Spatial representation of magnitude in gorillas and orangutans

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ABSTRACT

Humans mentally represent magnitudes spatially; we respond faster to one side of space when processing small quantities and to the other side of space when processing large quantities. We determined whether spatial representation of magnitude is a fundamental feature of primate cognition by testing for such space-magnitude correspondence in gorillas and orangutans. Subjects picked the larger quantity in a pair of dot arrays in one condition, and the smaller in another. Response latencies to the left and right sides of the screen were compared across the magnitude range. Apes showed evidence of spatial representation of magnitude. While all subjects did not adopt the same orientation, apes showed consistent tendencies for spatial representations within individuals and systematically reversed these orientations in response to reversal of the task instruction. Results suggest that spatial representation of magnitude is phylogenetically ancient and that consistency in the orientation of these representations in humans is likely culturally mediated.

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1. Introduction

Behavioral and neurobiological evidence indicates that human adults represent magnitude dimensions spatially (Dehaene, Bossini, & Giraux, 1993; Fischer, Castel, Dodd, & Pratt, 2003; Rusconi, Buetti, Walsh, & Butterworth, 2011). For example, picture the numbers one through 10. If you are like most native English speakers, you pictured them in a horizontal line with one on the left and 10 on the right. Spatial representation is involved in magnitude processing generally; it is not confined to processing of number specifically (Holmes & Lourenco, 2011; Walsh, 2003). The orientation of this spatial representation of magnitude varies with culture and task demands (Bachholt, Baumuller, & Brugger, 1998; Fischer, Shaki, & Cruise, 2009; Shaki & Petrusic, 2005; Shaki, Petrusic, & Leth-Steenensen, 2012; van Dijck & Fias, 2011). Across these variations, the spatial representation of magnitude is evident in that viewing or thinking about small magnitudes biases visual attention to one area of space while large magnitudes bias attention in the opposite direction. As a result, English speaking western adults are, in general, quicker to detect cues presented on the left after being primed with small numbers, and cues presented on the right after being primed with large numbers (Fischer et al., 2003). Similarly, when making numerical judgments, English speakers respond faster to small numbers with a leftward response and large numbers with a rightward response (Dehaene et al., 1993). These space-magnitude congruency effects have been most extensively studied using judgments of number (Dehaene et al., 1993), but are also found for comparisons along other dimensions such as size (Shaki, Petrusic, et al., 2012), order (Gevens, Reynvoet, & Fias, 2003), and emotional magnitude (Holmes & Lourenco, 2011).

Orientation of the spatial representation of magnitude varies across cultures, between individuals, and responds flexibly to experience. It is influenced by both reading and counting such that in contrast to English speakers, Palestinians, who read and count from right to left, respond faster on average to small numbers with a rightward response and large numbers with a leftward response (Shaki, Fischer, & Petrusic, 2009; Shaki, Petrusic, et al., 2012). These reliable group-level differences in orientation of the spatial representation of number are likely caused by long-term memory repre-
sentations acquired through cultural experience (van Dijck & Fias, 2011). Nonetheless, the orientation of spatial representation of magnitude is apparently not fixed by culture, as it can vary between individuals even within a cultural group. While English speaking adults performing a parity task show consistent, robust group-level left-to-right representations of number (Wood, Willmes, Nuerk, & Fischer, 2008), the few studies that present individual data indicate that as few as 56–66% of individual participants show this orientation (Nuerk, Wood, & Willmes, 2005; Wood, Nuerk, & Willmes, 2006). The remaining participants either show no clear orientation or the opposite right-to-left orientation. The orientation of spatial representations also changes in response to language priming, numerical range, real-world referents, and task instructions (Bachtold et al., 1998; Fischer et al., 2009; Shaki & Petrusic, 2005; Shaki, Petrusic, et al., 2012; van Dijck & Fias, 2011). For example, when asked whether a number is higher or lower than 6, English speakers show latency differences in opposite directions when referencing numbers on a ruler (left-to-right) than when referencing numbers on a clock face (right-to-left; Bachtold et al., 1998). Four is represented on the left as a “small” number when presented with a numerical range from 4 to 9, but on the right as a “large” number when presented in a range from 1 to 5 (Dehaene et al., 1993). Bilingual Russian-Hebrew speakers reverse the orientation of their spatial representation of number depending on the language used to prime the task (Shaki & Fischer, 2008).

Variability and flexibility in the orientation of spatial representations of magnitude are especially great when humans lack long-term memories defining prototypical arrangements in a domain. For example, adults comparing quantities 1–10 (e.g. select the smaller or larger item; Shaki, Petrusic, et al., 2012) show group level spatial representations in culturally preferred directions regardless of task instruction. However, if asked to compare animal sizes (e.g. snail vs. mouse), English speakers organize their representation with small animals on the left when asked to identify the smaller animal in the pair, but reverse this orientation when instructed to identify the larger animal in the pair. The spatial orientation of Arabic speakers also reverses in response to instructions, but in the opposite direction (Shaki, Petrusic, et al., 2012). Likewise, human adults judging the smaller or larger quantity in a pair of large, less commonly ordered numerals (6–50; Lee, Chun, & Cho, 2016) or in a pair of shape arrays (Lee et al., 2016; Patro & Shaki, 2016) show this same reversal in orientation when instructions are reversed. Apparently, in the absence of the strong norms governing specific orientation of representations, participants flexibly orient their spatial representations with the to-be-detected magnitude on the preferred point-of-reference side of space (left for English speakers, right for Arabic speakers; Patro & Shaki, 2016). Importantly, this systematic reversal in orientation is diagnostic of the presence of spatial representations - it would not occur if representations did not have spatial properties. Non-human animals do not have experience or cultural norms to dictate a consistent orientation of magnitude representation. Therefore if spatial representation of magnitude is a general cognitive process that exists outside of humans, non-human primates would likely show a similar reversal in orientation based on task instruction.

Recent evidence has suggested that animals as distantly related to humans as chickens (Gallus domesticus), may process magnitudes spatially (Rugani, Vallortigara, Priftis, & Regolin, 2015a, 2015b). However, it is probably premature to reach conclusions about the phylogeny of spatial processing of magnitude with evidence from only humans and chickens, which are separated by over 300 million years of divergent evolution, show major differences in brain laterality, and are tested using substantially different methods (Drucker & Brannon, 2014; Harshaw, 2015; Kumar & Hedges, 1998; Larsson, 2013; Mangalam & Karve, 2015; Rogers, Vallortigara, & Andrew, 2013; Shaki & Fischer, 2015). To determine the extent to which spatial representation is a fundamental basis for magnitude cognition across primates specifically, we tested for spatial-magnitude correspondence in two groups of apes: gorillas (Gorilla gorilla gorilla) and orangutans (Pongo pygmaeus & Pongo abelli) using a task similar to those used in humans. These species shared a common ancestor with humans approximately 8 and 15 million years ago respectively (Finstermeier et al., 2013). Non-human primates share many components of human magnitude processing abilities; they accurately judge differences in quantity, order items by magnitude, and show performance patterns consistent with human numerical estimation, such as the symbolic distance effect and conformity to Weber’s law (Beran, 2008; Brannon & Terrace, 2002; Cantlon & Brannon, 2006). They additionally show interactions between processing of space and various magnitudes (time: Merritt, Casasanto, & Brannon, 2010; order: Adachi, 2014; Drucker & Brannon, 2014; Gazes, Lazareva, Bergene, & Hampton, 2014; social dominance: Dahl & Adachi, 2014). As in humans, there is neural overlap between numerical and spatial processing in the intraparietal sulcus of monkeys (Hubbard, Piazza, Pinel, & Dehaene, 2005). Based on work with humans, we designed a task for apes that tests for the presence of a spatial representation of magnitude but does not make assumptions about the orientation of the representation. Given the individual variability in orientation shown by human adults (Wood et al., 2006), and the fact that apes do not have cultural norms to dictate a preferred orientation in spatial representation, there is not sufficient evidence to predict a consistent orientation of magnitude representation in these species. Apes were presented with a task in which they selected either the larger or smaller of two quantities of dots (Patro & Haman, 2012). Across pairs from small (2 versus 3) to large (9 versus 10) quantities, response latencies were compared for trials in which the correct choice required a leftward or a rightward response. If spatial representation of magnitude is an evolutionarily ancient foundation of magnitude processing, apes, like humans, should respond faster to one side of space when processing pairs of small quantities and faster to the other side of space when processing large quantities. Critically, if apes represent quantities for which they have no cultural norm similarly to how humans represent uncommon magnitude domains, we should observe that the orientation of the spatial representation is reversed between conditions in which the animals are required to pick small and pick large.

2. Method

2.1. Subjects and procedure

Subjects were 9 apes (4 gorillas, 5 orangutans; Table 1) housed at Zoo Atlanta. Subjects were presented with a quantity comparison task on a touch screen computer affixed to their indoor housing area. Subjects initiated each trial by touching a green start square in the lower center of the screen. Two white squares appeared on the left and right sides of the screen, each containing between two and 10 black dots (Fig. 1). Dots were randomly located within the stimulus borders. The total surface area of the dots presented in each white square was held constant across stimuli. This resulted in smaller diameter dots and larger overall dot perimeter the more dots were present in a display. The location of the “small” and “large” stimuli in a pair was counterbalanced pseudo randomly across trials, such that the lesser quantity of dots appeared on the left and right sides of the screen equally often. Subjects indicated their choice by touching within the borders of one of the two stimuli. During training, selection of the correct quantity was reinforced with an auditory reinforcer on 100% of trials, and a food pellet on 80% of trials.
The number of sessions to reach criterion did not differ between the pick small and pick large conditions or between the first and second trained conditions for either training (linear mixed model with subject as a random factor: main effect of condition: \( M_{\text{pick small}} = 8.56 \pm 5.98 \) sessions, \( M_{\text{pick large}} = 8.33 \pm 4.24 \), \( t(7) = 0.17, p = 0.870 \)), main effect of training order \( M_{\text{first}} = 8.56 \pm 4.48, M_{\text{second}} = 8.33 \pm 5.81, t(7) = -0.17, p = 0.870 \) or testing (linear mixed model with subject as a random factor: main effect of condition: \( M_{\text{pick small}} = 11.89 \pm 3.76 \) sessions, \( M_{\text{pick large}} = 13.89 \pm 5.53 \), \( t(7) = -1.01, p = 0.346 \), main effect of training order \( M_{\text{first}} = 12.11 \pm 5.04, M_{\text{second}} = 13.67 \pm 4.30, t(7) = 0.83, p = 0.436 \)).

### 2.2. Handedness testing

Handedness was measured for each animal using a simple computerized task. Subjects touched a white dot that appeared randomly in the center and 4 corners of the screen over 150 trials. The hand used for each touch was recorded, and the proportion of trials in which the subject used the left hand was calculated (Table 1).

### 2.3. Data analysis

All analyses include only trials from test sessions. Response latencies on novel test trials were calculated using median latencies on correct trials excluding outliers greater than three standard deviations above the mean (0.53% of trials excluded). To determine whether apes processed the magnitude of the stimuli, accuracy and response latencies were analyzed for distance effects and conformity with Weber’s law, both of which are diagnostic of magnitude processing. The distance effect is indicated by higher accuracy and shorter response latency with increasing differences between the quantities in the pair. Conformity to Weber’s law is indicated by higher accuracy and shorter response latency with increasing ratios of the larger to the smaller of the two quantities in the pair. These effects would be expected regardless of whether apes were relying on dot quantity or dot size to make their choices, as both represent magnitude dimensions.

To test for a spatial representation of magnitude, the difference in response latency between correct responses made to the right and those made to the left (rightward responses minus leftward responses) was calculated for each of the eight critical test pairs in which adjacent quantities were presented (i.e. 2–3, 3–4, 4–5, 5–6, 6–7, 7–8, 8–9, 9–10). For each of the nine subjects in each of the two conditions simple regression models were fit to estimate intercepts and slopes of the relationship between the quantity and right orientations. After completion of testing in the first condition (either pick large or pick small; Table 1), subjects received training and testing in the other condition.
the latency difference scores (Table 1). Spatial representation of magnitude would be indicated if animals responded faster to one side of space when processing small quantity test pairs (e.g. 2 vs 3; 3 vs 4) and faster to the other side of space when processing large quantity test pairs (e.g. 8 vs 9; 9 vs 10), and reverse this pattern between the pick small and pick large conditions. Unlike humans, apes lack cultural norms for representing magnitudes in a particular orientation. This lack of culture may lead individual apes to show different orientations, resulting in an average slope close to 0. However, if apes reverse the orientation of their representation of magnitude in response to task instructions, we expect a systematic reversal of individual slopes between the pick small and pick large conditions. Such a reversal would be evident as a negative correlation between slopes in the pick small and pick large conditions. We tested for this correlation using Spearman’s rank correlation test.

Although apes do not have human-like experience with reading or counting direction, factors such as species, condition order, or individual hand preferences (Fischer & Brugger, 2011) may determine the orientation of spatial representations. To determine the impact of these factors on slope orientation we fitted two Linear Mixed Models (LMMs; one for pick small and one for pick large) to the latency difference scores. These models included the lower quantity in each adjacent test pair as the independent variable. Species, condition order, and handedness were added to the models as fixed effect control variables interacting with the lower quantity in the pair. In addition, the intercept and the slope of the regression lines were allowed to vary randomly among subjects following normal distributions centered at zero.

LMMs were fitted using software R v.3.1.2 (R Core Team, 2014) and R package lme4 (R package lme4; Bates, Machler, Bolker, & Walker, 2015). The normality of the random effects and residuals was carefully inspected using normal-quantile plots and Shapiro tests and no deviation to the assumptions of the LMMs was detected. Whether the overall slopes of both LMM differed significantly from zero was tested with t-tests using the Satterthwaite approximation of the degrees of freedom (R package lmerTest; Kuznetsova, Brockhoff, & Christensen, 2015). The 0.05 significance threshold was used in all statistical tests.

The sample size used in this study (9 apes) was planned a priori and corresponded to the total number of apes available. No subjects were dropped from the study or from the analyses.

3. Results

3.1. Apes engaged in magnitude processing

Apes performed above chance on novel test trials (mean for all test pairs combined: M = 77.50 ± 4.30% correct; one sample t-test: t (8) = 19.18, p < 0.001), and on the critical subset of test trials with adjacent quantity pairs that were used for the spatial-magnitude analyses (2 vs 3; 3 vs 4, 9 vs 10, etc.; M = 71.01 ± 4.73% correct; one sample t-test: t(8) = 13.95, p < 0.001).

Across all training and test pairs, apes showed performance patterns consistent with magnitude processing (Cantlon & Brannon, 2006), a prerequisite for spatial-magnitude correspondence. Performance conformed to Weber’s law, with faster response latencies and higher accuracy associated with larger ratios between comparison quantities (Fig. 2; Spearman’s rank correlation: response latency: r(34) = 0.86, p < 0.001; accuracy: r(34) = 0.97, p < 0.001). The ratios used for these analyses and shown on the x-axis in Fig. 2 were calculated using the number of dots in each stimulus. As expected, the pattern of significance holds when the ratios are determined using dot diameter as well (Spearman’s rank correlation: response latency: r(34) = 0.85, p < 0.001; accuracy: r (34) = 0.96, p < 0.001). Additionally, performance was consistent with the distance effect, with shorter response latencies and higher...
accuracy associated with larger distances between quantities in a pair (Fig. 3; response latency: $F(7) = 27.71, p < 0.001$, linear contrasts $F(1,8) = 45.79, p < 0.001$; accuracy: $F(7) = 41.50, p < 0.001$, linear contrasts $F(1,8) = 62.82, p < 0.001$). Because low quantities 2, 3, and 4 were either always (pick small) or never (pick large) reinforced, a distance effect could result from differences in associative strength accrued during training. To determine if this was the case, follow up analyses were conducted on pairs from the pick small condition in which the low quantity stimulus was 4 (i.e. pairs 4–5, 4–6, 4–7, 4–8, 4–9, 4–10). Quantity 4 was always reinforced in training and quantities 5, 6, 7, 8, 9, and 10 were never reinforced in training. The relative associative strength of the stimuli was therefore constant across all distances in this subset of test pairs. The distance effect held across these pairs (response latency: $F(5) = 3.84, p = 0.006$, linear contrasts $F(1,8) = 4.95, p = 0.057$; accuracy: $F(5) = 8.17, p < 0.001$, linear contrasts $F(1,8) = 11.82, p = 0.009$), indicating that the distance effect resulted from the ratios of the comparison stimuli, not from differences in the reinforcement history of the stimuli.

3.2. Task instruction controlled the orientation of spatial representation

Like humans comparing animal sizes and large quantities, apes showed systematic reversal of the orientation of their spatial magnitude representation between the pick large and pick small instruction conditions. There was a significant negative correlation between individual slopes of the response latency regression lines between the pick small and pick large conditions (Fig. 4; Spearman rank correlation: $r(7) = -0.76, p = 0.018$) such that subjects who
showed a right-to-left orientation in the pick small condition (Fig. 5; positive slope; n = 5) tended to show a left-to-right orientation in the pick large condition (negative slope), and vice versa. The negative correlation also indicates stable individual tendencies for spatial representation across conditions; animals that showed the strongest spatial representation in one condition also showed the strongest spatial representation in the other condition.

3.3. Individual orientations did not differ systematically by species, handedness, or training order

LMM analysis indicated that apes showed individual variability in orientations of spatial magnitude congruity (likelihood ratio test of significance of random effects of subject identity on slopes: pick small: $X^2 (2, N = 9) = 6.64, p = 0.022$; pick large: $X^2 (2, N = 9) = 14.51, p < 0.001$). Therefore, the mean slope across all tested apes was not significantly different from 0 (pick small: $t(7.94) = -1.40, p = 0.20$; pick large: $t(8.06) = -0.33, p = 0.75$). Individual slopes did not vary systematically by species, handedness, or training order (LMM, t-tests with Satterthwaite approximation: all ps > 0.1).

4. Discussion

We found evidence for spatial representation of magnitude in nonhuman apes, suggesting that use of space to represent other dimensions is phylogenetically ancient. Like humans processing magnitudes in less familiar domains, apes reversed their orientation of spatial representation based on instruction, such that they accessed this representation from their preferred point of reference location in both conditions. Additionally, animals were consistent in the strength of their representations across conditions, with individual animals tending to show either strong or weak effects under both pick large and pick small instructions. While apes did not adopt a single orientation as a group, these results indicate stable tendencies for spatial representation within individuals.

Given the extensive experience most adult humans have with number lines and reading directions, it is not surprising that group level orientations for small number comparisons tend to be consistent across task instructions within human cultures (Ginsburg & Gevers, 2015; Lee et al., 2016; Shaki, Petrusic, et al., 2012). Individual differences in orientation and reversals in orientation in response to instructions similar to those shown by apes are only seen in humans when participants have no preexisting long term representation organizing the content of the domain being tested. Like apes, pre-school aged children, who also have limited cultural experience relative to adults, show variability in spatial orientation across individuals. For example, while 89% of British preschool children (3–6 years) presented with a line of objects counted them in a linear order, only 60% of those counted in the culturally typical left-to-right direction, while 40% counted in the right-to-left direction (Shaki, Fischer, & Gobel, 2012). Human adults performing a non-numerical quantity discrimination task similar to the one in the current experiment show instruction based reversal of spatial orientations consistent with that shown by apes (Patro & Shaki, 2016). This variability indicates that the tendency to organize information spatially may be a fundamental organizing feature of cognition, but that the orientation of those representations is impacted by culture and experience.

A limitation of our study is that we only tested ape species, and so cannot confidently draw conclusions outside of great apes. However, evidence from experiments with much more distantly related chicks (Gallus domesticus) may suggest that spatial representation of magnitude may be more widespread among vertebrates. Three day old chicks have been reported to show a leftward bias for small numbers and a rightward bias for large numbers (Rugani et al., 2015a, 2015b). Chicks trained to find food behind a target displaying 5 dots spontaneously chose the display on the left when presented with two identical choice stimuli smaller than the target (2 dots) and the display on the right when presented with choice stimuli larger than the target (8 dots). This may suggest a phylogenetically ancient predisposition to represent quantity in a left-to-right orientation. However, concluding that the behavior of chicks in this test is controlled by the same cognitive processes that result in many humans showing a left to right organization in magnitude processing may be premature for several reasons. First, the behavioral evidence from chicks indicates considerable inter-individual differences, with more than half the chicks failing to show the left-to-right orientation (Mangalam & Karve, 2015). Second, avian brains are highly lateralized compared with primates (Harshaw, 2015; Larsson, 2013; Rogers et al., 2013), and indeed evidence for laterality in nonhuman primates is mixed (Oleksiak, Postma, van der Ham, Klink, & van Wezel, 2011). Finally, avians and mammals diverged over 300 million years ago (Kumar & Hedges, 1998), so data from more species across this phylogenetic range are needed before conclusions can be drawn about common origins of cognitive processes. While Rugani et al. have addressed many of these points (Rugani, Vallortigara, Priftis, & Regolin, 2016a, 2016b, 2015a, 2015b), it remains possible that the left-to-right bias seen in humans and chicks may be the result of a convergence in behavior based on distinct cognitive processes—brain laterality in the chicks and cultural convention in English-speaking humans. In the present study four of the apes showed orientations of spatial representation in one direction while three showed orientations in the opposite direction. The remaining two apes show no clear orientation. These differences in orientation were not explained by species, training order, or handedness, although it remains possible that these differences could be explained by other idiosyncratic characteristics including experience with caregivers. These findings, combined with evidence of flexibility in the spatial orientation of magnitude representation in humans based on task instruction (Bachtold et al., 1998; Shaki, Petrusic, et al., 2012), culture (Shaki, Fischer, et al., 2012; Zohar-Shai, Tzelgov, Karni, & Rubinsen, 2017), language priming (Shaki & Fischer, 2008), and across individuals (Nuerk et al., 2005; Wood et al., 2006) suggest that physiological determinants may be of limited importance in determining the orientation of spatial representation in primates.

Because total surface area of the dots was controlled in the present task, total dot perimeter co-varied positively and dot size co-varied negatively with dot quantity. Previous findings suggest that non-human primates preferentially rely on quantity information over size or surface area (Brannon & Terrace, 2000), but it is not possible to determine from our results whether choices in this task were controlled by quantity, perimeter, or individual dot size. However, discrimination of quantity, size, and perimeter are all magnitude judgments, and gorillas and orangutans showed distance effects and patterns consistent with Weber’s law and typical of human performance on magnitude comparison tasks. These performance patterns indicate that apes were attending to a magnitude dimension of the stimuli, either size, perimeter, or quantity, and provide additional support for common magnitude representation processes in human and non-human primates (Beran, 2008; Brannon & Terrace, 2002).

The spatial organization of cognition shown by the apes may be a basic organizing feature of cognition (de Hevia, Girelli, & Cassia, 2012; McCrink & Opfer, 2014; Shaki, Fischer, et al., 2012; Walsh, 2003). Behavioral congruity between magnitude and space is present from early in development in humans. Pre-verbal pre-counting infants show interactions between number and space (de Hevia, Addabbo, Girelli, & Macchi-Cassia, 2014; de Hevia &
Spelke, 2010; Lourenco & Longo, 2010), and pre-counting children as young as 4 years of age show congruity between space and magnitude (Patro & Haman, 2012). Quantities may be represented topographically in parietal cortex, mimicking representations of space (Harvey, Klein, Petridou, & Dumoulin, 2013). Additionally, there is overlap in brain areas activated during the processing of magnitude and space in humans and non-human primates (Cutini, Scarpa, Scatturin, Dell’Acqua, & Zorzi, 2014; Hubbard et al., 2005), with the horizontal intraparietal sulcus implicated in both magnitude comparison and spatial attention (Hubbard et al., 2005; Rusconi et al., 2011). The results with apes in the present study combined with evidence from humans therefore add to a growing literature that suggests that spatial representation of magnitude is a fundamental characteristic of at least primate minds, and may be much more widespread among vertebrates.

6. Author note

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Author Contributions

R.P. Gazes developed the study concept and design. R.P. Gazes, J. M. Hope, and R.F.L. Diamond conducted the experiments and R.P. Gazes and J.M. Hope designed and analyzed the handedness task. D. Caillaud and R.P. Gazes conducted the statistical analyses. R.P. Gazes drafted the manuscript. R.P. Gazes, R.F.L. Diamond, R.R. Hampton, and T.S. Steinski provided critical revisions of the manuscript and interpretation of findings. All authors approved the final version of the manuscript for submission.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2017.07.010.

References


