

Overlapping and Distinct Neural Representations of Numbers and Verbal Transitive Series

Jérôme Prado^{1,2}, Ira A. Noveck² and Jean-Baptiste Van Der Henst²

¹Department of Psychology, University of Michigan, Ann Arbor, MI 48109-1043, USA and ²Laboratoire sur le Langage, le Cerveau et la Cognition (L2C2), UMR 5230, CNRS-Université de Lyon, 69675 Bron, France

It is a familiar and intuitive notion that human numerical and logical reasoning skills are tightly related. However, very little is known about the interaction between numerical knowledge and logical reasoning in the brain. Using functional magnetic resonance imaging in healthy subjects, we investigated ordered relations as they are expressed in number (4 is greater than 2) and in transitive reasoning (A is to the left of C after receiving; A is to the left of B; B is to the left of C) in order to determine the extent to which the same neural substrates support both. We found that representing an ordered series verbally learned by transitive reasoning draws on the representations of numbers in the anterior intraparietal sulcus. We further observed that, unlike numbers, transitive series are additionally encoded in the basal ganglia-dopamine system. Intraparietal and basal ganglia mechanisms are not active to the same extent at the same time. Although the intraparietal representations of number preferentially supports a verbal transitive series soon after learning, the basal ganglia are engaged when the series is well practiced. This finding suggests that the transient activation of number representations supports the representation of verbal transitive series until their late encoding in the basal ganglia-dopamine system by associative reinforcement mechanisms.

Keywords: basal ganglia, fMRI, intraparietal sulcus, numerical cognition, transitive reasoning

Introduction

The idea that human numerical and logical reasoning skills are related has fascinated philosophers and scientists for centuries (Houdé and Tzourio-Mazoyer 2003; Watanabe and Huber 2006). At the dawn of the modern cognitive science era, the developmental psychologist Piaget (1952) proposed that the ability to represent numbers is linked to the understanding of the logical relations between quantities, and much recent work on children's concept of number assumes the acquisition of reasoning principles (see Leslie et al. 2008). This link between number representation and reasoning is still predominant in modern educational systems, where children's logic is emphasized in the learning of mathematics (Nunes et al. 2007). Although the neuroimaging literature points to a role for the parietal cortex in representing both numerical (Cantlon et al. 2009) and logical (Goel 2007) relations, very little is known about the interaction between number knowledge and logical reasoning in the brain. In this work, we aim to determine the extent to which these 2 areas of human cognition share "neural" substrates by focusing on ordered relations.

There is good reason to suppose that the ability to discriminate numerical quantities and understand logical relations of, at least, order has ancient evolutionary roots. Indeed, these

competences are shared by preverbal children (Bryant and Trabasso 1971; Wynn 1992) and a large number of animal species (McGonigle and Chalmers 1977; Brannon and Terrace 1998; Brannon et al. 2001; Paz et al. 2004; Cantlon and Brannon 2006; Grosenick et al. 2007). For example, nonhuman primates are able to spontaneously determine which of 2 sets of dots is numerically larger (Brannon and Terrace 1998; Cantlon and Brannon 2006). Similarly, after learning by trial and error the ordinal relationships between overlapping pairs of items (e.g., $A > B$, $B > C$, $C > D$, and $D > E$) monkeys can spontaneously infer the relationship between items of a novel, nonoverlapping, pair (e.g., $B > D$; McGonigle and Chalmers 1977). (The symbol " $>$ " is used here as a general marker to indicate an adjective having a transitive relation such as "bigger than," "longer than," "to the left of," etc. . . .) The reasoning literature has investigated related phenomena under the heading "transitive reasoning" (Breslow 1981; Vasconcelos 2008).

These 2 areas—knowledge of numerical series and transitive reasoning—overlap in ways that go beyond their mere superficial resemblance. There is evidence indicating that they do share a common "behavioral" signature, that is, the "symbolic distance effect" (SDE). The SDE refers to the improved ability among participants to compare 2 numbers (Moyer and Landauer 1967) or ordered items (Potts 1974) as the symbolic distance between 2 juxtaposed stimuli increases. Thus, just as a participant can more quickly detect that 9, rather than 8, is greater than 7, the participant can more readily assess the relation $B > D$ than the relation $C > D$ when evaluating the linear ordering $A > B > C > D > E$.

The SDE raises the possibility that transitive reasoning and numerical processing share the same and (arguably) ancient neural mechanism. In line with this idea, some cognitive models have proposed that the same kind of mental representation embodies both transitive (Bryant and Trabasso 1971; Goodwin and Johnson-Laird 2005) and numerical series (Dehaene 1997). According to these models, both transitive series and numbers are thought to be represented on a spatial mental line so that the further apart the items (or numbers) are on the line the easier it is to discriminate between them. This account explains the behavioral SDE and is further supported by findings suggesting that numbers as well as transitive items are automatically associated with positions in space. For example, participants are systematically faster at discriminating between small numbers (Dehaene et al. 1993) and items at the beginning of a transitive ordering with their left hand than with their right hand (Prado et al. 2008). The reverse pattern is observed for large numbers and items at the end of a transitive ordering. Because the effect was primarily discovered on numbers, this behavioral effect is

termed the spatial-numerical association of response codes, or SNARC, effect (Dehaene et al. 1993).

In terms of neural activity, converging evidence from neuroimaging studies highlights the systematic involvement of the horizontal segment of the intraparietal sulcus (hIPS) in numerical manipulation (Pinel et al. 2004; Cantlon et al. 2006; Piazza et al. 2007). For example, this region is typically associated with a neural SDE (i.e., greater activity as the distance between numbers decreases) in number comparison tasks (Pinel et al. 2001). To date, no study has examined whether the hIPS also exhibits a neural SDE when reasoners process transitive series. There is some indication that it might. Two recent neuroimaging studies have demonstrated that the hIPS is activated when participants make order judgments related to ingrained series like letters (Fias et al. 2007) or months (Ischebeck et al. 2008). These results, together with a study showing that neurons in the hIPS of monkeys code the order of events (Nieder et al. 2006), suggest that the same brain region is involved in processing 2 of the fundamental characteristics of numbers, that is, quantity and serial order (Jacob and Nieder 2008). Although future electrophysiological studies might reveal whether these aspects are processed by the exact same neurons of the hIPS (Jacob and Nieder 2008), these data raise the possibility that representing ordinal relations between items in a transitive series is related to numerical processing mechanisms in the hIPS.

There is another possible explanation accounting for both the similar phylogenetic histories and the common behavioral effects (SDE and SNARC effect) observed in transitive reasoning and numerical cognition: Transitive and numerical series may rely on different mechanisms having both similar properties and phylogenetic histories. Specifically, it has been argued that transitive series (unlike numbers) are not supported by the hIPS but are related to associative reinforcement mechanisms in the basal ganglia-dopamine system (Frank et al. 2003; Frank 2005). This idea comes from the animal literature where the learning of a nonverbal transitive series is accomplished by presenting asymmetrically rewarded overlapping pairs of items (e.g., A+B-, B+C-, C+D-, D+E- where + indicates a positive and - a negative reward). In the above example, the anchors (A and E) have asymmetric reinforcement values (A is always rewarded, and E is never rewarded). Computational models have shown that these asymmetric values can transfer to the adjacent items (von Fersen et al. 1991; Delius and Siemann 1998; Frank et al. 2003). For example, because B is associated with the most rewarded item (A) and D is associated with the least rewarded item (E), B develops a greater associative value than D. Choosing B over D is entirely explained by the past reinforcement history for each item (von Fersen et al. 1991). This reasoning can be extended to all transitive items so that items at the top of the sequence develop greater dopamine values than those items at the bottom (Frank et al. 2003). This mechanism would entirely explain the SDE: It is easier to assess the relationship between 2 items with a large dopamine value difference than 2 items with a small difference (Frank et al. 2003; Vasconcelos 2008). Whether such associative reinforcement mechanisms can explain the SDE in verbal transitive reasoning tasks (where no “explicit” reward is involved) remains unexplored however.

Here we use functional magnetic resonance imaging (fMRI) in humans to examine the extent to which a transitive series draws on 1) those areas that are traditionally associated with

the representation of numbers in the hIPS or on 2) the basal ganglia-dopamine system involved in associative reinforcement. Prior to scanning, participants spontaneously inferred the ordinal structure of an arbitrary sequence of 8 items (i.e., $A > B > C > D > E > F > G > H$) by studying the adjacent relations between randomly presented overlapping items (e.g., $D > E$, $C > D$, $E > F$, $B > C$, $G > H$, $F > G$, $A > B$, and $E > F$). Brain activity and performance with the sequence were subsequently measured while subjects were asked to evaluate the truth value of test propositions describing all possible pairwise comparisons within the sequence (e.g., $B > D$?), covering 7 different symbolic distances while separating items in pairs (from 0 to 6 items separating the items of a given pair, see Fig. 1A, left). After performing this transitive reasoning task, the same participants were also required, in a separate block, to perform a number comparison task involving the presentation of all the pairwise comparisons within a sequence of 8 numbers (from 2 to 9), leading to the same 7 symbolic distances that separate the numbers (see Fig. 1B, left).

Comparing the neural correlates of the SDE observed in the transitive reasoning task to the neural correlates of the SDE observed in the number comparison task is critical for testing our hypotheses regarding the neural representation of transitive series. If a transitive series is supported by the same mechanisms that underlie the representation of numbers, then the hIPS should show a neural SDE in both transitive reasoning and number comparison tasks. If a transitive series is supported by associative reinforcement mechanisms, then a neural SDE should be observed in the basal ganglia but not in the hIPS in the transitive reasoning task.

Materials and Methods

Participants

Seventeen healthy right-handed volunteers participated in the study. Two participants were excluded from the analyses because their error rates in the transitive reasoning task were above 30%. The remaining 15 participants (3 males) were aged between 21 and 29 years (mean age: 23 years). All subjects were native French speakers and provided written informed consent prior to their participation in the study. Procedures were approved by the local ethics committee (CCPPRB of Lyon, France).

Experiment Timeline

Prior to scanning, participants were instructed and trained on both a number comparison and a transitive reasoning task. Participants began by carrying out 39 trials of the number comparison task in which they were required to compare the numerical value of 2 numbers presented simultaneously on both sides of a fixation point in the center visual field. Half of the participants assessed which was larger, the other half which was smaller. The same subjects were then trained on the transitive reasoning task. Specifically, subjects were asked to memorize a short paragraph describing a linear ordering of 8 adjacent geometrical shapes (each characterized in French by a 1-syllable name with a unique first letter). Below is an example.

The rectangle is to the left of the oval, the star is to the left of the triangle, the oval is to the left of the hexagon, the circle is to the left of the square, the arrow is to the left of the rectangle, the square is to the left of the star, and the triangle is to the left of the arrow.

Half of the subjects were presented with a spatial description using the preposition *to the left of* (*à gauche de*) and the other half with a spatial description using the preposition *to the right of* (*à droite de*). Participants were allowed to take as much time as necessary to study the paragraph and could take some notes on a separate sheet of paper. Both the spatial description and the notes were then removed and the subjects practiced 39 trials of the transitive reasoning task in which

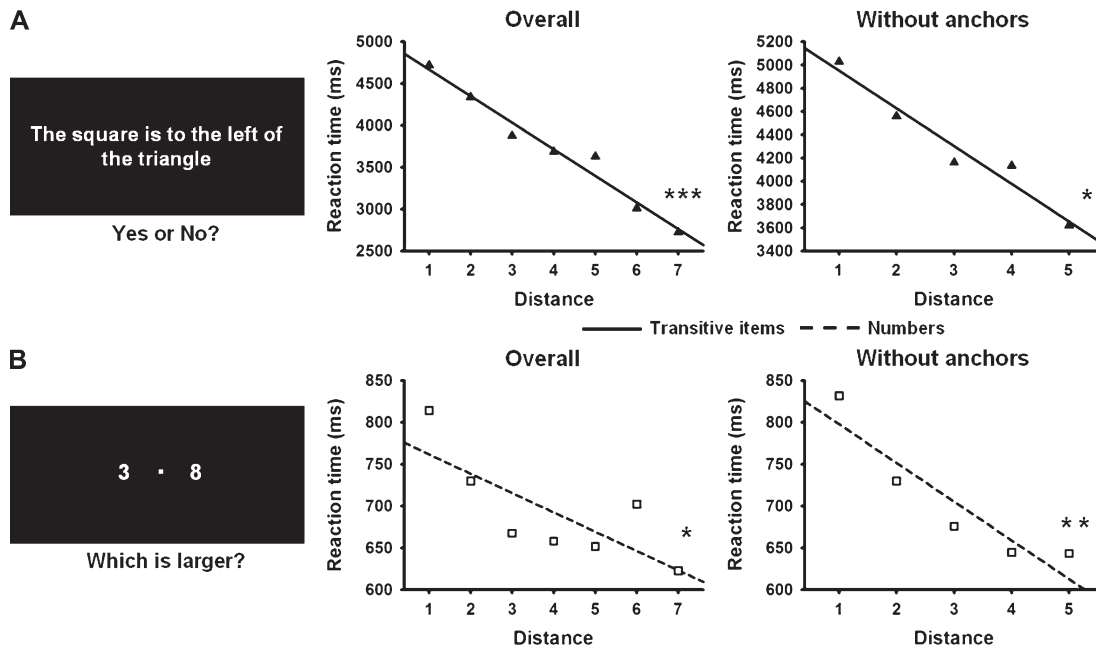


Figure 1. Tasks and behavioral performance. (A) Left: transitive reasoning task. Participants evaluate the truth value of spatial relations between items of a previously learned transitive series. Middle: reaction times linearly decreased as the distance between transitive items increased ($r^2 = 0.97$, $P < 0.001$). Right: reaction times linearly decreased as the distance between inner transitive items increased (i.e., anchor items were excluded; $r^2 = 0.85$, $P < 0.05$). (B) Left: number comparison task. Participants had to compare the magnitude of 2 numbers. Middle: reaction times linearly decreased as the distance between numbers increased ($r^2 = 0.60$, $P < 0.05$). Right: reaction times linearly decreased as the distance between inner numbers increased (anchor numbers were excluded; $r^2 = 0.95$, $P < 0.01$) * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

they were required to evaluate the truth value of statements related to the linear ordering of the shapes in the description (e.g., “the star is to the left of the triangle,” Yes or No?). Six different pairs were presented in each condition of distance except for the only pair involving 6 intervening items (and thus the 2 anchors), which was presented 3 times. The spatial preposition used in the statements (i.e., to the left of or to the right of) always matched the one used in the spatial descriptions, and the participants were told that they would be tested on the same linear ordering in the scanner. Participants were given feedback about their accuracy rate at the end of the practice session in both tasks. All the subjects included in the study performed at rates that were above 90% correct on both the number comparison and the transitive reasoning training sessions.

In the scanner, participants performed each task in a separate block, the transitive reasoning task being performed before the number comparison task. The task order was kept constant across subjects for 2 reasons. First, to increase accuracy, we wanted the participants to perform the transitive reasoning task immediately after the practice session, and it was not technically feasible to train the subject while they were in the scanner (because of the “paper-and-pencil” methodology described above). Second, this order ensured that the subjects did not have to maintain the linear ordering in working memory during the number comparison task. Indeed, previous research has shown that dual tasking (e.g., holding a list in working memory while performing a numerical task) significantly affects behavioral performance in numerical processing tasks (Lee and Kang 2002). In the transitive reasoning task, 78 test propositions (half valid and half invalid) were presented in order to cover all the pairwise spatial relations between the geometrical shapes in the array. There were 12 repetitions of each condition of distance except for the pair involving the 2 anchor items, which was presented 6 times. In the number comparison task, the stimuli were pairs of numbers (8 numbers from 2 to 9) presented simultaneously in the central visual field on both sides of a fixation dot. Seventy-eight pairs of numbers (half with the larger number on the left side of the fixation dot, half with the larger number on the right side) were presented in order to match the design of the transitive reasoning task (12 repetitions of each distance condition). In both tasks, each trial consisted of a fixation dot lasting from 3000 to 5000 ms followed by the presentation of the stimulus that remained

on the screen until the participant responded by pressing 1 of 2 corresponding response keys with their right hand (Yes/No response in the transitive reasoning task, Left number/Right number in the number comparison task).

Imaging Parameters

Images were collected using the 1.5T MRI system (Siemens Sonata Maestro Class) of the CERMEP—Imagerie du vivant in Lyon. The fMRI blood oxygen level-dependent signal was measured using a T_2^* -weighted echoplanar sequence (time repetition [TR] = 2500 ms, flip angle = 90° , time echo [TE] = 60 ms). In all, 26 axial slices (4.40 mm thick, field of view [FOV] = 23 cm, 64×64 matrix) were acquired per volume. Following functional image acquisition, a high resolution T_1 -weighted anatomical image (TR = 1880 ms, TE = 3.93 ms, FOV = 256 mm, flip angle = 15° , $176 \times 256 \times 256$ matrix, slice thickness = 1 mm) was collected for each subject.

fMRI Data Analysis

fMRI data were analyzed using SPM5 software (Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ac.uk>). The first 4 volumes in each session were discarded. Functional images were corrected for slice acquisition delays and spatially realigned to the first image of the first session to correct for head movements. The realigned functional images for each subject were then normalized into the Montreal Neurological Institute template using an affine transformation and voxels of $3.75 \times 3.75 \times 4.5$ mm³. Functional images were spatially smoothed with an isotropic Gaussian filter (8-mm full width at half maximum). Event-related statistical analysis was performed according to the general linear model (Josephs et al. 1997) using the standard hemodynamic response function. Events were time locked to the appearance of the stimulus in the numerical comparison task and to the midway point between the presentation of the statement and the motor response in the transitive reasoning task in order to account for the longer RTs observed in the transitive reasoning task (De Neys et al. 2008). The time series data were high-pass filtered (1/128 Hz), and serial correlations were corrected using an autoregressive AR(1) model.

Each correct trial was categorized according to a Task (transitive reasoning, numerical comparison) \times Anchoring (anchor, no anchor)

factorial design, leading to 4 different trial types. We included an additional parametric regressor for each of these trial types to probe whether and how the magnitude of the fMRI response in each trial varied with the distance between geometrical shapes (transitive reasoning task) and numbers (numerical comparison task). This model was estimated for each subject, and linear contrasts were calculated in order to investigate effects of interest.

Random effects analyses were applied to individual contrasts to account for between-subjects variance. The activations reported survived a voxel-level threshold of $P < 0.01$, uncorrected for multiple comparisons, and a cluster-level threshold of $P < 0.05$, corrected for multiple comparisons. Region of interest (ROI) analyses were performed using the SPM toolbox Marsbar (<http://marsbar.sourceforge.net/>). The ROI masks included all voxels within a 6-mm radius of each maximum. All P values reported are 2-tailed.

Results

In what follows, we first present the overall measures related to correct performance. This is followed by a description of the brain regions in which activity varied as a function of the distance between transitive items and/or numbers. These analyses lead us to consider the effect of practice on both behavior and brain activity in the transitive reasoning and number comparison tasks. Finally, we investigate whether and how the basal ganglia and the hIPS encode the relative order among the transitive items.

Distance between Transitive Items and Numbers Affects Performance

There are 3 main results to report with respect to these 2 kinds of standard problems. One, individual error rates did not exceed 9% in the transitive reasoning task (mean: 2.8%) and 2.6% in the number comparison task (mean: 0.6%). Two, in the

transitive reasoning task, no difference in reaction times was observed between the participants evaluating the preposition to the left of and those evaluating to the right of ($F_{1,13} = 0.28$, $P = 0.61$). Finally, analysis of correct RTs (Fig. 1) showed that responses were faster as the symbolic distance increased between transitive items ($F_{6,84} = 21.12$, $P < 0.001$) and numbers ($F_{6,84} = 8.59$, $P < 0.001$).

As expected, then, reaction times linearly decreased as the distance increased in both sequences (transitive series: $r^2 = 0.97$, $P < 0.001$; numbers: $r^2 = 0.60$, $P < 0.05$). This distance effect was persistent even when the pairs involving the anchor terms (A and H in the transitive reasoning task, 2 and 9 in the numerical comparison task) were removed from the analyses (transitive series: $F_{4,56} = 11.35$, $P < 0.001$; numbers: $F_{4,56} = 17.31$, $P < 0.001$). Without these anchor pairs (typically easier to process because they are the first and last items of the sequence; Potts 1974), reaction times remained linearly correlated with the variation of distance (transitive series: $r^2 = 0.85$, $P < 0.05$; numbers: $r^2 = 0.95$, $P < 0.01$). These results replicate previous findings (Moyer and Landauer 1967; Potts 1974) and show that subjects demonstrated a behavioral SDE when evaluating both the transitive and the numerical series.

Distance between Transitive Items and Numbers Affects Hips Activity

Analysis of fMRI data ($P < 0.01$ voxelwise, $P < 0.05$ corrected clusterwise) revealed that, within the brain structures involved in the transitive reasoning task, the left hIPS ($x = -39$, $y = -45$, $z = 42$, $Z = 4.53$), the left inferior frontal gyrus ($x = -57$, $y = 9$, $z = 18$, $Z = 3.63$), and the left premotor cortex ($x = -24$, $y = -9$, $z = 60$, $Z = 3.36$) were affected by the distance between transitive items (see Fig. 2). Within the brain regions activated

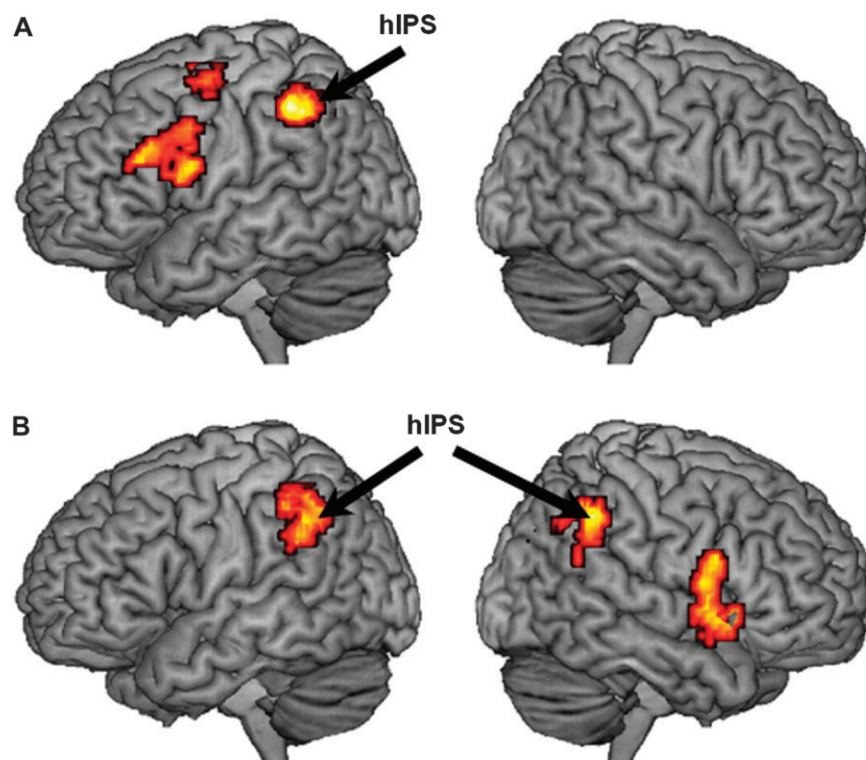


Figure 2. Surface projection of the brain regions showing both an overall task activation and a neural distance effect. (A) Transitive reasoning task. (B) Number comparison task. hIPS: horizontal segment of the intraparietal sulcus.

by the numerical comparison task, a neural SDE was observed in the bilateral hIPS (left: $x = -36, y = -51, z = 48, Z = 3.82$; right: $x = 51, y = -45, z = 45, Z = 3.99$) and the right inferior frontal gyrus ($x = 51, y = 12, z = 21, Z = 3.65$).

A boolean intersection of the 2 above maps (each at $P < 0.01$ voxelwise, $P < 0.05$ corrected clusterwise) revealed that the only region demonstrating a neural SDE in both transitive series and numbers was the left hIPS ($x = -39, y = -45, z = 42$; Fig. 3A). In this region, an ROI analysis showed that fMRI activity linearly decreased as the symbolic distance between transitive items and numbers increased (transitive series: $r^2 = 0.92, P < 0.001$; numbers: $r^2 = 0.89, P < 0.01$). This effect was still significant in the transitive reasoning task (but not in the number comparison task) when the anchor items were removed (transitive series: $r^2 = 0.96, P < 0.01$; numbers: $r^2 = 0.41, P = 0.24$). This overlap between the fMRI correlates of the transitive reasoning and number comparison tasks supports the idea that transitive series and number comparison tasks share the neural representation of numbers in the left hIPS.

Distance between Transitive Items, but not Numbers, Affects Basal Ganglia Activity

We found only one brain region in which the neural SDE was greater in the transitive reasoning than in the number comparison task ($P < 0.01$ voxelwise, $P < 0.05$ corrected clusterwise). This cluster was located in the left basal ganglia, at the level of the caudate nucleus ($x = -12, y = 3, z = 12, Z = 3.74$; see Fig. 3B). In this area, an ROI analysis revealed that fMRI activity linearly decreased as the distance between

transitive items increased ($r^2 = 0.88, P < 0.01$), but this effect was not observed in numbers ($r^2 = 0.03, P = 0.70$). Similar results were obtained when eliminating the anchor items (transitive ordering: $r^2 = 0.87, P < 0.05$; numbers: $r^2 = 0.43, P = 0.23$). That is, activity in the basal ganglia was modulated by the distance between transitive items but not between numbers (i.e., activity linearly increased as distance between transitive items decreased). This finding supports the idea that associative reinforcement mechanisms in the basal ganglia-dopamine system are involved in the representation of transitive series; we did not find evidence that this system is implicated in the representation of numbers.

Transitive Series Representations in the hIPS and Basal Ganglia Are Modulated by Practice

Unlike the number comparison task, the transitive reasoning task elicited a neural SDE in both hIPS and basal ganglia (see above). This finding might suggest that both structures 1) concomitantly represent the transitive series during the task or 2) are sequentially involved. To test between these competing hypotheses, we separated the first half of the trials (i.e., early trials) from the last half (i.e., late trials) for both the transitive reasoning and numerical comparison tasks and analyzed them independently. A linear SDE was observed on reaction times throughout the entire transitive reasoning (early trials: $r^2 = 0.90, P < 0.01$; late trials: $r^2 = 0.96, P < 0.001$) and number comparison (early trials: $r^2 = 0.65, P < 0.05$; late trials: $r^2 = 0.60, P < 0.05$) tasks. Overall, response times were longer

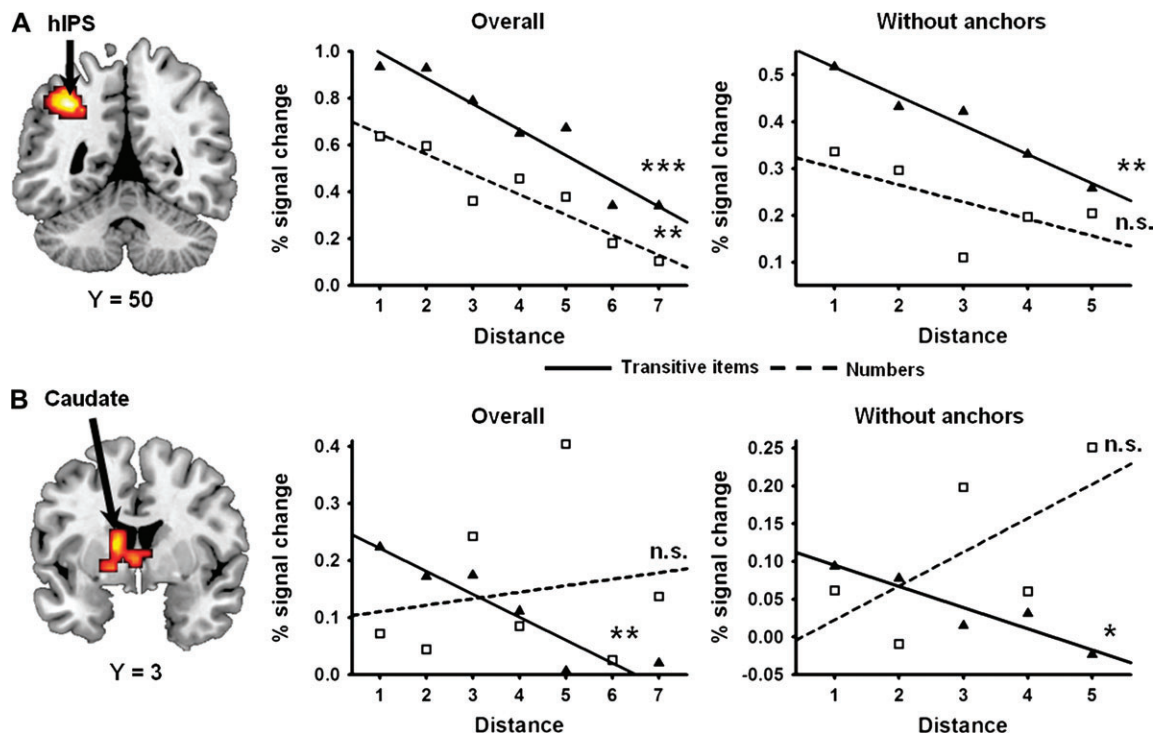


Figure 3. Neural distance effect in the hIPS and the left caudate nucleus. (A) Left: the hIPS was the only region showing a neural distance effect in both transitive reasoning and number comparison tasks. Middle: left hIPS activity linearly decreased as the distance between transitive items ($r^2 = 0.92, P < 0.001$; black triangles) and numbers ($r^2 = 0.89, P < 0.01$; empty squares) increased. Right: left hIPS activity linearly decreased as the distance between inner transitive items ($r^2 = 0.96, P < 0.01$; black triangles) and inner numbers ($r^2 = 0.41, P = 0.24$; empty squares) increased. (B) Left: the left caudate nucleus was the only region showing a greater neural distance effect in the transitive reasoning than in the number comparison tasks. Middle: left caudate activity linearly decreased as the distance between transitive items ($r^2 = 0.88, P < 0.01$; black triangles) and numbers ($r^2 = 0.03, P = 0.70$; empty squares) increased. Right: left caudate activity linearly decreased as the distance between inner transitive items ($r^2 = 0.87, P < 0.05$; black triangles) but not inner numbers ($r^2 = 0.43, P = 0.23$; empty squares) increased. hIPS: horizontal segment of the intraparietal sulcus. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s., non significant.

in early trials than in late trials in the transitive reasoning task (early trials: 4116 ms, late trials: 3543 ms; $t = 2.73$, $P < 0.05$). No difference was observed in the number comparison task (early trials: 699 ms, late trials: 701 ms; $t = -0.10$, $P = 0.93$).

With respect to fMRI, an ROI analysis revealed that the linear neural SDE in the hIPS was only reliable in the first half of the transitive reasoning task (early trials: $r^2 = 0.81$, $P < 0.001$; late trials: $r^2 = 0.25$, $P = 0.25$) (Fig. 4A). In the basal ganglia, however, the neural SDE was significant only in the last half of the transitive reasoning tasks (early trials: $r^2 = 0.09$, $P < 0.51$; late trials: $r^2 = 0.71$, $P < 0.05$; Fig. 4B). These differential effects over time were not observed in the number comparison task, where a linear neural SDE was observed during the entire task in the hIPS (early trials: $r^2 = 0.75$, $P < 0.05$; late trials: $r^2 = 0.61$, $P < 0.05$) and never found in the basal ganglia (early trials: $r^2 = 0.001$, $P = 0.95$; late trials: $r^2 = 0.35$, $P = 0.16$). These results suggest that number representations in the hIPS preferentially support transitive series soon after training, whereas associative processes in the basal ganglia are engaged as the series becomes well practiced.

Rank Order Differentially Affects Basal Ganglia and hIPS Activity

In order to investigate whether the serial position (or rank) of transitive items is represented in hIPS and basal ganglia, we performed additional ROI analyses of the fMRI data exclusively

focusing on the 7 adjacent pairs of the sequence (i.e., AB, BC, CD, DE, EF, FG, and GH).

First, analysis of behavioral performance on these pairs revealed a classic serial position effect (SPE; Bryant and Trabasso 1971), with faster RT when the pairs were located at both ends of the sequence than in the middle (Fig. 5A). That is, the variation of RTs from the first to the last ordered item was better explained by a quadratic ($r^2 = 0.54$, $P = 0.20$) than by a linear ($r^2 = 0.01$, $P = 0.83$) regression. The difference between both fits was marginally significant ($P < 0.10$). No relationship was observed between RTs and adjacent numbers (linear: $r^2 = 0.13$, $P = 0.43$; quadratic: $r^2 = 0.49$, $P = 0.25$).

Second, greater activity in the hIPS was observed when participants had to process items at the middle of the sequence rather than items at either end, mirroring the behavioral SPE observed (Fig. 5B, right). In other words, activity in the hIPS from the first to the last transitive item was better explained by a quadratic ($r^2 = 0.78$, $P < 0.05$) than by a linear ($r^2 = 0.03$, $P = 0.70$) regression. The difference between both fits was significant ($P < 0.05$). No relationship was observed between hIPS activity and adjacent numbers (linear: $r^2 = 0.38$, $P = 0.13$; quadratic: $r^2 = 0.41$, $P = 0.34$). This finding reveals that activity in the hIPS is associated with the behavioral SPE observed in transitive series.

Third, we found that activity in the left basal ganglia was greater when participants processed the first (e.g., the pair AB) than the last items (e.g., the pair GH) of the sequence

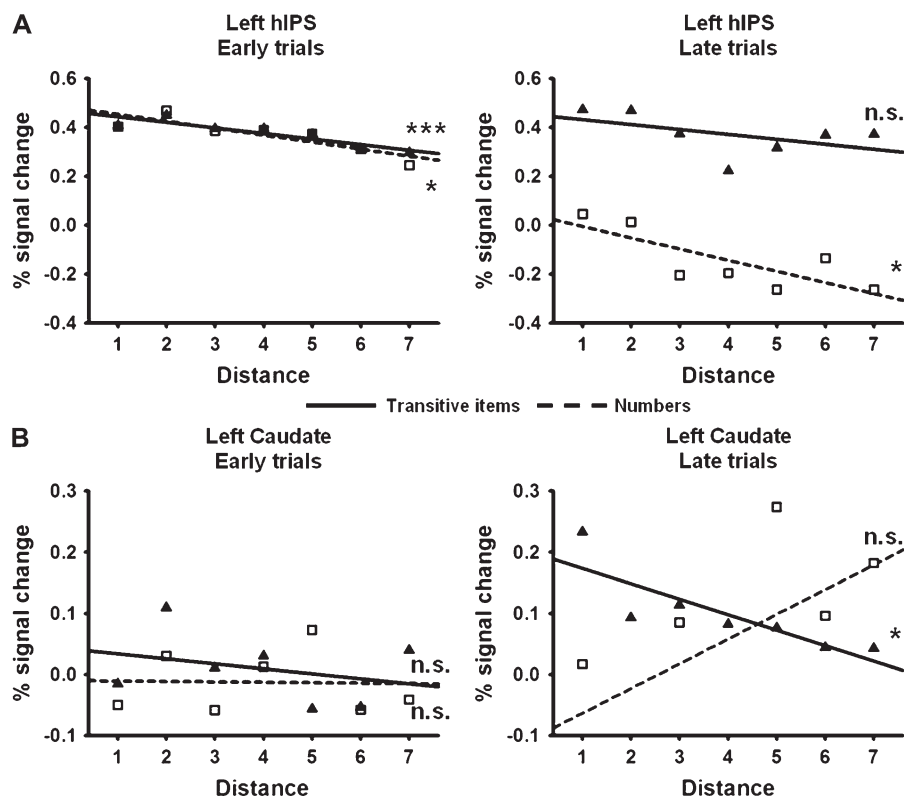


Figure 4. Neural distance effect in the left hIPS and the left caudate nucleus as a function of practice. (A) Left: in early trials, left hIPS activity was linearly correlated with the variation of distance between items in the transitive sequence ($r^2 = 0.81$, $P < 0.001$; black triangles) and numbers ($r^2 = 0.75$, $P < 0.05$; empty squares). Right: in late trials, left hIPS activity was not linearly correlated with the variation of distance between items in the transitive sequence ($r^2 = 0.25$, $P = 0.25$; black triangles) but was still correlated with the distance between numbers ($r^2 = 0.61$, $P < 0.05$; empty squares). (B) Left: in early trials, left caudate activity was correlated neither with the variation of distance between items in the transitive sequence ($r^2 = 0.09$, $P < 0.51$; black triangles) nor with the distance between numbers ($r^2 = 0.001$, $P = 0.95$; empty squares). Right: in late trials, left caudate activity was linearly correlated with the variation of distance between items in the transitive sequence ($r^2 = 0.71$, $P < 0.05$; black triangles) but not with the distance between numbers ($r^2 = 0.35$, $P = 0.16$; empty squares). hIPS: horizontal segment of the intraparietal sulcus. * $P < 0.05$, *** $P < 0.001$, n.s., non significant.

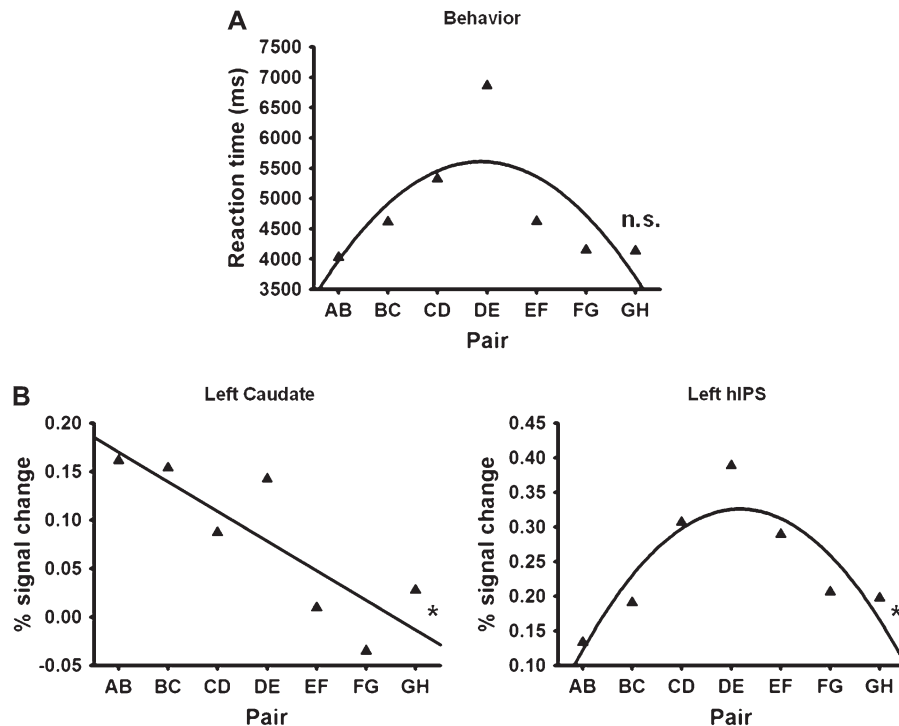


Figure 5. Adjacent pairs in the transitive sequence. (A) Variation of reaction time as a function of the position of the adjacent pairs in the sequence (AB representing the beginning and GH the end of the series) was better explained by a quadratic ($r^2 = 0.54$, $P = 0.20$) than by a linear ($r^2 = 0.01$, $P = 0.83$) regression. (B) Left: left caudate activity was linearly correlated with the position of the adjacent pairs in the sequence ($r^2 = 0.71$, $P < 0.05$). Right: left hIPS activity was quadratically correlated with the position of the adjacent pairs in the sequence ($r^2 = 0.78$, $P < 0.05$). * $P < 0.05$, n.s., non significant.

(Fig. 5B, left). More specifically, fMRI activity in the left caudate nucleus linearly decreased from the first to the last items of the sequence ($r^2 = 0.71$, $P < 0.05$). This result supports the hypothesis that the basal ganglia gradually encode the rank of items in a transitive sequence (Frank et al. 2003).

Discussion

In the present study, we investigated the link between the representations of transitive series and numbers in the human brain. In 2 separate tasks, participants were required to 1) assess the relationship between items from an ordered series previously learned by verbal transitive reasoning (transitive reasoning task) and 2) compare the magnitude of numbers (number comparison task). Transitive items and numbers were presented in pairs characterized by the distance separating each stimulus on their respective continuum (transitive series or numbers). Analysis of reaction times revealed that participants were faster to evaluate pairs of transitive items and pairs of numbers as the distance between stimuli increased. This behavioral SDE has long been shown in both the numerical cognition (Moyer and Landauer 1967) and transitive reasoning (Potts 1974) literatures. This effect traditionally supports the view that transitive series are supported by a spatial mental representation akin to the mental “number line” (Dehaene 1997), suggesting that transitive series may draw on the cerebral mechanisms involved in number processing. Our results reveal both overlapping and separate representations of transitive series and numbers in the human brain.

On the one hand, we found a unique brain region demonstrating a neural SDE in both transitive series and

numbers, that is, the left hIPS. The hIPS has been repeatedly found to be engaged in tasks involving numerical manipulation (Pinel et al. 2004; Cantlon et al. 2006; Piazza et al. 2007) and is thought to be the core of a quantity estimation mechanism in the human brain (Dehaene et al. 2003). Previous neuroimaging studies have found activation in the parietal lobes during transitive reasoning (Goel and Dolan 2001; Acuna et al. 2002; Goel et al. 2004; Heckers et al. 2004; Fias et al. 2007), but the present study provides the first demonstration that representing a verbal transitive series makes use of the same neural structure—the hIPS—that is involved in number processing. Specifically, this finding raises the possibility that the ability to represent ordinal relations between transitive items depends on the mechanisms involved in numerical comparisons. This is consistent with the notion that numbers are used not only to estimate quantities but also to evaluate ordinal relationships between elements within a hierarchy (e.g., the second is before the fourth; Jacob and Nieder 2008). Although it is still unclear whether the same parietal neurons encode both cardinal and ordinal aspects of numbers (Jacob and Nieder 2008), 2 recent fMRI studies have provided evidence that the hIPS is involved in representing familiar ordered series like months of the year (Ischebeck et al. 2008) and letters of the alphabet (Fias et al. 2007). Together with the present findings, these data suggest that the magnitude processing mechanisms in the hIPS might be engaged in representing familiar as well as recently acquired ordered information.

The presence of a neural SDE in the hIPS for both transitive series and numbers is also consistent with cognitive models of transitive reasoning and numerical cognition. These models argue that both transitive items (Huttenlocher 1968; Goodwin

and Johnson-Laird 2005) and numbers (Dehaene 1997) are organized along a linear continuum of partially overlapping representations. Because they are unambiguous, items at both ends of this spatial line (i.e., the anchors) should be more easily distinguishable than items in the middle of the line. In the transitive reasoning task, we observed such an SPE (Vasconcelos 2008) on participants' behavior, that is, reaction times when pairs of adjacent items were evaluated decreased as items were closer to the ends of the sequence. Interestingly, we found that activity in the hIPS mirrored this behavioral SPE, with a reduction of fMRI signal as items were closer to the ends of the sequence. This finding supports the idea that the hIPS houses a representation of the transitive series analog to a spatial "mental line." We did not observe any behavioral or neural SPE in the number comparison task. Although it is well known that small numbers are usually processed faster than large numbers (Gallistel and Gelman 1992), our task involved only highly familiar small numbers (from 2 to 9) and may not be well suited to investigating the so-called size effect in numerical series.

Overall, the pattern of results obtained in the hIPS lends neurological support for Piaget's pioneering intuitions that understanding numbers is linked to the comprehension of the logical relations between quantities. In his landmark work, Piaget (1952) indeed observed that children's ability to conserve numbers (i.e., understanding that a number of objects does not depend on their spatial arrangement) develops at the same time as the concept of ordinality. Although Piaget and his colleagues originally thought that these fundamental competences were not fully developed until the age of 7 (Piaget 1952), recent findings show that infants have a basic understanding of numerical quantities (Wynn 1992) and serial orders (Brannon 2002). Specifically, it has been argued that errors in number conservation tasks reflect failures at inhibiting a misleading strategy (i.e., the length-equals-number heuristic) rather than a lack of numerical competence per se (Houdé 2000). Support for this view has been given by studies showing that success in number conservation tasks with number-length interference is associated with 1) longer reaction times (Houdé and Guichard 2001) and 2) greater activity in an inhibitory control brain network (Leroux et al. 2006; Leroux et al. 2009) than success in tasks not involving such an interference.

On the other hand, our study reveals an important dissociation between the cerebral correlates of transitive and numerical series. In the left caudate nucleus, fMRI activity was linearly modulated by the distance between transitive items where no modulation was observed for numbers. This finding is in keeping with associative reinforcement models of transitive reasoning (von Fersen et al. 1991; Delius and Siemann 1998; Frank et al. 2003; Vasconcelos 2008). These models, coming from the animal behavior literature, argue that transitive reasoning does not rely on the mechanisms involved in numerical processing but rather on the dopaminergic neurons of the basal ganglia. Specifically, during learning, the striatal dopamine system is thought to associate a dopamine value with each item in the transitive series (Frank et al. 2003). Because a gradient of associative strength arises among all the stimuli in the transitive sequence, no explicit reasoning strategy is needed to complete a transitive reasoning task. Instead, participants would only need to rely on this associative gradient to rank transitive items: The greater the dopamine value of an item, the higher its rank in the transitive ordering.

Our study provides clear evidence for this kind of coding. We found that activity in the basal ganglia linearly increased as the rank of items in the sequence increased. Such an associative representation of the transitive sequence explains the behavioral SDE, that is, the ability to discriminate between 2 transitive items depends on the associative value difference between these items (Frank et al. 2003). In sum, these results suggest that processing transitive series does not rely solely on number representations in the hIPS but also on the basal ganglia-dopamine system.

The present findings further show that the hIPS and the basal ganglia have different patterns of temporal activity in the transitive reasoning task. That is, the hIPS was preferentially associated with a neural SDE at the beginning of the task, whereas the basal ganglia was implicated in this effect mostly at the end. This suggests that the analogical representations of numbers in the hIPS preferentially support the verbal transitive series early after acquisition and that the associative mechanisms of the basal ganglia preferentially support the series when it is well practiced. We speculate that the differential involvement of these neural mechanisms reflects the nature of the knowledge of the transitive ordering. In our paradigm, subjects were able to acquire the verbal transitive series after a short period of time spent studying the adjacent pairs. This relatively fast learning process might result from an explicit learning of the ordinal relations between transitive items, possibly mediated by the neurons coding the ordinal aspect of numbers in the hIPS (Nieder 2005). In contrast, the increased activation of the basal ganglia at the end of the task might be associated with an "implicit" learning of the sequence. Indeed, repeated exposure to the different pairs of items is necessary to strengthen the association between dopamine values and transitive items (Frank et al. 2003). Our findings suggest that such an associative learning occurs even in the absence of an explicit trial-by-trial reinforcement. Given the high accuracy rate observed at the end of the practice session, it is likely that the participants had a very good command of the transitive series and were thus aware of their behavioral performance on each trial. This "internal" cognitive feedback might be sufficient to associate a reinforcement value to each individual item over the course of the experiment (Aron et al. 2004).

The main regions observed in our study are the hIPS and the left caudate. However, it is important to consider the possible role of other brain regions in our experiment. For example, the transitive reasoning task also elicited a neural SDE in the left inferior frontal cortex (IFC). Activations in the left IFC have been found repeatedly in deductive reasoning tasks (Houdé and Tzourio-Mazoyer 2003; Goel 2007) and suggest that deductive reasoning relies on linguistic computations in addition to the analogical mechanisms of the parietal cortex. A neural SDE in the number comparison task was also observed in the IFC, although preferentially in the right hemisphere. Neuroimaging and electrophysiological studies have observed the involvement of the ventral and dorsal parts of the prefrontal cortex in numerical processing (Ansari 2008). Although the respective roles of the parietal and prefrontal regions in numerical cognition are still open to debate, it has been suggested that the prefrontal cortex might be particularly involved in associating numerical symbols (e.g., the Arabic numeral 2) with their nonsymbolic internal counterparts (e.g., the quantity 2). Support for this claim has been given by an electrophysiological study showing that several neurons of the

prefrontal cortex of monkeys are involved in representing both symbolic and nonsymbolic representations of magnitude (Diester and Nieder 2007).

In conclusion, the current study provides the first demonstration that representing a verbal transitive series relies on both number representations in the hIPS and associative mechanisms in the basal ganglia-dopamine system. Both mechanisms do not appear to be active at the same time. Although the hIPS preferentially supports the verbal transitive series soon after learning, the basal ganglia are more engaged when the series is well practiced. The transient activation of the hIPS may be specific to the representation of a verbal transitive series and might not be present when transitive reasoning is tested with more abstract tasks in humans (Van Opstal et al. 2008) or animals (Vasconcelos 2008). Nevertheless, in humans, this mechanism might be important to maintain an explicit representation of the verbal transitive series until associative reinforcement mechanisms allow for its implicit encoding in the basal ganglia.

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Address correspondence to Jérôme Prado, Department of Psychology, University of Michigan, East Hall, 530 Church Street, Ann Arbor, MI 48109, USA. Email: jprado@umich.edu.

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