



Original Articles

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, Bueti, 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 (Bachtold, Baumüller, & Brugger, 1998; Fischer, Shaki, & Cruise, 2009; Shaki & Petrusic, 2005; Shaki, Petrusic, & Leth-Steensen, 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 (Gevers, 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-

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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. Selection of the incorrect

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