SMA Selectively Codes the Active Accumulation of Temporal, Not Spatial, Magnitude

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Abstract

■ Estimating duration depends on the sequential integration (accumulation) of temporal information in working memory. Using fMRI, we directly compared the accumulation of information in temporal versus spatial domains. Participants estimated either the duration or distance of the dynamic trajectory of a moving dot or, in a control condition, a static line stimulus. Comparing the duration versus distance of static lines activated an extensive cortico-striatal network. By contrast, comparing the duration versus distance of dynamic trajectories, both of which required sequential integration of information, activated SMA alone. Indeed, activity in SMA, as well as right inferior oc-cipital cortex, increased parametrically as a function of stimulus duration and also correlated with individual differences in the propensity to overestimate stimulus duration. By contrast, activity in primary visual cortex increased parametrically as a function of stimulus distance. Crucially, a direct comparison of the parametric responses to duration versus distance revealed that activity in SMA increased incrementally as a function of stimulus duration but not as a function of stimulus distance. Collectively, our results indicate that SMA responds to the active accumulation of information selectively in the temporal domain. ■

INTRODUCTION

In the last decade, interest in the neural bases underlying timing processes has accelerated (Allman, Teki, Griffiths, & Meck, 2014; Merchant, Harrington, & Meck, 2013; Wittmann, 2013; Coull, Cheng, & Meck, 2011; Buonomano & Maass, 2009; Ivry & Schlerf, 2008; Buhusi & Meck, 2005). Evidence from neuroimaging studies has revealed a widespread timing-related network of activation including many cortical (prefrontal, temporal, and parietal corti-ces) and subcortical (basal ganglia and cerebellum) brain structures (Wiener, Turkeltaub, & Coslett, 2010; Coull & Nobre, 2008; Lewis & Miall, 2003). However, this extensive network of activation may not merely reflect the complex functional network involved in timing but may instead re-sult from the difficulty in isolating timing from other cogni-tive demands. Whereas durations up to approximately 200–300 msec may be coded as unique and autonomous, sensory-specific events (Spencer, Karmarkar, & Ivry, 2009; Karmarkar & Buonomano, 2007), estimating duration in the range of hundreds of milliseconds to seconds is a dy-namic process that depends on a number of accessory cog-nitive processes, such as sustained attention and working memory (WM; Ogden, Wearden, & Montgomery, 2014; Brown, Collier, & Night, 2013; Zélanti & Droit-Volet, 2011; Brown, 2008; Lustig, Matell, & Meck, 2005; Fortin & Rousseau, 1998; Zakay & Block, 1996). In the field of neuroimaging, several authors have tackled this problem by comparing the timing task with control tasks that make similarly dynamic demands, for example, averaging the length of a fluctuating line (Lewis & Miall, 2003) or the color of a flickering stimulus (Wiener, Lee, Lohoff, & Coslett, 2014; Tipples, Brattan, & Johnston, 2013; Bueti & Macaluso, 2011; Morillon, Kell, & Giraud, 2009; Coull, Nazarian, & Vidal, 2008; Livesey, Wall, & Smith, 2007; Coull, Vidal, Nazarian, & Macar, 2004). These studies revealed a more restricted timing network, primarily comprising SMA, inferior frontal cortex, adjacent anterior insula, BG, and superior temporal cortex. Indeed, a meta-analysis of over 40 neuroimaging studies of timing identified SMA and right inferior frontal cortex as being the only two regions common to both perceptual and motor timing and to timing in both the subsecond and suprasecond range (Wiener et al., 2010).

Despite obvious efforts to match control and timing tasks in terms of task difficulty, sustained attention, and WM in these fMRI studies, the way in which information was manipulated within WM differed. For the color or length tasks, information had simply to be integrated or averaged. Averaging can be achieved by integrating infor-mation from a random set or even subset (de Fockert & Marchant, 2008) of points during stimulus presentation. In the timing task, on the other hand, information has to be sequentially integrated between two anchor points in a particular direction or order, either by categorically com-paring information at onset and offset (e.g., Buonomano & Maass, 2009; Matell & Meck, 2000) or by continually accumulating information from stimulus onset to offset

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(Gibbon, Church, & Meck, 1984). This directionality is a fundamental feature of the flow of time, often referred to as "time's arrow." Indeed, the sequential or cumulative nature of timing is the reason for many of the behavioral dissociations that are observed when judging duration as opposed to other magnitude dimensions. For example, Droit-Volet, Clément, and Fayol (2008) demonstrated that psychophysical discrepancies in perceptual discrimination of duration, as opposed to length or number, vanished when spatial or numerical information was provided sequentially rather than simultaneously. In other words, if the total length, number, or duration of a sequence of stimuli had to be integrated and accumulated, the spatial and numerical tasks became as difficult as the timing task. Furthermore, in a follow-up study, Droit-Volet (2010) showed that the perceptual distortions induced by click trains, which were thought to be specific to the temporal domain, also applied to spatial and numerical judgments but only if these stimuli were presented sequentially and their individual magnitudes accumulated. More recently, Lambrechts, Walsh, and Van Wassenhove (2013) found that, if spatial and numerical information was presented in a similarly dynamic (i.e., sequential) way as temporal information, then duration judgments were unaffected by the size or number of stimuli, contrary to many previous findings that size (Xuan, Zhang, He, & Chen, 2007) or number (Dormal, Seron, & Pesenti, 2006) distorts estimates of duration. These behavioral findings suggest that, when timing is compared with another magnitude dimension that is equally sequential or dynamic, then psychophysical differences in judgments of duration versus other magnitudes are no longer seen. However, using a dynamic spatial task in which lines "grew" from left to right, Casasanto and Boroditsky (2008) and, later, Magnani, Oliveri, and Frassinetti (2014) found that duration judgments were biased by stimulus size.

We aimed to address this debate by using fMRI to investigate whether the neural timing network described above (SMA, right inferior frontal cortex, BG, superior temporal cortex) would still be observed when the control task is presented in a similarly sequential or dynamic way as the temporal task. We independently manipulated the integration of temporal (duration) versus spatial (distance) information using moving dot stimuli (see also Casasanto & Boroditsky, 2008, Experiment 5). Stimuli were identical for both tasks, but task instructions differed. Participants had to remember either when or where a dot initially appeared on a screen, monitor its trajectory, and then integrate this information to provide estimates of either duration (dynamic temporal condition) or distance (dynamic spatial condition). The spatial condition was thereby equated to the temporal condition in terms of retention of stimulus onset in WM and sequential integration of this information with stimulus offset. We also included static control tasks in which participants had to estimate either the duration of presentation (temporal) or the visual length (spatial) of a static line stimulus (see also Droit-Volet

et al., 2008). Although the static spatial task requires estimation of spatial magnitude, it does not require accumulation or integration of information. Comparing the static temporal task with the static spatial task should therefore reveal areas implicated not only in timing but also in the sequential integration of information that is essential for the temporal, but not the spatial, task. On the other hand, both the dynamic temporal and dynamic spatial task require the sequential integration of information, and so these should be subtracted out in a direct comparison of the two tasks, leaving only areas that are specific to the integration/accumulation of temporal information. These comparisons should allow us to dissociate regions of the timing network that are implicated in the sequential aspects of timing and those that are more specifically temporal.

In addition, the use of a spatial control task allows us to directly compare magnitude processing in the temporal and spatial domains. Neuroscientific investigation of magnitude has focused primarily on identifying common neural substrates for the processing of three distinct magnitude domains: space, time, and number (Dehaene & Brannon, 2010; Bueti & Walsh, 2009; Walsh, 2003). Although prior fMRI and TMS investigations of magnitude have compared spatial with numerical magnitude (e.g., Dormal, Dormal, Joassin, & Pesenti, 2012; Pinel et al., 2004) and temporal with numerical magnitude (e.g., Hayashi et al., 2013; Dormal et al., 2012; Dormal, Andres, & Pesenti, 2008), there are, as yet, no fMRI studies directly comparing temporal with spatial magnitude. Nevertheless, in a parallel line of research, activity in SMA has been shown to increase as a function of increasing physical (i.e., objective) stimulus duration (Wencil, Coslett, Aguirre, & Chatterjee, 2010; Macar, Vidal, & Casini, 1999) or even as a function of increasing perceived (i.e., subjective) duration (Tipples et al., 2013). In other words, SMA activity increases as a function of increasing temporal magnitude. We now draw these two lines of research together to investigate whether SMA activity varies specifically as a function of the increasing magnitude of temporal information (i.e., duration) or whether it is also implicated in the increasing magnitude of dynamic spatial information (i.e., distance).

METHODS

Participants

We examined 16 right-handed healthy volunteers (mean age = 26.1 [range = 21–40] years, 1 woman) with no record of neurological or psychiatric disorders and normal or corrected-to-normal vision. All participants gave informed written consent to the study protocol, which had been approved by the local research ethics committee. A behavioral pilot experiment (12 healthy young adults, 8 women) was conducted before the scanning session to confirm that the spatial and temporal tasks were matched for difficulty in the dynamic display condition.

Experimental Task

Participants performed a three-alternative forced choice task (Figure 1). The task was designed to measure temporal or spatial judgments of the same visual stimuli. Participants were required to judge whether a probe stimulus was shorter, equal, or longer than the previous sample stimulus, either in terms of duration or distance according to the cue word presented at the beginning of each trial. Trials started with the centrally presented cue (the word "duration" or "distance") presented for 800 msec, followed by a variable ISI (1–2 sec). Two visual stimuli were then presented consecutively (hereafter sample for the first stimulus and probe for the second stimulus), separated by a longer and more variable ISI (1.5–4 sec), which allowed the regional brain activity evoked by each stimulus to be disambiguated. Finally, after another variable ISI (1–2 sec), a response display was presented for 1500 msec, during which time participants registered their decision using one of three response keys. Intertrial intervals varied between 1 and 2 sec. Average trial length was ~9 sec. Experimental conditions (temporal [duration]/spatial [distance]) were presented in permuted order to ensure optimization of event-related signal strength (Josephs & Henson, 1999).

Static versus Dynamic Displays

Stimulus display was manipulated across blocks, with sample and probe stimuli being either static or dynamic (Figure 1). In the static condition, the stimulus was a white static line of variable length, presented against a black background for a variable duration. The position of the line on the screen varied from one presentation to another, being situated more to the left, in the center or to the right of the screen. In the dynamic condition,

the stimulus was a white moving dot, which moved smoothly from left to right against a black background, covering a variable distance over a variable duration. The start (and end) positions of the trajectory covered by the moving dot varied from one presentation to another, being situated more to the left, in the center or to the right of the screen. In both conditions, the screen turned black immediately upon stimulus offset. Importantly, the fMRI scanning environment was completely dark meaning that the participant had no visual cues (e.g., edges of the computer screen) against which the position of the stimulus could be localized. In both conditions, the stimulus was presented for one of four durations and had one of four distances. Crucially, in the dynamic condition, the spatial and temporal tasks were matched for WM load: Both types of judgment required the moment in time, or position in space, of initial stimulus onset to be retained in WM and to then be integrated with the moment in time, or position in space, of stimulus offset (see also Casasanto & Boroditsky, 2008, Experiment 5). By contrast, in the static condition, only temporal judgments required retention of stimulus onset and integration of onset and offset in WM. Spatial judgments in the static display had no WM requirements because all necessary perceptual information (line length) was given simultaneously at stimulus onset and remained constant until stimulus offset (i.e., the line had a fixed length throughout its presentation).

Stimulus and Response Details

For both static and dynamic displays, the magnitude of sample and probe stimuli varied in four steps from 400 to 1600 msec in the temporal task (400/800/1200/1600 msec) and from 4 to 16 spatial units in the spatial

Figure 1. Task details. Participants judged whether a probe stimulus was shorter (S), equal (=), or longer (L) than the previous sample stimulus, either in terms of duration in the temporal task or in terms of distance in the spatial task. Stimuli were either dynamic trajectories (moving dot) or static lines. Responses were provided with index/middle/ring finger button presses, and stimulus–response contingencies were varied across trials. Sample and probe stimuli were separated by a variable ISI (1.5–4 sec). Intertrial intervals (black screen), as well as the ISIs between cue and sample and between probe and response (black screens), varied between 1 and 2 sec.
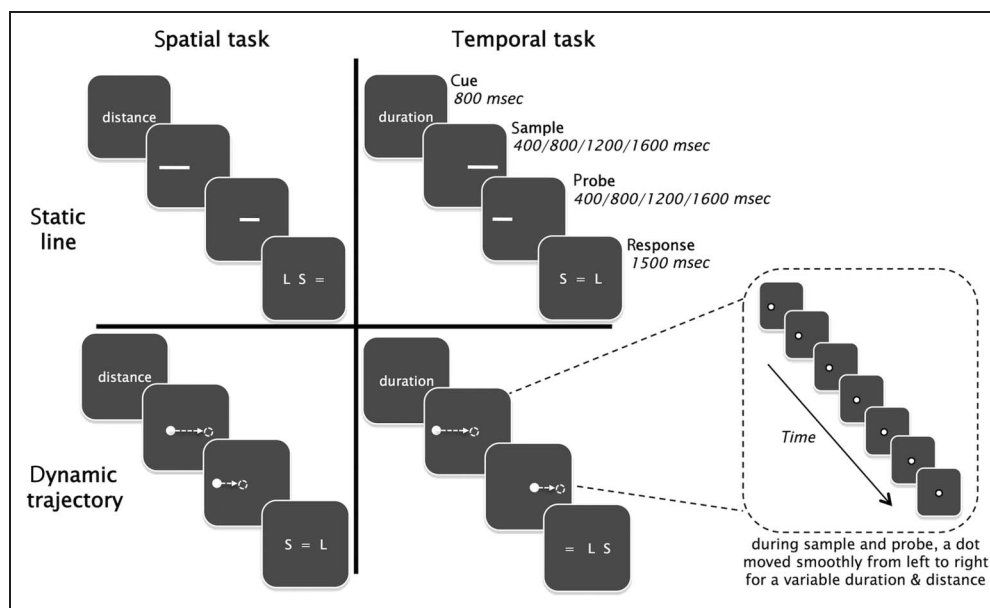
task (4/8/12/16 spatial units, corresponding to visual angles of 0.8°/1.6°/2.4°/3.2°). So that participants could not anticipate the eventual distance of a stimulus simply from its starting position on the screen, all four stimulus distances started from the same point on the screen. To minimize the possibility that participants would then simply estimate stimulus distance from its end position on the screen, the location at which each stimulus was presented varied from one trial to the next, giving a wide variation in possible end points. The stimulus could be presented on the left, around the center, or on the right of the screen. The leftmost start point was 3.2° to the left of screen centre, that is, −3.2° (with end points of −2.4°/−1.6°/−0.8°/0° for the 4/8/12/16 stimulus lengths, respectively); the central start point was 1.6° to the left of screen center, that is, −1.6° (with end points of −0.8°/0°/0.8°/1.6° for the 4/8/12/16 stimulus lengths, respectively); and the rightmost start point was exactly at screen center, that is, 0° (with end points of 0.8°/1.6°/2.4°/3.2° for the 4/8/12/16 stimulus lengths, respectively).

For static displays, stimulus duration was varied (400/800/1200/1600 msec) in the temporal task, whereas stimulus length was held constant (10 spatial units, corresponding to a visual angle of 2°). Correspondingly, stimulus length was varied (4/8/12/16 spatial units) in the spatial task, whereas stimulus duration was held constant (1000 msec). For dynamic displays, the duration for which the stimulus was presented and the distance for which it traveled varied simultaneously in both temporal and spatial tasks. Duration and distance were partially (rather than fully) orthogonalized to equate the number of trials in which the difference between sample and probe was either zero (e.g., sample = 400 msec, probe = 400 msec), small (e.g., sample = 400 msec, probe = 800 msec), or large (e.g., sample = 400 msec, probe = 1200 msec). Specifically, we used the following combinations: 400 msec/4 (400 msec refers to duration; and 4, to the number of spatial units for distance), 400 msec/8, and 400 msec/12; 800 msec/4, 800 msec/8, and 800 msec/16; 1200 msec/4, 1200 msec/12, and 1200 msec/16; and 1600 msec/8, 1600 msec/12, and 1600 msec/16. We also manipulated the relative magnitude of sample and probe to obtain equal numbers of trials in which the probe was shorter, equal, or longer than the sample (eight trials each per condition in each block). As duration and distance varied simultaneously for each stimulus, trajectory speed was not uniform across combinations (i.e., the dot moved faster for the "400 msec/12" stimulus than for the "400 msec/8" stimulus). We minimized speed bias effects on duration perception (e.g., Brown, 1995) by counterbalancing the relative speed of sample and probe (i.e., equal number of trials in which the speed of the probe was either slower or faster than that of the sample). We also counterbalanced the spatial position of sample and probe stimuli (i.e., equal numbers of trials in which the probe was presented to the left/right of the sample) to minimize potential effects of spatial location on perception of duration (e.g., Vicario et al.,

2008). Finally, we also equated the number of trials in which the correct answer in one dimension would be either congruent or incongruent with the correct answer in the other dimension. For example, a trial in which the sample was "1600 msec/12" and the probe was "400 msec/4" would be congruent because the "shorter" answer would be correct for both duration and distance. On the other hand, a trial in which the sample was "400 msec/12" and the probe was "1200 msec/12" would be incongruent because the answer would be "longer" for duration but "same" for distance.

On a trial-by-trial basis, index/middle/ring finger button-press responses were orthogonalized with respect to shorter/equal/longer decisions. For example, the index finger button-press response was associated with "shorter" decisions in a third of the trials, to "equal" decisions in another third of trials, and to "longer" decisions in the remaining trials. Importantly, participants did not know the response configuration of any particular trial until the response display was presented at the end of the trial. This manipulation allowed us to minimize motor preparation confounds during the critical sample and probe stages of the trial (see also Coull et al., 2008).

fMRI Acquisition

Scans were acquired at the Marseille fMRI Centre (http://irmfmrs.free.fr) using a 3-T (3T-MAGNEX) Bruker Medspec 30/80 Advance whole-body MRI system (Ettlingen, Germany), equipped with a head coil. EPI was used to obtain T2*-weighted fMRI images in the axial plane, using an interleaved slice acquisition sequence. The acquired image volume consisted of 32 × 4 mm transverse slices, with an interscan interval of 2.13 sec. The size of this image volume allowed us to scan the entire cerebral cortex and most of the cerebellum. A structural MRI was also acquired (using a standard T1-weighted scanning sequence, 1-mm^3 resolution) to allow anatomically specific localization of significant areas of brain activation. A 2 × 2 factorial design, comprising the factors of dimension (time/space) and display (static/dynamic), yielded four experimental conditions: time static, space static, time dynamic, and space dynamic. The temporal and spatial conditions were intermixed, in permuted order, within the same block of 48 trials (24 trials per condition), whereas the static and dynamic display was manipulated across blocks. Presentation order of the static and dynamic conditions was counterbalanced across participants.

A secondary aim of the study was to examine modulation of temporal- or spatial-specific brain activity as a function of stimulus magnitude (duration or distance). However, a block of 48 trials gave only six trials of each of the four durations in the temporal condition and six trials of each of the four distances in the spatial condition. Therefore, we included two additional blocks of the dynamic condition (with different trial randomization) in the scanning session to ensure a sufficient number of trials

of each duration/distance. Three blocks of the dynamic condition gave a total of 18 stimuli for each of the four durations in the temporal task and each of the four distances in the spatial task. Because duration and distance were orthogonal, this also gave us 18 stimuli at each of the four distances in the temporal task and 18 at each of the four durations in the spatial task. Presentation order of the three dynamic blocks was counterbalanced across participants. In total, four scanning runs (260 or 261 image volumes, approximately 8 min per run) were acquired for each participant (one static block and three dynamic blocks). An initial familiarization session, performed outside the scanner, ensured participants had understood task instructions. Because of a technical malfunction, one of the participants performed the static block plus only two of the dynamic blocks.

Behavioral Data Analysis

The percentage of correct responses during each of the four blocks was recorded during fMRI scanning and analyzed, using paired t tests, to determine whether there were significant differences in performance of the temporal and spatial tasks in static or dynamic displays. We further analyzed behavioral data from the three dynamic blocks to examine whether performance accuracy varied as a function of the magnitude of stimulus duration or distance. Trials from all three dynamic blocks were binned into five categories, according to the relative magnitude (either duration or distance) of the probe stimulus compared with the sample: probe much shorter than sample (a probe–sample ratio of 0.25–0.5), probe slightly shorter than sample (ratio = 0.6–0.7), probe approximately equal to sample (ratio = 0.75–1.33), probe slightly longer than sample (ratio = 1.5–2), or probe much longer than sample (ratio = 3–4). Temporal trials were binned as a function of the relative duration of probe to sample stimuli, whereas spatial trials were binned as a function of the relative distance of probe to sample stimuli. The percentage of correct responses in each bin was calculated and analyzed using a 2 × 5 repeated-measures ANOVA with Task (temporal/spatial) and Relative magnitude (probe shorter/longer than sample) as within-subject factors. Finally, we used data from the three dynamic blocks to explore possible influences of stimulus distance on the subjective perception of duration (Casasanto & Boroditsky, 2008; Xuan et al., 2007) or of stimulus duration on the subjective perception of distance (Lambrechts et al., 2013). This time, temporal trials were binned as a function of the relative distance of probe to sample stimuli. Conversely, spatial trials were binned as a function of the relative magnitude of probe to sample stimuli. Binning data in this way allowed us to examine the mutual interference between temporal and spatial information. We indexed perceived duration by designating trials as either correct, overestimates, or underestimates. We then calculated the proportion of

total errors that were overestimates [i.e., overestimates/ (underestimates + overestimates)]. Errors were classified as overestimates if the probe and sample were of the same magnitude but the participant judged the probe to be longer or if the probe was shorter than the sample but the participant judged it to be longer or of equal length. The proportion of total errors in which duration/ distance had been overestimated was calculated for each of the five bins and analyzed using a 2 × 5 repeated-measures ANOVA with Task (temporal/spatial) and Relative magnitude (probe shorter/longer than sample) as within-subject factors. Post hoc Newman–Keuls tests were used to explore significant effects. Statistical threshold was fixed at $p < .05$ for all behavioral analyses.

fMRI Data Analysis

Image processing and statistical analysis of fMRI data were conducted with SPM8 (http://www.fil.ion.ucl.ac. uk/spm/software/spm8). The first five images of each run allowed for magnetic field saturation and were discarded. All remaining functional images were slice-time corrected using the middle slice in time as reference (Slice 31; 32 slices total; interleaved acquisition). These images were then realigned to correct for head movement between scans. Each structural MRI was coregistered to the corresponding mean realigned functional image to put structural images into the functional brain space. All functional images were then spatially normalized by matching each image to the standard SPM8 EPI template, resampled to 3-mm isotropic voxel size, and spatially smoothed using isotropic Gaussian kernels of 8-mm FWHM.

We then conducted event-related analysis of the preprocessed fMRI data. Stimulus-evoked neural responses were modeled as single events, time-locked to the onset of the sample and probe stimuli, and convolved with the canonical hemodynamic response function. The data were high-pass filtered (cutoff frequency = 0.0083 Hz), and global changes were removed by proportional scaling. Analysis of the data was performed using the general linear model to obtain parameter estimates of event-related activity at each voxel for each condition and to generate SPMs of the t statistic, which were transformed to maps of corresponding Z values. Statistical maps of significant change in the amplitude of response were initially thresholded at $p < .001$ (uncorrected for multiple comparisons) at the voxel level, with the threshold for significance being set at $p < .05$, corrected for multiple comparisons (FWE) at either the voxel or cluster level (41 voxels). We report all areas that survived this corrected threshold during interrogation of the whole-brain volume. We also report any additional clusters that did not survive the whole-brain threshold but did survive a threshold of $p < .05$ FWE corrected at the voxel level in selected ROIs using small volume correction. ROIs for the perception of duration were anatomically defined (using the automated

anatomical labeling [AAL] database; Tzourio-Mazoyer et al., 2002) and selected a priori on the basis of previous fMRI investigations of perceptual timing of single visual stimuli (Tipples et al., 2013; Bueti & Macaluso, 2011; Wencil et al., 2010; Wiener et al., 2010; Coull et al., 2004, 2008; Livesey et al., 2007). Specifically, we interrogated AAL-defined SMA, inferior frontal gyrus, anterior insula, dorsolateral pFC, superior temporal cortex, and BG. Given its long-standing implication in timing, we also interrogated AAL-defined cerebellum, although it is more usually associated with timing of multiple intervals or with motor timing (Wiener et al., 2010; Lewis & Miall, 2003). Anatomically defined (AAL) ROIs for perception of distance were selected a priori on the basis of prior neuroimaging investigations of spatial attention (Corbetta & Shulman, 1998) and size perception (Pooresmaeili, Arrighi, Biagi, & Morrone, 2013; Sperandio, Chouinard, & Goodale, 2012; Murray, Boyaci, & Kersten, 2006; Grill-Spector & Malach, 2004) and comprised inferior and superior parietal cortices and primary and extrastriate visual cortices. All ROIs were bilateral. Right inferior parietal cortex was also included as an ROI for duration, as well as distance, estimation, based on its role in magnitude processing generally (Bonato, Zorzi, & Umiltà, 2012; Dormal et al., 2012; Walsh, 2003). Three separate first-level analyses (detailed below) were conducted for each of the 16 participants.

Temporal and Spatial Perception in Static versus Dynamic Displays

The first analysis aimed simply to identify regions that were activated significantly more by temporal versus spatial processing when stimulus presentation was either static or dynamic. To equate statistical power across static and dynamic presentations, we analyzed data from the static block and from one of the three dynamic blocks. The dynamic block was chosen on the basis of task performance (see Results).

For each single participant, we modeled events of interest time-locked to the onset of the sample and probe stimuli, comprising the factorial combination of the two experimental factors, task (time/space) and display (static/dynamic), to give us four experimental conditions: time static, space static, time dynamic, and space dynamic. The single-participant model also included regressors modeling events of no interest for each run: six motion correction parameters, one regressor time-locked to the onset of the cue, one regressor time-locked to the onset of the response, and one regressor modeling error trials (including nonresponses). Modeling error trials separately meant that the four regressors of interest modeled correct trials only, which minimized any differences in task performance across conditions. For each participant, we specified contrasts of interest to identify regions activated by temporal versus spatial processing, separately in static or dynamic displays. Specifically, we compared trials in which temporal and spatial judgments were based on static

line stimuli, that is, [time static − space static] and vice versa; trials in which temporal and spatial judgments were based on dynamic moving-dot stimuli, that is, [time dynamic − space dynamic] and vice versa; and finally, the comparison of these two contrasts, that is, [(time static − space static) − (time dynamic − space dynamic)] and vice versa, which identified regions selectively recruited by temporal as compared with spatial judgments for static versus dynamic displays (i.e., the interaction between dimension and display). The resulting statistical maps (contrast images) were then entered into a second, group level of analysis. Three analyses (one for each contrast of interest), each containing the 16 relevant single-participant statistical maps, were performed. Statistical inferences for each contrast were derived using one-sample t tests. Parameter estimates (beta values) in significantly activated regions were extracted using the MarsBaR ROI toolbox (Brett, Anton, Valabregue, & Poline, 2002) and plotted for each of the four experimental conditions to aid data interpretation.

Parametric Modulation of Temporal- or Spatial-specific Networks by Stimulus Magnitude

The second analysis aimed to identify regions whose activity increased linearly with stimulus magnitude, either duration or distance. Wencil et al. (2010) have already identified regions whose activity increased as a function of stimulus duration. We plan to take this analysis one step further by comparing areas whose activity varies as a function of stimulus duration with those whose activity varies as a function of stimulus distance. Wencil et al. (2010), and more recently, Henry, Herrmann, & Obleser, (2015) also identified regions whose activity increased as a function of task difficulty. However, our experimental aim was to identify regions tracking the magnitude of duration (i.e., the elapse of time), not the discriminability of duration.

To have enough trials of each of the four durations/distance, this analysis was composed of data from all three dynamic blocks. Therefore, this analysis included data from the dynamic blocks only, not the static one. Across the three blocks, for each single participant, we modeled events of interest separately at the onset of the sample and of the probe for both tasks (time/space) to give four experimental conditions: time sample, time probe, space sample, and space probe. Each single-participant model also included the nine regressors of no interest, defined above (movement parameters, cue, response, errors). In addition, to identify areas whose activity increased as a function of stimulus magnitude, we included two parametric modulations that weighted sample and probe events as a function of their duration or distance. Weights of 4, 8, 12, or 16 were assigned to stimuli whose duration was 400, 800, 1200, or 1600 msec, respectively, or whose distance was 4, 8, 12, or 16 spatial units, respectively. Note that duration and distance modulations were included for both

temporal and spatial tasks, with distance modulations being orthogonalized with respect to duration modulations. Orthogonalization of the regressors ensured that any activations revealed by the parametric modulation of distance were not confounded by concurrent parametric modulation of duration. This was necessary because, on average, long distance stimuli (16 units) were presented for longer durations (800/1200/1600 msec) than short (4 units) distance stimuli (400/800/1200 msec).

For each participant, we specified contrasts to identify regions whose activity increased linearly as a function of duration during temporal trials (i.e., the parametric modulation of time sample or time probe by duration, hereafter "Time × Duration") or areas whose activity increased as a function of distance during spatial trials (i.e., the parametric modulation of space sample or space probe by distance, hereafter "Space × Distance"). Modeling error trials separately meant that the four regressors of interest modeled correct trials only, meaning that the magnitude of the stimuli modeled by these regressors had been accurately perceived by the participant. This is important because it ensured that parametric modulation contrasts reflected objective stimulus magnitude rather than a subjectively distorted perception of magnitude. The resulting statistical maps of each of these four parametric modulations were then entered into a full factorial design at a second, group level of analysis, with dimension (Time × Duration/Space × Distance) as one factor and stimulus (sample/probe) as the other. At this group level, we first defined contrasts that identified regions whose activity was modulated as a function of stimulus duration during temporal trials (Time × Duration) or as a function of distance during spatial trials (Space × Distance), averaged across sample and probe stimuli. These contrasts identified brain regions implicated in processing temporal or spatial magnitude generally. We then defined difference contrasts that directly compared these magnitude modulations with one another, which identified areas responding selectively to the increasing magnitude of temporal information versus the increasing magnitude of spatial information, that is, [(Time × Duration) − (Space × Distance)] and [(Space × Distance) − (Time × Duration)]. These contrasts were defined separately at the sample and probe stages of the task. To disambiguate areas of timing-related activation from space-related deactivation (or vice versa), the [(Time × Duration) − (Space × Distance)] contrast was masked inclusively by the (Time × Duration) contrast, whereas the [(Space × Distance) − (Time × Duration)] contrast was masked inclusively by the (Space × Distance) contrast. It is important to note that this masking procedure does not change the statistical value of activations of interest but simply removes deactivations of no interest from the whole-brain map. Beta values of the parametric modulations were extracted using the MarsBaR ROI toolbox (Brett et al., 2002) and plotted for each of the four experimental conditions to aid data interpretation.

Correlation between Objective and Subjective Measures of Stimulus Duration

Finally, we correlated activity from regions whose activity was significantly modulated by stimulus duration with individual differences in performance of the temporal task. This correlation allowed us to examine whether activity in an area that increases as a function of increasing objective stimulus duration also increased as a function of increasing subjective duration (i.e., overestimates of stimulus duration). We repeated the analysis described in Parametric Modulation of Temporal- or Spatial-specific Networks by Stimulus Magnitude section above (i.e., data from all three dynamic blocks, with parametric modulations indexing stimulus duration or distance for each of the four events of interest), except that this time the four regressors of interest modeled both correct and error trials (i.e., error trials were not modeled in a separate regressor of no interest). It was necessary to model error trials as well as correct trials in the regressors of interest so that we could capture activity related to the incidence of overestimates (i.e., errors), not only that related to correct trials. This resulted in a model with four regressors of interest (time sample, time probe, space sample, and space probe), each with two parametric modulations (duration and distance) and eight regressors of no interest (six movement parameters, cue, and response). As mentioned above, we identified areas whose activity increased as a function of increasing stimulus duration averaged across both the sample and probe stages of the task (i.e., the Time × Duration contrast) to identify regions that were implicated generally in processing temporal magnitude. For each individual participant, beta values were extracted from these areas for the time probe event (which was the event on which the temporal estimate was being made) using MarsBaR (Brett et al., 2002). This gave a value that represented the processing of increasingly longer probe durations. We then defined a behavioral index that represented the subjective perception that probe duration was longer than normal. Each participant's propensity to overestimate stimulus duration was calculated as the proportion of total errors [i.e., overestimates/(underestimates + overestimates)]. Across participants, we correlated the behavioral index of overestimation (i.e., subjective perceived duration) to the beta value representing increasing stimulus duration (i.e., objective stimulus duration) using Pearson product–moment correlations.

RESULTS

Behavioral Data

Temporal versus Spatial Accuracy in Static and Dynamic Displays

In the static block, as expected, performance accuracy (Table 1) was significantly higher in the spatial task than

Table 1. Mean Accuracy (Percent Correct ± Standard Error) in the Temporal and Spatial Tasks for the Static and Dynamic Displays

	Temporal (%)	Spatial (%)
Static	79.9 (±2.25)	91.1 (±3.56)
Dynamic 1	61.9 (±3.77)	72.4 (±2.81)
Dynamic 2	63.9 (±3.63)	69.9 (±3.23)
Dynamic 3	56.5 (±3.9)	65.7 (±3.03)

The dynamic task was performed three times, with a different trial randomization in each block.

the temporal one ($t(15) = 3.53, p < .005$). Unexpectedly, however, spatial performance was also more accurate than temporal performance in Dynamic block 1 ($t(14) = 2.88, p < .05$) and in Dynamic block 3 ($t(15) = 2.32, p < .05$). In Dynamic block 2, on the other hand, accuracy was not significantly different between the temporal and spatial tasks ($t(15) = 1.51, p = ns$). We therefore used these behavioral results to guide our choice of the dynamic block to be included in the fMRI analysis of static versus dynamic blocks: Dynamic block 2 was the only block in which the comparison of temporal and spatial tasks would not be confounded by task difficulty.

For the three dynamic blocks, we also examined accuracy as a function of the relative magnitude of the probe compared with the sample stimulus (Table 2). Although performance was significantly better on the spatial task than the temporal task ($F(1, 15) = 16.09, p < .01$), the effects of relative magnitude on accuracy were similar for the temporal and spatial tasks ($F(4, 60) = 2.30, p = ns$). Specifically, the more similar the magnitude of the sample and probe stimuli (in terms of either duration or distance), the more likely the participant was to make an error ($F(4, 60) = 26.28, p < .001$).

Table 2. Mean Accuracy (Percent Correct ± Standard Error) in the Temporal and Spatial Dynamic Tasks as a Function of the Relative Magnitude of the Probe Compared with the Sample Stimulus

	Temporal (%)	Spatial (%)
Probe ≪ sample	81.25 (±5.24)	89.58 (±2.99)
Probe < sample	71.88 (±5.74)	83.33 (±4.63)
Probe = sample	51.30 (±3.21)	53.99 (±2.99)
Probe > sample	66.93 (±4.91)	80.21 (±3.79)
Probe ≫ sample	67.19 (±5.07)	89.58 (±2.99)

The probe could be much shorter (≪), slightly shorter (<), equal to (=), slightly longer (>), or much longer (≫) than the preceding sample in terms of either duration (temporal task) or distance (spatial task). Data are averaged across all three dynamic blocks.

Interference between Temporal and Spatial Magnitude in Dynamic Displays

For the three dynamic blocks, we also measured the proportion of overestimates as a function of relative magnitude. The proportion of overestimates was significantly higher in the temporal, than the spatial, task ($F(1, 15) = 11.49, p < .005$) and also when the probe was longer, rather than shorter, than the sample ($F(4, 60) = 12,726, p < .0001$). These main effects were qualified by a significant interaction between Task and Relative magnitude ($F(4, 60) = 34.51, p < .0001$): The relative magnitude of the unattended dimension influenced the proportion of overestimates in the attended dimension in both tasks, but in opposite directions. Specifically, the spatial attributes of the stimuli strongly modulated perceived duration ($F(4, 60) = 34.51, p < .0001$): The longer the distance covered by the probe stimulus compared with that covered by the preceding sample, the more participants overestimated the duration of the probe (Figure 2). Conversely, the temporal attributes of the stimuli also modulated perceived distance, although to a slightly lesser extent ($F(4, 60) = 9.05, p < .0001$) and in the opposite direction (Figure 2). The shorter the duration of the probe stimulus compared with that of the sample stimulus, the more participants overestimated the distance covered by the probe.

fMRI Data

Temporal versus Spatial Processing in Static Displays

Estimating the duration rather than length of static lines significantly activated the SMA, inferior frontal gyrus bilaterally,
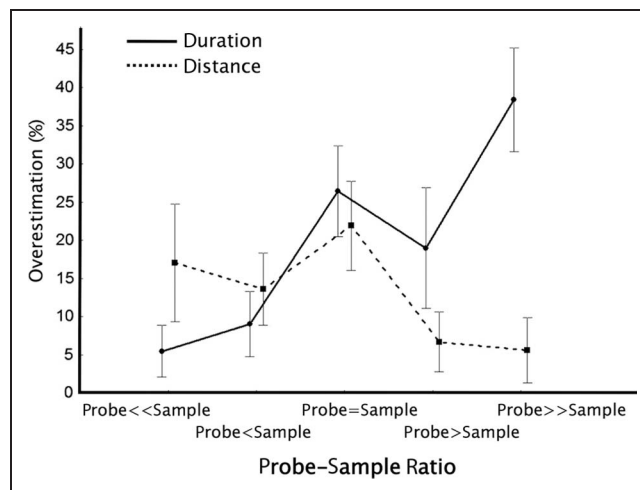
Figure 2. Influence of the nonpertinent stimulus magnitude on duration/distance estimates. The percentage of trials in which the duration (solid line) of the probe stimulus was overestimated increased when its distance was longer than that of the sample stimulus. Conversely, the percentage of trials in which distance (dotted line) of the probe stimulus was overestimated increased when its duration was shorter than that of the sample stimulus. Overestimation was calculated as a proportion of total errors. Error bars represent standard errors.

Table 3. Brain Regions Differentially Activated by the Discrimination of Stimulus Duration (Temporal) versus Stimulus Distance (Spatial) When the Stimuli to Be Discriminated Were Either Static Lines or Dynamic Trajectories

Anatomical Structure	x, y, z Coordinates (mm)	Cluster Size (Voxels)	Z Score
(A) Temporal–spatial			
Static display			
SMA	−3, −4, 67	77	4.22
Left inferior frontal gyrus (operculum)	−57, 2, 10	214	4.95
Right inferior frontal gyrus (operculum)	57, 5, 16	509	4.90
Left anterior insula	−36, 23, 1	42	4.12
Left superior temporal gyrus	−54, −46, 19	157	4.30
Right middle temporal gyrus	60, −25, −8	47	4.20
Right globus pallidus and putamen	18, −4, 1	99	4.40
Dynamic display			
Data from Dynamic block 2 only			
SMA	6, −7, 73	71	4.03
	−3, 2, 55		3.93
Data from all three dynamic blocks			
SMA	−3, 2, 55	88	4.13
Static–dynamic display			
Left anterior insula	−45, 11, −8	28	4.27*
Dynamic–static display			
–	–	–	–
(B) Spatial–temporal			
Static display			
Left superior parietal cortex	−15, −73, 46	145	4.74
Right superior parietal cortex	30, −76, 55	172	5.45
Medial frontal cortex	−6, 56, 22	48	4.04
Left inferior parietal cortex	−36, −49, 52	13	3.90*
Right inferior parietal cortex	36, −55, 52	18	3.98*
Left inferior occipital cortex	−48, −76, −11	40	4.63*
Primary visual cortex	9, −82, 7	13	3.55*
Dynamic display			
–	–	–	–

*Activations are significant at $p < .05$ corrected for multiple comparisons at the whole brain level or in anatomically defined ROIs.

left anterior insula, BG, and middle/superior temporal cortex bilaterally (Table 3A, Figure 3A). We then compared duration-specific processing in the static condition to duration-specific processing in the dynamic condition (i.e., the interaction term) to isolate regions that were activated by the timing task only when it was compared with a static control task, not when it was compared with a dynamic one.

This contrast revealed activity in left anterior insula only (Table 3A). In contrast to this predominantly rostral pattern of timing-related activity, estimating line length versus duration preferentially engaged inferior and superior parietal cortices bilaterally, primary visual cortex, left inferior occipital cortex, and a single cluster in ventromedial frontal cortex (Table 3B).
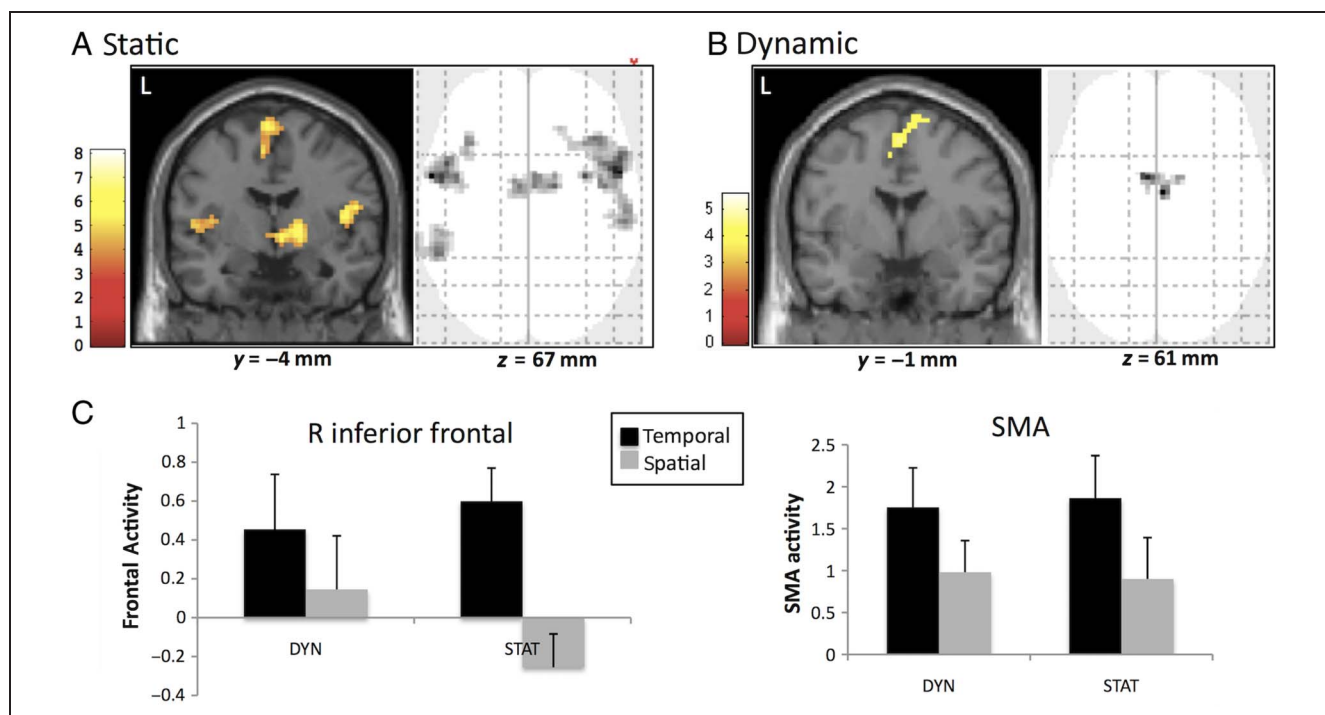
Figure 3. Regions activated significantly more by the temporal versus spatial task in static and dynamic displays. (A) Estimating the duration rather than length of static line stimuli activated an extensive cortico-striatal timing network. (B) The extent of this timing network was dramatically reduced when the temporal task was compared with a spatial task that was equally dynamic, comprising a single focus of activation in SMA. Significant clusters of activation are superimposed on a standard anatomical MRI image, and the axial sections of the "glass-brain" view are included to illustrate the selectivity of the SMA response in the dynamic temporal condition. (C) Plots show activity in the SMA and right inferior frontal cortex clusters identified by the comparison of temporal and spatial tasks in the static condition. Activity is plotted for the temporal and spatial tasks in both the dynamic (DYN) and static (STAT) conditions. SMA is activated significantly more by the temporal versus spatial task whether stimuli are dynamic or static, whereas right inferior frontal cortex is activated significantly more by the temporal versus spatial task only when stimuli are static.

Temporal versus Spatial Processing in Dynamic Displays

This contrast was composed of data from Dynamic block 2, which was the only block in which performance of the temporal and spatial tasks was matched (see above). Estimating the duration taken by the moving dot to complete its trajectory, rather than the distance it had covered, significantly activated SMA only (Table 3A, Figure 3B). Interestingly, one of the peak coordinates of this cluster (x, y, and z coordinates [mm] = -3, 2, 55) overlapped almost exactly with that reported in Wiener et al.'s (2010) meta-analysis (0, 2, 53). By contrast, there were no areas that were preferentially engaged by estimating the distance covered by the moving ball, rather than its duration. We then compared duration-specific processing in the dynamic condition with duration-specific processing in the static condition (i.e., the interaction term). However, this contrast revealed no significant areas of activation (Table 3A).

Given the remarkable specificity of the SMA activation, we sought to confirm this result with a larger data sample and so compared duration versus distance estimation using data from all three dynamic blocks. Again, estimation of the duration rather than distance of a moving dot significantly activated SMA only (Table 3A). Furthermore,

as before, there were no areas preferentially engaged by distance, rather than duration, estimation. Although performance was, on average, significantly worse for the temporal task than the spatial task when data from all three blocks were taken into consideration, we minimized difficulty confounds in the fMRI data by analyzing correct trials only. In addition, it is noteworthy that the results are almost identical whether we analyzed data from all three blocks or only the block in which spatial and temporal performance was matched (Table 3A).

Increasing Magnitude of Stimulus Duration or Distance

Duration modulation. During the temporal task, activity in SMA and right inferior occipital cortex increased as a function of the duration of sample and probe stimuli (i.e., the parametric modulation Time × Duration; Table 4A, Figure 4A). Figure 4B shows linear fits of activity from the SMA and right inferior occipital cortex clusters as a function of stimulus magnitude. In both regions, activity increased as a function of the duration of either the sample or probe stimulus.

Crucially, we then directly compared areas whose activity increased as a function of duration in the temporal task with those whose activity increased as a function

**Table 4.** Brain Regions Whose Activity Increases with Stimulus Magnitude

Anatomical Structure	x, y, z Coordinates (mm)	Cluster Size (Voxels)	Z Score
(A) Time × Duration			
SMA	0, −4, 64	75	5.01
Right inferior occipital cortex	30, −97, −5	92	5.31
(B) Space × Distance			
Primary visual cortex	0, −88, 19	129	4.55
Left inferior occipital cortex	−24, −61, −20	45	3.73
Right inferior occipital cortex	15, −67, −11	34	4.13*
(C) Time × Duration − Space × Distance			
SMA	3, −4, 64	14	4.36*
(D) Space × Distance − Time × Duration			
Primary visual cortex	9, −88, 22	111	4.53
Right inferior occipital cortex	15, −70, −8	21	4.11*

(A) Brain regions whose activity increased as a function of the duration of the sample and probe stimuli in the temporal task. (B) Brain regions whose activity increased as a function of the distance of the sample and probe stimuli in the spatial task. (C) Brain regions whose activity selectively increased as a function of the duration of the sample stimulus, but not its distance, in the temporal task. (D) Brain regions whose activity selectively increased as a function of the distance of the probe stimulus, but not its duration, in the spatial task.

*Activations are significant at $p < .05$ corrected for multiple comparisons at the whole brain level or in anatomically defined ROIs.
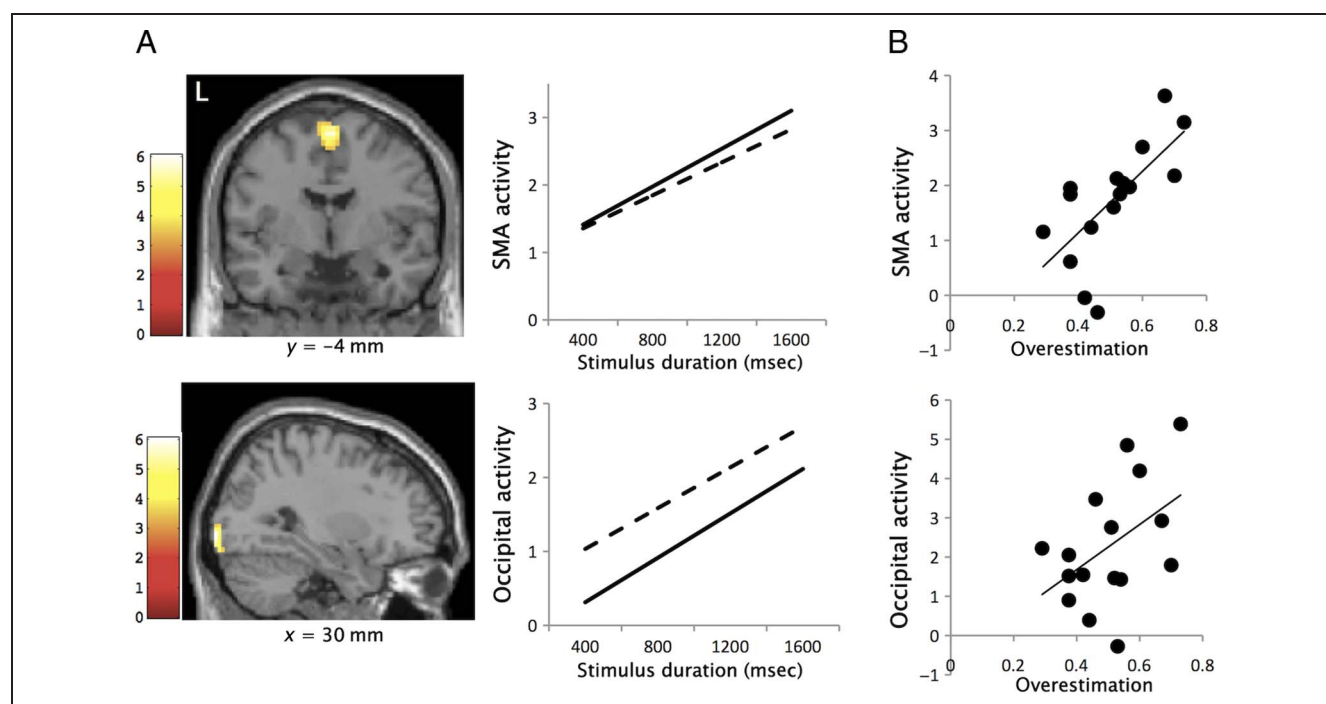
Figure 4. Parametric increases in regional brain activity as a function of objective and subjective durations. (A) In the dynamic temporal task, activity in SMA (top) and right inferior occipital cortex (bottom) increased as a function of objective stimulus duration. Accompanying plots show linear fits of regional brain activity as a function of the duration (400/800/1200/1600 msec) of either the sample (solid line) or probe (dashed line) stimulus. (B) Activity in SMA and right inferior occipital cortex also increased as a function of subjective stimulus duration: The higher the activity during presentation of the probe stimulus, the more likely the participant was to overestimate its duration. Overestimation was calculated as a proportion of total errors.
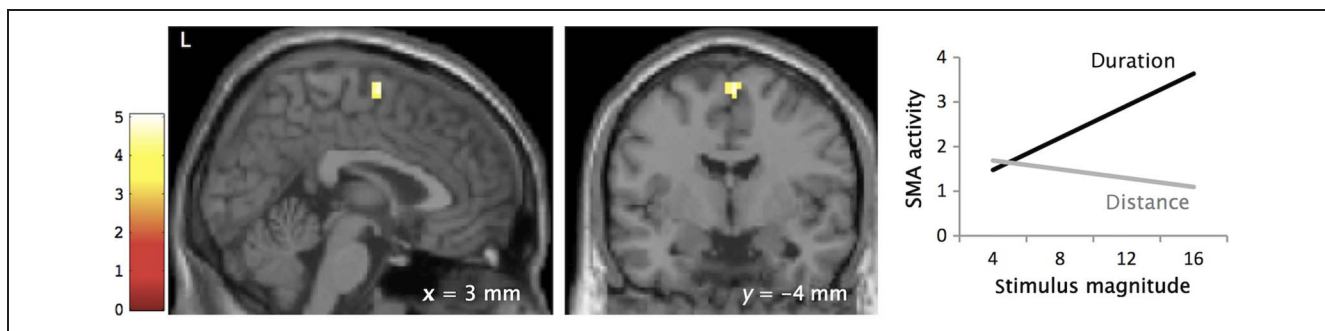
Figure 5. Differential parametric increases in activity as a function of stimulus duration versus stimulus distance. Activity in SMA increased as a function of the duration (400/800/1200/1600 msec) of the sample stimulus in the temporal task, but not as a function of its distance (4/8/12/16 spatial units) in the spatial task. The accompanying plot shows the linear fits of regional brain activity as a function of stimulus magnitude (duration/distance). Significant clusters of activation are superimposed on sagittal and coronal slices of a standard anatomical MRI image.

of distance in the spatial task. This comparison was conducted separately for the sample and probe stimuli so as to isolate duration-related processing during presentation of the sample, which is the stage of the task nonconfounded by comparison and decision processes. During presentation of the sample stimulus, activity in SMA (Table 4C) increased as a function of duration but not as a function of distance (Figure 5). There were no other areas of significant activity at either the sample or probe stage of the task. Although activity in right inferior occipital cortex also increased as a function of duration but not as a function of distance during presentation of both sample (x, y, and z coordinates = 21, −100, −8; Z = 4.59) and probe stimuli (x, y, and z coordinates = 33, −94, −14; Z = 4.12), these activations did not survive the significance threshold corrected at the whole-brain level. Because we did not have an a priori hypothesis that visual cortex would be preferentially activated by duration versus distance processing, we could not perform small volume correction analysis on these clusters. We report them here only for completeness.

We further explored the data by plotting how activity in SMA and right inferior occipital cortex was modulated by stimulus duration when duration was either task relevant (and therefore explicitly attended) in the temporal task or task irrelevant (and therefore either ignored or

only implicitly attended) in the spatial task. Figure 6 shows linear fits of activity as a function of duration in the temporal versus spatial tasks. Whereas activity in right inferior occipital cortex increased as a function of duration in temporal and spatial tasks equally, activity in SMA increased as a function of stimulus duration in the temporal task more than in the spatial task. In other words, the parametric response of right inferior occipital cortex to the magnitude of stimulus duration was independent of the requirement to attend to stimulus duration. On the other hand, the parametric response of SMA to stimulus duration was higher when stimulus duration was task relevant in the temporal task than when it was task irrelevant in the spatial task.

We aimed to quantify this pattern of effect by conducting an additional whole-brain analysis in which we specified contrasts that would identify areas whose activity increased as a function of duration in the spatial task and those whose activity increased as a function of distance in the temporal task (i.e., as a function of the nonpertinent dimension in each task). These contrasts were first specified at the individual participant level and then entered into a full factorial design at the group level, with dimension (Space × Duration/Time × Distance) as one factor and stimulus (sample/probe) as the other. During the spatial task, activity increased in inferior occipital

Figure 6. Parametric changes in activity as a function of stimulus duration in temporal or spatial tasks. Stimulus duration is task relevant in the temporal task (black lines) but task irrelevant in the spatial task (gray lines). Data are plotted as a function of stimulus duration (400, 800, 1200, and 1600 msec). In SMA, activity increases as a function of duration in both spatial and temporal tasks, although the activation is stronger when duration is task relevant in the

temporal task. By contrast, in right inferior occipital cortex, activity also increases as a function of duration in both spatial and temporal tasks, and there is no distinction in the size of the response when duration is task relevant (temporal task) or not (spatial task).
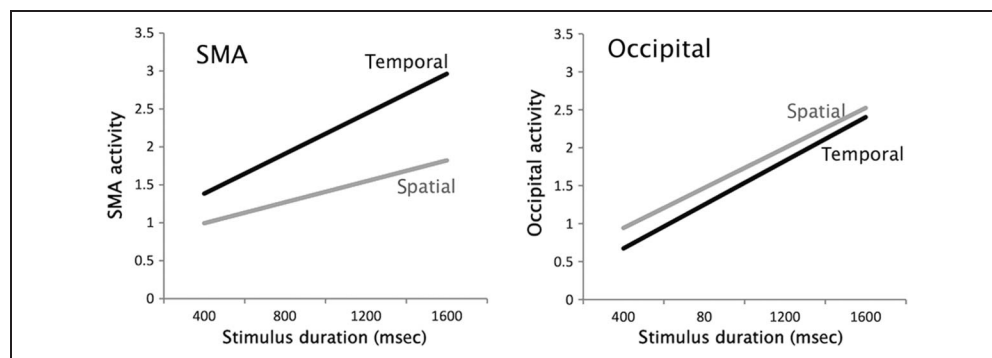
cortex as a function of the duration of sample and probe stimuli in both left (x, y, and z coordinates $= -30$, -97, -8; $Z = 4.91$, $p < .05$, whole-brain corrected) and right (x, y, and z coordinates $= 30$, -97, -5 and -30, -97, -8; $Z = 5.26$, $p < .005$, whole-brain corrected) hemispheres. There were no other areas of activation. During the temporal task, there were no areas whose activity significantly increased as a function of stimulus distance.

Distance modulation.   During the spatial task, activity increased in medial occipital cortex (primary visual cortex) and inferior occipital cortex bilaterally as a function of the distance covered by the sample and probe stimuli (i.e., the parametric modulation Space × Distance; Table 4B). We then directly compared areas whose activity increased as a function of distance with those whose activity increased as a function of duration. There were no significant changes in activity during presentation of the sample stimulus. However, activity in two regions of medial occipital cortex increased as a function of distance but not as a function of duration during presentation of the probe. These areas of activation were located in primary visual cortex and visual area V3 (Table 4D).

Common magnitude modulation.   We looked for areas of overlap among regions whose activity increased with increasing duration during the temporal task and those whose activity increased with increasing distance during the spatial task to potentially identify a common substrate for increasing magnitude that is independent of dimension (temporal/spatial). However, the conjunction of one contrast with another revealed no areas of overlap, for either the sample or probe stimuli.

Brain–Behavior Correlations

Pearson correlations revealed significant correlations between individual differences in task performance and regional brain activity in both SMA ($r = .68$, $p < .005$) and right inferior occipital cortex ($r = .46$, $p < .05$): The higher the regional brain activity during presentation of the probe stimulus, the more likely the participant was to overestimate its duration (Figure 4C).

DISCUSSION

When a perceptual timing task was compared with a static spatial control condition (line length estimation), we observed activation of a distributed network comprising SMA, bilateral inferior frontal gyrus (operculum), left anterior insula, BG, and bilateral middle/superior temporal cortex. However, when the perceptual timing task was compared with a spatial control task that was similarly dynamic, requiring that the location of stimulus onset be retained in WM and then sequentially integrated with the location of stimulus offset to provide a measure of cumulative distance, the only area that was significantly

activated was SMA. In addition, parametric analyses revealed that activity in SMA increased linearly as a function of duration during the dynamic temporal task but not as a function of distance during the dynamic spatial task. By directly comparing the increasing magnitude of one dimension with the increasing magnitude of another, our data not only confirm SMA's fundamental role in timing (Schwartze, Rothermich, & Kotz, 2012; Wiener et al., 2010) but, more specifically, highlight the direct, monotonic relationship between the level of activity in SMA and the sequential integration of information selectively in the temporal, not spatial, dimension.

Dynamic Integration of Temporal versus Spatial Information

The first main result from this study was that estimation of stimulus duration selectively activated SMA, despite the fact that the dynamic control task (distance estimation) similarly required information at stimulus onset to be retained in WM and to be sequentially integrated with information available at stimulus offset. In addition, duration and distance discrimination accuracy was equivalent in the block of trials for which fMRI data were compared, suggesting tasks were equally difficult. The only difference between timing and control tasks was the nature of the information being integrated: temporal or spatial. Because the sequential processing component was matched across tasks, SMA appears to be preferentially engaged by the temporal component of the timing task. Dormal, Andres, Dormal, and Pesenti (2010) have previously reported that sequential, rather than simultaneous, presentation of dot arrays activated SMA as well as inferior frontal cortex bilaterally. However, this study contrasted sequential versus simultaneous processing in a particular dimension (number), whereas we contrasted sequential processing between dimensions (temporal and spatial). Taken together, these results suggest that, although SMA may be involved in sequential processing generally, it is preferentially implicated in the sequential integration of temporal information. Interestingly, none of the other regions of the distributed timing network identified by the comparison of the timing to the spatial task in the static condition (inferior frontal gyrus, insula, BG, temporal cortex) survived the contrast with the dynamic spatial task. These areas might therefore be implicated in sequential or WM processing generally (see also Dormal et al., 2010), rather than processing of temporal information specifically.

Parametric Increases in Regional Brain Activity as a Function of Duration

The importance of SMA for duration processing was confirmed by further parametric analysis of all three dynamic blocks. Specifically, we replicated previous results that SMA activity increases as a function of physical stimulus

duration during a perceptual timing task (Wencil et al., 2010) and that activity in this region correlates with individual differences in the propensity to overestimate stimulus duration (Herrmann, Henry, Scharinger, & Obleser, 2014; Tipples et al., 2013). Specifically, the higher the activity in SMA during presentation of the probe, the more likely a participant was to overestimate its duration. Therefore, the second main result of our study was that activity in SMA increased as a function of both objective (physical) and subjective (perceived) stimulus durations. This is the first time that data from a single fMRI study have revealed correlations between regional brain activity and the magnitude of objective, as well as subjective, stimulus duration. These findings suggest that similar mechanisms underlie the neural representation of both physical and perceived duration: A stimulus that is misperceived as long shows the same pattern of neural activity as a stimulus that is physically long. More generally, the finding of parametric increases in regional brain activity as a function of duration supports the hypothesis that time is represented continuously in the brain (at least for durations in the range of 400–1600 msec), rather than as a comparison of two snapshots of activity at stimulus onset and offset (Mendez, Perez, Prado, & Merchant, 2014; Bueti & Macaluso, 2011). It's possible, however, that different brain regions may index stimulus duration depending on specific task requirements: For example, Bueti and Macaluso (2011) found that activity in putamen, superior temporal cortex, and right inferior frontal cortex/anterior insula, but not SMA, increased as a function of perceived duration during a temporal reproduction task. The generality of our findings in SMA must now be tested with other temporal paradigms, such as motor timing (rather than the perceptual paradigm used here), rhythmic timing (rather than single-interval timing), or timing of empty intervals (rather than filled durations).

Activity in right inferior occipital cortex also varied as a function of stimulus duration. This is consistent with findings from several electrophysiological studies in monkeys (Jaramillo & Zador, 2011; Ghose & Bearl, 2010; Anderson & Sheinberg, 2008; Janssen & Shadlen, 2005; Ghose & Maunsell, 2002; Riehle, Grun, Diesmann, & Aertsen, 1997), as well as fMRI studies in humans (Bueti & Macaluso, 2011; Bueti, Bahrami, Walsh, & Rees, 2010), showing duration-related changes in activity of sensory-specific (or task-specific) processing areas, such as visual or auditory cortex. In fact, we found that occipital cortex activity increased as a function of stimulus duration whether temporal processing was explicitly required for the task (temporal task) or not (spatial task). Therefore, modulation of inferior occipital cortex as a function of the duration of our visual stimuli is likely to represent the coding of information over time in a low-level, sensory-specific processing region. Furthermore, by plotting duration-related increases in activity during a temporal task (for which duration was pertinent) with those in a spatial task (for which duration was nonper-

tinent), we were able to dissociate the functional contributions of visual cortex and SMA to duration processing. Whereas the parametric response to stimulus duration in right inferior occipital cortex was equivalent whether stimulus duration was task relevant (temporal task) or not (spatial task), the parametric response to duration in SMA was higher when stimulus duration was being actively attended (i.e., in the temporal task). This dissociation suggests that temporal information is coded passively in low-level, sensory-specific processing areas (i.e., visual cortex) but is actively accumulated in the SMA (see also Van Wassenhowe, 2009).

Parametric Increases in Activity as a Function of Increasing Duration versus Distance

We confirmed prior results that activity in SMA increases as a function of both objective and subjective stimulus durations. However, we refined these findings by directly comparing areas whose activity was modulated by increasing duration during the temporal task with those that were modulated by increasing distance during the spatial task. This contrast allowed us to control for processes linked to the amodal accumulation of information generally. To conclude that an area accumulates temporal information, it is not sufficient to merely show that its activity increases as a function of duration. It is necessary to show that its activity increases selectively as a function of duration. In addition, we measured these duration-specific increases in activity independently at sample and probe stages of the task. This helped us to isolate straightforward accumulation of temporal information from more complex processes of temporal comparison. As argued by Wencil et al. (2010), processes related to the sequential integration, or "accumulation," of temporal information should be explored at the sample stage of the task because the probe stage is confounded by concurrent comparison and decision processes (see also Harrington, Zimbelman, Hinton, & Rao, 2010; Coull et al., 2008). The third, and perhaps most critical, finding of our study was that activity in SMA increased selectively with the increasing stimulus duration of the sample stimulus but not with its increasing distance. Our data therefore extend previous results (Herrmann et al., 2014; Wencil et al., 2010) by demonstrating that activity in SMA increases in line with accumulation of temporal information specifically, not with the accumulation of spatial information or, perhaps even, of magnitude generally.

Single-cell recordings in monkeys have demonstrated a close relationship between stimulus duration and activity in SMA. For example, neural firing in SMA increases as a function of duration when monkeys are implicitly timing a predictable interval (Akkal, Escola, Bioulac, & Burband, 2004) or when they are explicitly reproducing an interval designated either by a previously learned visual cue (Mita, Mushiake, Shima, Matsuzaka, & Tanji, 2009) or an isochronous sequence of tones (Crowe, Zarco, Bartolo, & Merchant, 2014; Merchant, Zarco, Pérez, Prado, & Bartolo,

2011). Merchant, Pérez, Zarco, and Gámez (2013) have even recently found evidence for duration tuning in SMA, with the same cells firing to particular durations whatever the modality (visual/auditory) or structure (reproduction of single or multiple intervals) of the timing task. Similarly, in humans, EEG recordings have shown that the amplitude of the contingent negative variation (CNV), an electrophysiological index of temporal preparation usually recorded over medial frontal electrodes, varies in line with duration when participants are implicitly timing a predictable interval (Praamstra, Kourtis, Kwok, & Oostenveld, 2006) or explicitly comparing the duration of a probe stimulus with that of a previously memorized standard (Ng, Tobin, & Penney, 2011; Van Rijn, Kononowicz, Meck, Ng, & Penney, 2011; Pfeuty, Ragot, & Pouthas, 2003, 2005; Macar & Vidal, 2003; Macar et al., 1999).

However, as argued previously (Van Rijn et al., 2011; Harrington et al., 2010; Wencil et al., 2010; Coull et al., 2008), the reproduction or probe phase of a timing task is confounded by concurrent comparison and decision processes. Wiener et al. (2012) addressed this issue by recording CNV amplitude during the initial encoding or sample phase of the task. Using a sophisticated combination of TMS and EEG methodologies, they confirmed that TMS-induced increases in perceived duration of the sample duration correlated with increases in CNV amplitude. Our own fMRI findings therefore complement the existing body of electrophysiological data by confirming not only that activity in SMA increases as a function of duration during the relatively "purer" sample stage of the task but that this increase in activity is selective to the accumulation of temporal, not spatial, information. It is therefore unlikely to simply reflect the accumulation of magnitude information generally. Electrophysiological recordings in monkey lateral prefrontal cortex have already demonstrated that distinct populations of cells code for decisions based on duration versus distance information (Genovesio, Tsujimoto, & Wise, 2012). Our whole-brain fMRI results suggest that duration and distance judgments are not only coded by distinct populations of cells but by anatomically distinct brain regions.

Relevance to Magnitude Processing

It is important to emphasize that our results are not incompatible with existing literature describing a role for right parietal cortex in magnitude processing (Bonato et al., 2012; Bueti & Walsh, 2009; Walsh, 2003). The aim of such studies is to identify a common neural basis for magnitude processing, irrespective of the type of magnitude information being processed (e.g., duration, size, or number). In the current study, by contrast, we did not compare each task with a sensorimotor control to identify areas of neuroanatomical overlap (e.g., Dormal et al., 2012). Instead, we explored the brain for areas whose activity increased in line with increasing degrees of magnitude in the temporal (duration) versus spatial

(distance) domain. Putting our results together with previous findings, it appears that, although right parietal cortex is engaged whenever the participant is processing any kind of dimension that can vary in magnitude (e.g., time, space, or number), incremental variations in that magnitude are actually represented in dimension-specific regions of the brain (e.g., SMA and right inferior occipital cortex for the visual stimuli used in the current study).

Consistent with the idea of a common neural basis for magnitude processing, behavioral studies have shown that one form of magnitude processing can bias perception of other forms. For example, the magnitude of spatial or numerical information can influence the perception of time (see Bonato et al., 2012, for a review): If the magnitude of a task-irrelevant dimension (number, size, luminance) is large, stimulus duration is overestimated (Xuan et al., 2007; Dormal et al., 2006). However, several authors have found evidence for asymmetric interference between magnitude dimensions, with spatial (Magnani et al., 2014; Mendez, Prado, Mendoza, & Merchant, 2011; Casasanto & Boroditsky, 2008) or numerical (Dormal et al., 2006) magnitude influencing temporal perception more than temporal magnitude influences spatial or numerical perception. However, this asymmetry may be less evident when both spatial and temporal dimensions are equally dynamic (Lambrechts et al., 2013; Droit-Volet et al., 2008), suggesting that the cumulative nature of temporal processing plays an important role in these effects. Our own behavioral data support this interpretation: The relative magnitude of the task-irrelevant dimension induced spatial, as well as temporal, distortions of our dynamic stimuli. Specifically, the relatively longer the distance of a dynamic trajectory, the more its duration was overestimated, and the relatively shorter the duration of a dynamic trajectory, the more its distance was overestimated. These findings are consistent with the classic kappa (Cohen, Hansel, & Sylvester, 1954; Abe, 1935) and tau (Helson, 1930) effects, respectively, which are measured using a series of empty intervals (which invoke an illusion of movement and speed) rather than continuous trajectories as discussed here.

Intriguingly, temporal and spatial distortions were influenced by task-irrelevant magnitude in diametrically opposite ways. Probe duration was overestimated when probe distance was relatively longer than the sample, supporting prior studies (e.g., Xuan et al., 2007). By contrast, probe distance was overestimated when probe duration was relatively shorter than the sample. In fact, this surprising result also confirms prior findings: Lambrechts et al. (2013) found that the shorter the duration of a dynamic display, the larger the accumulated surface size was estimated to be. It was suggested that, in dynamic displays, when judgments of spatial or numerical magnitude depend on the integration of information over time, shorter stimulus durations lead to a higher concentration of spatial information per unit time, leading participants to overestimate spatial size (Lambrechts et al., 2013). In

summary, our behavioral data, first of all, underline the mutual influence of spatial and temporal information upon perception, indicative of a common system for processing magnitude, and second, confirm that this influence is bidirectional, although asymmetric, when the dynamic, cumulative properties of the spatial and temporal stimuli are matched.

Conclusion

Comparing the duration versus distance of dynamic trajectories activated SMA alone, suggesting that this region is specific for the sequential accumulation of information in the temporal, rather than spatial, domain. Moreover, SMA activity increased parametrically as a function of stimulus duration, not distance, and also correlated with individual differences in the propensity to overestimate stimulus duration. Although activity in right inferior occipital cortex also increased with stimulus duration, this was evident during the spatial, as well as temporal, task, indicating passive, low-level coding of temporal information. Duration-related increases in SMA by contrast were greater during the temporal task, indicating active accumulation of temporal information.

Acknowledgments

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