higher levels of processing, such as LIP, a visual area where receptive fields of cells move with each eye movement. This would be particularly exciting, as recent well-controlled single-cell studies on awake monkeys have firmly implicated that area in timing the duration of visual events [15,16].

Whatever the mechanisms involved in the adaptation effects, these and other results [8,11] show that judging time is no simple task for the brain. Centralised cross-modal clocks cannot account for the new results, but nor can their existence be completely excluded, given the cross-modal correlation and learning in duration discrimination [5,6]. However, the new results fit well with recent thinking that suggests that, at least for short intervals, time may not be encoded explicitly as a metric, but as a spatio-temporal pattern within a distributed network of neurons [17,18]. Relative time between events may be transformed into

specific patterning in neural maps, interpretable with the same type of machinery used to decode cortical representation of spatial images.

Much previous work on dynamic perception has shown that for the brain time and space are not processed separately, but can influence each other strongly [19]. The new study [8] points to another example of the interaction between the two dimensions, showing that time analysis can depend on spatial position. Einstein's stunning insight that revolutionised physics a century ago was that space and time are in some sense 'the same stuff' and can be treated in the same way. Perhaps a similar conceptual leap is needed to understand space-time in the brain. While this line of thinking is clearly highly speculative, we have suggested that the effects of saccades on temporal judgements may be a relativistic-like consequence of rapidly shifting receptive-fields at the time of saccades, that also cause spatial compression [20] (schematically illustrated in Figure 2). It remains to be seen whether this approach will provide a useful framework to study spatial and temporal neural events.

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## Krill Migration: Up and Down All Night

A new study showing Antarctic krill sink when their stomachs are full has provided indirect evidence that krill undergo multiple daily vertical migrations. Such behavior could make a significant contribution to carbon sequestration by the deep oceans.

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Many small pelagic animals undertake extensive daily vertical migrations, sometimes travelling hundreds of meters to and from the food-rich surface layers of the ocean. The classic paradigm has organisms ascending to the upper layers at night to feed and returning to deeper waters during the day to avoid visual predators, predominantly fish. It has long been assumed that they make only one round trip every 24 hr [1].

While the vertical migration of populations can be monitored by sampling with nets and other devices, uncovering the movements of individuals has been more problematic. Indirect evidence — analysis of gut contents — has suggested that animals move in and out of the feeding zone, as individuals collected from deep waters at night often contain prey that are only present in surface waters [2]. Direct verification of this, however, has been lacking. A new

study [3] has provided tantalising evidence that one of the most numerically and ecologically important small pelagic species, Antarctic krill (*Euphausia superba*, Figure 1), undertake more than one vertical migration per day. As they reported recently in *Current Biology*, by examining the swimming behavior of tethered krill, Tarling and Johnson [3] have shown that individuals actively reposition themselves lower in the water column when their stomachs are full.

Antarctic krill are negatively buoyant and so must swim continuously to remain in the surface layers; if they stop swimming, they sink. Fortunately they can exert some control over their rate of descent by adopting a parachute mode, in which they fan out their swimming legs and open their feeding baskets, to decrease