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

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Summary

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 upon prefrontal and parietal regions.

Introduction

Every action we take and every stimulus we perceive has a temporal dimension. The mechanisms used to measure time are currently a topic of intensive investigation, with the number of neuroimaging studies seeking to define and describe them growing rapidly. As yet, 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 activity. Contrary to this, we suggest that much of the current ambiguity on this topic may be due to inappropriate grouping of studies which use very different time measurement tasks and may draw upon distinct neural timing systems. If this is the case, it should be possible to isolate the various systems by careful grouping of the literature based on task parameters. Here, we use precisely that approach, dividing studies by three general task characteristics: duration measured, use of movement to define a temporal estimate, and continuity and predictability of the task.

Our decision to characterize studies based upon interval duration and use of movement builds on previous suggestions that these factors discriminate between two or more time measurement systems. Evidence suggesting different neural systems for timing at different duration ranges includes distinct psychophysical characteristics [2], responses to pharmacological agents [2-6], impairment by dual task scenarios [7], and, most recently, brain activation patterns (Lewis & Miall unpublished data, [8]) during the measurement of sub and supra-second intervals. The timing of brief intervals is frequently linked with motor control since 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 located within the motor system and may be used to measure brief intervals even in the absence of movement [9;10]. This timing could be accomplished using cortically modulated central pattern generators in the spinal cord, motor cortex based temporal pattern generation [11-13], or temporally predictable changes in activity of buildup cells [14;15]. The cerebellum could also be involved [16;17], and shows particularly appropriate circuitry for the measurement of brief intervals [18-21]. We therefore suggest 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 based upon the predictability and continuity of the time measurement task arises from two proposals. First, that the extent to which time is attended within a given task helps to determine which neural system is used to measure it. This idea is linked to the possibility of different systems for the measurement of short and long intervals since several authors have suggested that time measurements in the sub-second range are essentially automatic while measurements in the multi-second range require attention [3;6]. Our second proposal is that 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 is based upon studies of automatic movement which have shown that attention is not required for the performance of over-learned motor tasks [22]. The consistent timing achieved in these tasks [23] must also be performed in absence of attention, very likely drawing upon an over-learned motor plan or program [23;24]. Once selected and initiated, such a program 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 this circuitry for continuous predictable, as compared to discontinuous or unpredictable, time measurement tasks.

**The Hypothesis**

Based upon 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 behavioral tasks examined here, and that each of the task characteristics discussed helps to partially determine which system is active in any given task. One 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 likely recruits circuits within the motor system that can measure time without attentional modulation. Central pattern generators would provide an ideal mechanism for this system, since they are characterized by continuous rhythmic output. The other, 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 likely draws upon multi-purpose cognitive circuits within the prefrontal and parietal cortices [25]; in particular, activity is expected in areas associated with attention and working memory [3;6;26;27].

**The neuroimaging literature**

Table 1 summarizes the published neuroimaging literature of primate time measurement [8;10;15;28-53] by listing the areas of brain activity reported in each study. Anatomical labels are listed across the top row of the table, with laterality specified just below. Individual studies are listed row by row. Shaded cells within each row indicate peaks of significant activity as reported by the authors. To be inclusive, we report results from the most lenient comparison between conditions presented in each study i.e. test versus rest.
rather than a more rigorous control as in [32], but see our bibliographic annotations for exact details. In papers reporting multiple datasets, each set is included as a separate row in the table (see [8;32;47;49-51]). Tasks are categorized 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.

Table 2 lists the percentages of eligible studies that show activity in any given area when grouped by various combinations of their task characteristics (Rows A-J). More commonly activated regions are color coded from yellow to red. 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 tables. 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 3 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 vs. ‘automatic’ tasks (see Row J); those to the left are commonly activated in cognitive but not in automatic related tasks (gray cells in Row J), and vice versa for those on the right (blue cells in Row J); those in the center are not strongly biased to either task type (white cells in Row J).

Perhaps the most important observation to make about Table 2 is that the patterns observed when studies are divided based upon combinations of task characteristics (Rows B-I) produce a more coherent picture, with a higher proportion of studies in a category activating the same areas, than the pattern observed when studies are combined across all categories (Row A). If these diverse tasks all draw 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 vs. Rows F-I), the observed pattern strongly supports the possibility of anatomically distinct neural mechanisms.

Looking specifically at the categories emphasizing automatic related task characteristics (Rows F-G) we see that of these studies show very frequent activity in the motor system, with bilateral SMA and left sensorimotor cortex most commonly activated and only slightly less frequent activity in right cerebellum and PMC, and in left thalamus and basal ganglia. Activity in the right superior temporal gyrus is also common, while the prefrontal and majority of parietal cortices activate only rarely.

Turning to the categories emphasizing cognitive control related task characteristics (Rows B-E), we see that while some regions frequently observed in association with automatic timing also activate here (right PMC and bilateral SMA), there is also considerable activity in the prefrontal and parietal cortices, with a bias to the right cortical hemisphere, and in the left cerebellum. This pattern suggests that, although use of the cognitively controlled system does not preclude involvement of some parts of the automatic system, additional areas are also recruited for tasks with these characteristics.
Before reading too much into these patterns we should consider whether all of the observed activity is truly associated with timing mechanisms or whether some of it might be due to confounds.

**Challenges to the hypothesis – confounds**

Because our analysis uses the most inclusive contrast from each dataset examined, much of the activity we describe could 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 – in some cases no – movement or movement preparation occurred during scanning. This is the case for activity in right cerebellar hemisphere [30;37;51;52], premotor cortex [29;34;41;52], SMA [34;41;52], and left basal ganglia [41;52;54] in tasks requiring only covert decisions, memory encoding, memory rehearsal of rhythms, or detection of oddballs. Since this activity is not due to movement (although motor imagery may occur), it may be genuinely linked to timing.

Turning to the sensory systems, several studies have described activity in the superior temporal lobe during time measurement tasks involving no auditory cues [28;31;33]. Others have shown auditory activity during task phases occurring after auditory cue cessation, such as continuation tapping after auditory synchronization [47], or memory encoding after presentation [51]. This activity may be associated with auditory imagery used for the task [47], and since it occurs most often in automatic timing tasks, specifically in those not involving supra-second intervals (Rows G & H), auditory imagery may be preferentially used under these circumstances. By contrast, the absence of occipital activity in tasks without visual stimuli makes it unlikely that this region is associated with temporal processing.

The areas which commonly activate during cognitively controlled tasks include regions known for involvement in working memory (dorsolateral prefrontal cortex), recall (ventrolateral prefrontal cortex), and attention (intraparietal sulcus and inferior parietal lobe), all of which processes are believed necessary for cognitively controlled time measurement [3;6;26;27]. Because tasks associated with the cognitively controlled system are quite different from those associated with the automatic system, it could be argued that the prefrontal and parietal activity observed during the former when lenient comparisons are applied is due to confounding task characteristics – for example, memory or decision related processes – rather than time measurement alone. That these same regions are active even when more complete cognitive subtractions are used [8;15;48] however, suggests their *bona fida* involvement in temporal processing.

**Conclusions**

A clear dissociation in brain activity is seen when neuroimaging studies of time measurement are divided based upon the interval to be measured, use of movement to define time, and the continuity or predictability of the task. This 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 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 likely fulfill memory and attentional requirements, respectively. Prefrontal cortex is thought to be quite flexible in function, containing modules which can be recruited on-demand for any one of a number of tasks [25]. It is possible that, while some timing functions can be performed within the less flexible neural circuits in the automatic system, direct attention to a timing task leads to recruitment of these flexible, multi-purpose modules to construct a more versatile, but temporary, clock system.
Reference List

   Target intervals were presented by vibrotactile stimulation then reproduced by button pressing. We present data from the comparison of all timing conditions versus cued button pressing control.


   8 ss indicated via a button press whether visually presented intervals were longer or shorter than standards (0.6 and 3 s, in separate datasets). The control involved similar judgments regarding physical length of visual stimulus. We present data for time versus length at each duration.


Subjects indicated deviations in rhythm, pitch, or color of auditory or visual stimuli. We merged results from auditory and visual rhythm monitoring versus pitch/color monitoring.


We present fMRI data from the temporal production task versus cued button presses.


We report fMRI results from synchronization versus rest.


We report PET signal increases during same/different judgments of auditory rhythms versus rest. Region as specified by authors are used since coordinates are not presented.


We present data from detection of long deviant sounds versus hearing standard length sounds.

feedback about time estimation is related to a right hemisphere activation measured by PET. Exp.Brain Res. 2000, 130:328-337.
We present data for comparison of valid versus invalid duration feedback conditions in a temporal production task.
The spatial or temporal locus of a forthcoming instruction to move was pre-cued. We present time versus rest data from PET and fMRI experiments separately.
The time of a forthcoming cue to move was specified by valid or invalid pre-cues at two intervals. We present merged data from the contrast of all conditions versus rest.
All timing related activity reported is collapsed into one row of Table 1.
We collapse together results from synchronization to auditory and visual cues versus rest continuation versus rest.
Results from all uni-manual tapping conditions versus rest, and from comparisons between the bimanual tapping tasks are collapsed into a single row.
We present data from discrimination between tactile stimuli of different velocities versus rest.
We present results for temporal discrimination versus random button pressing control.
We report results from all self-paced tapping tasks versus rest.
We show results for memory timed movements versus rest.
41. Larsson J, Gulyas B, Roland PE: Cortical representation of self-paced finger
We report results from self-paced movement versus rest.

We report data from the synchronized versus cued press contrast.


We present data from temporal discrimination versus random response control.

PET data was presented separately for two monkeys, making temporal judgments versus spatial judgments; we merged results from both.

Authors present PET data from isochronous production versus baseline and repeated sequence versus isochronous in both auditory and visual conditions. To be inclusive we list areas where signal increased in either contrast and in either modality.

We collapse across results from synchronize, continue, listen, and discriminate versus rest as the latter are included in the former, but report separately the two datasets for two intervals.

We present fMRI results from temporal discrimination task versus random button-press control. Data was separated in 2.5 s epochs, but we list activity during any epoch.

We present separately results of tapping synchronization versus rest for long and short intervals, although both were acquired in a single experiment.

Subjects synchronized tapping with visual cues. Results for synchronization at 5 s versus 0.6 s are presented separately for adults and adolescents. Results from an ADHD group are excluded.

51. Sakai K: Neural representation of a rhythm depends on its interval ratio.
Two experiments, which we present as separate lines in Table 1. In both, encoding of complex versus isochronous rhythms was compared. Results from these comparisons are merged for all rhythms presented in each experiment.


We report fMRI data from encoding of rhythms versus control condition in which subjects ignored temporal information.


We present data from temporal measurement versus forward & backwards counting.


Excluded because a comprehensive list of activated regions is not provided.


Excluded because only schizophrenic versus control group data are reported.


We exclude this study because the reported activities are associated with learning rather than timing.


We exclude this study because activities relate to learning and retention rather than to rhythm production.


Table 1: areas of activity reported in reviewed studies

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Table 1: Summary of results from the majority of published neuroimaging studies of timing in primates. More information about our choice of which contrasts to include in this table is given in the bibliography. We include one study of our own which is not yet published, but currently under review [8]. Several published studies were excluded [54-58] (see bibliographic annotations for details). Cells containing an X indicate that a brain region was not scanned; and that study is excluded from further calculations (Table 2).

Abbreviations:  F Pole = frontal pole, DLPFC = Dorsolateral Prefrontal Cortex, VLPFC = Ventrolateral Prefrontal Cortex, PMC = lateral premotor area, S. Par. = superior parietal gyrus, IPS = intraparietal sulcus, Inf. Par. = inferior parietal gyrus, Cing. = cingulate gyrus, SMA = supplementary motor area, M1 = primary motor cortex, S1 = primary somatosensory cortex, CB Lat. = lateral cerebellum, CB med. = medial cerebellum, Occip. = occipital lobe, SMA = supplementary motor area, S. Temp = superior temporal gyrus, Basal G. = basal ganglia.

Anatomical definitions used: DLPFC includes BA 9 and 46; VLPFC includes BA 45, 47, & 11; frontal pole includes BA 10. SMA and pre-SMA are combined as SMA, anterior and posterior cingulate are combined as cingulate, and frontal operculum is included in PMC [59], 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 localizations specified by authors are ambiguous (i.e. insula/operculum), they are indicated in both areas.
Table 2: Percentage of studies active in each area

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**DIFFERENCE SCORE** rows B-E: J
Table 2: The data from Table 1 has been categorized by task characteristics and the percentages of studies reporting activity in each region, calculated using only studies with the appropriate combinations of task characteristics, are indicated. See main text for details.

KEYWORDS:
Time perception; timing; functional imaging; automatic movement; neural clock;