Consciousness of subjective time in the brain

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"Mental time travel" refers to conscious experience of remembering the personal past and imagining the personal future. Little is known about its neural correlates. Here, using functional magnetic resonance imaging, we explored the hypothesis that mental time travel into "nonpresent" times (past and future) is enabled by a special conscious state (chronesthesia). Well-trained subjects repeatedly imagined taking one and the same short walk in a familiar environment, doing so either in the imagined past, present, or future. In an additional condition, they recollected an instance in which they actually performed the same short walk in the same familiar setting. This design allowed us to measure brain activity correlated with "pure" conscious states of different moments of subjective time. The results showed that the left lateral parietal cortex was differentially activated by nonpresent subjective times compared with the present (past and future > present). A similar pattern was observed in the left frontal cortex, cerebellum, and thalamus. There was no evidence that the hippocampal region is involved in subjective time travel. These findings provide support for theoretical ideas concerning chronesthesia and mental time travel.

episodic memory | autonoetic consciousness | imagined time | parietal lobule | intraparietal sulcus

uman beings spend a good deal of their waking moments thinking about what has happened in the past and what might happen in the future. When this thinking involves themselves as observers or participants in the happenings, it has metaphorically been referred to as mental time travel. Although the seeds of the scientific study of mental time travel were sown in the 20th century (1-5), it was only recently that its systematic investigation was launched. Several different approaches have been pursued, including behavioral/cognitive analyses (6-12), studies using functional neuroimaging techniques (13-16), as well as electrophysiological studies (17).

In a typical functional neuroimaging study of mental time travel, subjects' brains are scanned while they are (i) thinking thoughts about the past, usually in the form of remembering events that they have experienced, or (ii) thinking comparable thoughts about the future, usually in the form of imagining events that they might experience at some time yet to come. The findings of several studies have pointed to widely distributed neural regions that show differential activity in both past and future thinking. These common regions include bilateral frontotemporal and medial temporal cortices, the hippocampus, and posterior cingulate and retrosplenial regions (18).

The commonalities of the past and future, especially in relation to the prefrontal cortex, were initially suggested as a part of the theory of episodic memory (3), specifically in relation to autonoetic consciousness (19). More recently, these commonalities have been seen as stemming from previously experienced visual–spatial contexts of envisioned events (16). They have been variously interpreted in terms of concepts such as "constructive episodic simulation" (20), "self-projection" (21), "scene construction" (22), and "the prospective brain" (23, 24).

One issue that has arisen in the context of thinking about mental time travel has to do with the nature of the time in which the metaphorical "travel" occurs (cf. 22). What is this nonpresent "time" in which remembering of past events and imagining of future events takes place in the physical present? It cannot be the same "clock and calendar" time that figures prominently in physical sciences and governs many practical affairs of everyday life, because "past" and "future," necessarily defined with respect to a sentient observer, do not exist in the physical reality but are products of the human mind (25, 26). For this reason, the time of which past and future moments are parts has been referred to as "subjective time" (4).

Here we report a preliminary study in which we held the contents ("message") of mental time travel constant while experimentally varying the moments of imagined time-past, present, and future. In the core experimental conditions, trained, fully informed subjects, in repeated functional magnetic resonance imaging (fMRI) scanning sessions, imagined themselves taking a short walk from point A to point B in a highly familiar setting (i) "yesterday" (PAST), (ii) "right now" (PRESENT), or (iii) "tomorrow" (FUTURE). A fourth experimental condition comprised the canonical task of past thinking (episodic memory retrieval) by having the participants recollect an instance in which they actually performed the same short walk in the same highly familiar setting (REMEMBER). Two other conditions served as reference conditions: silently counting backward by threes from a given three-digit number (COUNT) and rest with eyes closed (REST). As a historical note, it is worth mentioning that mental walk, albeit in the present, as well as counting backward by threes constituted two of the three conditions in a pioneering regional cerebral blood-flow study of cognition reported by Roland and Friberg 25 y ago (27).

Our main interest was to examine whether imagining walking in the past and in the future would differentially engage some brain regions relative to imagining doing the same task right in the imagined present. The task to do (imagining a walk) was identical across conditions—the conditions differed only with regard to subjective time of the imagined activity. Candidate brain regions which hypothetically might code for subjective time include the (medial) prefrontal cortex (16, 19), hippocampus (8), and parietal cortex (28, 29).

Results

For the four time conditions (PAST, PRESENT, FUTURE, RE-MEMBER), the subjects recorded their opinion of the quality of the mental walk on a four-point scale. On average, in all four conditions, the higher ratings 3 and 4 were given in >80% of the trials.

The imaging data were analyzed in a mixed ANOVA model with a total N of 20 observations across participants and scan days. The ANOVA was adjusted for the nonindependence induced by scanning the participants repeatedly. There were marked interindividual differences as well as intraindividual differences across scan days. Here, based on the ANOVA model, we report effects that were consistent across individuals and scan days.

First, we present results on overall similarities between imagery and remembering. A counting baseline served as reference task, as this condition should control for basic sensory-motor as well as cognitive (e.g., working memory) processes. Consistent with previous findings (13, 18), comparisons of the REMEMBER task

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with the COUNT baseline task, and IMAGERY (past+present +future) with the same baseline task revealed highly overlapping patterns of brain activity (Fig. 1). Specifically, both REMEMBER and IMAGERY recruited a frontoparietal network in the left hemisphere.

Second, we addressed the main issue of brain activity in relation to mental time travel by contrasting conditions involving nonpresent time (REMEMBER; imagining in the past and in the future) with "present time" (imagining a walk here and now). This contrast identified a region in the left parietal cortex (Fig. 2; x,y,z = -34, -76,50; Z = 3.88). Additional activations were observed in the right cerebellum (x,y,z = 8, -84, -24; Z = 3.46), in a midbrain region extending into the bilateral thalamus (x,y,z = 2, -6,14; Z = 3.71), and in the left middle frontal gyrus (x,y,z =-34,16,42; Z = 3.50). A plot of the blood-oxygen-level-dependent (BOLD) signal change in the parietal cortex region revealed that it was elevated relative to PRESENT in all nonpresent time conditions (Fig. 2). A similar pattern was seen for the cerebellum, thalamus, and frontal cortex.

In a follow-up analysis, we restricted the condition of nonpresent time to imagining in the past and in the future (i.e., we excluded the REMEMBER condition) and contrasted this experimental condition with imagining in the present. A highly similar pattern was revealed as when REMEMBER was included in the comparison, with the same left parietal cortex as well as the cerebellum, thalamus, and frontal cortex regions. No differential activity was observed in or near the hippocampus, even at a very liberal threshold (0.01 uncorrected).

Given the observed differences between brain responses related to thinking about the past or future relative to the present, as a control analysis, we contrasted directly the PAST and FU-TURE conditions. The brain responses related to these two conditions were highly similar and no significant differences were observed (P < 0.001 uncorrected).



Fig. 1. Similarities in brain activity patterns for remembering and imagery are projected on a left cortical rendering view of the brain. Brain regions activated during the episodic retrieval task relative to the counting baseline task are plotted in red, and brain regions revealed in the comparison of imagery (past, present, and future) relative to counting are plotted in yellow. The overlap in activation patterns for REMEMBER (R) and IMAGERY (I) was pronounced in the inferior frontal cortex (*x*, *y*, *z*: R = -34, 38, -16, Z = 5.07; I = -34, 38, -16, Z = 4.49), fusiform gyrus (*x*, *y*, *z*: R = -32, -48, -10, Z = 5.73), posterior cingulum/precuneus (*x*, *y*, *z*: R = -10, -60,62, Z = 6.23; I = -16, -58,60, Z = 5.83), and inferior parietal cortex (*x*, *y*, *z*: R = -40, -76,46, Z = 6.45; I = -40, -76,46, Z = 4.49). Threshold for illustration: *P* < 0.001 uncorrected.



Fig. 2. Brain activity related to mental time travel. The contrast of nonpresent time (PAST, FUTURE, REMEMBER) with the present revealed differential activation in the left parietal cortex. The activation difference in the left parietal cortex was plotted relative to present for each of the nonpresent time conditions. Threshold for illustration: P < 0.005 uncorrected.

A final set of analyses explicitly addressed the relation between REMEMBER and IMAGERY of the past. As reported (Fig. 2), these conditions engaged overlapping regions relative to IM-AGERY of the present (Table 1). However, in addition, RE-MEMBER recruited a more extensive set of regions, and a direct comparison between REMEMBER and IMAGERY of the past revealed several regional differences (Table 1). Thus, actual retrieval of previously experienced events engaged a more extensive brain system than simply imagining performing a walk in the past.

Discussion

Chronesthesia is defined as a form of consciousness that allows individuals to think about the subjective time in which they live and that makes it possible for them to mentally travel in such time (30). Our findings show that under conditions in which variables other than the imagined moments of personal past, present, and future are held constant, some brain regions exhibit differential activity that is systematically related to the subjects' conscious, "chronesthetic" states.

Relative to the mental act of imagining oneself carrying out a familiar activity at the present time, imagining the same task done yesterday or tomorrow led to differential engagement of the left lateral parietal cortex near the intraparietal sulcus (Brodmann areas 39, 40, and 7), as well as regions in the left frontal cortex, right cerebellum, and thalamus. These regions were also recruited during episodic remembering of the same content. Common activity related to the remembered past and imagined future has been previously reported by Addis and her coworkers (13), and both the parietal cortex and cerebellum have been associated with mental time travel (16). In addition, frontal regions have frequently been discussed in relation to mental time travel (21, 31). There was no evidence in the data that the hippocampal region is involved in subjective time travel. This null finding might be interpreted to mean that the hippocampus is more related to the informational content (the message) of a phenomenal experience, which was held constant, rather than to the conscious temporality of the experience (32). Similarly, in a recent lesion study it was concluded that imagining the future is independent of the hippocampus (33).

The left lateral parietal region that here was related to mental time travel partly overlaps a left angular region shown to be recruited during both past and future thinking (28) and with parietal regions implicated in self-projection in past, present, or future time (29). However, a contribution of the present study is the demonstration that the parietal response was elevated for nonpresent time periods relative to the present. As such, our findings specifically relate the parietal cortex to transformations in subjective time. This functional account is supported by studies linking the left parietal cortex to first-person perspective simulation (34). Also, albeit on a much smaller timescale, the parietal

Contrast	Brain region	Voxels (k)	Z	<i>x</i> -talai	<i>y</i> -talai	<i>z</i> -talai
REMEMBER > PRESENT	Parietal cortex_L	758	4.54	-38	-72	46
	Precuneus_R	6,776	3.04	6	-53	67
	Precuneus_L		3.02	-12	-50	43
	Frontal_Mid_L	809	4.06	-34	16	42
	Frontal_Sup_R	190	3.96	22	27	39
	Cerebellum	372	3.55	14	-80	-16
	Midcingulum	214	3.41	-2	-6	30
	Cerebellum_R	391	3.27	12	-45	-40
	Cerebellum_L		2.58	-18	-41	-40
	Temporal cortex_L	339	3.23	-50	-26	-7
	Frontal_Mid_Orb_L	130	3.14	-38	58	-5
	Cerebellum	312	3.12	32	-83	-26
	Frontal_Sup_Medial_L	167	3.11	-10	37	37
PAST > PRESENT	Parietal cortex_L	119	3.45	-34	-71	50
	Cerebellum	169	3.31	10	-80	-16
REMEMBER > PAST	Paracentral_Lobule_R	309	4.41	12	-16	73
	Frontal_Mid_R	118	4.75	24	29	39
	Cingulum_Mid_L	1,900	4.20	-8	-37	42
	Cuneus_L	158	3.64	-8	-59	25
	Angular_L	61	3.51	-40	-70	42
PAST > REMEMBER	_	—	_	—	—	_

Table 1. Similarities and differences between REMEMBER and IMAGERY of the past

Relative to IMAGERY of the PRESENT, both the REMEMBER and PAST conditions engaged the left parietal cortex and the cerebellum. In addition, REMEMBER recruited an extensive set of regions in frontal, parietal, and temporal cortices (P < 0.001, uncorrected; k > 50).

cortex has been assigned a role in representing time during timeperception tasks (35). clude that a concept such as subjective time, or something like it, is necessary to make sense of our findings.

Consistent with our finding that the same left parietal region was recruited during episodic memory retrieval, parietal cortex activation has repeatedly been observed in relation to episodic memory tasks (36). Demands on remembering temporal event information have been shown to modulate the magnitude of parietal cortex activation (37), and parietal cortex activity has been found to be increased during successful retrieval of old relative to new information (38). Importantly, the subjective perception that information is old has also been shown to modulate activity in the left parietal cortex (39, 40). These findings converge with the present set of observations in showing that the left parietal cortex is engaged during veridical episodic remembering, subjective (false) perception that information is old, and in imagining past and future events. Chronesthesia may well be a common denominator across these conditions.

The proposed link between the parietal cortex and consciousness of subjective time may further be related to recent studies of the neural correlates of sensory consciousness. Conscious visual experiences reflect increased activity in dorsal frontal and parietal regions (41), and the parietal cortex was found to be part of a distributed network interacting with prefrontal regions in relation to awareness in sensory learning (42). Indeed, consciousness per se seems to depend on interactions in a posterior lateral corticothalamic network that includes a complex of brain regions in the posterior parietal cortex (43). An interesting task for future studies will be to scrutinize the potential relation between consciousness, the parietal cortex, and sense of time.

It has been questioned whether the concept of subjective time is necessary for accounting for similarities in brain activity during past and future thinking (22). A largely identical pattern of brain activity has been found to be recruited during imagining fictitious experiences (8), and it has been argued that the commonalities in brain activity instead can be accounted for by the process of scene construction (22). Inasmuch as any scene construction that may have occurred in the conditions of our study was held constant by the design of the study, it seems reasonable to conMethods

Subjects. Five healthy, young adult females (mean age: 27.6 y; range: 26–30 y) participated in this experiment. None of the subjects had any history of neurological or psychiatric disorders. Moreover, all subjects had complete knowledge of what the study was about and were recruited only after the procedure was explained to them. Some individuals excluded themselves from the study, because they did not think that they could perform the tasks. Those individuals who reported that they were able to perform the tasks, thereby including themselves in the study, then received extensive training on the tasks before the first scan session in a separate practice session. During the training, subjects performed the tasks inside a scanner simulator. All subjects gave informed written consent to participation in accordance with the Baycrest Research Ethics Board.

Design. All subjects participated in four scanning sessions on separate days over a 2-wk period. They were scanned (fMRI) in each of five conditions in each session. Three conditions-PAST, PRESENT, and FUTURE, collectively referred to as IMAGINING-involved imagining taking a walk in these three times. The fourth condition-REMEMBER-involved bringing to mind and playing the "mental tape" of a walk that had been actually taken in the past. The three IMAGINING conditions and REMEMBER will be collectively referred to as TIME conditions. The fifth condition-COUNT-served as a control. It involved a nonspatial, nontemporal activity: mentally counting backwards by threes from a given number. The imagined walks in PAST, PRESENT, and FUTURE, as well as REMEMBER, took place in a highly familiar location where the subjects had taken the walk on many occasions. A scanning session was divided into four "blocks." Each block consisted of 10 "trials." On each trial the subject performed a "task" that corresponded to one of the five conditions. Before the experiment began, each subject had selected four different walks to be used in the experiment. Within each subject, across the four sessions, the four experimental conditions-PAST, PRESENT, FUTURE, and REMEMBER-were counterbalanced with the subject's four walks. The walks were held constant within a block and varied across the blocks within a session. This design allowed us to observe the neural correlates of the three IMAGINING and the REMEMBER conditions while the imagined or remembered "content" was the same in all of them.

Procedure. The procedure within a session was identical for all subjects. Their brain was scanned continuously throughout a block. Within a block, each of

the five tasks was used on two trials. The two trials of a given condition always occurred in immediate succession. The order of the tasks was varied semirandomly across blocks, sessions, and subjects. Each trial within a block began with a 3-s presentation on an instruction screen of the identifying name of the task and, in the case of the three imagining conditions, the subjective moment of time to be used. An auditory tone closed the instruction screen and cued the subject to close her eyes and start the designated mental task for 30 s. A second tone was presented at the end of the 30 s, which cued the subject to open her eyes and record her assessment of the quality of her own performance on the task. For the four time conditions (PAST, PRESENT, FUTURE, and REMEMBER) the subject chose one of four buttons on a keypad. For the COUNT condition, the subject indicated whether she finished the trial on an even or odd number. The subject had 8 s to give her response, and did not move on until the 8 s had passed. In total, each trial lasted 41 s.

Imaging Parameters. Images were acquired on a 3-T Siemens Magnetom Trio whole-body scanner with a matrix 12-channel head coil at the Rotman Research Institute of Baycrest. Functional volumes were obtained using a wholehead T2*-weighted echo-planar image sequence [repetition time (TR): 2 s; echo time (TE): 30 ms; flip angle: 70°; 28 oblique axial slices with interleaved acquisition; $3.1 \times 3.1 \times 5$ -mm voxel resolution; field of view (FOV): 20 cm; acquisition matrix: 64×64]. The first 10 volumes were discarded to allow the magnetization to reach steady state. Physiological data (heart and respiration rate) were acquired during the scanning session. Anatomical images were acquired using an MP-RAGE (magnetization-prepared rapid gradientecho) sequence (TR: 2 s; TE: 2.63 ms; 160 oblique axial slices, with a 1-mm³ voxel size; FOV: 25.6 cm; acquisition matrix: 256 × 256), either before or after the functional images were acquired. Instructions were presented visually through a mirror mounted on the coil that reflected images from a projector located at the bottom of the scanner. Finger-press responses were recorded with an MRI-compatible response pad.

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Functional MRI Data Preprocessing and Analysis. The experiment yielded 20 nonindependent datapoints. Functional images were analyzed using Statistical Parametric Mapping software (SPM8; Wellcome Neuroimaging Laboratory, London, United Kingdom). The images were slice-timed to correct for time differences between slices, realigned to correct for linear movement artifacts, unwarped to correct for nonlinear movement artifacts, normalized to achieve images in MNI space (Montréal Neurological Institute), and finally spatially low-pass-filtered with a Gaussian kernel of 8 mm in x, y, and z directions. The time series were high-pass-filtered with 10 mHz. No global normalization was performed, but an autoregressive function was used to compensate for serial correlations. Boxcar functions were made for PAST, PRESENT, FUTURE, REMEMBER, COUNT, and BASE (rest) conditions. The boxcar functions were convolved with the canonical hemodynamic response function (HRF) to form a regressor with natural hemodynamics. Another six regressors (for x, y, z, pitch, roll, and vaw) from the movement correction were applied, to capture variance due to movement. After the regression, contrasts were made for "PAST-BASE," "PRESENT-BASE," "FUTURE-BASE," "REMEMBER-BASE," and "COUNT-BASE." A three-factor ANOVA was made with the following factors: "subject" (1-5), which was set to independent and unequal variance; "day" (1-4), which was set as dependent but with equal variance; and "condition" (1-5; previously mentioned contrasts), which was set as dependent but with equal variance. Contrasts were made from the ANOVA by zeroing the regressors for subject and day and only using the condition regressors. The β -plots consist of the three β -value differences relative to baseline across all voxels. The bars are averaged over subjects and days, with the SE of the mean shown as a vertical line.

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