

Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging

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A recent review of neuroimaging data on time measurement argued that the brain activity seen in association with timing is not influenced by specific characteristics of the task performed. In contrast, we argue that careful analysis of this literature provides evidence for separate neural timing systems associated with opposing task characteristics. The 'automatic' system draws mainly upon motor circuits and the 'cognitively controlled' system depends upon prefrontal and parietal regions.

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Abbreviations

fMRI functional magnetic resonance imaging
PMC lateral premotor area
SMA supplementary motor area

Introduction

Every action we take and every stimulus we perceive has a temporal dimension. The neural mechanisms used to measure time are currently a topic of intensive investigation – the number of neuroimaging studies seeking to define and describe them is growing rapidly, including more than 20 studies published since the year 2000. To date, no strong consensus has been reached about which brain regions are involved in time measurement; however, a recent review [1**] argues that the specific characteristics of the performed timing task do not affect the observed pattern of brain activity. Contrary to this, we suggest that much of the current ambiguity on the topic of neural time presentation may be due to the inappropriate grouping of studies that use very different time measurement tasks, thus drawing upon distinct neural timing systems. If this is the case, it should be possible to isolate the various neural systems involved in time measurement by a careful grouping of the literature, on the basis of the different task parameters used. In this review, we use precisely that approach, dividing studies of time representation according to three general task characteristics: the duration measured, the use of movement to define a

temporal estimate, and the continuity and predictability of the task.

The importance of stimulus characteristics

Our decision to characterise studies in relation to interval duration and to use of movement builds on previous suggestions that these factors discriminate between two or more different time measurement systems. Evidence suggesting the existence of different neural systems for timing at different duration ranges includes: distinct psychophysical characteristics at different durations [2]; differential responses to pharmacological agents [2–6]; differential impairment of performance by dual task [7]; and, most recently, different patterns of brain activation during the measurement of sub-second and supra-second intervals (PA Lewis, RC Miall, unpublished data).

The timing of brief intervals is frequently linked with motor control because voluntary movements are typically of sub-second durations, and can be reproduced with extreme temporal consistency. The circuitry used to ensure this consistency is likely to be located within the motor system and may be used to measure brief intervals even in the absence of movement [8,9]. This timing could be accomplished using cortically modulated central pattern generators in the spinal cord, temporal pattern generation originating from the motor cortex [10–12], or temporally predictable changes in the activity of build-up cells: preparatory cells that gradually increase in activity prior to movement [13,14]. The cerebellum may also be involved in motor timing [15,16] and shows particularly appropriate circuitry for the measurement of brief intervals [17–20]. Our division of studies on the basis of interval length and involvement of movement therefore stems from the suggestion that motor circuitry may be involved in time measurement under some circumstances, specifically during the measurement of sub-second durations or durations defined by movement.

Our division of studies according to the predictability and continuity of the time measurement task is rooted in two proposals. First, several authors have suggested that time measurements in the sub-second range are automatic, whereas measurements in the multi-second range require attention [3,6]. Second, continually measuring intervals in a repeating cycle, or in a non-repeating but pre-learned and therefore predictable pattern, requires less direct attention than the discrete measurement of non-continuous trials. This proposal arises from studies of automatic movement showing that attention is not required for the performance of over-learned motor tasks [21]. The

consistent timing achieved in these tasks [22] must also be performed in the absence of attention, and is very likely to draw upon an over-learned motor plan or programme [22,23]. Once selected and initiated, a motor programme can be executed without requiring direct attention. The measurement of a continuous series of predictable or over-learned movements should therefore require attention only during the selection and initiation phases.

Taken together with the suggestion that motor circuitry can be used to measure temporal intervals even in the absence of movement, these two proposals suggest the preferential use of motor circuitry for continuous, predictable (as opposed to discontinuous or unpredictable) time measurement tasks.

The hypothesis: automatic versus cognitively controlled timing

On the basis of our predictions regarding how the three task characteristics discussed above draw on different neural resources, we propose that two distinct systems exist for measuring time in the types of behavioural tasks examined here. We also submit that each of the task characteristics discussed above helps to partially determine which system is active in any given task. One hypothesised system, which we will designate the 'automatic' timing system, is primarily involved in the continuous measurement of predictable sub-second intervals defined by movement. Automatic timing is likely to recruit circuits within the motor system that can measure time without attentional modulation. Central pattern generators would provide an ideal mechanism for this system, as they are characterised by continuous rhythmic output. The other hypothesised system, which we will designate the 'cognitively controlled' timing system, is more involved in the measurement of supra-second intervals not defined by movement and occurring as discrete epochs. Cognitively controlled timing is likely to draw upon multi-purpose cognitive circuits within the prefrontal and parietal cortices [24]; in particular, activity is expected in areas associated with attention and working memory [3,6,25,26].

Neuroimaging studies

Figure 1 summarises the published neuroimaging literature on primate time measurement [PA Lewis, RC Miall, unpublished data, 1^{••},9,14,27–47^{••},48–52]. It lists the areas of brain activity reported in each study in response to time measurement tasks. Tasks are categorised according to whether or not a duration greater than one second was measured, whether measured intervals were defined by movement, and whether time measurement was continuous, with predictable intervals. The take home message is shown by the pattern of highlighted boxes in the figure: there is great variability between studies, but activity clusters in the upper left and bottom right corners of the table.

Figure 2 shows the percentages of studies reporting activation in a given brain area as a proportion of all studies that imaged that area and used a particular combination of timing task characteristics. An important observation to make from Figure 2 is that the activity patterns observed when studies are divided according to combinations of task characteristics (Rows [b]–[i]) produce a more coherent picture, with a higher proportion of studies in a specific category activating the same areas, than the pattern observed when studies are combined across all categories (Row [a]). If diverse tasks all drew upon the same neural timing mechanism, we might expect a stronger consensus in Row (a). Because different networks appear to be activated by tasks with different combinations of characteristics (Rows [b]–[e] versus Rows [f]–[i]), the observed pattern strongly supports the possibility of anatomically distinct neural mechanisms in time measurement.

Looking specifically at the categories emphasising automatic-related task characteristics (Rows [f]–[g]) we see very frequent activity in the motor system — the bilateral supplementary motor area (SMA) and the left sensorimotor cortex are most commonly activated; the right cerebellum and lateral premotor area (PMC) are only slightly less frequently activated; the left thalamus and the basal ganglia are also activated. Activity in the right superior temporal gyrus is also common, whereas the prefrontal cortex and the majority of parietal cortices activate only rarely.

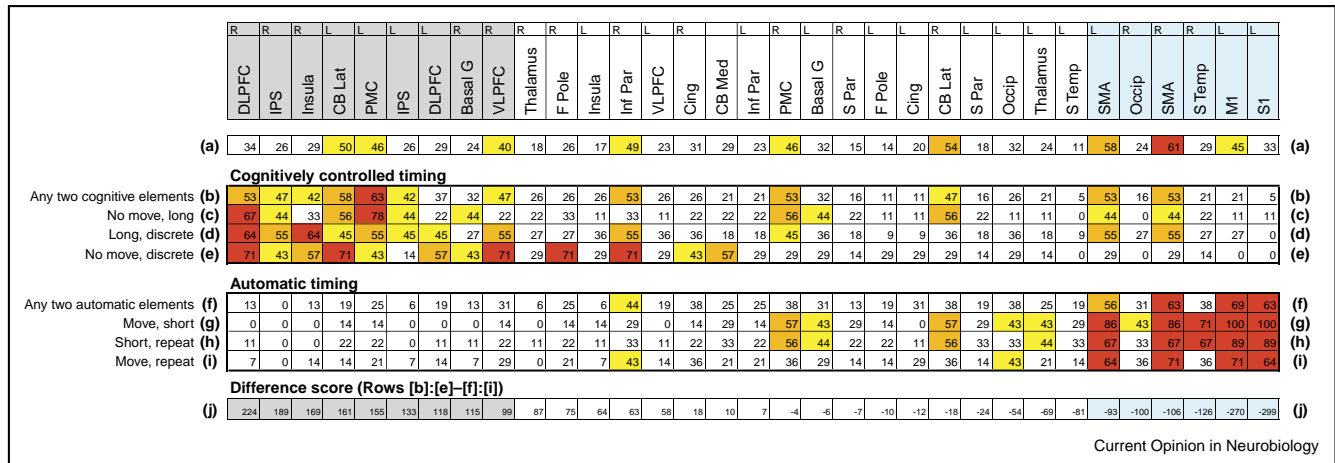
Turning to the categories emphasising cognitive-control-related task characteristics (Rows [b]–[e]), we see that although some regions frequently observed in association with automatic timing (right PMC and bilateral SMA) also activate in these conditions, considerable activity occurs in the left cerebellum and in the prefrontal and parietal cortices, with a bias to the right cortical hemisphere. This pattern suggests that, although the use of the cognitively controlled system does not preclude involvement of some parts of the automatic system, additional areas are recruited for tasks with these characteristics.

Before reading too much into the observed patterns, we should consider whether all of the activity discussed is truly associated with timing mechanisms or whether some of it might be due to confounding factors.

Challenges to the hypothesis — confounds

Because our analysis uses the most inclusive contrast from each dataset examined, much of the activity we describe may be due to task-related but non-temporal processes. Auditory, visual, and primary sensorimotor cortical activity found in association with automatic timing, for instance, might simply be due to sensory stimuli and motor responses. Some regions of the motor system, however, are active even in studies where very little

Figure 2



A summary of the activation patterns seen in Figure 1. The data from Figure 1 have been categorised by task characteristics. The percentages of studies reporting activity in specific regions in response to timing, calculated using only studies with the appropriate combinations of task characteristics, are indicated. More commonly activated regions are colour-coded from yellow (low activation) to red (high activation). For clarity, only areas that were active in at least 10% of all eligible studies are shown; many areas reported only in a minority of studies are therefore excluded from both figures. Row (a) shows the percentages of activity, calculated across all 35 datasets reviewed. Row (b) deals with studies in which any two of three task characteristics examined were associated with the cognitively controlled system. Rows (c)–(e) specify the three possible pairings of characteristics. Rows (f)–(i) follow a similar model, but for task characteristics associated with the automatic system. Columns are arranged from left to right by difference in the summed percentages in the cognitive tasks versus the automatic tasks (see Row [j]): those to the left are commonly activated in cognitive but not in automatic related tasks (grey cells in Row [j]), and vice versa for those on the right (blue cells in Row [j]); those in the centre are not strongly biased to either task type (white cells in Row [j]). Abbreviations as in Figure 1.

movement or movement preparation (and in some cases none at all) occurred during scanning. This is the case for activity in the right cerebellar hemisphere [29,36,50,51], the premotor cortex [28,33,40,51], the SMA [33,40,51], and the left basal ganglia [40,51,53], in timing tasks requiring only covert decisions, memory encoding, memory rehearsal of rhythms, or detection of oddballs. Because this activity is not due to movement (although motor imagery may occur), it may be genuinely linked to timing.

Turning to the involvement of sensory systems, several studies have described activity in the superior temporal lobe during time measurement tasks involving no auditory cues [27,30,32]. Others have shown auditory activity during task phases occurring after auditory cue cessation, such as continuation of tapping after auditory synchronisation [46], or memory encoding after presentation [50].

This activity may be associated with auditory imagery used for the task [46], and because it occurs most often in automatic timing tasks, specifically in those not involving supra-second intervals (Rows [g] and [h]), auditory imagery may be preferentially used under these circumstances. In contrast, the absence of occipital activity in tasks without visual stimuli makes it unlikely that this region is associated with temporal processing.

The areas that commonly activate during cognitively controlled tasks include regions known for their involvement in working memory (e.g. the dorsolateral prefrontal cortex), recall (e.g. the ventrolateral prefrontal cortex), and attention (e.g. the intraparietal sulcus and inferior parietal lobe), all of which processes are believed necessary for cognitively controlled time measurement [3,6,25,26]. Because tasks associated with the cognitively

(Figure 1 Legend Continued) encoding of rhythms versus the control condition, in which subjects ignored temporal information. [52] We present data from temporal measurement versus forward and backwards counting. [53] The authors report PET studies of music performance, perception, and comprehension in musicians and non-musicians. These studies suggest that the neural systems underlying music are distributed throughout the left and right cerebral and cerebellar hemispheres, with different aspects of music processed by distinct neural circuits. However, this study is excluded from Figure 1 because a comprehensive list of activated regions is not provided. Abbreviations: Basal G, basal ganglia; CB Lat, lateral cerebellum; CB Med, medial cerebellum; Cing, cingulate (anterior and posterior) DLPFC, dorsolateral prefrontal cortex (includes Brodmann’s areas 9 and 46); F Pole, frontal pole (includes Brodmann’s area 10); Inf Par, inferior parietal gyrus; IPS, intraparietal sulcus; M1, primary motor area; Occip, occipital lobe; S1, primary somatosensory area; S Par, superior parietal gyrus; S Temp, superior temporal gyrus; VLPFC, ventrolateral prefrontal cortex (includes Brodmann’s areas 45, 47, and 11). The SMA and the pre-SMA are combined as SMA; the frontal operculum is included in PMC [58], as are the frontal eye fields. The transverse temporal gyrus is included in superior temporal gyrus. Cerebellar nuclei are included in the appropriate cerebellar hemisphere. Where the laterality is not given, or is <5 mm, it is shown as bilateral. If localisations specified by authors are ambiguous (i.e. insula/operculum), they are indicated in both areas.

controlled system are quite different from those associated with the automatic system, it could be argued that the prefrontal and parietal activities observed during the former, when lenient comparisons are applied, are due to confounding task characteristics — for example, memory-related or decision-related processes — rather than to time measurement alone. That these same regions are active even when more complete cognitive subtractions are used [PA Lewis, RC Miall, unpublished data, 14,47**], however, suggests their genuine involvement in temporal processing.

Conclusions

A clear dissociation in brain activity related to timing is seen when neuroimaging studies of time measurement are divided according the interval to be measured, the use of movement to define time, and the continuity or predictability of the task. This dissociation cannot be explained by confounding task characteristics alone, and thus provides support for the existence of two distinct systems for time measurement. One, which we term the ‘automatic’ system, is closely linked to the motor and premotor circuits, with some involvement of the auditory cortex. This system does not draw much upon the prefrontal or parietal cortices. It may track time using temporal pattern generators, the temporally predictable increase or decrease of activity in build-up cells, or one of the various timing capabilities of the cerebellum. Auditory imagery may also be used. The other system, termed ‘cognitively controlled’, draws heavily upon the prefrontal and parietal cortices, which are likely to fulfil memory and attentional requirements, respectively. The prefrontal cortex is thought to be quite flexible in function, containing modules that can be recruited on demand for any one of several tasks [24]. It is possible that, although some timing functions can be performed within the less flexible neural circuits of the automatic system, direct attention to a timing task leads to the recruitment of flexible, multi-purpose modules to construct a more versatile, but temporary, clock system.

Acknowledgements

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