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Research report

Neural systems supporting timing and chronometric counting: an FMRI study

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Abstract

At least two strategies are available to humans for estimating multisecond intervals. One depends on an interval timing system that is common to many species. The other is the language-based strategy of chronometric counting. These two strategies are easily distinguished by the psychophysical properties of their behavioral correlates: counting supports substantially more precise estimates than are possible using the more general interval timing system. The present study investigates the neural systems that underlie the execution of these different strategies. Eighteen adults reproduced a 16-s interval either by internally timing or covertly counting the duration. Comparison of counting and timing to a resting baseline suggested that these strategies engage some nonoverlapping neural systems. Counting, but not timing, strongly activated Broca's area, primary motor cortex in the mouth region, and right cerebellum, all of which are associated with internal speech. Counting also activated parts of the medial premotor circuit, including the putamen, supplementary motor area (SMA) proper, and cingulate motor area (CMA), that have been associated with reproducing isochronous and syncopated rhythms of elements lasting hundreds of milliseconds. During timing, only a portion of this circuit, the SMA proper and CMA, was engaged. Both timing and counting interfered with semantic processing during the resting state, evidenced by task-related decreases in the left inferior and middle frontal gyri, right superior frontal gyrus, left angular gyrus, and bilateral posterior cingulate cortex. This study suggests that counting activates a corticostriatal network associated with millisecond, rhythmic timing. In contrast, timing long durations without the benefit of linguistic strategies for subdividing counts reduces activity in this circuitry.
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Theme: Neural basis of behavior
Topic: Cognition

Keywords: Neural system; Internal timing; Time perception; Counting; fMRI

1. Introduction

The ability to time intervals ranging from milliseconds to hours is a cognitive capacity found widely among fish, birds, and mammals [7,54,61]. A model called Scalar Expectancy Theory has been highly successful in accounting for various properties of interval timing that are apparent across species [12,13]. Interval timing relies upon distributed corticostriatal networks and neurotransmitter systems that have been identified in some detail in animals [37] and humans [19], and their functional significance is beginning to be elucidated using a variety of psychophysical, pharmacological, electrophysiological, and functional neuroimaging methods [24,38].

The study of human timing presents an additional challenge in that humans frequently use a language-based strategy, called chronometric counting, to estimate durations [15]. A counting strategy allows multisecond durations to be estimated with greater precision than is possible using only the interval timing system [48]. When counting, estimation of a single long interval is reduced to a consecutive series of estimates of brief intervals in the millisecond range. The functional consequence of this subdivision process is that counting displays very different psychophysical properties

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than does timing [26]. For timing, the standard deviation of the response distribution scales proportionally with the timed duration, a scalar property that is an instantiation of Weber's law [12]. For counting, it is the *variance* of the response distribution, rather than the standard deviation, that scales with the counted duration. Thus, for counting, the standard deviation of the response distribution scales proportionally to the square root of time. In practical terms, counting improves our ability to estimate durations beyond a few seconds over the natural timing ability conferred by our brain's interval timing system, and the relative improvement in precision that counting provides increases as the counted duration lengthens.

Previous animal research has suggested that counting and timing may rely on common neural mechanisms [39,40]. Thus, while a counting strategy violates the scalar property globally, the distributions of individual counts themselves *do* obey the scalar property [65,66]. This observation suggests that humans may in fact use the interval timing system to generate individual counts when counting, although the molar effect of summing those individual counts results in greater precision than would be expected from the scalar property expressed by timing.

The fact that counting and timing produce clearly distinguishable patterns of behavioral data raises the question of whether performing these strategies depends upon similar or distinct neural systems. To date, several neuroimaging studies have examined counting in humans, but these have focused on counting as a means of quantifying simultaneously presented visual stimuli [45,52] or successively presented auditory stimuli [41] rather than for the explicit purpose of estimating an interval of time.

Given the possibility that individual counts may in fact depend upon the interval timing system for their generation, we hypothesized that timing and chronometric counting would activate largely overlapping brain networks that are associated with the clock process. However, we expected counting to engage additional cognitive operations that are not required by interval timing itself, such as internal verbalization to express the current count and increased attention and working memory to maintain the count. These additional operations might either amplify the same neural systems activated by interval timing or activate entirely different brain areas than those recruited by timing. The following experiment was performed to evaluate these competing hypotheses by directly comparing the patterns of neural activation evoked when participants performed a temporal reproduction task under either counting or timing instructions.

2. Materials and methods

2.1. Participants

Eighteen healthy adults participated, ages 21–47 (mean = 30.2, standard deviation = 7.5; 10 males). They were recruited from students and staff at the Medical College of Wisconsin (MCW) and were compensated US$15/h. All provided written informed consent according to the guidelines of the MCW Institutional Review Board.

2.2. Apparatus

Stimuli were presented and responses collected using a custom program written in E-Prime v. 1.1 (Psychology Software Tools). Visual stimuli were rear-projected onto an opaque frosted-glass screen located at the participant's feet. Participants viewed the screen through right-angle prism glasses. A nonferrous key press pad was used to record participants' responses.

2.3. Experimental design

We explicitly compared counting and timing of a 16-s interval by the same group of subjects using the peak-interval timing procedure, also known as the "peak procedure" [6,51]. All participants had previous experience with both tasks because they had been tested in a similar behavioral experiment outside the scanner [26].

The experiment was composed of six functional imaging runs, that alternated between the timing and counting tasks. Participants were asked to focus on a white fixation cross displayed in the center of the screen. Each imaging run was preceded by three training trials in which a vertically oriented, blue rectangle appeared on the screen for 16 s then changed color to magenta for 1.5 s. The training trial allowed encoding of the interval to be reproduced during the subsequent imaging run. The intertrial interval (ITI) for the training trials was 1 s.

Each functional imaging run began with a 12-s presentation of the fixation cross on a black background. Each task had 21 trials per run. The total run duration was 720 s. The signal to be timed or counted was the duration of a blue rectangle that subtended approximately 3.6 × 3.0 degrees of visual angle and was overlaid with the white fixation cross. In the testing trials, participants made a single key press with their right index finger when they believed the 16-s duration they learned in the training trials had elapsed. Visual feedback was provided randomly on half the trials immediately after the key press. The feedback display, which remained on for 1 s, consisted of a histogram that was divided into 20 time bins of 1.6 s each and ranged from 0–32 s. The letter "T" was presented below the *x*-axis to indicate the target duration on a relative time scale without providing information about its absolute duration. A white bar filled one of the bins indicating when the participant's response occurred. A green line above the graph indicated good performance (within ± 30% of the target duration). Earlier and later regions had a red line above them. Trials were separated by randomly selected intertrial intervals of 11, 15, or 19 s.

2.4. Tasks instructions

The stimulus presentation parameters were identical for each task; only the instructions differed. The instructions common to both tasks were as follows: "Use your right index finger to make a single response when you think the color change should occur. You will get feedback after a random half of the trials. Try to use the feedback to improve your performance on subsequent trials. Please maintain your focus throughout the run on the fixation cross in the middle of the screen."

In a timing run, participants were instructed not to count, use any other process of subdivision (such as foot tapping, humming, singing, etc.), or use any external timing mechanism. They were instructed to use their internalized perception of the temporal duration of the blue rectangle presented during the training trials to guide their performance during the testing trials. In a counting run, participants were instructed to count mentally without moving their mouth as follows: "one-thousand, *one*. . ., one-thousand, *two*. . .," etc. This instruction insured that all participants counted using the same strategy at a rate of approximately 1 count per s. This chronometric counting strategy allowed participants to determine a count during the training trials corresponding to the duration that had elapsed when the color change occurred. That count was then used during the testing trials to decide when to respond.

2.5. Scanning procedure

Event-related fMRI was performed on a 1.5T GE Signa scanner equipped with a three-axis, local-gradient head coil and an elliptical, end-capped, quadrature radiofrequency coil. Foam padding was used to limit head motion within the coil. Prior to functional imaging, a high-resolution, three-dimensional, whole-brain volume was collected for anatomic localization and coregistration using a spoiled, gradient-recalled at steady-state pulse sequence (TE = 5 ms, TR = 24 ms, 40° flip angle, NEX = 1, slice thickness = 1.2 mm, FOV = 24 cm, resolution = 256 × 192). Functional images were collected using a single-shot, blipped, gradient-echo, echo-planar pulse sequence (TE = 40 ms, TR = 2 s, 90° flip angle, FOV = 24 cm, resolution = 64 × 64 matrix). Nineteen contiguous 7-mm sagittal slices were acquired to provide coverage of the entire brain. Each run began with six blank images (12 s) prior to task onset to allow the MR signal to reach equilibrium. Three hundred sixty images (720 s) were collected per run.

2.6. Behavioral data analysis

For each task, response times from all trials were pooled into a single frequency distribution with 0.5-s bins to generate a response distribution, which was normalized by maximum response rate to allow comparison across individuals. These normalized peak functions were fit with two-parameter Gaussian curves (mean and standard deviation) using the SPSS PeakFit program (v. 4.11, SYSTAT Software, 2001). A least-squares method that minimized the residuals determined the best-fitting Gaussian function. Two measures of interest were extracted from the fitted curves: the mean of the distribution (*peak time*) and the width of the distribution at half the maximum height (FWHM, or *spread*). *Peak time* is a measure of timing accuracy. *Spread* is a measure of timing precision that is numerically equivalent to 2.355 standard deviations. *Peak time* and *spread* were separately analyzed using a repeated-measures ANOVA that tested the within-subject effect of task (counting vs. timing).

Group-averaged response distributions for each task were generated by summing participants' normalized response distributions, smoothing the group distributions with a three-point moving average, and height-normalizing them by the percent of maximum responses per bin.

2.7. fMRI data analysis

Functional images were analyzed using Analysis of Functional NeuroImages (AFNI) software [9]. The first 12 s and last 4 s of each run were discarded, and the six runs of 352 images each were concatenated. The time series of images was spatially 3D-registered to reduce the effects of head motion. The response to each task was calculated by averaging single trials separately for counting and timing from trial onset to 34 s after trial onset. Using a local baseline calculated by averaging the values in the first and last averaged volumes, percent signal change was calculated for each time point in the response curve. For group analyses, individual subject data were converted to standard Talairach stereotaxic space [60] and blurred using a 6-mm FWHM Gaussian filter. For voxel-wise analyses, the variable of interest was the area under the percent-signal-change response curve (AUC) during the time period prior to the typical hemodynamic delay of the motor response (2–18 s after trial onset). A voxel-wise, one-sample *t*-test with 18 subjects ($df = 17$) was used to compare counting or timing AUC during this period to the zero baseline. Clusters in which the AUC was significantly different from zero in either task were defined as regions of interest (ROIs), and the response curves for each task were plotted as percent signal change. Large clusters containing insula, putamen, and inferior frontal gyrus were separated into foci of activation along minima conforming to regions of white matter. In addition, a voxel-wise, paired *t*-test ($df = 17$) directly compared counting vs. timing AUC. Data were thresholded at a voxel-wise p value of 0.001 using a minimum cluster size threshold of 400 μl. These values were determined by a Monte Carlo simulation using the AFNI program *AlphaSim* and correspond to a false positive cluster detection rate of $p < 0.05$ for the entire brain volume.

Task subtractions were performed for Counting–Baseline, Timing–Baseline, and Counting–Timing. Left and right lateral surfaces of the hemispheres and a midsagittal view were rendered on a fiducial brain using CARET [63]. Semitransparent axial slices through the basal ganglia ($z = 0$ to $+9$ mm) and cerebellum ($z = -20$ to -25 mm) were rendered using AFNI.

3. Results

3.1. Behavioral performance

The group-averaged response distributions in Fig. 1 closely conform to those previously published in a similar behavioral experiment [26]. Both counting and timing strategies produced temporally accurate performance, as indexed by the peak of their corresponding response distributions, which occurred at the target time of 16 s. *Peak times* for the two tasks were equivalent [counting = 15.9 ± 0.2 s (mean ± standard error of the mean); timing = 16.2 ± 0.2 s; $F(1,17) = 2.16$, *n.s.*], showing that counting and timing are equally accurate methods for reproducing a 16-s duration. However, counting produced substantially more reliable estimates, as indicated by the reduced *spread* of its response distribution (counting = 2.4 ± 0.2 s; timing = 6.9 ± 0.5 s). The *spread* was significantly smaller for counting than timing [$F(1,17) = 92.14$, $p < 0.0001$].

3.2. Functional imaging data

Fig. 2 displays renderings of the Counting–Baseline, Timing–Baseline, and Counting–Timing subtractions. Increases in relative MR signal intensity are indicated in red and decreases are shown in blue. Tables 1 and 2 provide a summary of the significant activation clusters for each subtraction.

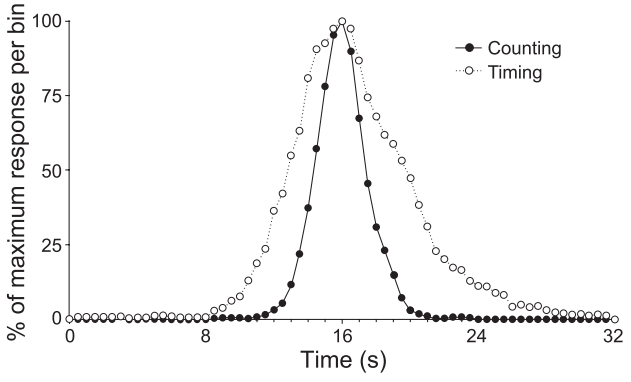


Fig. 1. Response distributions plotted on a relative response axis for the counting and timing tasks.

3.2.1. Counting vs. baseline

Counting resulted in increased bilateral activation relative to baseline in the supplementary motor area (SMA) proper and cingulate motor area (CMA), primary motor cortex (M1; mouth region), inferior frontal gyri (IFG; pars opercularis, BA 44), and putamen (Put). Counting also activated the left insula and a right-lateralized focus in the cerebellum located in the culmen in lobule V and declive in lobule VI [53]. In contrast, counting was associated with decreased activation relative to baseline in the IFG pars triangularis and orbitalis (45/47).

3.2.2. Timing vs. baseline

Timing resulted in increased bilateral activation in the SMA proper, CMA, insula, and primary visual cortex (V1). In contrast, timing produced lateralized decreases in activation relative to baseline in the left IFG (pars triangularis, BA 45)/left MFG (BA 46), left middle frontal gyrus (MFG; BA 6/9), left angular gyrus (AG), right superior frontal gyrus (SFG; BA 8), and bilateral posterior cingulate (Post Cing).

3.2.3. Counting vs. timing

Counting was associated with greater activation than timing bilaterally in the SMA proper, M1 (mouth area), putamen, and left IFG (BA 44). No areas were activated more strongly by timing than by counting.

3.3. Time course of functional activity

Our hypothesis that counting and timing would use fundamentally similar neural processes led us to examine the time course of activation in all regions activated by either task (Table 1). Fig. 3 shows the time courses from 16 of the 17 identified regions of interest (ROI) affected (increases or decreases) by either counting or timing. One ROI not shown (right SFG, BA 8) was very similar to the other negative time courses for both tasks. The majority of positive time courses appeared bimodal with an initial rise after trial onset and a second rise after the onset of the motor response. Negative time courses appeared unimodal and reached a nadir shortly after the motor response.

The positive signal changes were distributed fairly symmetrically across the hemispheres, whereas the negative signal changes tended to be more lateralized to the left hemisphere. The differences between the counting and timing time courses were maximal in the primary motor cortex bilaterally in the mouth region. Other areas where the time course was of higher amplitude for counting than timing included the left IFG (corresponding to Broca's area), SMA proper/CMA, putamen bilaterally, and the right cerebellum, although the latter region displayed sufficient within-subject variability in our voxel-wise analysis such that the difference between the two conditions did not prove significant. For the majority of time courses, the amplitude for timing was substantially less than the ampli-

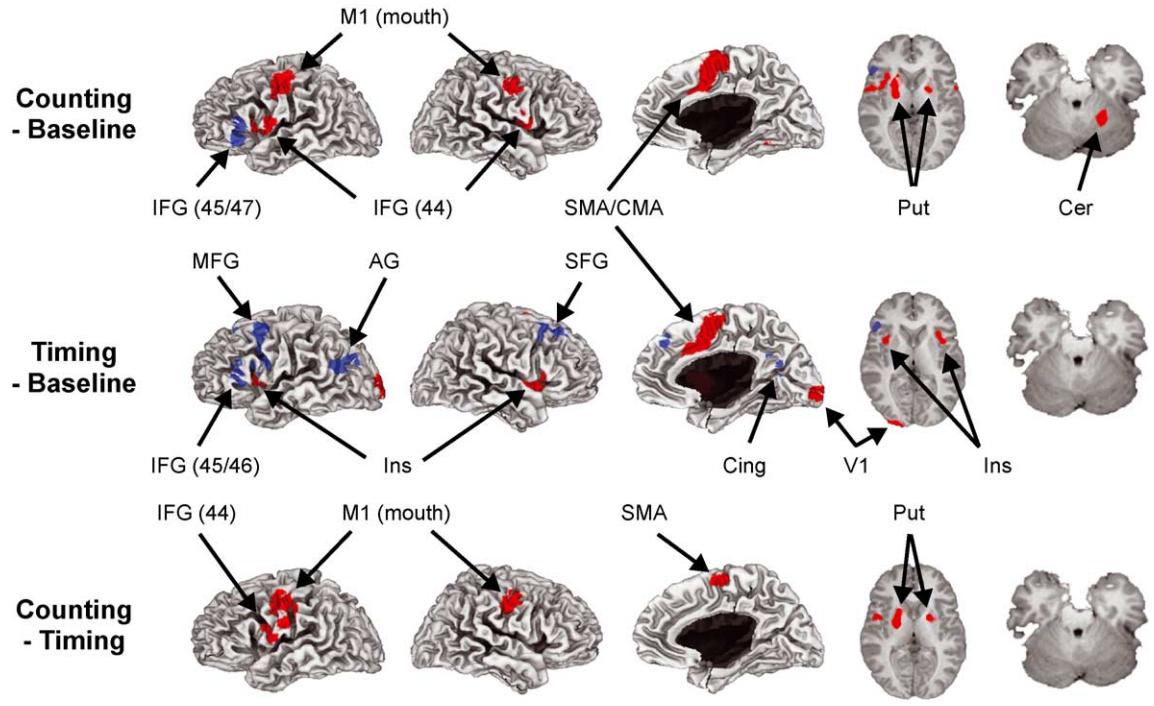


Fig. 2. Left and right lateral and midline hemispheric renderings (columns 1, 2 and 3) and axial slices through the basal ganglia (column 4) and cerebellum (column 5). Primary motor cortex (M1), inferior frontal gyrus (IFG), supplementary motor area (SMA), cingulate motor area (CMA), putamen (Put), cerebellum (Cer), middle frontal gyrus (MFG), angular gyrus (AG), superior frontal gyrus (SFG), insula (Ins), posterior cingulate (Cing), primary visual cortex (V1). Basal ganglia and cerebellar axial slices are centered approximately +4.5 and −22.5 mm from the AC/PC line, respectively; left is on reader's left.

tude for counting. In light of the basal ganglia's importance in timing, we conducted a follow-up analysis that examined changes in signal intensity from baseline in the putamen for each time point after trial onset. A transient, but significant ($p < 0.05$) increase in signal was observed in the right putamen 4 s after trial onset for timing.

4. Discussion

Our results showed that counting produced equally accurate but less variable estimates than timing, consistent with previous work (e.g., Refs. [11,16,26,65]). In humans, counting is thought to minimize the scalar effects of clock sources of variability by subdividing a long duration with shorter, internally generated counts [26]. However, counting and timing may use the same internal clock as their timing source [65]. The law of large numbers implies that the greater the number of counts used to estimate a particular duration, the less variable will be the estimate of that duration. However, each count requires the full set of processes related to using the internal clock: starting, comparing, deciding, stopping, and resetting. Counting may also reduce memory and decision variability because durations would not be sampled from a potentially large distribution of values in long-term memory for comparison with the current time. Counting simplifies the decision process and minimizes the use of long-term memory because it requires comparison with only a single abstract numerical representation for the participant to determine when to respond. However, use of working memory may increase as participants keep track of the current count. This view implies that counting should increase activation in systems associated with both clock and working memory processes. Our main fMRI results were consistent with this prediction, showing that counting, but not timing, activated a network of brain regions associated with subvocal rehearsal during working memory. Counting also produced greater activation than timing in the medial premotor circuit, which has been associated with reproducing intervals in the range of several hundred milliseconds to several seconds. We now turn to a discussion of these results.

4.1. Counting activates internal subvocal rehearsal systems

The most striking differences between counting and timing were found in regions classically associated with internal speech. Converging evidence using different tasks and neuroimaging techniques implicates the left inferior frontal cortex (BA 44), left ventral premotor cortex, and right cerebellum in mediating verbal rehearsal [3,22,42,55,58]. There were also striking differences between counting and timing in activation of bilateral primary motor cortex in a region associated with tongue or mouth movements and articulation [2,5,8,30,34,44,67]. All of these regions showed sustained activation during counting, but

Table 1
Regions demonstrating significant departures from baseline MR signal intensity levels for counting and timing from 2 to 18 s after trial onset (voxel-wise, one-sample *t*-tests, $df = 17$, $p < 0.05$)

Task comparison	Side	BA	μl	*x*	*y*	*z*
Counting>baseline						
Frontal						
SMA proper/CMA	B	6/32	7485	1	−1	52
M1 (mouth)	L	4	3137	−45	−11	44
M1 (mouth)	R	4	798	50	−11	42
IFG	L	44	774	−51	1	9
IFG	R	44	609	54	−1	14
Insula	L	–	1158	−34	11	9
Subcortical						
Putamen	L	–	3769	−20	2	5
Putamen	R	–	1682	21	5	3
Cerebellum (V/VI)	R	–	884	23	−51	−21
Baseline>counting						
Frontal						
IFG	L	45/47	1549	−48	27	5
Timing>baseline						
Frontal						
SMA proper/CMA	B	6/32	6044	3	6	45
Insula	R	–	1870	36	10	4
Insula	L	–	581	−35	8	9
Occipital						
V1	L	17	1609	−19	−96	4
V1	R	17	639	13	−93	−4
Baseline>timing						
Frontal						
MFG	L	6/9	5448	−33	10	39
SFG	R	8	2492	22	22	46
IFG	L	45/46	1649	−46	25	14
Parietal						
AG	L	39	983	−47	−65	20
Post. cingulate	B	23	577	−5	−59	17

Right (R), left (L), bilateral (B). Brodmann areas (BA). volume of activation in microliters (μl). *x*, *y*, and *z* = Talairach coordinates of center of mass in millimeters. Supplementary motor area (SMA), cingulate motor area (CMA), primary motor cortex (M1), inferior frontal gyrus (IFG), primary visual cortex (V1), middle frontal gyrus (MFG), superior frontal gyrus (SFG), angular gyrus (AG), posterior cingulate (post. cingulate).

no significant changes from baseline during timing. The most parsimonious explanation of the counting results is that participants subvocalize their count in a way that covertly engages this rehearsal network. This interpretation accounts for the left IFG activation in Broca's area, which is associated with internal speech [23]. Likewise, subvocal rehearsal tasks engage the right cerebellum as part of verbal processing [42,57]. Of particular relevance to our study is that activation in right cerebellar lobule VI is specifically sensitive to verbal working-memory load, suggesting that it processes input from left frontal articulatory-control systems in the IFG [10]. Thus, regions involved in internal speech are activated strongly when people use a counting strategy to reproduce an interval.

While timing a 16-s interval did not activate the IFG in our study, other work has shown that auditory rehearsal networks support the estimation and reproduction of shorter intervals (i.e., 300–1200 ms) [49,50], which typically do not benefit from using counting strategies [16]. In these studies, estimating or reproducing the duration of *tones* is mediated largely by a right hemisphere IFG (BA 44) and superior temporal gyrus (BA 22) network, which appears to sustain the internal rehearsal of nonlinguistic auditory representations [42]. Our results suggest that explicit instructions to not engage in counting suppress nonlinguistic rehearsal processes as well. At the same time, the modality of the timed event, which was *visual* in the present study, elicits activity in systems that support visual representations. It was notable that timing, but not counting, significantly engaged V1 bilaterally. Fig. 3 shows that V1 activity was sustained throughout the 16-s interval in the timing task, whereas in the counting task it decreased or returned to baseline shortly after the onset of the trial. Although the counting time course of V1 activation in the left hemisphere appears to be significantly different from baseline, the relatively greater variability of its time points prevented their reaching statistical significance in the more conservative analysis employed to identify the ROIs. One might speculate that the timing task encourages participants to pay more attention to the visual stimulus, resulting in increased V1 activation through top-down attentional mechanisms [29]. In contrast, an instruction to estimate a visual event using a counting strategy may motivate participants to redirect more of their attention to the current count, thereby engaging subvocal rehearsal systems.

4.2. Counting activates the medial premotor circuit

Counting strongly activated regions comprising the medial premotor circuit [1] including bilateral putamen and the

Table 2
Regions demonstrating significant differences between counting and timing from 2 to 18 s after trial onset (voxel-wise, paired *t*-tests, $df = 17$, $p < 0.05$)

Task comparison	Side	BA	μl	*x*	*y*	*z*
Counting>timing						
Frontal						
SMA	B	6	1509	0	−7	59
M1 (mouth)	L	4	3401	−50	−11	38
M1 (mouth)	R	4	972	51	−12	41
IFG	L	44	658	−47	1	11
Subcortical						
Putamen	L	–	3735	−21	−2	8
Putamen	R	–	962	22	0	7
Timing>counting						
None						

Right (R), left (L), bilateral (B). Brodmann areas (BA). Volume of activation in microliters (μl). *x*, *y*, and *z* = Talairach coordinates of center of mass in millimeters. Primary motor cortex (M1), supplementary motor area (SMA), inferior frontal gyrus (IFG).

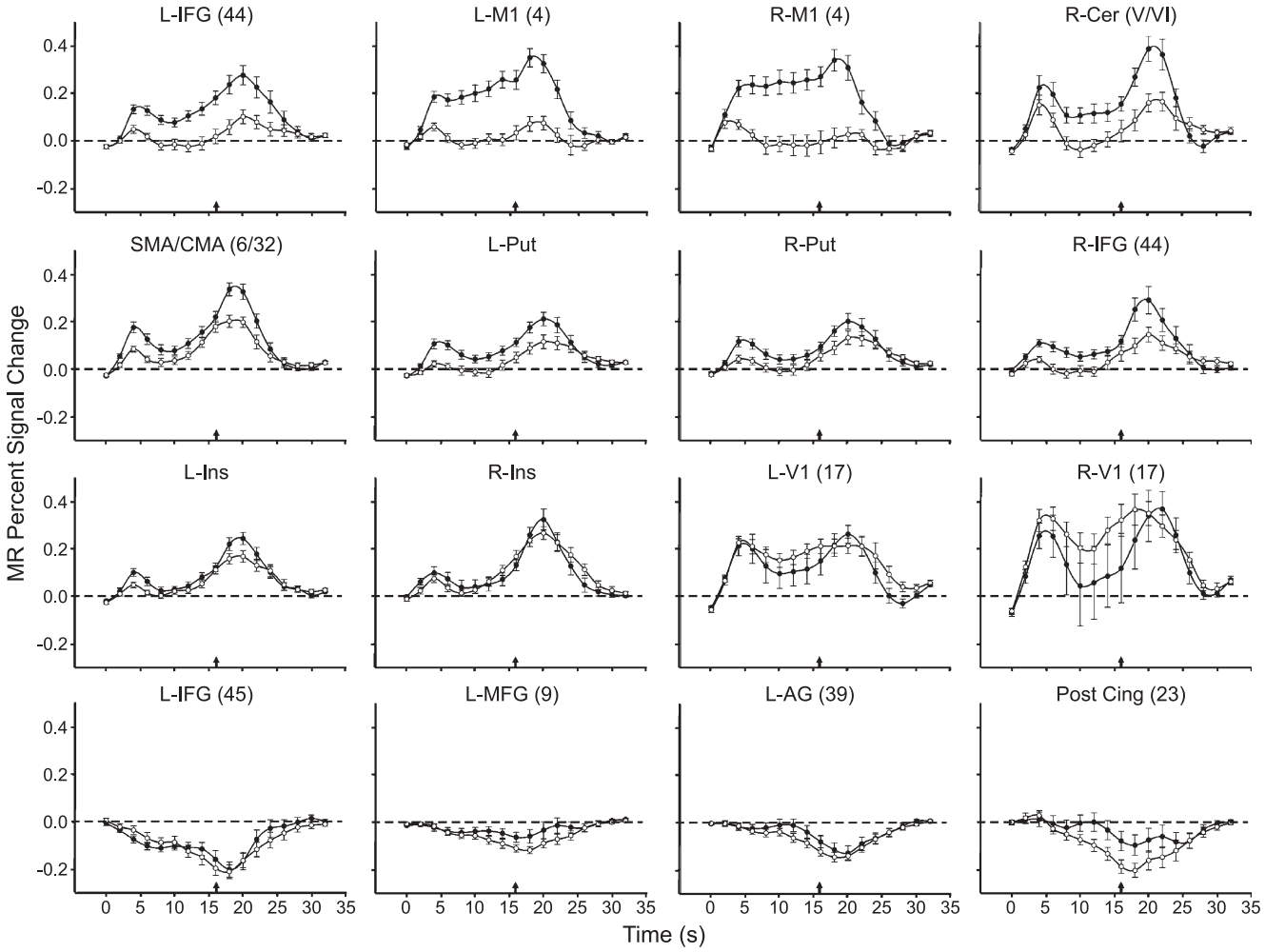


Fig. 3. Selected event-related averaged time courses extracted from 16 regions of interest (Table 1) for the counting (●) and timing (○) tasks. Left (L), right (R), primary motor cortex (M1), supplementary motor area (SMA), cingulate motor area (CMA), insula (Ins), putamen (Put), inferior frontal gyrus (IFG), middle frontal gyrus (MFG), superior frontal gyrus (SFG), angular gyrus (AG), posterior cingulate (Post Cing), primary visual cortex (V1), cerebellum (Cer). Error bars represent standard errors of the mean. Small arrows located at 16 s on the *x*-axes indicate the most typical time of the motor response.

SMA proper. In humans, this corticostriatal network has been associated with generating precisely timed, isochronous rhythms lasting several hundred milliseconds and syncopated rhythmic sequences lasting a few seconds [28,43,49].

The SMA was engaged most robustly by the counting task but was also activated by the timing task. Our results suggest that the SMA may be necessary for using a counting strategy and may also play a key role in computing time. Although SMA activation accompanies both temporal and nontemporal discriminations (e.g., pitch) [50], suggesting that its function is not unique to timekeeping operations, it is closely associated with internally generated planning or anticipatory processes [62]. Other work has shown that the SMA responds to the duration of events [31,32]. EEG recordings and lesion studies in humans have shown that the SMA is involved in temporal regulation [18,31,64].

While other studies have reported SMA, but not basal ganglia, activation during the timing of shorter durations (<2 s) [17,27], the majority have found that interval timing on a variety of tasks is associated with basal ganglia activation [14,19,20]. Assuming that counting requires timing of shorter subintervals, the bilateral putamen activation we observed while participants counted is consistent with animal studies, which show that the basal ganglia are the targets of dopaminergic inputs that alter the rate of the clock process during interval timing of durations lasting 2–60 s [25,33,36,37]. Contrary to our expectations, the putamen was not activated by the timing task if the entire 16-s premovement period is examined, although a small, transient increase in putamen activation was observed bilaterally 4–6 s after trial onset (see Fig. 3). Our results indicate that timing activates elements of the medial premotor circuit much less than does counting.

Finally, it is notable that our results in the counting task closely resembled our fMRI study of motor timing, in which healthy adults repeatedly tapped at a pace of 300 or 600 ms [49]. Similar to the present study, activation was found in the medial premotor circuit (putamen, SMA proper), suggesting that similar corticostriatal networks support the reproduction of short intervals and chronometric counting. These results contrast with our studies of time discrimination, wherein interval encoding is more closely associated with activation in a "complex circuit" involving the caudate and pre-SMA [21,46,50]. Taken together, these results raise the intriguing possibility that distinct corticostriatal circuitry may support timing for different purposes.

4.3. "Deactivation" by timing and counting

Several areas showed decreases in MR signal during the tasks relative to the resting baseline. These regions, which included the angular gyrus, dorsal prefrontal cortex, posterior cingulate, and anterior inferior frontal gyrus, comprise a network that consistently shows deactivation across a variety of tasks [35,47,56]. Many authors have interpreted this deactivation as evidence that cognitive processes such as thinking, planning, and monitoring the environment occur during "rest" and are interrupted or suppressed during task performance [35,47,59]. For example, several of these regions have been implicated in semantic processing [4]. We speculate that subjects engaged in such processes during the relatively long rest intervals between trials of the present study, and that these processes were interrupted when the task resumed, producing deactivation. As in previous studies, the areas showing deactivation were relatively left-lateralized, suggesting at least some overlap with language systems. This network of areas is generally deactivated somewhat less by counting than by timing, possibly because the linguistic aspects of the counting task weakly engaged the network and thereby reduced the difference between the task and resting states.

5. Conclusions

The present findings replicated previous behavioral results showing that while both counting and timing sustain temporally accurate performance, counting produces more reliable estimates, as indicated by decreased variability in the distribution of responses. Our fMRI results extended this work by illuminating the neural basis for chronometric counting of long durations. Consistent with behavioral models, counting activated brain regions associated with internal subvocal rehearsal systems and working memory, and also a corticostriatal network that has been associated with the clock process, the medial premotor circuit. However, this circuit was only partially activated during timing, suggesting that other systems may also play an important role in interval timing. Finally, both counting and timing interfered with semantic processing presumed to occur during the baseline "rest" period.

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