COGNITIVE NEUROSCIENCE

Different reference frames on different axes: Space and language in indigenous Amazonians

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Spatial cognition is central to human behavior, but the way people conceptualize space varies within and across groups for unknown reasons. Here, we found that adults from an indigenous Bolivian group used systematically different spatial reference frames on different axes, according to known differences in their discriminability: In both verbal and nonverbal tests, participants preferred allocentric (i.e., environment-based) space on the left-right axis, where spatial discriminations (like "b" versus "d") are notoriously difficult, but the same participants preferred egocentric (i.e., body-based) space on the front-back axis, where spatial discrimination is relatively easy. The results (i) establish a relationship between spontaneous spatial language and memory across axes within a single culture, (ii) challenge the claim that each language group has a predominant spatial reference frame at a given scale, and (iii) suggest that spatial thinking and language may both be shaped by spatial discrimination abilities, as they vary across cultures and contexts.

INTRODUCTION

Space is fundamental to human cognition, but people mentally represent space in qualitatively different ways. For example, it will be apparent to many readers looking at Fig. 1 that the chair is on the left and the ball is on the right. Although this egocentric (i.e., perspective-dependent) description may seem natural to some (*1*, *2*), it is far from universal. For example, among Tenejapan Tzeltal speakers of Mexico (*3*) or Yupno speakers of Papua New Guinea (*4*), the ball might be said to be "uphill" or "downhill" of the chair. Such descriptions use allocentric space, coordinate systems defined by features of the environment, independent of the observer's perspective, such as the slope of a mountain, the rotation of the planet (i.e., east and west), or the sides of a room (window side and door side). These egocentric and allocentric frames of reference (FoRs) constitute fundamentally different ways of representing the spatial relations among objects at any scale (*1*, *2*, *5*, *6*), from the monumental (e.g., the city is west of the mountains) to the miniscule (e.g., the freckle is on her left cheek). Although language groups typically have multiple FoRs at their disposal, they tend to use one type preferentially on a given spatial scale, according to cross-linguistic studies (*1*, *2*, *7*–*10*).

In addition to talking differently about space, people also show differences in spatial reasoning and memory, even when they are not using language, as revealed by a variety of behavioral tasks. People use different nonlinguistic FoRs to learn new dance routines (*11*), remember the location of hidden objects (*5*), track the path of moving objects through a maze (*3*) or across three-dimensional space (*12*), and reconstruct novel configurations of objects [(*2*); see Figs. 2 and 3]. The key manipulation in each of these tasks is the rotation of the participant between learning and testing, which reveals their implicit spatial strategies. For example, in spatial reconstruction tasks like those we use here (Fig. 2, right), participants learn to reconstruct a novel array of objects at a study table and then rotate 180° to face the test table, where they are asked to reproduce the same array. Critically, their behavioral response depends on which nonlinguistic FoR they use. If they use egocentric space, as is typical among adults in the United States and in other industrialized groups, their response array will be a 180° rotation of the original, preserving the position of array objects from the observer's perspective (i.e., objects that were on their right remain on their right; see Fig. 2). By contrast, if they use allocentric space, their response array will be a simple translation of the original (without rotation), preserving its spatial structure with respect to external coordinates (like the room or landscape), as is common in some unindustrialized groups, according to cross-cultural studies. In short, different FoRs define different ways of talking and thinking about space.

Beyond dictating the way people conceptualize space itself, FoRs also shape the representation of abstract, nonspatial domains like time and number, which people implicitly spatialize along a

Fig. 1. Where is the ball? In language elicitation tasks like this one (*9*), people use different spatial FoRs in their verbal descriptions (e.g., The ball is to the right/in front/east of the chair).

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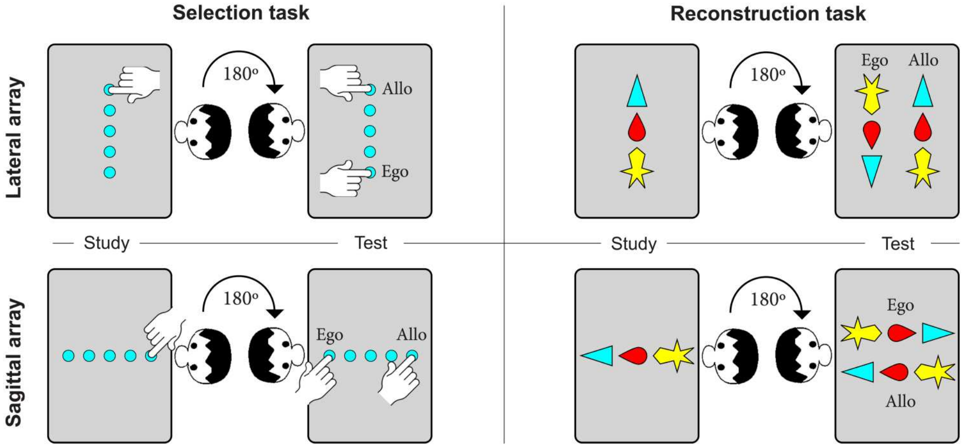

Fig. 2. Methods of experiment 1. Participants performed two nonverbal tests of spatial FoRs, in which they encoded the spatial arrangement of objects arrayed along either the lateral or sagittal axis.

variety of spatial continua (*13*–*18*). For example, whereas many adults in industrialized cultures conceptualize time along a left-right mental timeline [an egocentric FoR; (*14*)], people in some indigenous cultures spatialize time using absolute FoRs, as revealed by their spontaneous co-speech gestures: They implicitly associate the past with east or downhill and the future with west or uphill (*16*, *17*, *19*). To the extent that such abstract concepts are supported by representations of space, people with different spatial frameworks have different conceptual frameworks (*4*).

For decades, researchers have debated what factors determine the spatial FoRs that people use and why. Some researchers have attributed differences in spatial memory to differences in spatial language [e.g., (*1*, *2*, *7*, *20*); but see (*12*, *21*)]. This proposal is supported by studies showing a correspondence between the nonlinguistic FoR that people use in spatial memory tasks (like the rotation tasks described above) and the linguistic FoR that is most prevalent in their community. Although language may play a causal role in spatial memory, linguistic relativity accounts are incomplete for three reasons. First, much of the evidence linking spatial language with spatial memory is based on cross-cultural comparisons, and therefore cannot rule out confounding effects of language and culture (*22*). Second, the correlation between preferred linguistic and nonlinguistic FoR is far from perfect, leaving substantial variation in spatial thinking unexplained, both within and across groups (*1*, *2*, *23*). Evidence from verbal interference tasks suggests that language does not play an online role in determining nonlinguistic FoR use (*24*). Third, even if differences in spatial language could fully account for differences in spatial thinking, this link could not in principle address the larger question: Why is there variation in FoR use in language or in thought?

According to (*21*), "the causal engine both for the engrained spatial reasoning styles and the fashions of speech that we find in different communities may well be a derivative of their ambient spatial circumstances." But which circumstances matter and why? There is some evidence suggesting that FoR use may ultimately be shaped by local ecology, topography, levels of urbanization, sociocultural differences, or other contextual factors (*1*, *4*, *6*, *7*, *21*, *22*, *25*–*27*), but it remains unclear whether and how each of these factors affect FoR use. In short, there is ample evidence of differences in spatial FoRs within and across groups (in both language and behavior), but "no attested mechanism" (*1*) for this variation. As a potential explanation, we consider variation in spatial perception and memory, using spatial axis as our test bed.

To date, researchers have typically relied on the left-right axis in behavioral tests of FoR use, largely ignoring other spatial axes [see Fig. 2, top row]. Even when multiple axes have been tested (2, *3*, *5*, *9*, *10*, *12*, *22*, *23*, *27*, *28*, 29), data from the sagittal axis are often excluded from analysis (*2*), left uninterpreted (*22*), or pooled with data from other axes (*5*, *9*, *10*, *29*). Yet, research in cognitive linguistics and cognitive neuroscience shows that the lateral axis is peculiar. People are notoriously bad at distinguishing left and right, not only in language [e.g., "No, your other left!"; (*30*–*32*)] but also in visuospatial perception and memory; people fail to distinguish shapes, images, and letters that are left-right mirror images of each other (like "b" and "d") more than they confuse up-down mirror images (like "d" and "q") or other spatial transformations (*33*–*38*). This mirror invariance is evident not only in the brain and behavior of humans (*39*–*41*) but also of nonhuman animal species, including macaques (*42*), rats (*43*), and octopus (*44*), suggesting that it is an evolutionarily ancient feature of visuospatial perception (*45*, *46*). Although its causes are uncertain, mirror invariance has been attributed to the bilateral symmetry of the brain (*45*), deficiencies in interhemispheric coordination (*47*), and an evolved ability for recognizing objects from a variety of perspectives on a horizontal plane (*42*, *46*). It could also reflect the form of the human body, which is symmetrical across the lateral axis only, and therefore provides no clear way to distinguish the poles of left-right space (*48*).

The ability to reliably discriminate left-right mirror images [sometimes called enantiomorphy; (*49*)] develops slowly in contexts where it is learned, perhaps continuing into the second decade of life (*40*). In contexts without high literacy rates, and where left-right distinctions may have little cultural relevance, people continue to show mirror invariance throughout adulthood (*50*–*52*). For example, among Mopan and Tenejapan Mayans, adults tend not to distinguish objects or shapes from their left-right mirror images, describing and categorizing them together, even when observing both simultaneously (*34*, *50*). The difficulty of lateral space

Fig. 3. A Tsimane′ woman studies a lateral array of objects in the Reconstruction task.

is also reflected in language: Many language groups (perhaps as many as a third of languages worldwide) lack any terms denoting left and right regions of space (*7*, *50*), and in those that do have such terms, children are notoriously slow to learn their meanings (*30*, *31*). In short, people experience different spatial continua differently, the lateral axis is uniquely difficult, and the degree of this difficulty varies across groups.

We hypothesized that these basic differences in spatial perception and memory underlie differences in people′s FoR use [(*3*); cf. (*28*)]. In most contexts, the spatial relations among any two objects can be characterized by multiple spatial continua, some of which are defined egocentrically (e.g., the observer′s front) and some of which are defined allocentrically (e.g., the slope of the landscape). We propose that when faced with this choice, people tend to use the spatial continuum that is easiest to perceive or remember, whether that continuum is defined egocentrically or allocentrically. On this spatial discrimination hypothesis, people′s FoR use should reflect not only the features of their environment [e.g., the presence of salient landmarks or gradients; (*21*)] but also the characteristics of their egocentric spatial perception. Namely, people should use the left-right axis (or any other egocentric axis) to encode spatial relations only to the extent that they can reliably distinguish the poles of that axis in a given context. People who struggle with left-right spatial distinctions should rely more on other spatial continua (i.e., those defined by the environment) to encode the same spatial relations, especially in contexts in which this allocentric alternative is highly discriminable. On this view, much of the observed variation in FoR use may reflect differences in left-right spatial discrimination, which is known to vary within and across groups. Consistent with this account, some previous findings suggest that left-right spatial discrimination abilities are correlated with FoR use across cultures, and over development (*2*, *3*, *5*, *23*, *34*, *40*, *53*): People with better left-right spatial discrimination abilities tend to use egocentric FoRs on the lateral axis, where FoR use has typically been tested.

Here, we compared FoR use across the lateral (left-right) and sagittal (front-back) spatial axes among the Tsimane′, a group of farmer-foragers indigenous to the Bolivian Amazon (*54*). Tsimane′ culture and language provide a good test bed in which to measure variation in FoR use. Unlike American adults, Tsimane′ adults generally have little formal education, low levels of literacy, and few of the cultural artifacts that emphasize left-right discrimination in industrialized cultures (e.g., digital interfaces, cars, and faucets). As a result, mirror invariance very likely remains strong among Tsimane′ adults, as it does for many illiterate people across ages and cultures (*34*, *49*, *55*, *56*). Moreover, studies of Tsimane′ spatial language suggest a prevalence of allocentric spatial terms [e.g., upriver and downriver; see (*57*)], perhaps because Tsimane′ people spend considerable time navigating complex terrain on foot, starting in childhood (*58*). Such allocentric tendencies allowed us to test the strongest prediction of the spatial discrimination hypothesis—that people who favor allocentric FoRs on the lateral axis might nevertheless favor egocentric FoRs on the sagittal axis. By contrast, adults from Western, Educated, Industrialized, Rich, and Democratic [WEIRD; (*59*)] groups, who have substantial practice unlearning mirror invariance, tend to use overwhelmingly egocentric FoRs, even on the lateral axis (*1*, *2*), and therefore should be expected to show little or no difference across axes—a null effect—on any account.

We tested Tsimane′ adults′ FoR use in two experiments, one focused on spatial memory and the other focused on spatial language, allowing us to test two hypotheses about their determinants. First, if FoR use is governed by the relative discriminability of competing spatial continua, then participants should show stronger egocentric tendencies on the sagittal axis, where egocentric spatial distinctions are relatively easy, than on the lateral axis, where egocentric distinctions are more difficult. Alternatively, people could "fixate predominantly on just one frame of reference" [(*7*); also see (*6*)], in which case Tsimane′ participants′ spatial behavior should not differ systematically across spatial axes. Second, whereas many previous studies have evaluated the relationship between spontaneous spatial language and memory across groups, here, we evaluated this relationship within a single language group. If "the details of the linguistic representation are faithfully reflected in non-linguistic coding for spatial arrays" (*3*) at the individual level, then any cross-axis difference in FoR use should be found both in people′s spatial memory and in their spatial language.

RESULTS

Experiment 1: Frames of reference in spatial memory

In experiment 1, we tested nonlinguistic FoR use across spatial axes in a sample of 30 Tsimane′ adults, using two nonverbal spatial memory tasks described below. In both, participants studied a spatial array at a study table and then gave a behavioral response at a test table, after turning around 180°, as shown in Fig. 2. In each task, participants′ behavioral responses could be consistent with an egocentric FoR (i.e., the result of rotation), an allocentric FoR (i.e., the result of translation), or neither (see Fig. 2). Critically, each participant performed the tasks on two different axes. In the lateral condition, the array was oriented along the participants′ left-right axis; in the sagittal condition, the array was oriented along their front-back axis, and the order of these conditions was counterbalanced across participants.

In the Selection task, participants touched one of five identical cups as designated by the experimenter and then, after turning around, were asked to touch the cup in the "same" position at the test table (see Materials and Methods). Participants correctly identified the middle cup 92.5% of the time (95% in trial 1 and 90% in trial 6), indicating clear understanding of the task, before and after the critical trials. In critical trials, participants could choose the cup in the same position egocentrically, allocentrically, or neither (see Fig. 2, left). Overall, 50% of responses were egocentric, 46% were allocentric, and only 4% did not correspond to either. The rate of these unclassifiable responses did not differ significantly across axes (i.e., lateral: five responses; sagittal: four responses; β = 6.85, SEM = 4.85, *P* = 0.15). Figure 4 (left) shows the proportions of egocentric versus allocentric responses on each axis, with between-subject binomial 95% confidence intervals.

To analyze these results, we used mixed-effects logistic regression models of individual responses with random subject slopes and intercepts. We included fixed effects of schooling, age, and axis order (e.g., lateral followed by sagittal) and their interactions with axis. All models and analyses are available online at osf.io/qmxd6. We used the "emmeans" package in R (*60*, *61*) to evaluate the effect of axis and to compare FoR use on each axis to chance (i.e., 50%). As evident in Fig. 4 (left), participants' responses were reliably allocentric on the lateral axis (71.3% allocentric; β = − 2.17, SEM = 0.97, *P* = 0.03), but this pattern reversed on the sagittal axis, where participants had a reliable preference for egocentric responses (75.9% egocentric; β = 2.99, SEM = 1.32, *P* = 0.02). Critically, participants' FoR use differed significantly across axes (β = − 5.15, SEM = 1.59, *P* = 0.001), an effect that interacted with education; participants with more years of formal schooling showed a weaker effect of axis (β = − 2.05, SEM = 1.02, *P* = 0.04), perhaps because reading experience improves left-right spatial discrimination, allowing people to rely on that continuum when encoding spatial relations. This reversal of FoR use at the group level was also found in the majority of individual participants, two-thirds of whom responded more allocentrically on the lateral axis and more egocentrically on the sagittal axis.

In the Reconstruction task, participants memorized a novel array of three distinct objects and then, after turning around, reconstructed the array from memory (see Materials and Methods). The position and orientation of each object corresponded to an egocentric FoR, an allocentric FoR, or neither (see Fig. 2, right). We found a high rate of agreement between the position and orientation of individual objects, 92% of which corresponded to the same FoR. Overall, participant responses were 56% egocentric, 35% allocentric, and 9% neither. The rate of these unclassifiable responses (i.e., mostly responses in which position and orientation conflicted) did not differ significantly across axes (i.e., lateral: 9 objects; sagittal: 18 objects; β = − 1.12, SEM = 1.99, *P* = 0.57). Figure 4 (right) shows the proportions of egocentric versus allocentric responses on each axis, with between-subject binomial 95% confidence intervals.

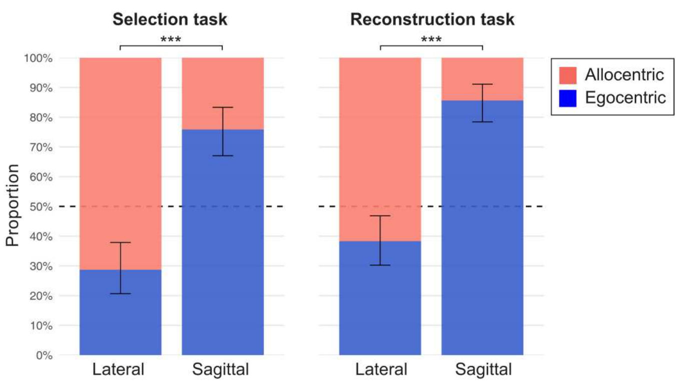

Fig. 4. Results of experiment 1. In both tasks, participants preferentially responded allocentrically on the lateral axis and egocentrically on the sagittal axis. Dashed lines show chance performance (i.e., 50%), and error bars show between-subject binomial 95% confidence intervals.

Using the same regression models as in the Selection task, we found the same qualitative pattern of results: FoR use differed reliably across axes (β = − 11.4, SEM = 3.2, *P* = 0.0003; see Fig. 4, right). On the lateral axis, participants showed a slight preference for allocentric responses, but this pattern did not differ reliably from chance (62% allocentric; β = − 1.55, SEM = 1.20, *P* = 0.20). Again, they showed the opposite pattern on the sagittal axis, with a reliable preference for egocentric responses (86% egocentric; β = 9.90, SEM = 3.12, *P* = 0.002). We found the same group-level reversal when we analyzed objects' positions (β = − 7.78, SEM = 2.37, *P* = 0.001) and orientations (β = − 7.49, SEM = 3.03, *P* = 0.01) separately, and when analyzing individual participants, two-thirds of whom made more allocentric responses on the lateral axis and more egocentric responses on the sagittal axis. Together, these findings show that people's spatial memory is not characterized by a single predominant FoR, even for the same set of objects in the same environment. Rather, an individual's preferred nonlinguistic FoR can reverse across axes.

In principle, participants' preference for allocentric reconstructions of lateral arrays could reflect a lack of relevant egocentric language: Many language groups entirely lack terms for left and right, and some only use such terms to describe body parts, not regions of space (*6*, *7*, *50*). People who lack knowledge of such terms also tend to avoid egocentric FoRs on the lateral axis, including adults (*3*, *12*, *27*) and children (*23*, *28*). To evaluate whether our behavioral effects reflected deficiencies in participants' spatial language, we tested their knowledge and spontaneous use of Tsimane' words denoting left and right (see Materials and Methods). Nearly every participant (92%) correctly labeled their left and right hands, and some participants (28%) spontaneously used these terms to describe regions of space in a simple language elicitation task (in which most utterances were spatially ambiguous; see the Supplementary Materials for detailed results). Therefore, participants preferred using allocentric FoRs on the lateral axis in the spatial memory tasks despite the general availability of left-right words in their language, suggesting that language may not have been the primary determinant of their behavioral responses. In principle, both spatial memory and spatial language use could reflect the difficulty of left-right spatial discrimination, a hypothesis we turn to in experiment 2.

Experiment 2: Frames of reference in spatial language

In previous studies, a correlation between linguistic and nonlinguistic FoR use has led some researchers to posit that differences in spatial memory reflect differences in spatial language (*1*, *6*, *7*). However, most studies have relied on comparisons across human groups that differ not only in their spatial language but also in myriad other ways. To avoid the inferential complexities inherent to cross-cultural comparisons, some studies have evaluated within-group effects, comparing people's nonlinguistic FoR use (e.g., in spatial problem solving or co-speech gesture) with their mastery of egocentric spatial language (e.g., their ability to place objects on the "left" or "right"), with mixed results (*12*, *22*, *23*, *28*, *29*, *62*–*65*). However, if the goal is to clarify when and why people use a given FoR in a given context, then we must test not only people's knowledge of egocentric language but also their spontaneous use of it: Even people who can use egocentric spatial terms correctly in labeling tasks could disprefer those terms in everyday speech. Here, we tested participants' spontaneous use of spatial language, allowing us to compare preferences for linguistic and nonlinguistic FoRs across axes within a single population.

In experiment 2, in a new sample of 36 Tsimane' adults, we conducted a two-axis version of the director-matcher task (*66*, *67*), an established paradigm designed to elicit spatial language (see Fig. 5). In each director-matcher pair, one participant (i.e., the director) viewed a series of object configurations composed of two animal figures (i.e., a chicken and a pig) and was asked to describe it to the other participant (i.e., the matcher) so that they could construct an identical arrangement with their own pair of animal figures. Although the director and matcher were seated side by side (facing the same direction), an opaque screen prevented them from seeing each other's object arrays (or gestures), encouraging the director to encode unambiguous spatial information in speech (e.g., "the chicken is on the right of the pig and both animals are facing upriver"; see Table 1 for more examples). If patterns of spatial memory reflect patterns of spatial language (*1*, *6*, *7*), then the cross-axis pattern we observed in participants' nonverbal spatial behavior in experiment 1 should extend to their verbal descriptions. Alternatively, language groups could converge on a single predominant FoR in language [e.g., for ease of communication; (*3*, *7*)], even while preferring different FoRs on different axes for nonlinguistic reasoning.

Testing was video- and audio-recorded, and director utterances were translated into Spanish by a professional Tsimane'-Spanish interpreter (with native Tsimane' language skills) who was blind to hypotheses. These Spanish translations were then coded independently by two of the authors (B.P. and I.B.), one of whom is a Spanish-English bilingual who was blind to hypotheses at the time of coding. For each trial, they classified the director's descriptions of objects' location and orientation using the MesoSpace classification system (*68*), which consists of six classes: relative, direct, object-centered, geomorphic, landmark-based, and absolute. This system encourages careful coding and allows for simple translation into other FoR classifications systems (see Materials and Methods). To assess the reliability of Tsimane'-Spanish translations, we compared FoR classifications across two translations (n = 7 participant pairs) and found high agreement, both for the six-class typology (81%; Cohen's κ = 0.76) and for the simpler two-class typology (83%; Cohen's κ = 0.75). Likewise, to assess the reliability of FoR coding, we compared FoR classifications across coders and found high agreement, both for the six-class typology (73%; Cohen's κ = 0.65) and for the simpler two-class typology (86%; Cohen's κ = 0.78).

Whereas in the Reconstruction task each trial yielded three data points (i.e., one for each object in an array), here each trial yielded a maximum of two data points, one utterance about object position and another about object orientation. This allowed us to evaluate the rates of FoR use in participants' speech whether they used the same FoR or different FoRs to describe these two spatial aspects. A small number of trials (3%) were coded as incorrect by one or both coders and were excluded from analyses, as were practice trials. Overall, directors' spatial language was 40% egocentric, 40% allocentric, and 20% unclassifiable. Figure 6 shows the relative prevalence of classifiable responses by FoR. Of the egocentric utterances, most (64%) were classified as relative and the rest (36%) were classified as direct (see Table 1 for examples). Of the allocentric utterances, the vast majority (72%) were landmark-based, 25% were absolute, and just 3% were object-based. None were geomorphic. We coded up/downriver as absolute rather than geomorphic, as this spatial gradient seems to apply beyond the context of the river.

To test differences in FoR use across axes, we used a mixed-effects logistic regression model of spatial language (excluding unclassifiable utterances) with random subject slopes and intercepts. We included fixed effects of schooling, age, aspect, and facing direction (i.e., aligned or misaligned with the river) and their interactions with axis. As before, we used the emmeans R package (*60*, *61*) to contrast FoR use within and across spatial axes (i.e., lateral versus sagittal) and aspects (i.e., position versus orientation). Although the rates of egocentric and allocentric FoRs were equal overall, they differed reliably across axes ($\beta = -1.83$, SEM = 0.72, P = 0.01), as in the behavioral data from experiment 1. As shown in Fig. 6, participants used marginally more allocentric language on

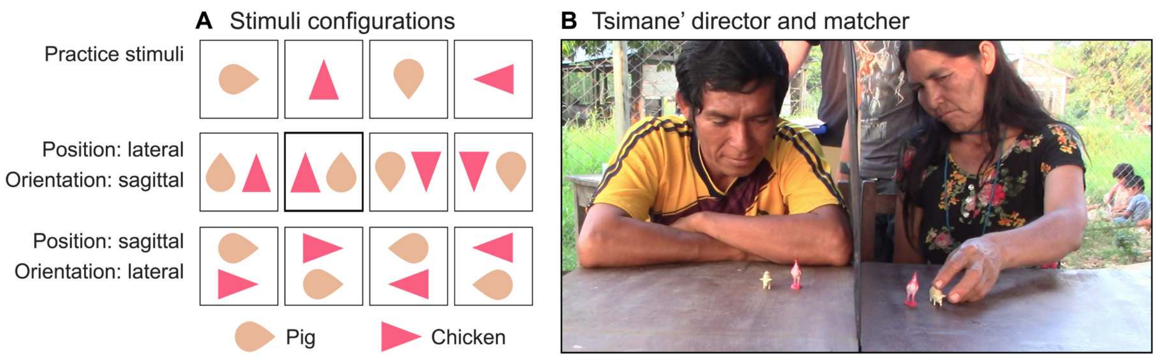

Fig. 5. Methods of experiment 2. (**A**) Configurations of animal figures presented to the director, as seen from above. Top row shows practice trials. Middle row shows configurations in which the lateral axis was relevant to position and the sagittal axis was relevant to orientation. Bottom row shows configurations in which the sagittal axis was relevant to position and the lateral axis was relevant to orientation. (**B**) A director (left) describes a configuration of animal figures [highlighted in (A)] to a matcher (right), separated by an occluder.

Table 1. Spatial language use by FoR in the director-matcher task.

Anchor	FoR (MesoSpace)	Proportion	Example
Egocentric	Direct	14%	The animals are facing me
	Relative	25%	The pig is on my side and the chicken is on the other side
Allocentric	Object-based	01%	The pig is on the chicken's right
	Landmark	29%	The pig is on the side toward the road
	Geomorphic	–	–
	Absolute	10%	The pig is upriver from the chicken
Other	Unclassifiable	20%	The pig is facing that way

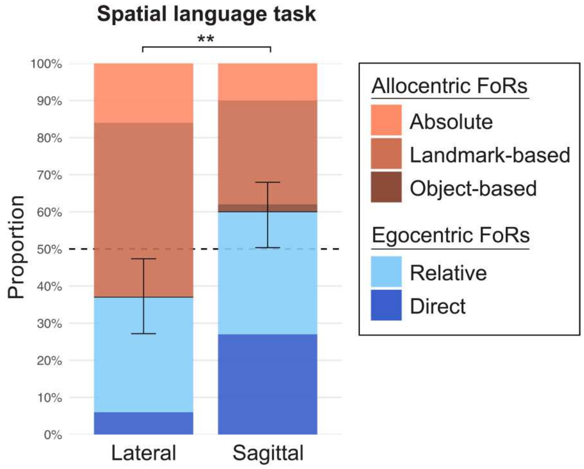

Fig. 6. Results of experiment 2. Participants' linguistic FoR use reversed across axes: They used more allocentric spatial language to describe lateral relations and used more egocentric spatial language to describe sagittal relations. The dashed line shows chance performance (i.e., 50%), and error bars show between-subject binomial 95% confidence intervals.

the lateral axis (β = − 1.27, SEM = 0.71, $P = 0.07$) and used numerically (but not significantly) more egocentric language on the sagittal axis (β = 0.56, SEM = 0.35, $P = 0.11$). This group-level pattern was found in the majority of individual participants, 61% of whom used more egocentric language on the sagittal axis than on the lateral axis.

We also found a large main effect of spatial aspect (β = − 3.36, SE = 0.71, $P < 0.0001$). Participants preferentially used egocentric language (76%) when describing object location (e.g., "The pig is toward me") and used allocentric language (70%) when describing object orientation (e.g., "The animals are facing the door"), perhaps because participants projected the likely path of the animal figures onto their surroundings, leading them to use the landmarks along that path (e.g., the door) in their descriptions of orientation (see fig. S4 for plot). Accordingly, whereas landmark-based FoRs made up only 9% of position descriptions, they made up a large plurality (49%) of orientation descriptions. Aspect also interacted significantly with axis (β = − 3.90, SEM = 1.61, $P = 0.02$), indicating that the effect of axis on FoR use was driven primarily by utterances about orientation (β = − 3.36, SEM = 1.13, $P = 0.003$), not position (β = 0.56, SEM = 0.95, $P = 0.55$). The proportion of unclassifiable utterances was significantly larger on the lateral axis (32%) than on the sagittal axis (9%; β = 2.65, SEM = 0.75, $P = 0.0004$), perhaps because left-right distinctions are less salient and/or because left-right language can be ambiguous with respect to FoR.

Participants dispreferred egocentric spatial language when describing lateral spatial relationships despite their knowledge of left-right terms. In our tests (see Materials and Methods), all 36 participants generated the Tsimane' words for left and right and 30 of them (83%) correctly applied them to their hands (the others swapped these labels). Participants were also oriented with respect to two allocentric spatial continua: When asked to point upriver, participants' average pointing direction was almost exactly southwest (223° ± 9°), toward the mountains, and when asked to point East, they pointed almost due East on average (94° ± 7°). See the Supplementary Materials for full methods and results of these tasks. This allocentric orientation may have subtly influenced participants' use of spatial language, which differed depending on their facing direction. When describing spatial relations that aligned with the flow of the river (e.g., when one object was positioned downriver of the other or both were facing downriver), they showed a slight preference for allocentric language (54% allocentric). This pattern reversed when these spatial relationships were misaligned with the river (47% allocentric). However, this effect did not approach statistical significance (β = 0.27, SEM = 1.37, $P = 0.85$) and did not interact with axis (β = 0.47, SEM = 1.38, $P = 0.74$).

DISCUSSION

The way people conceptualize space varies across contexts, but the origin of this variation has remained unresolved. Here, we tested whether FoR use varies across egocentric spatial axes known to differ in their discriminability: Lateral spatial distinctions are more difficult than sagittal distinctions. In two experiments, participants' FoR use changed across axes accordingly. In experiment 1, Tsimane' adults preferentially used allocentric space to encode lateral arrays of objects but used egocentric space to encode sagittal arrays, as revealed by two nonverbal tests of spatial memory. In experiment 2, Tsimane' adults showed the same pattern of FoR use in their spatial language, using more allocentric language to describe lateral spatial distinctions and more egocentric language to describe sagittal distinctions. This cross-axis reversal in both spatial memory and spatial language requires reconsidering the development and dynamics of FoRs.

Even while acknowledging effects of context on FoR use (*21*, *29*), researchers have long characterized language groups according to what appeared to be their "predominant" FoR [e.g., (*1*, *2*, *5*–*7*, *11*, *20*, *69*)]. It is on this basis that the cross-cultural correlation between linguistic and nonlinguistic FoR use has been evaluated—by comparing the FoR that is predominant in spatial language to the FoR that is predominant in spatial memory. However, these interpretations are based primarily on tests of the lateral axis alone. Some previous studies have reported differences in nonlinguistic FoR use across axes (*3*, *12*, *22*, *23*, *27*, *28*) and noted the existence of "strong" and "weak" spatial axes in some groups (*3*, *50*, *70*). However, these findings have not challenged existing classification conventions, in part because they did not show qualitative differences in FoR use across axes. Rather, they showed differences of degree only: Participants preferred the same FoR on both axes, just to different extents, consistent with the claim that each group has a single predominant FoR. By contrast, here we showed that different FoRs can predominate on different axes, challenging the claim that groups—or even individuals—conform to a single predominant FoR at a given spatial scale.

What then is the relationship between spatial language and memory? Previous studies have found that linguistic and nonlinguistic FoR use tend to covary across groups [at least as measured on the lateral axis; (*1*, *6*, *7*, *71*)], but these cross-group effects could reflect any number of linguistic or cultural differences. Some studies have found a within-group relationship between people's nonlinguistic FoR use and their mastery of spatial words [like left and right; (*12*, *22*, *62*, *63*); but see (*23*, *28*, *29*, *64*, *65*)]. Our results show such a within-group correspondence in people's spontaneous FoR use when egocentric and allocentric responses were equally valid: Tsimane' participants showed the same cross-axis difference in their linguistic FoR preferences as in their nonlinguistic FoR preferences. Although this pattern is consistent with the claim that "habitual use of particular linguistic concepts modifies non-linguistic concepts" (*71*), it is equally consistent with the opposite causal claim (i.e., habitual use of nonlinguistic concepts shapes patterns in language), as well as with a common cause account, on which both spatial language and spatial reasoning are shaped by the same cultural and environmental factors.

Whatever the causal link between spatial language and spatial reasoning, the use of a particular language cannot explain the individual differences in FoR use observed within the same language group (e.g., why do some Tzeltal-speakers use egocentric spatial strategies, while others use allocentric strategies?), nor can it explain the variation in linguistic FoR use that has been observed across language groups (e.g., why do Tzeltal speakers preferentially use allocentric language, while U.S. Americans preferentially use egocentric language?): Linguistic differences cannot explain themselves. Rather, this variation within and across groups, if not arbitrary, likely reflects a variety of nonlinguistic factors, such as topography, urbanization, material culture, and other features of the spatial context (*1*, *4*, *6*, *7*, 12, *21*, *22*, *25*–*27*). As (*21*) articulates, "The quest is for a unified explanation of when and why individuals or populations...solve spatial problems in varying ways."

We suggest that one of the nonlinguistic determinants of FoR use may be people's perception of space, as governed by the spatial discrimination hypothesis. Since spatial relations (e.g., the relative locations of two objects) are experienced by people in context, they can all be defined by many spatial continua, some of which are egocentric and some of which are allocentric. On this account, all else being equal, people encode spatial relations using the spatial continuum along which those relations are easier to perceive or remember. If so, then the FoR that a person uses in a given context should vary according to the relative discriminability of the competing spatial continua; contexts or experiences that make a given continuum easier to perceive or remember should increase people's reliance on that continuum to structure their spatial language and spatial memory, whether that continuum is defined by the body or the environment (*28*). In this sense, people may not be choosing among spatial reference frames (e.g., egocentric versus allocentric) per se, but among specific spatial continua (e.g., left-right versus uphill-downhill).

This account can explain the differences we observed among Tsimane' adults, whose patterns of FoR use reflected known differences in the spatial discriminability of egocentric axes (i.e., poor discrimination on the lateral axis compared to the sagittal axis). In principle, two features of our experimental setup could have incidentally contributed to this cross-axis difference. First, the experimenters stood on either side of participants as they performed the Selection and Reconstruction task, which could have encouraged allocentric responding if participants preferentially used the experimenters' bodies as landmarks (among many stable features of the environment) or took their perspective on the task materials. This skeptical account does not apply to experiment 2, in which experimenters stood behind the director-matcher pairs, and therefore shared their point of view (and were out of sight). Second, the cross-axis difference we observed could in part reflect differential use of distance information. In our tasks, sagittally arrayed objects could be distinguished by their distance from the participant (i.e., near-far), but laterally arrayed objects could not (*3*, *28*, *64*). However, if distance information had a larger effect (if any) on participants' responses on the sagittal axis than on the lateral axis, this difference was not evident in their spontaneous spatial language: Although participants sometimes used distance terms to describe the positions of objects in the spatial language task (e.g., "the chicken is close to me/the wall"), the prevalence of such utterances did not differ significantly across spatial axes or interact with axis in predicting FoR use (see the Supplementary Materials for detailed analyses). Moreover, participants in experiment 2 used different FoRs on different axes when describing object orientation (i.e., facing direction) but not when describing object position, the aspect of space for which distance would be most relevant. In principle, the differential usefulness of distance information across axes (i.e., the ability to compute "distance from me") could contribute to mirror invariance, giving animals a heuristic by which to compute differences across sagittal space more easily than across lateral space. Whatever their causes, differences in spatial discrimination can explain variation in FoR use not only across axes but also across cultures and over development. As we outline below, previous findings reveal a correlation between spatial discrimination and FoR use at these other levels as well.

Decades of cross-cultural work on FoRs show greater egocentric tendencies among literate people from industrialized groups and greater allocentric tendencies in people who do not read or write, including many from horticultural groups (*5*, *7*, *71*). Other cross-cultural research shows a corresponding trend in mirror invariance: Whereas people from literate groups typically learn to distinguish left-right mirror images, many people from low-literacy populations show mirror invariance into adulthood, conflating shapes and objects with their left-right reflections (*34*, *35*, *49*, *55*, *72*). These group-level differences in spatial discrimination ability likely reflect differences in the spatial structure of people's everyday environment and material culture, beyond the practice of reading and writing. For example, whereas using a sink requires making lateral spatial distinctions (e.g., left is hot and right is cold), using a well does not; whereas safely crossing a busy street in the United States requires looking left-then-right for oncoming cars, safely crossing a river requires looking upriver for hazards. Although research on FoR use and spatial discrimination have remained largely separate, these abilities have been tested in some of the same groups: Of nine language groups tested, only those with good left-right spatial discrimination abilities (i.e., Dutch and Japanese) preferred egocentric FoRs on the lateral axis (*2*, *3*, *34*, *50*). Although purely correlational, this pattern suggests that cross-cultural differences in FoR use could in part be explained by cross-cultural differences in spatial discrimination.

A similar pattern is observed over the course of cognitive development. In industrialized cultures, mirror invariance is strongest during early childhood, when children struggle to distinguish letters like b and d (*36*, *56*), habitually conflate shapes with their left-right mirror images (*33*, *37*, *40*) and happily write their own names backward [e.g., in English from right to left; (*73*)]. This left-right spatial confusion is also reflected in language learning: Children struggle with words for left and right for years after they have mastered words for up and down, front and back (*30*, *31*). Perhaps as a consequence of this difficulty with left-right discrimination, young children [like many nonhuman animals; (*5*, *42*)] tend to prefer allocentric FoRs on tests of the lateral axis, even in cultures where adults prefer egocentric FoRs (*23*, *28*). We suggest that it may only be by overcoming this mirror invariance (e.g., by learning to distinguish b and d) that children in some cultures develop into largely egocentric adults (*30*, *31*, *40*, *72*). In principle, the posited link between spatial discrimination ability and FoR use could also obtain across individual adults in the same group. Individual differences are found in adults' spatial discrimination abilities and in their FoR preferences, even in groups whose language strongly favors one FoR (*1*, *2*, *22*, *34*, *35*, *49*, *72*), but to our knowledge, no within-group correlation has been measured. Whether across axes, cultures, ages, or individuals, FoR use may be shaped by "any variable affecting perception of, attention to, or memory for, the differences between the sides of an axis" (*74*).

This proposal offers a potential resolution to a longstanding debate on the developmental starting point of spatial concepts, before language or culture exert any influence. From Immanuel Kant (*75*) to Isaac Newton (*76*) and Jean Piaget (*77*), much of Western science and philosophy has assumed egocentric space as the primary basis for spatial reasoning (*78*, *79*). However, the empirical record for this claim is mixed: Although some evidence from young infants suggests that people may first conceptualize space egocentrically (*80*), other studies suggest otherwise [e.g., (*81*, *82*)]. Some studies in children and nonhuman primates show greater facility with allocentric spatial thinking [(*5*); cf. (*64*)]. These seemingly contradictory findings have left scholars without a clear answer to the question: Which FoR is developmentally primary, and which is learned? The present findings suggest that this question may be misguided. Rather than representing spatial relations egocentrically or allocentrically by default, people may use a variety of spatial FoRs flexibly in different contexts (and on different axes) starting early in life (*64*, *82*–*85*), according to the affordances of their spatial experience.

MATERIALS AND METHODS

All studies were conducted in the summer of 2019 near San Borja, Bolivia. We collaborated closely with T. Huanca from the Centro Boliviano de Investigación y de Desarrollo Socio Integral (CBIDSI), who provided translators, logistical coordination, and expertise in Tsimane' culture. Studies were approved by the Gran Consejo Tsimane' (Tsimane' Grand Council), as well as the Institutional Review Board of UC Berkeley.

Experiment 1: FoRs in spatial memory

Participants

Participants were Tsimane' adults (age, 19 to 64 years; schooling, 0 to 12 years) who provided informed consent and were compensated with goods. All 30 participated in the Selection task, and 25 of them also participated in the Reconstruction task, followed by a series of spatial language tasks.

Selection task

In the Selection task (Fig. 2, left), adapted from the "chips task" in (*70*), participants viewed five identical plastic cups on the study table, arrayed either laterally or sagittally. The experimenter and translator stood to either side of the participant, between the tables. In each trial, the experimenter touched one of the cups in the study array and asked the participant to do the same, to ensure that they had encoded which was the target cup. The participant then turned around 180° to face the test table, where five additional cups were also arrayed in the same orientation, and was asked to touch the cup that was in the "same" position as in the test array. The experimenter followed a standard sequence for each participant, touching each cup without speaking (lateral sequence: middle, left, right, mid-left, mid-right, and middle; sagittal sequence: middle, near, far, mid-near, mid-far, and middle). As the middle cup had a single correct answer regardless of FoR, these trials served as a comprehension check. Note that each test array therefore yielded four critical responses, which were coded as egocentric, allocentric, or unclassifiable.

Reconstruction task

The Reconstruction task (Fig. 2, right) was based on the "animals-in-a-row" task used by (*2*), but we used other objects with asymmetric fronts and backs (e.g., a pen, coffee scoop, and spoon). Each axis was tested twice using two sets of three objects, and the order of sets and axes was crossed and counterbalanced across participants. In each trial, participants were presented with a (lateral or sagittal) array of three objects at the study table, where they practiced reconstructing the array (Fig. 3). Any errors during these practice trials were pointed out by the experimenter. After having correctly reconstructed the array twice at the study table (i.e., correct position and orientation along primary axis), participants turned around 180° to face the test table and were asked to reconstruct the array again there. The experimenter and translator stood to either side of the participant, between the tables. The experimenter recorded the position and orientation of each object in the response arrays. In our main analyses, these objects were classified as egocentric or allocentric only when both their position and orientation implied the same FoR; otherwise, they were considered unclassifiable.

Basic spatial language tasks

After participants completed the nonverbal tasks, we performed three simple tests of their spatial language. First, we asked them to describe the position of a target object in each of four positions around a reference object (i.e., right, left, far, and near sides; see fig. S1) and recorded the spatial language they used in response. Second, we asked them to label each of their hands and we recorded their responses. Last, we asked them to manually point toward poles defined by two different allocentric FoRs—north (*Rocve*) and upriver (*Ñichche'*)—and recorded the headings in which they pointed using a digital compass. For full methods and results of these tasks, see the Supplementary Materials.

Experiment 2: FoRs in spatial language

Participants

Participants were 36 Tsimane' adults (age, 20 to 77 years; schooling, 0 to 12 years) who did not participate in experiment 1, composing 18 pairs. They provided informed consent and were compensated with goods.

Spatial language elicitation

We used the director-matcher task (*66*, *67*) to elicit verbal descriptions of spatial relations across the lateral and sagittal axes. Each pair of participants was seated side by side at a pair of testing tables, one on each side of a visual occluder (see Fig. 5). The experimenter and translator(s) stood behind the participants, facing the same direction. The orientation of the tables was counterbalanced across sessions such that participants faced in one of four directions defined by the river-based coordinate system used by the Tsimane': upriver (225°), downriver (45°), and the two orthogonal directions (i.e., across river: 135° and 315°). Each participant played only one role in testing (i.e., either director or matcher), which was assigned a priori according to the side on which they sat (i.e., left or right side; counterbalanced across sessions).

At the start of each session, each participant received plastic figures of a chicken and a pig—both of which are commonly observed in Tsimane' villages—and was instructed in their native language. Whereas matchers were free to manipulate their objects as they liked, directors only observed and described the objects that the experimenter placed on their side of the occluder. When seated, participants could not see each other's faces, gestures, or objects, requiring the director to convey all information orally (see Fig. 5A). Practice trials consisted of four single-object trials (i.e., rightward chicken, toward chicken, away pig, and left pig), which were presented in a predetermined random order. Once the director gave verbal directions and the matcher was satisfied with their configuration of objects, the director was asked to stand, look over the occluder, and inspect the matcher's configuration. During practice trials, participants repeated incorrect trials until they achieved a correct match. After completing all four practice trials correctly (within eight attempts), they advanced to the critical trials. In critical trials, configurations always included both animals, but they varied in their position (i.e., what animal was on which side) and orientation, which the two animals always shared (i.e., both facing left, right, away, or toward the participant). Crossing these variables resulted in eight critical trials (see Fig. 5B), which were presented in a predetermined random order. To encourage thoughtful direction, the director continued to inspect the matcher's responses at the end of each critical trial, but was not permitted to repeat any trial.

After the director-matcher task, we asked directors to label their two hands and tested their orientation in absolute spatial coordinates—upriver and east—using the same procedures as in experiment 1.

Spatial language translation and coding

An experienced Tsimane'-Spanish translator with native Tsimane' language skills and blind to experimental hypotheses produced written translations of director utterances in each trial from video recordings. Using these translations, two of the authors (B.P. and I.B.) independently coded which FoR was used to describe position and orientation in each trial, according to the six-type classification system detailed in (*68*). One of these coders (I.B.) is a native Spanish speaker and was blind to experimental hypotheses at the time of coding. Position and orientation were coded and analyzed separately because speakers can (and often did) use different FoRs to encode these two spatial aspects (e.g., "The pig is upriver of the chicken and both are facing me"). When participants described position or orientation ambiguously (i.e., plausibly corresponding to multiple FoRs) or not at all (e.g., "The animals are on the table"), this language was coded as unclassifiable.

In addition to the written translations, coding of directors' spatial language was informed by (i) diagrams of the object configurations that the director was describing, (ii) participants' absolute facing direction (i.e., heading), and (iii) their seating positions (i.e., which side was the director on). We used these contextual variables to inform our coding when verbal information alone could not disambiguate FoR. For example, the diagrams served to clarify the meaning of left/right terms, which cannot be categorized out of context; the sentence "the pig is on the left and the chicken is on the right" is ambiguous when the animals are facing in the same direction as the speaker, as left and right here can refer either to the sides of the animals (e.g., "the pig is on the chicken's left"; an intrinsic FoR) or to the sides of the speaker (e.g., the pig is on my left; an egocentric FoR). Such utterances were therefore coded as unclassifiable, and because they were unique to the lateral axis, they contributed to the cross-axis difference in unclassifiable utterances that we observed. Only when the animals faced in another direction (which they did three-quarters of the time), could we disambiguate the use of left/right terms. Likewise, participants heading was useful for interpreting uses of up (*arriba*) and down (*abajo*). In consultation with our native Tsimane' interpreters, we coded these as absolute (i.e., upriver and downriver) when these terms described a location or orientation that was plausibly upriver (225°) or downriver (45°), as subsequent testing revealed that participants were well oriented with respect to this allocentric continuum (see the Supplementary Materials).

After coding all utterances independently, the coders resolved differences through discussion. Following the classification system used in experiment psychology (*6*, *21*), we coded as egocentric those FoRs in which the anchor is the body of an observer (i.e., relative and direct) and coded as allocentric FoRs anchored to aspects of the environment (i.e., object-centered, geomorphic, landmark-based, and absolute).

Supplementary Materials

This PDF file includes:

Experiments 1 and 2
The role of distance information
Figs. S1 to S4

View/request a protocol for this paper from *Bio-protocol*.

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