

Uncoupling Sensation and Perception in Human Time Processing

Nicola Binetti¹, Alessandro Tomassini², Karl Friston³, and Sven Bestmann^{3,4}

Abstract

■ Timing emerges from a hierarchy of computations ranging from early encoding of physical duration (time sensation) to abstract time representations (time perception) suitable for storage and decisional processes. However, the neural basis of the perceptual experience of time remains elusive. To address this, we dissociate brain activity uniquely related to lower-level sensory and higher-order perceptual timing operations, using event-related fMRI. Participants compared subsecond (500 msec) sinusoidal gratings drifting with constant velocity (standard) against two probe stimuli: (1) control gratings drifting at constant velocity or (2) accelerating gratings, which induced illusory shortening of time. We tested two probe intervals: a 500-msec duration (Short) and a longer duration required for an accelerating probe to be perceived as long as the standard (Long—individually determined).

On each trial, participants classified the probe as shorter or longer than the standard. This allowed for comparison of trials with an “Objective” (physical) or “Subjective” (perceived) difference in duration, based on participant classifications. Objective duration revealed responses in bilateral early extrastriate areas, extending to higher visual areas in the fusiform gyrus (at more lenient thresholds). By contrast, Subjective duration was reflected by distributed responses in a cortical/subcortical areas. This comprised the left superior frontal gyrus and the left cerebellum, and a wider set of common timing areas including the BG, parietal cortex, and posterior cingulate cortex. These results suggest two functionally independent timing stages: early extraction of duration information in sensory cortices and Subjective experience of duration in a higher-order cortical–subcortical timing areas. ■

INTRODUCTION

Duration estimation is a fundamental ability for successful interactions with our environment. Evaluating and comparing durations of sensory events is thought to require the interplay between parietal, premotor, cingulate, and prefrontal cortices and subcortical regions in the BG, cerebellum, and thalamus (Merchant & Yarrow, 2016; Coull, Nazarian, & Vidal, 2008). Although research has shed light on various processes that enable our sense of duration, such as the extraction and representation of duration information, or the mnemonic and decisional processes required for duration comparison and classification, the biological basis of the subjective experience of time remains scarcely understood (Wittmann & Meissner, 2018; Trojano, Caccavale, De Bellis, & Crisci, 2017; Bueti & Macaluso, 2011; Wittmann, 2009).

Sensory input conveys durational information, with evidence from neural network modeling (Buonomano, Bramen, & Khodadadifar, 2009), brain stimulation (Salvioni, Murray, Kalmbach, & Bueti, 2013), and neuroimaging studies

(Bueti, Bahrami, Walsh, & Rees, 2010; Bueti & Macaluso, 2010), suggesting that early striate and extrastriate (V5/MT) regions play a key role in temporal encoding and STM, independent of low-level visual feature processing.

The ability to compare durations of stimuli belonging to different sensory modalities or to reproduce the duration of a sensory stimulus with an equivalently timed motor response implies that duration information can be represented in a more abstract format. Several models of time perception propose that time is quantified by means of a linear accumulation of timing evidence (Ivry & Richardson, 2002; Rosenbaum, 2002; Wing, 2002; Treisman, 1963). This seems compatible with the build-up of activity before an event, which covaries with stimulus duration, as seen in nonhuman primate (Janssen & Shadlen, 2005; Leon & Shadlen, 2003) and human electrophysiology recordings (Pfeuty, Ragot, & Pouthas, 2005; Macar & Vidal, 2004; Pouthas, Garnero, Ferrandez, & Renault, 2000).

Indeed, imaging studies reveal multiple regions sensitive to time accumulation when contrasting timing tasks with equivalent nontiming controls. For example, differences in visual stimulus duration lead to larger activity in the anterior portion of the SMA (preSMA) and the ACC (Pouthas et al., 2005). Bueti and Macaluso (2011) assessed the relationship between the subjective experience of time and corresponding neural responses in a more direct approach for identifying the biological substrates of time

¹UCL Interaction Centre, University College London, ²MRC Cognition and Brain Sciences Unit, University of Cambridge, ³Wellcome Centre for Human Neuroimaging, UCL Queen Square Institute of Neurology, ⁴Department of Movement and Clinical Neurosciences, UCL Queen Square Institute of Neurology, University College London

accumulation (Buetti & Macaluso, 2011). The authors observed that activity in the right putamen, right mid insula, and right mid/superior temporal cortex correlated with an illusory lengthening of time, suggesting a distributed cortical and subcortical time accumulation network. These findings are consistent with recent models proposing that timekeeping is distributed and carried out in parallel. For example, the striatal beat frequency model suggests that striatal spiny neurons act as temporal integrators of cortical and thalamic oscillatory clock signals (Buhusi & Meck, 2005; Matell, Meck, & Nicolelis, 2003) across both duration estimation and duration reproduction tasks and independently of sensory modality.

Duration discrimination further relies on working memory processes to store and compare duration of nonsimultaneous stimuli. Lateral premotor and right inferior frontal cortices have been linked to the mnemonic components of comparison/reproduction timing tasks (Pouthas et al., 2005; Schubotz & von Cramon, 2001; Kawashima et al., 1999). Although typically observed in timing research, SMA is more generically linked to working memory, typically recruited in perceptual and motor tasks (Rao, Mayer, & Harrington, 2001; Kawashima et al., 1999; Rao et al., 1997). Early auditory (Franssen, Vandierendonck, & Van Hiel, 2006) and visual (Salvioni et al., 2013) processing areas are involved in maintaining STM traces of temporal information in working memory. Finally, the comparison of these memory traces must lead to a categorical decision of which stimulus lasted longer (Lindbergh & Kieffaber, 2013). Studies have linked the cingulate cortex to these decision-making stages in duration discrimination tasks (Pouthas et al., 2005; Rao et al., 2001).

However, there is still a limited understanding of what subset of timing areas uniquely contribute to our subjective experience of time (Hayashi, van der Zwaag, Buetti, & Kanai, 2018; Trojano et al., 2017; Wittmann, Van Wassenhove, Craig, & Paulus, 2010; Wittmann & Paulus, 2008). Here, we address at which stage—within a timing hierarchy—our perceptual experience of duration (i.e., a duration “percept”) emerges. To this end, we contrasted activity related to the low-level encoding of duration features embedded in a sensory signal (sensitive to differences in time—duration sensation) from activity related to the subjective, higher-order perception of duration (sensitive to perceived differences in time—duration perception), which inform categorical duration judgments.

Participants evaluated the duration of sequential drifting sinusoidal gratings in a classic standard/probe comparison task. Participants compared subsecond (500 msec) sinusoidal gratings drifting with constant velocity (standard) against two probe stimuli: (1) control gratings drifting at constant velocity or (2) accelerating gratings, which induced an illusory shortening of time (Bruno, Ayhan, & Johnston, 2015; Sasaki, Yamamoto, & Miura, 2013; Binetti, Lecce, & Doricchi, 2012; Matthews, 2011). The inclusion of accelerating stimuli dissociated objective and subjective duration effects. On each trial, participants classified the

probe as lasting shorter or longer than the standard. This allowed for identifying brain activity uniquely related to an objective difference in probe duration (Objectively Long vs. Objectively Short) or to a subjective difference in probe duration (Subjectively Short vs. Subjectively Long), based on participants’ duration classifications. Although there is no dedicated sensor for time, duration is a feature that characterizes a physical stimulus. We hypothesized that visual areas, which are sensitive to features embedded within a sensory signal, should primarily respond to variations in objective duration (Salvioni et al., 2013; Buetti et al., 2010), that is, reflecting duration sensation. This extracted information would then inform a conscious percept of time, that is, duration perception. Objective and perceived duration, however, do not always agree, as evidenced by time distortions that highlight the constructive nature of timing (Eagleman, 2008). We reasoned that the subjective experience of duration would engage higher-order areas and in some measure should be less sensitive to objective differences in duration.

We found two independent (i.e., nonoverlapping) sets, one sensitive to objective duration and comprising bilateral early extrastriate areas and one sensitive to subjective duration, including the left superior frontal gyrus and the left cerebellum, and to a lesser degree the BG, parietal cortex, and posterior cingulate cortex. Direct comparisons of Subjective and Objective activations confirmed a pattern of activation that was consistent with that observed in the Subjective contrast and not with the Objective contrast, thus further supporting the notion of independent sets of brain activations. These data suggest two functionally independent, hierarchically segregated systems for sensory and perceptual representations of duration.

METHODS

Participants

Twenty-eight participants were recruited in the study (19 women, age = 27.7 ± 6.3 years, range = 20–48 years). All participants had normal or corrected-to-normal vision. Informed consent was obtained from all participants before starting the experiment. Five participants were excluded from the analysis of functional data because of poor psychometric fits (with left tail $>.25$ and right tail $<.75$ probability) for Accelerating probe data collected during the structural scan. The functional data of the remaining 23 participants is reported below (15 women, age = 28.5 ± 6.5 years, range = 20–48 years). The study was approved by the University College London ethics committee and was in agreement with research guidelines and regulations. Experimental protocols conformed to the guidelines of the Declaration of Helsinki.

Apparatus

Visual stimuli were back-projected with an LCD projector displaying at 1024×760 (60 Hz) onto a translucent screen at

end of the MRI bore. Participants viewed the screen through a mirror mounted on a 32-channel head coil. Participants wore silicone earplugs and overear headphones through which they received instructions. Stimulus presentation and response collection were implemented on MATLAB 2011a (The MathWorks), running the Cogent toolbox library (www.vislab.ucl.ac.uk/cogent.php).

Task and Stimuli

Participants performed duration comparisons in a visual Standard–Probe binary choice task. Participants were tested on two variants of the task, the first during a 12-min structural scan (Phase 1) and the second during two 22-min functional scan runs (Phase 2).

Identifying the Accelerating Drift Timing Bias for Perceptually Consistent Timing Categories (Phase 1)

Participants sequentially viewed Standard and Probe durations (Figure 1A), delivered through horizontally drifting sinusoidal carriers set within a stationary Gaussian envelope (drifting Gabor patch encompassing approximately 5° of visual angle, with a 0.6 cpd spatial frequency). The central portion of the patch was occupied by a Gaussian blob, which encompassed 0.5° of visual angle, on top of which a fixation cross was overlaid. The Standard stimulus

drifted rightward with Constant velocity (0.42 rad displacement per draw cycle) for 500 msec. The Probe stimuli were characterized by Constant or Accelerating drift and variable duration (for animation lasting nFrames equivalent to 500 msec or required to match point of subjective equality [PSE], drift was approximated by a fourth-degree polynomial function, $y = 976.87 \times x^4 - 49620 \times x^3 + 9.1337e^{+05} \times x^2 - 6.2571e^{+06} \times x + 1.0829e^{+07}$, for x was between 1 and 30 in nFrames steps and y was successively scaled to guarantee that the Probe's average drift velocity was equal to the Standard drift velocity). Horizontal shifts progressively increased (accelerated) across draw cycles, with an average velocity that matched that of the Constant drift Standard. Previous studies reveal that accelerating stimuli appear to last shorter than stimuli of equal duration that move at constant velocity (Bruno et al., 2015; Sasaki et al., 2013; Binetti et al., 2012; Matthews, 2011). Probe duration was selected based on randomly perturbed estimates of the PSE, yielded by a QUEST adaptive staircase routine across 200 trials (Watson & Pelli, 1983). Stimuli were separated by a 500-msec ISI, where only the central fixation cross was displayed. At the end of the trial, participants were required to indicate with a right hand button press which stimulus, the first or second, lasted longer. Standard and Probe stimulus order was counterbalanced across trials. The purpose of this task was that of identifying the PSE of the Accelerating drift stimuli for each participant,

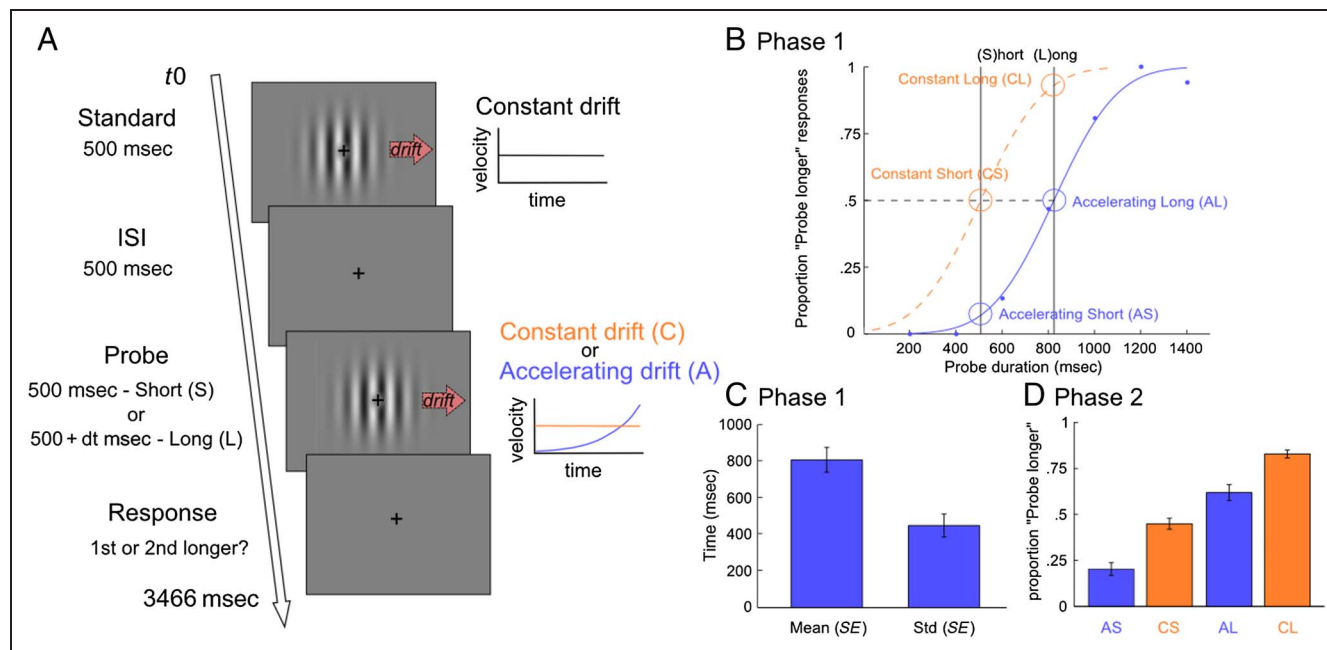


Figure 1. (A) Time course of events in trial during functional scans. The Standard grating drifted rightward with Constant velocity for 500 msec, whereas the Probe grating had Constant or Accelerating drift, lasting 500 msec or a duration that matched the participant's PSE for accelerating stimuli. Stimuli were separated by a 500-msec ISI. At the end of the trial, participants indicated which stimulus lasted longer (first or second). Standard and Probe order was counterbalanced across trials. (B) During the structural scan (Phase 1), we identified the participant's PSE for Accelerating stimuli, that is, duration required for an Accelerating probe to appear equally long to the Constant standard. During the functional scans (Phase 2), participants were presented Constant (C) and Accelerating (A) stimuli lasting 500 msec (S) or longer durations equivalent to the participant's PSE (L), yielding four stimulus categories: CS, CL, AS and AL. (C) Mean and variability (standard deviation) of the PSE for Accelerating stimuli to be perceived equally long to the 500-msec Constant drift Standard, as calculated during the structural scan (Phase 1). Error bars depict the SEM. (D) Proportion of "Probe lasted longer" responses for the four stimulus categories presented during the functional scans (Phase 2).

that is, the duration required for the Accelerating stimulus to be perceived equally long to the Constant drift Standard. This was aimed at generating duration categories that were perceptually consistent across participants. We predicted, based on previous observations (Binetti et al., 2012; Matthews, 2011), that the Accelerating drift would produce a PSE greater than the 500-msec Standard duration, indicating a compression of perceived duration, that is, the Probe would have to last longer than the Standard in order for the two to appear equally long.

Dissecting Activity Sensitive to Objective and Subjective Differences in Duration (Phase 2)

After completing the structural scan, participants performed a similar task during two functional scan runs. The task varied with respect to the previous one in two respects: (1) Participants now estimated both Accelerating and Constant drift probes, presented in alternating blocks of six trials, and (2) only two Probe durations were tested (Figure 1A, B): a 500-msec duration (Short—equivalent to the standard duration) and the duration required for an Accelerating probe to appear equally long to the standard (>500 msec, Long—the PSE determined on an individual basis in Phase 1). This yielded four stimulus combinations: Constant-Short (CS), Accelerating-Short (AS), Constant-Long (CL), and Accelerating-Long (AL). To maintain attentional set, incidental Constant and Accelerating stimuli at two flanker durations were included (Short flankers and Long flankers—the duration required for an Accelerating probe to generate 10% and 90% of “Probe longer” responses, respectively; not shown in Figure 1). This ensured the participants were engaged by occasionally exposing them to easy trials (in which Standard and Probe were noticeably different). Probe duration (Short, Long, and flankers) was randomly selected across trials. Participants were presented 140 Short probes (70 Constant drift + 70 Accelerating drift), 140 Long probes (70 Constant drift + 70 Accelerating drift), and 56 flankers (28 Short Constant drift flankers + 28 Long Accelerating drift flankers), for a total of 336 trials per run. Every 48 trials, participants had a 12-sec resting period where only the central fixation cross was displayed (six resting periods per run). Phase 2 was aimed at identifying brain activity uniquely related to an Objective difference in probe duration (Long vs. Short probes) or to a Subjective difference in probe duration, based on duration classifications (Subjectively Short vs. Subjectively Long), revealing responses linked to duration sensation and perception, respectively.

Behavioral Data Analysis

Randomly perturbed QUEST estimates were binned (seven linearly spaced time bins ranging between 100 and 1500 msec), and the proportion of “Probe longer” responses per time bin was calculated. We fit each participant’s responses with a cumulative Gaussian (Figure 1B). The 50% point of this function

yielded an estimate of the participant’s PSE for Accelerating drift, that is, the duration required for an Accelerating Probe to be perceived equally long to the Constant drift Standard. A PSE larger than the 500-msec Standard would indicate that accelerating drift induces a compression of time as the Probe has to last longer than the Standard in order for the two to appear equally long. The PSE values for Accelerating drift, calculated for each participant, determined the duration of Long stimuli presented in Phase 2. Behavioral data were analyzed with JASP 0.8.1.1 (<https://jasp-stats.org/>).

fMRI Data Acquisition

Whole-brain 3-D gradient-echo EPI (Lutti, Thomas, Hutton, & Weiskopf, 2013) data were acquired on a Siemens Trio 3T scanner equipped with a 32-channel head coil for signal reception. Functional data were acquired over two sessions (2249 volumes total per participant). Acquisition parameters were as follows: 3 mm isotropic resolution, echo time = 15.85 and 34.39 msec (multiecho acquisition), repetition time = 1.1 sec per volume. Each volume was acquired with an acceleration of 3 in the through-slab direction and a speed-up factor of 2 in the in-plane direction, and the images were reconstructed using the GRAPPA algorithm (Griswold et al., 2002) as implemented on the scanner console. The first five volumes were discarded to allow for steady-state magnetization. A flip angle of 15° was used.

Field maps were acquired before the functional runs for subsequent correction of geometric distortions in EPI data at high field strength using a multiecho gradient-echo with 3-mm isotropic resolution and echo times of 10 msec/12.46 msec (short/long, respectively). Whole-brain T1-weighted anatomical images of each participant’s brain were acquired using an optimized 3-D modified driven equilibrium Fourier transform imaging sequence (Deichmann, Schwarzbauer, & Turner, 2004) with 1-mm isotropic resolution. The sequence used an inversion time of 910 msec, echo time = 2.48 msec, repetition time = 7.92 msec, and flip angle = 16°.

fMRI Data Analysis

Data were analyzed using SPM12 (Wellcome Trust Centre for Neuroimaging, University College London). Preprocessing included realignment and unwarping using individual field maps, coregistration of EPI to individual anatomical images, spatial normalization to the Montreal Neurological Institute (MNI) space, and spatial smoothing using an 8-mm FWHM Gaussian kernel.

We disambiguate Objective and Subjective duration by contrasting stimuli based on their physical duration (Long—L vs. Short—S) or based on the classification of duration as indicated through participant responses (Probe judged shorter—0 vs. Probe judged longer—1). The general linear model included 13 event-related regressors modeling responses to each event in our 2 × 2 × 2 factorial design. The first eight involved combinations of stimulus type

(Accelerating—A/Constant drift—C), stimulus duration (Short—S/Long—L), and perceived duration (Perceived Short—0/Long—1), modeled relative to the onset of the Probe stimulus. Additionally, the onset of short (Regressor 9) and long (Regressor 10) flanker stimuli, the onset of (Regressor 11) eye blinks, (Regressor 12) pauses, and the onset participants' button presses (Regressor 13) were included. All event-related responses were modeled as stick functions; apart from pauses that were modeled as continuous 12-sec events. In addition to event regressors, a total of 23 nuisance regressors were included to account for motion and physiological effects of no interest. A physiological noise model was constructed using an in-house MATLAB toolbox (Hutton et al., 2011) to remove variance accounted for by cardiac and respiratory responses. The model comprised 17 physiological regressors in total: 6 for respiratory phase, 1 for respiratory volume, and 10 for cardiac phase. Finally, to discount motion-related artifacts that eluded rigid body motion correction, the six motion regressors obtained during realignment were included.

In this paper, we focus on the simple main effects of Objective and Subjective duration (Short vs. Long) by testing two contrasts. Objective duration was explored by contrasting (CL1 + AL1 + CL0 + AL0)–(CS1 + AS1 + CS0 + AS0). Subjective duration was explored by contrasting stimuli based on the participant duration classifications, independently of their objective duration: Subjective contrast (CS1 + AS1 + CL1 + AL1)–(CS0 + AS0 + CL0 + AL0). For whole-brain analyses, statistical parametric maps of each contrast were characterized in terms of significant clusters, using a cluster-defining threshold of $p = .001$; the 0.05 family-wise error (FWE)-corrected critical cluster size was 100 voxels. We also report additional findings descriptively at $p = .001$, uncorrected for subsequent confirmation. We also directly contrasted Subjective and Objective duration to identify activations that significantly differed between these conditions.

Experimental data and codes used in the study are available upon direct request, consistent with University College London's guidelines and regulations.

RESULTS

Behavioral Data

We computed the PSE for Accelerating drift stimuli. As anticipated, we found that Accelerating drift induced a substantial compression of perceived time: on average, Accelerating drift stimuli had to last 806 ± 324 msec to be perceived equally long to the 500-msec Constant drift Standard (Figure 1C).

We submitted proportion of “Probe longer” responses to a repeated-measures ANOVA with Stimulus Type as within-subject factor (AS vs. CS vs. AL vs. CL; Figure 1D) and participant Age (binned, above and below mean) and Sex as covariates. The analysis revealed a main effect of Stimulus Type, $F(3, 57) = 51.99, p < .001, \eta_p^2 = .71$; we observed

no modulatory effect of Age, $F(3, 57) = .2, p = .89, \eta_p^2 = .003$, or Sex, $F(3, 57) = 1, p = .4, \eta_p^2 = .01$, on Stimulus Type. *t*-Test comparisons showed that, relative to Constant drift stimuli, Accelerating drift stimuli yielded significantly smaller proportions of “Probe longer” responses, both for Short (AS vs. CS: $t(22) = -4.6, p < .0001, d = -.96$) and Long (AL vs. CL: $t(22) = -4.78, p < .00001, d = -.99$) durations.

We also tested whether proportions of “Probe longer” responses for AS, CS, AL, and CL stimuli differed from chance-level performance (.5 proportion of “Probe longer responses”). Bonferroni corrected *t* tests revealed that, despite lasting the same as the Standard, the proportion of “Probe longer” responses for AS stimuli significantly differed from chance level, $t(22) = -8.61, p < .00001, d = -1.79$, due to an illusory shortening of time induced by acceleration. Unsurprisingly, proportion of “Probe longer” responses for CL stimuli also significantly differed from chance level, $t(22) = 14.83, p < .00001, d = 3.09$, as these did not accelerate and physically lasted longer than the Standard. Proportion of “Probe longer” responses for AL stimuli showed a borderline significant difference from chance level, $t(22) = 2.73, p = .049, d = .57$. Because Long durations were selected based on each participant's PSE for accelerating stimuli observed in Phase 1, AL stimuli were perceived on average similar in duration to the Standard despite their physical difference in duration. Finally, proportion of “Probe longer” responses for CS stimuli, which shared duration and drift profile with the Standard, did not significantly differ from chance level, $t(22) = -1.74, p = .38, d = -.36$.

Imaging Analyses

Our general linear model design enabled contrasting stimuli based on differences in Objective duration (Objectively Long = L vs. Objectively Short = S) or based on the classification of duration provided by participant responses on a trial-by-trial basis, Subjective duration (Subjectively Long = 1 vs. Subjectively Short = 0). This design accounts for low-level feature processing, attentional, decisional, and motoric task demands, which are equally shared across conditions. We performed two contrasts to identify brain activity uniquely related to Objective and Subjective differences in duration (Figure 2A).

Objective Duration Contrast Reveals Activity Bilateral Early Visual Extrastriate Areas

Objective duration was explored by contrasting longer versus shorter stimuli, independently of participant responses (Figure 2B, top). Activated areas were confined to visual regions including right inferior occipital gyrus ($p = .002$ FWE cluster-corrected; peak coordinate [36 -88 6], $t(1, 22) = 4.96$) and the left occipital pole ($p = .003$ FWE cluster-corrected; peak coordinate [-22 -96 14], $t(1, 22) = 4.82$). For exploratory purposes, we also evaluated the

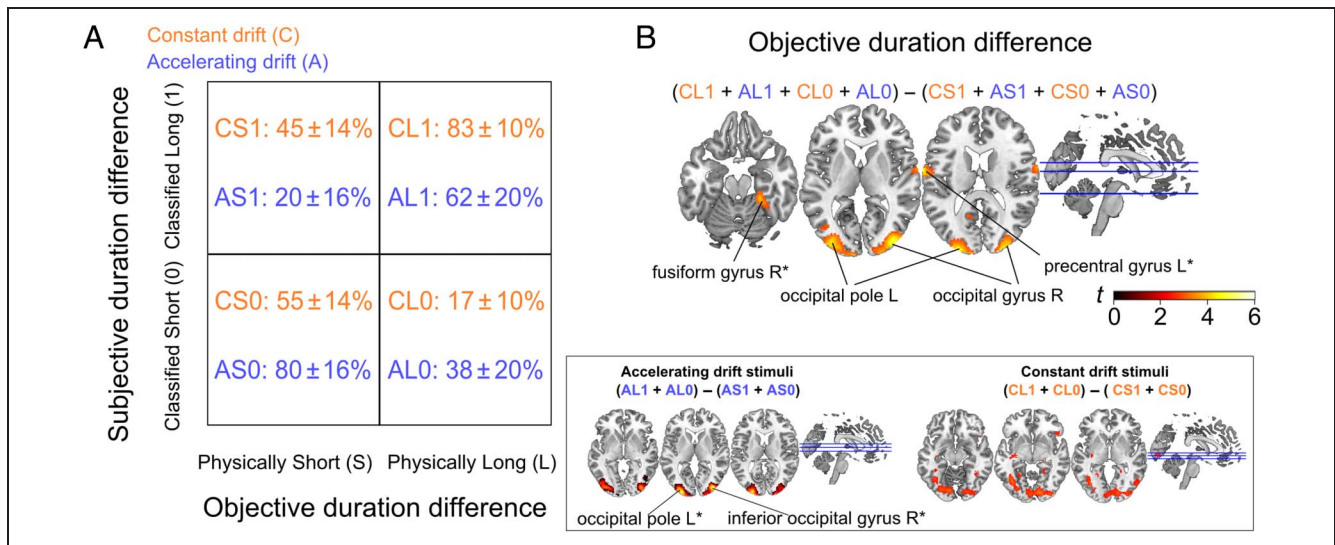


Figure 2. (A) Objective and Subjective duration contrasts, based on the subjective (columns) or objective stimulus duration (rows). Percentages depict the distribution of Short (S) and Long (L) Control (C) and Accelerating (A) stimuli across Objective/Subjective duration categories. (B) Axial slices depicting activations for the contrast identifying objective duration difference, collapsed across stimuli categories (top). Lower panels show the activity changes within each stimulus category. Activation images thresholded for t scores > 2.8 (all stimuli and Accelerating stimuli) and t scores > 2.3 (Constant stimuli). * $p < .001$, uncorrected.

Objective duration contrast at a more lenient $p < .001$ threshold (uncorrected), which showed additional activity in the left precentral gyrus (peak coordinate $[-66 -4 16]$, $t(1, 22) = 4.53$) and the right fusiform gyrus (peak coordinate $[24 -36 -20]$, $t(1, 22) = 4$).

We further explored Objective duration for Accelerating and Constant stimuli separately (Figure 2B, bottom). Accelerating drift stimuli ((AL1 + AL0) - (AS1 + AS0)) revealed a cluster of activation in the right inferior occipital gyrus ($p = .005$ FWE cluster-corrected; $p = .046$ voxelwise FWE correction; peak coordinate $[-36 -86 2]$, $t(1, 22) = 6.18$) and in the left occipital pole ($p < .001$ FWE cluster-corrected; peak coordinate $[-24 -96 8]$, $t(1, 22) = 5.67$). For Constant drift stimuli ((CL1 + CL0) - (CS1 + CS0)), no regions reached either FWE cluster-corrected significance ($p < .05$) or significance at more lenient statistical thresholds ($p < .001$, uncorrected). We explored Objective duration for Constant drift stimuli at a more lenient threshold ($p < .01$ uncorrected), which showed an equivalent pattern of activity to the Accelerating drift stimuli, with a cluster of activation in the left and right occipital gyri. Although these patterns of activity were equivalent for Accelerating and Constant drift stimuli, the former were more effective at revealing differences in time sensation.

Subjective Duration Contrast Reveals Activity in the Left Superior Frontal Gyrus and the Left Cerebellum

Subjective duration was explored by contrasting stimuli based on a participant's duration classification, independently of their physical duration (Figure 3, top). We identified a cluster of activation in the medial segment of the left superior frontal gyrus ($p = .002$ FWE cluster-

corrected; peak coordinate $[-2 28 42]$, $t(1, 22) = 5.61$) and on the left lateral lobe of the cerebellum ($p = .041$ FWE cluster-corrected; peak coordinate $[-46 -60 -38]$, $t(1, 22) = 5.17$). In addition, at a more lenient statistical threshold (i.e., $p < .001$ uncorrected), activations included the right putamen (peak coordinate $[26 -6 8]$, $t(1, 22) = 3.89$), the left caudate ($[-8 8 4]$, $t(1, 22) = 3.81$), the right anterior insula ($[32 18 -8]$, $t(1, 22) = 3.93$), the left parietal cortex (supramarginal gyrus $[-46 -50 56]$, $t(1, 22) = 4.3$) and the left occipital fusiform gyrus ($[-16 -98 -14]$, $t(1, 22) = 3.81$). We explored Subjective duration for each stimulus drift type separately (Constant and Accelerating; Figure 3, bottom). Accelerating drift stimuli ((AS1 + AL1) - (AS0 + AL0)) showed a cluster of activation in the medial segment of the left superior frontal gyrus ($p < .001$ FWE cluster-corrected; peak coordinate $[-4 26 42]$, $t(1, 22) = 5.69$) and marginally significant activations ($p < .001$ uncorrected) in the left and right lateral lobes of the cerebellum (left: peak coordinate $[-44 -62 -44]$, $t(1, 22) = 5.81$; right: peak coordinate $[26 -80 -46]$, $t(1, 22) = 5.41$), left superior frontal gyrus (peak coordinate $[-14 18 62]$, $t(1, 22) = 4.65$), left middle frontal gyrus (peak coordinate $[-40 56 -4]$, $t(1, 22) = 4.27$), right supra-marginal gyrus (peak coordinate $[60 -40 38]$, $t(1, 22) = 3.53$), right angular gyrus (peak coordinate $[54 -52 40]$, $t(1, 22) = 4.19$), and left caudate (peak coordinate $[-8 8 4]$, $t(1, 22) = 3.8$), all areas generally associated with tasks that require integration of somatosensory signals and timing tasks (Jones & Jahanshahi, 2011; Buhusi & Meck, 2005; Nenadic et al., 2003; Rao et al., 2001; Ivry & Keele, 1989). More specifically, the BG and pFC are believed to be involved in magnitude representations used in perceptual timing tasks (Buhusi & Meck, 2005). Constant drift

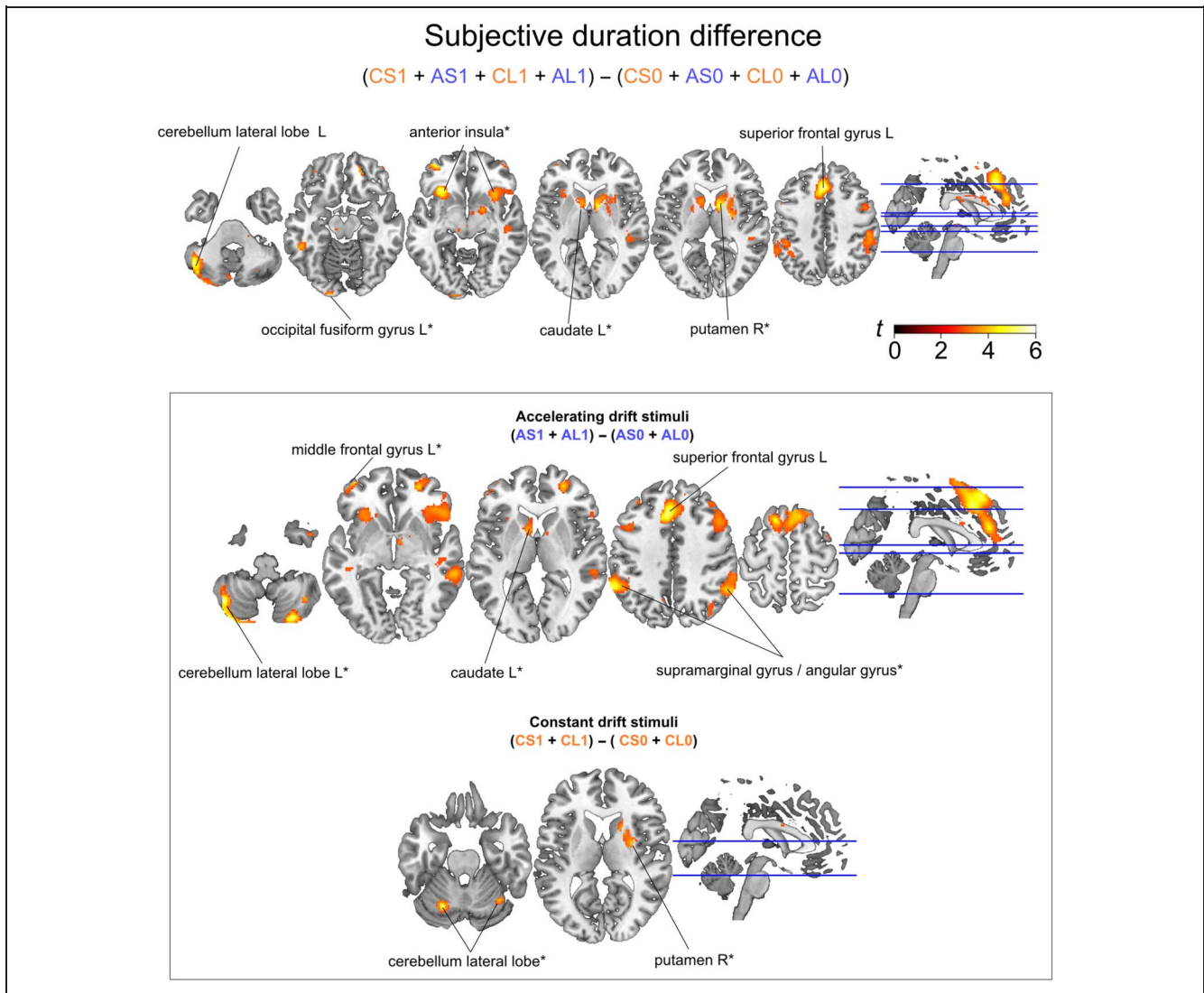


Figure 3. Subjective duration contrast activations, collapsed across stimuli categories (top) or within each stimulus category separately (bottom). Activation images thresholded for t scores > 2.8 . $*p < .001$, uncorrected, for display purposes.

stimuli ((CS1 + CL1) - (CS0 + CL0)) revealed only marginally significant activations on the left and right lateral lobe of the cerebellum ($p < .001$ uncorrected, left: peak coordinate $[-22 -66 -24]$, $t(1, 22) = 5.51$; right: peak coordinate $[36 -60 -24]$, $t(1, 22) = 3.86$) and the right putamen ($p < .001$ uncorrected, peak coordinate $[30 -2 10]$, $t(1, 22) = 3.93$).

Subjective–Objective Duration Direct Comparison Confirms Differences in Frontal–Medial Areas

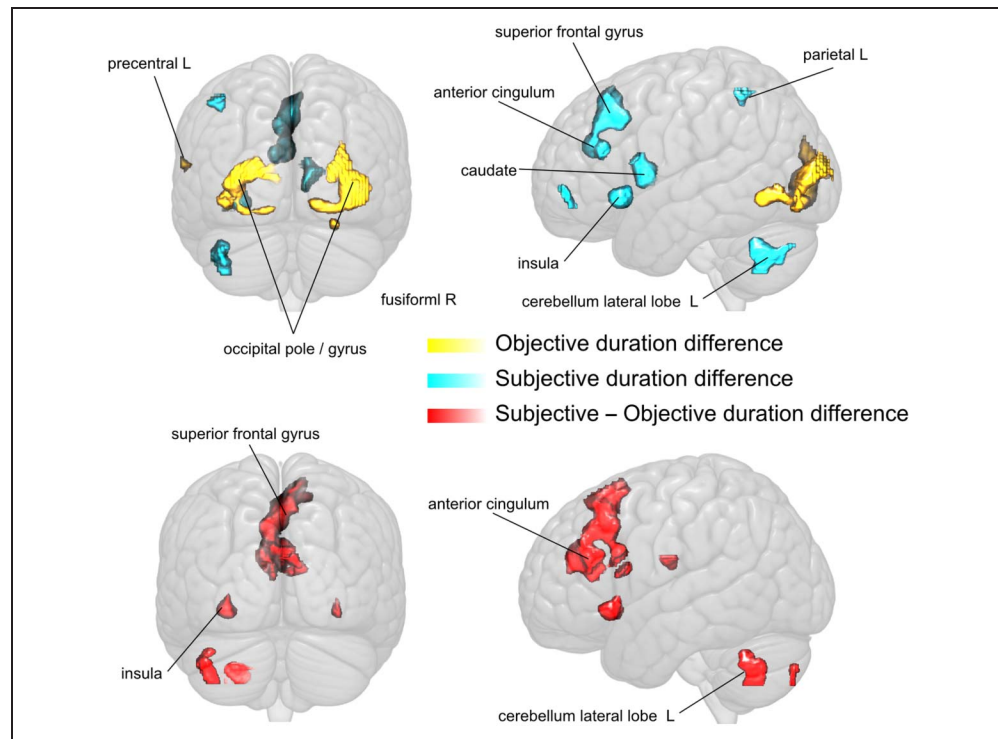
Objective and Subjective activations were directly contrasted to formally assess differences between networks uniquely processing timing sensation and perception, identified by the simple main Objective and Subjective contrasts. Paired-sample t tests revealed a cluster of activity in frontal–medial areas, peaking in dorsal ACC BA 32 ($p < .001$ FWE cluster-corrected; peak coordinate $[-12 32 24]$, $t(1, 22) = 5.22$).

This cluster included left superior frontal gyrus, which was the strongest activation observed in the Subjective contrast ($p < .001$ FWE cluster-corrected; peak coordinate $[-4 26 40]$, $t(1, 22) = 5.22$). At a more lenient statistical threshold (i.e., $p < .001$ uncorrected), we observed a pattern of activations that were consistent with what observed in the Subjective duration contrast, notably including the insula (left: peak coordinate $[-32 -20 -8]$, $t(1, 22) = 5.08$; right: peak coordinate $[32 18 -10]$, $t(1, 22) = 3.89$) and the left lobe of the cerebellum (peak coordinate $[-26 -86 -42]$, $t(1, 22) = 5.08$; Figure 4).

DISCUSSION

We identified brain activity uniquely sensitive to Objective differences in duration (time sensation) and Subjective differences in duration (time perception) while accounting for low-level feature processing, attentional, decisional, and

Figure 4. Rendered, semi-transparent view depicting brain regions sensitive to Objective (yellow) and Subjective (blue) duration (t scores > 2.8 and Objective cluster size > 12 voxels or Subjective cluster size > 35 voxels).



motoric task demands, which were balanced across conditions. We found that Objective duration was reflected in activity increases in early visual areas (left occipital pole and right inferior occipital gyrus), whereas Subjective duration was reflected in activity increases across a cortical/subcortical network comprising the left superior frontal gyrus and the left lateral cerebellum (Table 1). A more lenient threshold ($p < .001$, uncorrected) revealed additional activity increases in the BG (right putamen, left caudate), the right supramarginal gyrus, and right angular gyrus, all areas typically associated with perceptual timing tasks. Interestingly, there was no overlap between these networks, suggesting a clear dichotomy between activity linked to Objective and Subjective duration (Figure 4).

Timing Is Achieved throughout a Distributed Cortical and Subcortical Hierarchy

Timing relies on mechanisms that guarantee a quasi-linear correspondence between objective and perceived duration, at least within the millisecond-to-second range. As with all perceptual systems, timing is constructive, where sensory and nonsensory (e.g., contextual, prior experience) information are integrated across processing stages. Indeed, neuroimaging, brain lesion, and neurophysiological evidence reveal a highly modular and distributed architecture (Merchant, Harrington, & Meck, 2013). Furthermore, recent studies reveal a chronotopic organization of time (Harvey, Dumoulin, Fracasso, & Paul, 2020; Protopapa et al., 2019). Adaptation studies show duration selectivity in neural populations of the inferior parietal lobule, the posterior temporal

cortex, the middle frontal gyrus, the middle cingulate cortex, the caudate, putamen, the inferior temporal gyri (Hayashi et al., 2015), and the SMA (Protopapa et al., 2019). Given the repeated presentation of two durations in our study (500 and ~ 800 msec—average PSE), a subset of activations (parietal, cingulate cortex, putamen, and caudate) may additionally reflect adaptation-like effects uncovered in these previous studies.

Primate electrophysiology (Shuler & Bear, 2006; Ghose & Maunsell, 2002) and human neuroimaging (Buetti et al., 2010; Buetti & Macaluso, 2010) studies have shown that time information modulates activity in primary visual areas, suggesting an involvement of sensory cortices in memory and encoding stages of time perception (Salvioni et al., 2013). Studies contrasting timing against carefully matched nontiming tasks have identified the cerebellum and BG/striatum as candidate time accumulation structures, whereas frontal and parietal areas are more likely involved with attentional, working memory and decisional aspects of the task (Ferrandez et al., 2003; Nenadic et al., 2003; Belin et al., 2002; Rao et al., 2001). Physiological and imaging studies have narrowed down brain activity that is modulated by time and therefore more specifically linked to timekeeping. Direct recordings in macaque parietal cortex show a build-up of response frequency as a function of duration (Janssen & Shadlen, 2005). Similarly, amplitude of evoked brain responses originating in frontal brain areas (contingent negative variation) covary with elapsed duration (Herbst, Chaumon, Penney, & Busch, 2015; Pfeuty et al., 2005). These findings suggest that areas involved with the accumulation of timing evidence should be sensitive

Table 1. FWE Cluster-corrected Peak Coordinates of Activation for Objective and Subjective Duration Contrasts and Objective/Subjective Duration for Accelerating Stimuli

<i>Contrast</i>	<i>Location in Stereotaxic Space: MNI</i>	<i>Cluster Size</i>	<i>pFWE</i>	<i>t Value (Peak)</i>	<i>Label (Neuromorphometrics)</i>
Objective	38 -88 6	712	.002	4.96	Right IOG (inferior occipital gyrus)
Objective	-22 -96 14	622	.003	4.82	Left OP (occipital pole)
Subjective	-2 28 42	608	.002	5.61	Left MSFG (superior frontal gyrus medial segment)
Subjective	-46 -60 -38	294	.041	5.17	Left cerebellum exterior
Objective (Accelerating stimuli)	36 -86 2	512	.005	6.18 Also pfwe = 0.046 voxelwise	Right IOG (inferior occipital gyrus)
Objective (accelerating stimuli)	-24 -96 8	886	$p < .001$	5.67	Left OP (occipital pole)
Subjective (accelerating stimuli)	-44 -62 -44	367	.055	5.81	Left cerebellum exterior
Subjective (accelerating stimuli)	-4 26 42	1285	$p < .001$	5.696	Left MSFG (superior frontal gyrus medial segment)

to differences in duration, which is a feature expected from hypothetical time accumulation mechanisms.

Objective or Subjective Differences in Duration as Handles of Time Accumulation Mechanisms

Based on this evidence, Pouthas and coworkers (2005) investigated what areas within a timing network were specifically modulated by duration, aimed at identifying physiological correlates of time accumulator/s (Pouthas et al., 2005). A timing versus nontiming task contrast identified a timing network comprising the frontal, mesiofrontal (preSMA), parietal cortices, and BG. This was followed by contrasting Long versus Short stimuli, revealing activity sensitive to difference in duration in the preSMA, the ACC, the right inferior frontal gyrus (corresponding to Broca's area), the lateral premotor cortex bilaterally, and the right caudate nucleus. PreSMA and the caudate nucleus were identified as candidate accumulator mechanisms, consistently with neuropsychological (Jahanshahi et al., 2010; Malapani, Deweer, & Gibbon, 2002; Harrington, Haaland, & Hermanowitz, 1998) and pharmacological (Coull, Hwang, Leyton, & Dagher, 2012) evidence linking frontostriatal dopaminergic activity to timing. The authors argued that the ACC activation reflected attentional control related to the response selection component of the task, where longer durations require longer sustaining of attention (Wu et al., 2017; Peru, Pavesi, & Campello, 2004).

As with all constructive processes, our perception of duration is not necessarily veridical. This is clearly evidenced by time distortions induced by endogenous factors such as fluctuations of arousal (Binetti, Harrison, Mareschal, & Johnston,

2017) or dopamine levels (Marinho et al., 2018) or through manipulations of stimulus features, such as stimulus number, size, or luminance (Xuan, Zhang, He, & Chen, 2007) or motion dynamics (Binetti et al., 2012; Matthews, 2011; Kanai, Paffen, Hogendoorn, & Verstraten, 2006). Based on this, perceived duration, opposed to objective duration of a stimulus, should provide a more robust handle on timekeeping. Buetti and Macaluso (2011) focused on the relationship between the perceptual experience of time and corresponding neural activity by inducing illusory time dilation via visual motion (faster moving stimuli = time overestimation) of stimuli in a duration reproduction task (Buetti & Macaluso, 2011). Contrasting the timing task versus a nontiming control revealed activity in the putamen, the mid-insula, the SMA, the mid/superior temporal gyri, the right VI lobule of the cerebellum, and the TPJ. Importantly, the authors identified activity that covaried with perceptual duration estimates (reproduction errors) in the right putamen, the right mid-insula, and the superior temporal cortex, revealing accumulation behavior across various brain structures. However, a limitation of studies relying on timing versus nontiming comparisons is that, despite being carefully matched in difficulty and sensory features, they can introduce discrepancies in attentional, strategic, or decisional demands (Pouthas et al., 2005).

Disentangling Activity Uniquely Sensitive to Objective and Subjective Differences in Duration

In this study, we combined approaches comparing Objective and Subjective differences in duration, within a single protocol strictly focused on comparisons within

timing conditions. Opposed to prior studies, this approach did not rely on a nontemporal control task. Both Objective and Subjective contrasts accounted for processing of low-level visual features of stimuli, attentional, decisional, and motoric task demands, which were equally shared across conditions.

Objective duration was associated with activity increases in early visual areas (left occipital pole and right inferior occipital gyrus), corresponding to bilateral early extrastriate area, as previously reported in animal (Onoe et al., 2001) and human imaging studies (Bueti et al., 2010). Importantly, early sensory areas have been associated with the extraction of time features from the sensory signal (Salvioni et al., 2013), and Objective differences in duration did not modulate activity in areas beyond the visual system that are involved with cognitive (i.e., nonsensory) components of timing. For exploratory purposes, we investigated brain activity at a more lenient threshold ($p < .001$, uncorrected). We found activations in the left precentral gyrus, which has been frequently documented in time estimation (Ortuño, Guillén-Grima, López-García, Gómez, & Pla, 2011) and reproduction tasks (Jech, Dušek, Wackermann, & Vymazal, 2005), as well as the right fusiform gyrus, which has been linked to attention and working memory in visual duration discrimination tasks (Pouthas et al., 2000). The fusiform gyrus therefore was the latest visual processing stage whose activity was modulated by objective duration information. We observed no activity in V5, which was expected, given that stimuli of different durations were equated in average velocity.

Subjective duration was reflected in activity increases in the medial segment of the left superior frontal gyrus, on the border between the dorsal anterior cingulate and the pFC, and the left cerebellum. The dorsal anterior cingulate is involved in reward-based decision-making (Bush et al., 2002) and in focusing attention toward task-relevant features (Weissman, Gopalakrishnan, Hazlett, & Woldorff, 2004), whereas the pFC has been frequently linked to timing performance in neuropsychological (Koch, Oliveri, Carlesimo, & Caltagirone, 2002) and brain stimulation studies (Koch, Oliveri, Torriero, & Caltagirone, 2003) and has been associated with attention to time information (Coull, Vidal, Nazarian, & Macar, 2004). Notably, both the superior frontal gyrus (Murai, Whitaker, & Yotsumoto, 2016; Jones & Jahanshahi, 2011) and the cerebellum (Murai et al., 2016; Lewis & Miall, 2003; Ivry & Keele, 1989) are commonly identified in standard/probe comparisons (Wiener, Turkeltaub, & Coslett, 2010). At more lenient thresholds ($p < .001$, uncorrected), we observed activations in the parietal cortex, a hub for abstract representations of quantities (Bueti & Walsh, 2009), posterior cingulate cortex, the angular gyrus, and the BG (right putamen and left caudate), all areas associated with perceptual timing tasks (Nenadic et al., 2003; Onoe et al., 2001; Rao et al., 2001; Ivry & Keele, 1989). Notably, we also observed activations in the anterior insula, which has been previously observed in imaging (Bueti & Macaluso, 2011; Wittmann et al., 2010)

and brain lesion (Trojano et al., 2017) timing studies. The insula is believed to mediate the subjective awareness of duration through the integration of interoceptive signals (Wittmann & Meissner, 2018; Craig, 2009a, 2009b). Also, a recent meta-analysis on conscious visual awareness revealed a distributed network involving the superior frontal gyrus, the caudate, insula, and the fusiform gyrus (Bisenius, Trapp, Neumann, & Schroeter, 2015), all areas observed in the subjective duration contrast. Importantly, Objective and Subjective contrasts yielded independent, nonoverlapping sets of activations, confirmed by direct comparisons of Subjective and Objective activations. This suggests functional independence of sensory and perceptual timing stages, which has also been reported in the frequency domain in an MEG study (Noguchi & Kakigi, 2006).

Conclusion

We identify within a timing network a subset of brain areas that are uniquely related to Objective differences in duration and Subjective differences in duration, thus disentangling time sensation and perception. We argue that early visual extrastriate regions extract duration features from the sensory signal (time sensation), without directly mediating a subjective duration experience, whereas superior frontal gyrus and the cerebellum relate to higher-order timekeeping, attentional and decisional processes subtending the subjective experience of duration and ensuing behavior (time perception). Importantly, time sensation and perception arise from functionally independent processing stages in the cortical hierarchy.

Acknowledgments

N. B. was supported through the Newton International Fellowship (Fellowship Number FN111112) awarded by the British Academy and the Royal Society. S. B. was supported by the European Research Council Starter Grant (ActSelectContext; 260424). The Wellcome Centre for Human Neuroimaging is supported by core funding from the Wellcome trust (203147/Z/16/Z). K. F. was funded by a Wellcome Trust Principal Research Fellowship (Ref: 088130/Z/09/Z). We thank Peter Zeidman for his excellent suggestions with the data analysis and interpretation of findings.

Reprint requests should be sent to Nicola Binetti, Gower St., Bloomsbury, WC1E 6BT, University College London, United Kingdom, or via e-mail: nicolabinetti@gmail.com.

REFERENCES

- Belin, P., McAdams, S., Thivard, L., Smith, B., Savel, S., Zilbovicius, M., et al. (2002). The neuroanatomical substrate of sound duration discrimination. *Neuropsychologia*, *40*, 1956–1964.
- Binetti, N., Harrison, C., Mareschal, I., & Johnston, A. (2017). Pupil response hazard rates predict perceived gaze durations. *Scientific Reports*, *7*, 3969.
- Binetti, N., Lecce, F., & Doricchi, F. (2012). Time-dilation and time-contraction in an anisochronous and anisometric visual scenery. *Journal of Vision*, *12*.

- Bisenius, S., Trapp, S., Neumann, J., & Schroeter, M. L. (2015). Identifying neural correlates of visual consciousness with ALE meta-analyses. *Neuroimage*, *122*, 177–187.
- Bruno, A., Ayhan, I., & Johnston, A. (2015). Changes in apparent duration follow shifts in perceptual timing. *Journal of Vision*, *15*, 2.
- Bueti, D., Bahrami, B., Walsh, V., & Rees, G. (2010). Encoding of temporal probabilities in the human brain. *Journal of Neuroscience*, *30*, 4343–4352.
- Bueti, D., & Macaluso, E. (2010). Auditory temporal expectations modulate activity in visual cortex. *Neuroimage*, *51*, 1168–1183.
- Bueti, D., & Macaluso, E. (2011). Physiological correlates of subjective time: Evidence for the temporal accumulator hypothesis. *Neuroimage*, *57*, 1251–1263.
- Bueti, D., & Walsh, V. (2009). The parietal cortex and the representation of time, space, number and other magnitudes. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *364*, 1831–1840.
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, *6*, 755–765.
- Buonomano, D. V., Bramen, J., & Khodadadifar, M. (2009). Influence of the interstimulus interval on temporal processing and learning: Testing the state-dependent network model. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *364*, 1865–1873.
- Bush, G., Vogt, B. A., Holmes, J., Dale, A. M., Greve, D., Jenike, M. A., et al. (2002). Dorsal anterior cingulate cortex: A role in reward-based decision making. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 523–528.
- Coull, J. T., Hwang, H. J., Leyton, M., & Dagher, A. (2012). Dopamine precursor depletion impairs timing in healthy volunteers by attenuating activity in putamen and supplementary motor area. *Journal of Neuroscience*, *32*, 16704–16715.
- Coull, J. T., Nazarian, B., & Vidal, F. (2008). Timing, storage, and comparison of stimulus duration engage discrete anatomical components of a perceptual timing network. *Journal of Cognitive Neuroscience*, *20*, 2185–2197.
- Coull, J. T., Vidal, F., Nazarian, B., & Macar, F. (2004). Functional anatomy of the attentional modulation of time estimation. *Science*, *303*, 1506–1508.
- Craig, A. D. (2009a). Emotional moments across time: A possible neural basis for time perception in the anterior insula. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *364*, 1933–1942.
- Craig, A. D. (2009b). How do you feel—Now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70.
- Deichmann, R., Schwarzbauer, C., & Turner, R. (2004). Optimisation of the 3D MDEFT sequence for anatomical brain imaging: Technical implications at 1.5 and 3 T. *Neuroimage*, *21*, 757–767.
- Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, *18*, 131–136.
- Ferrandez, A. M., Hugueville, L., Lehericy, S., Poline, J. B., Marsault, C., & Pouthas, V. (2003). Basal ganglia and supplementary motor area subattend duration perception: An fMRI study. *Neuroimage*, *19*, 1532–1544.
- Franssen, V., Vandierendonck, A., & Van Hiel, A. (2006). Duration estimation and the phonological loop: Articulatory suppression and irrelevant sounds. *Psychological Research*, *70*, 304–316.
- Ghose, G. M., & Maunsell, J. H. (2002). Attentional modulation in visual cortex depends on task timing. *Nature*, *419*, 616–620.
- Griswold, M. A., Jakob, P. M., Heidemann, R. M., Nittka, M., Jellus, V., Wang, J., et al. (2002). Generalized autocalibrating partially parallel acquisitions (GRAPPA). *Magnetic Resonance in Medicine*, *47*, 1202–1210.
- Harrington, D. L., Haaland, K. Y., & Hermanowitz, N. (1998). Temporal processing in the basal ganglia. *Neuropsychology*, *12*, 3–12.
- Harvey, B. M., Dumoulin, S. O., Fracasso, A., & Paul, J. M. (2020). A network of topographic maps in human association cortex hierarchically transforms visual timing-selective responses. *Current Biology*, *30*, 1424–1434.
- Hayashi, M. J., Ditye, T., Harada, T., Hashiguchi, M., Sadato, N., Carlson, S., et al. (2015). Time adaptation shows duration selectivity in the human parietal cortex. *PLoS Biology*, *13*, e1002262.
- Hayashi, M. J., van der Zwaag, W., Bueti, D., & Kanai, R. (2018). Representations of time in human frontoparietal cortex. *Communications Biology*, *1*, 233.
- Herbst, S. K., Chaumon, M., Penney, T. B., & Busch, N. A. (2015). Flicker-induced time dilation does not modulate EEG correlates of temporal encoding. *Brain Topography*, *28*, 559–569.
- Hutton, C., Josephs, O., Stadler, J., Featherstone, E., Reid, A., Speck, O., et al. (2011). The impact of physiological noise correction on fMRI at 7 T. *Neuroimage*, *57*, 101–112.
- Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience*, *1*, 136–152.
- Ivry, R. B., & Richardson, T. C. (2002). Temporal control and coordination: The multiple timer model. *Brain and Cognition*, *48*, 117–132.
- Jahanshahi, M., Jones, C. R., Zijlmans, J., Katzenschlager, R., Lee, L., Quinn, N., et al. (2010). Dopaminergic modulation of striato-frontal connectivity during motor timing in Parkinson's disease. *Brain*, *133*, 727–745.
- Janssen, P., & Shadlen, M. N. (2005). A representation of the hazard rate of elapsed time in macaque area LIP. *Nature Neuroscience*, *8*, 234–241.
- Jech, R., Dušek, P., Wackermann, J., & Vymazal, J. (2005). Cumulative blood oxygenation-level-dependent signal changes support the 'time accumulator' hypothesis. *NeuroReport*, *16*, 1467–1471.
- Jones, C. R., & Jahanshahi, M. (2011). Dopamine modulates striato-frontal functioning during temporal processing. *Frontiers in Integrative Neuroscience*, *5*, 70.
- Kanai, R., Paffen, C. L., Hogendoorn, H., & Verstraten, F. A. (2006). Time dilation in dynamic visual display. *Journal of Vision*, *6*, 1421–1430.
- Kawashima, R., Inoue, K., Sugiura, M., Okada, K., Ogawa, A., & Fukuda, H. (1999). A positron emission tomography study of self-paced finger movements at different frequencies. *Neuroscience*, *92*, 107–112.
- Koch, G., Oliveri, M., Carlesimo, G. A., & Caltagirone, C. (2002). Selective deficit of time perception in a patient with right prefrontal cortex lesion. *Neurology*, *59*, 1658–1658.
- Koch, G., Oliveri, M., Torriero, S., & Caltagirone, C. (2003). Underestimation of time perception after repetitive transcranial magnetic stimulation. *Neurology*, *60*, 1844–1846.
- Leon, M. I., & Shadlen, M. N. (2003). Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron*, *38*, 317–327.
- Lewis, P. A., & Miall, R. C. (2003). Distinct systems for automatic and cognitively controlled time measurement: Evidence from neuroimaging. *Current Opinion in Neurobiology*, *13*, 250–255.
- Lindbergh, C. A., & Kieffaber, P. D. (2013). The neural correlates of temporal judgments in the duration bisection task. *Neuropsychologia*, *51*, 191–196.
- Lutti, A., Thomas, D. L., Hutton, C., & Weiskopf, N. (2013). High-resolution functional MRI at 3 T: 3D/2D echo-planar

- imaging with optimized physiological noise correction. *Magnetic Resonance in Medicine*, 69, 1657–1664.
- Macar, F., & Vidal, F. (2004). Event-related potentials as indices of time processing: A review. *Journal of Psychophysiology*, 18, 89–104.
- Malapani, C., Deweer, B., & Gibbon, J. (2002). Separating storage from retrieval dysfunction of temporal memory in Parkinson's disease. *Journal of Cognitive Neuroscience*, 14, 311–322.
- Marinho, V., Oliveira, T., Rocha, K., Ribeiro, J., Magalhães, F., Bento, T., et al. (2018). The dopaminergic system dynamic in the time perception: A review of the evidence. *International Journal of Neuroscience*, 128, 262–282.
- Matell, M. S., Meck, W. H., & Nicolelis, M. A. (2003). Interval timing and the encoding of signal duration by ensembles of cortical and striatal neurons. *Behavioral Neuroscience*, 117, 760–773.
- Mathews, W. J. (2011). How do changes in speed affect the perception of duration? *Journal of Experimental Psychology: Human Perception and Performance*, 37, 1617–1627.
- Merchant, H., Harrington, D. L., & Meck, W. H. (2013). Neural basis of the perception and estimation of time. *Annual Review of Neuroscience*, 36, 313–336.
- Merchant, H., & Yarrow, K. (2016). How the motor system both encodes and influences our sense of time. *Current Opinion in Behavioral Sciences*, 8, 22–27.
- Murai, Y., Whitaker, D., & Yotsumoto, Y. (2016). The centralized and distributed nature of adaptation-induced misjudgments of time. *Current Opinion in Behavioral Sciences*, 8, 117–123.
- Nenadic, I., Gaser, C., Volz, H. P., Rammesayer, T., Häger, F., & Sauer, H. (2003). Processing of temporal information and the basal ganglia: New evidence from fMRI. *Experimental Brain Research*, 148, 238–246.
- Noguchi, Y., & Kakigi, R. (2006). Time representations can be made from nontemporal information in the brain: An MEG study. *Cerebral Cortex*, 16, 1797–1808.
- Onoe, H., Komori, M., Onoe, K., Takechi, H., Tsukada, H., & Watanabe, Y. (2001). Cortical networks recruited for time perception: A monkey positron emission tomography (PET) study. *Neuroimage*, 13, 37–45.
- Ortuño, F., Guillén-Grima, F., López-García, P., Gómez, J., & Pla, J. (2011). Functional neural networks of time perception: Challenge and opportunity for schizophrenia research. *Schizophrenia Research*, 125, 129–135.
- Peru, A., Pavesi, G., & Campello, M. (2004). Impairment of executive functions in a patient with a focal lesion in the anterior cingulate cortex. Evidence from neuropsychological assessment. *Functional Neurology*, 19, 107–111.
- Pfeuty, M., Ragot, R., & Pouthas, V. (2005). Relationship between CNV and timing of an upcoming event. *Neuroscience Letters*, 382, 106–111.
- Pouthas, V., Garnero, L., Ferrandez, A. M., & Renault, B. (2000). ERPs and PET analysis of time perception: Spatial and temporal brain mapping during visual discrimination tasks. *Human Brain Mapping*, 10, 49–60.
- Pouthas, V., George, N., Poline, J. B., Pfeuty, M., VandeMoortele, P. F., Hugueville, L., et al. (2005). Neural network involved in time perception: An fMRI study comparing long and short interval estimation. *Human Brain Mapping*, 25, 433–441.
- Protopapa, F., Hayashi, M. J., Kulashakar, S., van der Zwaag, W., Battistella, G., Murray, M. M., et al. (2019). Chronotopic maps in human supplementary motor area. *PLoS Biology*, 17, e3000026.
- Rao, S. M., Harrington, D. L., Haaland, K. Y., Bobholz, J. A., Cox, R. W., & Binder, J. R. (1997). Distributed neural systems underlying the timing of movements. *Journal of Neuroscience*, 17, 5528–5535.
- Rao, S. M., Mayer, A. R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience*, 4, 317–323.
- Rosenbaum, D. A. (2002). Time, space, and short-term memory. *Brain and Cognition*, 48, 52–65.
- Salvioni, P., Murray, M. M., Kalmbach, L., & Buetti, D. (2013). How the visual brain encodes and keeps track of time. *Journal of Neuroscience*, 33, 12423–12429.
- Sasaki, K., Yamamoto, K., & Miura, K. (2013). The difference in speed sequence influences perceived duration. *Perception*, 42, 198–207.
- Schubotz, R. I., & von Cramon, D. Y. (2001). Interval and ordinal properties of sequences are associated with distinct premotor areas. *Cerebral Cortex*, 11, 210–222.
- Shuler, M. G., & Bear, M. F. (2006). Reward timing in the primary visual cortex. *Science*, 311, 1606–1609.
- Treisman, M. (1963). Temporal discrimination and the indifference interval. Implications for a model of the “internal clock”. *Psychological Monographs*, 77, 1–31.
- Trojano, L., Caccavale, M., De Bellis, F., & Crisci, C. (2017). The brain and the subjective experience of time. A voxel based symptom-lesion mapping study. *Behavioural Brain Research*, 329, 26–34.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33, 113–120.
- Weissman, D. H., Gopalakrishnan, A., Hazlett, C., & Woldorff, M. (2004). Dorsal anterior cingulate cortex resolves conflict from distracting stimuli by boosting attention toward relevant events. *Cerebral Cortex*, 15, 229–237.
- Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010). The image of time: A voxel-wise meta-analysis. *Neuroimage*, 49, 1728–1740.
- Wing, A. M. (2002). Voluntary timing and brain function: An information processing approach. *Brain and Cognition*, 48, 7–30.
- Wittmann, M. (2009). The inner experience of time. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 364, 1955–1967.
- Wittmann, M., & Meissner, K. (2018). The embodiment of time: How interoception shapes the perception of time. In M. Tsakiris & H. De Preester (Eds.), *The interoceptive mind: From homeostasis to awareness* (p. 63). Oxford: Oxford University Press.
- Wittmann, M., & Paulus, M. P. (2008). Decision making, impulsivity and time perception. *Trends in Cognitive Sciences*, 12, 7–12.
- Wittmann, M., Van Wassenhove, V., Craig, B., & Paulus, M. P. (2010). The neural substrates of subjective time dilation. *Frontiers in Human Neuroscience*, 4, 2.
- Wu, D., Deng, H., Xiao, X., Zuo, Y., Sun, J., & Wang, Z. (2017). Persistent neuronal activity in anterior cingulate cortex correlates with sustained attention in rats regardless of sensory modality. *Scientific Reports*, 7, 43101.
- Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, 7, 1–5.