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Space and Time in the Parietal Cortex: fMRI Evidence for a Neural Asymmetry

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Abstract

How are space and time related in the brain? This study contrasts two proposals that make different predictions about the interaction between spatial and temporal magnitudes. Whereas ATOM implies that space and time are symmetrically related, Metaphor Theory claims they are asymmetrically related. Here we investigated whether space and time activate the same neural structures in the inferior parietal cortex (IPC) and whether the activation is symmetric or asymmetric across domains. We measured participants' neural activity while they made temporal and spatial judgments on the same visual stimuli. The behavioral results replicated earlier observations of a space-time asymmetry: Temporal judgments were more strongly influenced by irrelevant spatial information than vice versa. The BOLD fMRI data indicated that space and time activated overlapping clusters in the IPC and that, consistent with Metaphor Theory, this activation was asymmetric: The shared region of IPC was activated more strongly during temporal judgments than during spatial judgments. We consider three possible interpretations of this neural asymmetry, based on 3 possible functions of IPC.

Keywords: ATOM, Metaphor, Space, Time, fMRI, Parietal lobe

Introduction

It is clear that spatial and temporal magnitudes interact in the brain and mind, but the exact nature of this interaction is a matter of debate. According to one account, A Theory Of Magnitude (ATOM; Walsh, 2003), space, time and other prothetic domains (i.e. that can be experienced as more or less in magnitude) interact because they are represented by a common metric, located in the inferior parietal cortex (IPC; Walsh 2003; Bueti & Walsh 2009). Support for this model comes from behavioral experiments showing cross-dimensional interference between different prothetic dimensions, as well as from neuroimaging studies showing that magnitude processing in various dimensions activates overlapping areas of IPC, mainly in the right hemisphere (see Bueti & Walsh 2009 for review). According to ATOM, these different magnitudes share a representational substrate because they need to be integrated for successful execution of actions: Bueti and Walsh (2009) note that, "There is no such thing as getting to the right place at the wrong time" (pg. 1832). Like Locke (1689/1995) before them, ATOM theorists imply that space and time are symmetrically related. Indeed, if different prothetic domains are represented by the same metric, there is no *a priori* reason to assume that one domain should depend asymmetrically on another.

According to a second theoretical proposal, Metaphor Theory (MT), space and time are asymmetrically related: Temporal representations depend on spatial representations, more than vice versa. This asymmetry is fundamental to MT, which posits that representations of abstract concepts depend, in part, on representations of more concrete, perceptible domains (Lakoff & Johnson, 1980; 1999). Since time is an abstract entity that we can never see or touch, it is argued to rely on spatial representations for conceptual scaffolding. Evidence for this asymmetric relationship comes from psychophysical studies showing asymmetric cross-dimensional interference between distance and duration: Task-irrelevant spatial magnitude influences temporal judgments more than task-irrelevant temporal magnitude influences spatial judgments (Bottini & Casasanto, 2010; Casasanto & Boroditsky, 2008; Casasanto, Fotakopoulou, & Boroditsky, 2010; Merritt, Casasanto, & Brannon, 2010; see also Boroditsky, 2000).

These cross-domain asymmetries were predicted by MT but not by ATOM. Yet, the available data leave open a possibility: Perhaps spatial and temporal magnitudes are *encoded* symmetrically. The observed asymmetry could arise subsequently, as magnitudes are re-represented during retrieval or response planning. If so, this finding would help to reconcile ATOM and MT, suggesting that initial stages of magnitude processing may be ATOMIC even if later stages are metaphoric.

To test this proposal, we used fMRI to measure neural activity during spatial and temporal magnitude reproduction tasks. First, we compared activity during the encoding of spatial and temporal magnitudes to establish whether space and time interact at this stage, and whether they do so in the IPC. Second, by defining this area of overlap as a Region of Interest (ROI) and by comparing neural activity during the encoding of space and of time, we contrasted predictions of MT and ATOM. Both theories predict that encoding space and time should activate overlapping areas: On the basis of previous findings, we assume areas within IPC. MT predicts that this common area will be activated more by time than by space, because people involuntarily encode more irrelevant spatial information during temporal encoding than vice versa. ATOM does not predict any cross-domain asymmetry in the region of overlap.

Methods

Participants

18 healthy native English speakers (16 right-, 1 left-handed, 1 ambidextrous, 9 male, mean age = 23.7, range: 20-31) took part in the current experiment. All participants provided informed consent and were compensated for their participation.

Materials

Lines of varying lengths were presented for varying durations. Durations ranged from 1000 ms to 4000 ms in 600 ms increments. Displacements ranged from 100 to 400 pixels in 60 pixel increments. The six durations were fully crossed with the six spatial displacements, producing 36 unique lines. Half of the lines were red and half were blue. Color was randomly assigned and counter-balanced across conditions and participants. Lines grew horizontally across the screen from left to right, along the vertical midline. The starting position of the lines was, on average, at 337 pixels from the left border of the screen, with the starting point randomly jittered (± 25 pixels) so the monitor could not be used as a reliable reference frame for spatial estimations. Participants responded with a joystick (Current Designs, Philadelphia, USA; model: HHSC-JOY-1). Participants used their right hand to control the joystick for cursor movement and their left index finger for button responses.

Procedure

Participants engaged in four different tasks: spatial reproduction, temporal reproduction and two color identification control tasks. Each trial started with a white cue that was presented for 1 second and indicated which dimension participants would need to reproduce for this trial (an “X” for space, an hourglass for time, and different colored squares for the two control conditions). This cue was followed by a single growing line that stayed on the screen until it reached its maximum spatial and temporal extent and then disappeared. After a period of 5 sec. (\pm random jitter; range = 0-1 sec.), a response cue and a cursor appeared until participants performed the required task or until a time-out period of 12 seconds had elapsed.

In the space condition (S), the X-icon appeared in either the upper- or lower-left corner of the screen (location counterbalanced across participants). To reproduce the distance that the line had traveled, participants moved the cursor from the center of the screen to the center of the icon, clicked once, moved the cursor rightwards in a straight line and then clicked a second time. The distance between the clicks represented the estimated displacement of the line. In the time condition (T), the hourglass-icon appeared in the lower- or upper-left corner of the screen (i.e. in the corner opposite the space cue). To reproduce duration, participants moved the cursor to the center of

the icon, clicked once, waited for the amount of time the line had been on the screen, and clicked a second time in the same spot. The time between the two clicks represented the duration of the line (procedure adapted from Casasanto & Boroditsky, 2008).

Finally, two color identification conditions were included as controls: the “color half” (CH) and “color-full” (CF) conditions provided a low level visual control for the target lines, and also allowed us to subtract out activity due to motor preparation prior to responses. Each color condition required the same motor response as one of the target conditions. In the “color-half” condition (CH), participants saw two squares appear, each consisting of a red and a blue half. The left square was presented in the same corner in which the spatial response cue was presented for that participant and the second square was presented 250 pixels to the right of the left one. Participants first moved the cursor to the half of the left square that matched the color of the line, clicked once, moved the cursor rightwards in a straight line to the half of the right square that matched the color of the line and clicked again. Both squares were identical within a given trial (e.g. 2 red-blue squares), but the order of the colored halves was counter-balanced across trials (50% red-blue; 50% blue-red). In the “color-full” condition (CF), participants saw a blue and a red square appear in the upper- and lower-left corners of the screen (square position was counterbalanced across trials) and clicked twice on the square that had the color of the presented line.

Before entering the scanner, participants read the instructions and performed 3 practice trials of each condition. While in the scanner, participants performed each of the four tasks for each of the 36 unique lines (4 x 36 = 144 trials in total). Lines were presented randomly within condition, and the order of conditions varied pseudo-randomly (maximum of 3 trials of the same condition in a row).

fMRI Data Acquisition

fMRI data were acquired on a Siemens Avanto 1.5 T MRI system (Siemens, Erlangen, Germany) using a standard birdcage head-coil for RF transmission and signal reception. T2*-weighted BOLD-sensitive images were acquired using a gradient EPI sequence (Echo Time (TE) = 40 ms; Repetition Time (TR) = 2.28 s; 32 axial slices in ascending order; voxel size = 3.3x3.3x3.0 mm³). For each subject we also acquired a T1-weighted high-resolution anatomical scan (TE = 2.95 s, TR = 2.25 s, voxel size = 1.0x1.0x1.0 mm³, 176 sagittal slices, field of view = 256).

fMRI Data Analysis

Functional data were preprocessed and analyzed with SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>). Preprocessing involved the removal of the first 5 volumes to allow for T1 equilibration effects. Images were spatially realigned

with rigid body registration, temporally realigned to the middle slice (slice 17), co-registered to each participant's structural scan, normalized to a standard EPI template in MNI space and resampled at an isotropic voxel size of 2 mm. To remove baseline-drifts and low frequency signal changes, a 1/128 Hz temporal high-pass filter was applied. The normalized images were then smoothed with an isotropic 8 mm FWHM Gaussian kernel.

The preprocessed data were analyzed on a subject-wise basis using an event-related approach. The time series were entered into a GLM with separate regressors for the encoding and response phase for each condition (respectively modeled at one second before stimulus offset and response onset for S, T, CH and CF), which were then convolved with a canonical hemodynamic response function. Although response phase regressors were added to the model for completeness, they were not analyzed further and will not be discussed. Finally, nuisance regressors were added to account for disturbances caused by small head movements.

To examine neural activity specific to spatial and temporal encoding, we computed two contrast images for each participant individually ([S-CH] and [T-CF]). These were then entered into separate second level random effects analyses to compute the space- and time-specific activations on the group level. Each of these two analyses consisted of a one-sample t-test to reveal activations significantly different from zero across the contrast images from all participants. A double threshold was applied to protect against Type I errors: only voxels with a $p < .001$ (uncorrected) and a volume exceeding 41 voxels (328 mm³) were considered (volume sizes were defined by Monte Carlo Simulation, $p < .001$, Slotnick, 2011).

To reveal the neural overlap between spatial and temporal encoding, we performed a conjunction analysis on the 2 second-level contrast images ([S-CH] \cap [T-CF]). Based on our *a priori* hypothesis, bilateral clusters of IPC activity that emerged from the conjunction were extracted and defined as our ROI's. From these ROI's, we extracted separate contrast values for the [S-CH] and the [T-CF] contrasts for each subject, using the MarsBaR package (Brett, Anton, Valabregue, & Poline, 2002; <http://marsbar.sourceforge.net>, v.042).

Results

Behavioral Results

First we tested whether spatial and temporal reproduction was affected by variation in the task-irrelevant stimulus dimension. The spatial and temporal extents of the stimuli and responses were normalized, so that slopes could be compared across domains¹. We calculated the normalized

¹The data from one participant were excluded due to excessively low within-dimension performance on both tasks (both slopes were two standard deviations below group averages).

slopes of the effect of irrelevant spatial information on duration reproduction (ST) and the effect of irrelevant temporal information on spatial distance reproduction (TS) for each participant separately (Fig. 1). The results showed significant cross-dimensional interference effects: The spatial extent of stimuli predicted the variation in the temporal responses (Wald $X^2(1) = 23.55$, $p = .001$) and the duration of stimuli predicted the variation in spatial responses (Wald $X^2(1) = 12.21$, $p = .001$). Importantly, these effects were asymmetric: Spatial information affected duration reproduction more than temporal information affected distance reproduction (Wald $X^2(1) = 8.00$, $p = .01$).

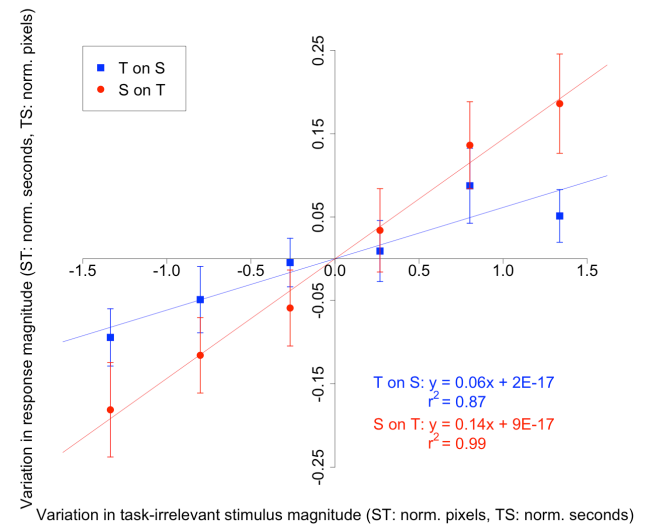


Figure 1: Cross-domain interference effects. **TS (Blue):** Effect of line duration on spatial distance reproduction. **ST (Red):** Effect of line displacement on duration reproduction. Error bars indicate SEM.

To investigate within-domain performance, we used the normalized stimulus and response values to calculate the normalized slopes of the effect of spatial variation on spatial reproduction (SS) and temporal variation on temporal reproduction (TT), for each participant separately. Although the results show strong effects both of actual space on estimated space (SS: Normalized slope = 0.98; Wald $X^2(1) = 10139$, $p = .001$) and of actual time on estimated time (TT: Normalized slope = 0.88 Wald $X^2(1) = 1465$, $p = .001$), they also show a significant difference between within-dimension effects: participants were significantly better at spatial than at temporal reproduction (Difference of normalized slopes = 0.10 Wald $X^2(1) = 20.41$, $p = .001$).

This difference in within-domain performance between space and time is potentially problematic for the interpretation of the between-domain asymmetry. If performance in one domain is nearly perfect, estimates in this domain may be less susceptible to interference than estimates in

the other domain (Bottini & Casasanto, 2010). To rule out this concern, we re-ran the regression model after equating for within-dimension performance. Following Casasanto, et al. (2010), we excluded the data from participants with low TT-slopes until the within-dimension performance was the same for Space and Time (i.e. until $SS = TT$; $N = 7$). Even after equating within-dimension performance, a strong space-time asymmetry persisted: the spatial extent of stimuli predicted the variation in the temporal responses more than vice versa (Wald $X^2(1) = 12.56$, $p = .001$), as in previous experiments (e.g., Casasanto & Boroditsky, 2008; Merritt et al., 2010).

Imaging Results

Patterns of Activation As the ROI analysis was our main point of focus, we provide only a cursory overview of the whole-brain results. During spatial encoding ([S-CH]), we observed bilateral activations in parietal areas (including the IPC, intraparietal sulcus (IPS) & superior parietal gyrus), extrastriate visual cortex (extending into the inferior temporal gyrus) and frontal areas (precentral gyri, IFG, anterior insulae (AI), middle frontal gyri, SMA & medial superior frontal gyri). During temporal encoding ([T-CF]), we found activations in the parietal cortex (bilateral IPC, IPS, & supramarginal gyri; right angular gyrus), left dorsal extrastriate cortex and a range of bilateral frontal activations (precentral gyri, AI, DLPFC, SMA, anterior cingulate and medial superior frontal gyri). Additional activity was observed in bilateral superior temporal gyri, right inferior temporal gyrus and subcortical areas (thalamus and basal ganglia).

To reveal neural activations common to spatial and temporal encoding, we performed a conjunction analysis on both aforementioned contrasts ([S-CH] \cap [T-CF]; Fig. 2, left). Overlapping activations were found in bilateral parietal cortex, ranging from lateral IPC into the IPS and including part of the supramarginal gyrus in the right hemisphere. Additional clusters of activity included the left extrastriate cortex, just anterior to the cuneus, and a posterior part of the right inferior temporal gyrus. Frontal activations included bilateral DLPFC and parts of both precentral gyri (extending ventrally into the IFG and AI). Furthermore, we observed right-lateralized dorsal activation of the posterior middle and superior frontal gyri, extending into the superior frontal sulcus. Finally, the conjunction revealed medial frontal activations comprising the SMA, the medial superior frontal gyri and the middle and anterior cingulate.

ROI Analysis To investigate whether space and time encoding activated the bilateral IPC clusters revealed by the conjunction analysis symmetrically or asymmetrically, we defined the left and right IPC clusters as our two ROI's and extracted the contrast values per subject for each con-

dition of interest. These contrast values were entered into a regression model, with Condition (Space; Time), Hemisphere (Left; Right) and their interaction (Condition*Hemisphere) as within-subject factors and Subject as a repeated random effect. The IPC was activated more strongly by temporal encoding than by spatial encoding (main effect of Condition: Wald $X^2(1) = 4.65$, $p = .03$). Furthermore, both domains activated the right IPC more than the left IPC (main effect of Hemisphere: Wald $X^2(1) = 6.79$, $p = .01$), but the relationship between spatial and temporal activation did not differ between hemispheres (Condition*Hemisphere interaction: Wald $X^2(1) = .073$, $p = .79$). Since previous studies have tended to implicate the right IPC in magnitude processing, we analyzed the ROI in each hemisphere separately. The main effect of Condition was significant in the right hemisphere ($T > S$, Wald $X^2(1) = 5.14$, $p = .02$), and marginally significant in the left-hemisphere ($T > S$, Wald $X^2(1) = 3.49$, $p = .06$) (Fig. 2, right).

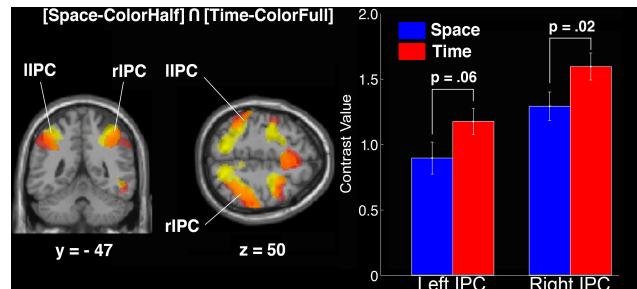


Figure 2: Left: IPC activated by both space and time. *Yellow:* areas activated by spatial encoding ([S-CH]); *Red:* areas activated by temporal encoding ([T-CF]); *Orange:* areas activated by both ([S-CH] \cap [T-CF]). **Right:** Contrast values for space and time for the left and right IPC clusters.

Although these findings demonstrate that the IPC was differentially activated by spatial and temporal encoding, we must consider a skeptical account of this neural asymmetry. Our behavioral results indicated that, for some participants, temporal encoding was less accurate than spatial encoding, and may therefore have been more effortful. In principle, a difference in cognitive effort could be responsible for the observed cross-domain asymmetry in the IPC. If the observed asymmetry were due to more effort during temporal vs. spatial encoding, then adding a measure that reflects this difference in effort to the regression model as a covariate should reduce or eliminate the main effect of Condition.

To address this possibility, we calculated the difference between the normalized slopes of within-dimension performance in the space and the time condition (SS-TT) for each participant and included this difference score in the model. Even when cognitive effort was controlled for, we observed the same robust cross-domain asymmetry effects. Both IPC clusters were still activated more by tem-

poral than by spatial encoding (main effect of Condition: Wald $X^2(1) = 4.19$, $p = .04$), with stronger overall right hemisphere activation (main effect of Hemisphere: Wald $X^2(1) = 4.24$, $p = .04$). The main effect of this behavioral measure of cognitive effort, however, was not significant (Wald $X^2(1) = 2.42$, $p = .12$), nor was its three-way interaction with Dimension and Hemisphere (Wald $X^2(1) = 1.60$, $p = .66$). These analyses show that the cross-domain asymmetry in BOLD activity in the IPC ROIs cannot be attributed to the observed differences in within-domain performance (i.e., to the finding that temporal estimates were less accurate, and potentially more effortful, than spatial estimates).

Discussion

This study investigated whether representations of space and time interact at encoding and, if so, whether their relationship is symmetric or asymmetric. Consistent with both ATOM and MT, we observed that encoding spatial and temporal magnitudes activated overlapping clusters of a widespread neural network, most notably in the bilateral IPC. Of primary interest, our behavioral and ROI data provide converging support for an asymmetric relationship between these two domains, as predicted by MT. The behavioral findings indicated that when people reproduced duration they incorporated task-irrelevant spatial information, more so than they incorporated task-irrelevant temporal information when reproducing spatial extent. Our fMRI results showed that this behavioral asymmetry corresponded to a neural asymmetry: the IPC was more active during temporal encoding than during spatial encoding. The asymmetry between space and time is already present during encoding of spatial and temporal stimuli.

Further interpretation of the asymmetric IPC activation requires addressing the question of what exactly is being represented in the IPC. On one possibility, the IPC is the locus of a domain-general magnitude metric that accumulates undifferentiated bits of information (Buetti & Walsh, 2009, Walsh, 2003), in any prosthetic domain. In our task, the activation of the IPC might reflect the degree to which this metric accumulates bits from *both* domains simultaneously. Our behavioral results indicated that task-irrelevant spatial information was being encoded during time trials, more than task-irrelevant temporal information was being encoded during space trials. Hence, the IPC metric would have accumulated more task-irrelevant magnitude information (along with the task-relevant magnitude information) during time trials than during space trials, resulting in the increased BOLD signal. This account can potentially reconcile ATOM with MT: It is compatible with ATOM's claim of an IPC-based general magnitude representation, and is also consistent with MT, as the asymmetric IPC activation indicates an asymmetric interaction between space and time.

A second possibility is that magnitudes from different domains are represented independently in different parts of the brain (Cohen Kadosh et al. 2008), and that the IPC hosts a mechanism by which cross-domain magnitude representations are selected and integrated according to contextual demands.

A range of empirical data supports this interpretation. Several studies have shown that, during magnitude judgments, the activation of parietal areas around the IPS is modulated by the degree of interference from irrelevant dimensions (Ansari, Fugelsang, Dhital, & Venkatraman, 2006; Cohen Kadosh, Cohen Kadosh & Henik, 2008; Pineda, Piazza, Le Bihan, & Dehaene, 2004; Cohen Kadosh, Cohen Kadosh, Linden, et al., 2007; Kaufmann et al., 2005). Moreover, studies of magnitude-irrelevant visual processing find that the IPC is activated by the need to suppress task-irrelevant distractors (Friedman-Hill, Robertson, Desimone, & Ungerleider, 2003; Marois, Chun, & Gore, 2000; Wojciulik & Kanwisher, 1999). These processes are mostly right-lateralized (Chun & Marois, 2002; Marois, Chun, & Gore, 2000; 2004) and they are independent from task difficulty (Marois et al., 2000; Wojciulik & Kanwisher, 1999).

Our task required participants to selectively attend to the relevant dimension of the stimuli and filter out the irrelevant dimension (i.e., space or time), which varied orthogonally. The greater IPC activation we observed during temporal encoding could reflect the increased demands posed on the 'magnitude selector/integrator' to filter out the task-irrelevant spatial information. Whereas this interpretation is consistent with MT, it contradicts one of the core claims of ATOM by positing that spatial and temporal magnitude representations are distinct: What is in common is the process of selecting and integrating relevant magnitude information.

Finally, on a third possibility, encoding space and time activated nearby but separate neural populations in the IPC, but the low spatial resolution of fMRI does not allow us to separate them (see Shuman & Kanwisher 2004 for similar arguments). On this view, spatial encoding would have mainly activated the spatial representations, whereas temporal encoding would have activated both temporal and spatial representations. Not only could this account for the BOLD asymmetry (the combined activation of the two separate neural populations in same voxels during time processing leads to a higher BOLD signal), it could also explain the behavioral pattern. If temporal encoding activates neural populations that code for space more than vice versa, due to the "source domain-target domain" link posited by metaphor theorists, there should be more opportunity for crosstalk during time encoding than during space encoding. This notion of separate but closely interacting neural representations of space and time is consistent with MT, but argues against ATOM's claim of a shared representational basis of all prosthetic magnitudes.

In summary, here we show a neural asymmetry between space and time that underlies the behavioral asymmetry found here and in multiple previous studies of distance and duration estimation. We consider three possible interpretations of these behavioral and neural asymmetries, all of which are consistent with MT, but only the first of which is compatible with ATOM. If the first account is correct and the IPC is the locus of a domain-general magnitude metric, ATOM and MT can be reconciled and the apparent contradiction in behavioral data resolved. The two other proposals are only consistent with MT and argue directly against ATOM's main claim of a shared IPC-based magnitude metric. Rather, they suggest that space and time are represented by distinct but closely interacting neural structures, either in the IPC, or in the form of a broadly distributed network. Further studies are needed to decide among these possibilities and clarify the role of the IPC in representing or integrating magnitudes.

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