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No Sex or Age Difference in Dead-Reckoning Ability among Tsimane Forager-Horticulturalists

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Abstract Sex differences in reproductive strategy and the sexual division of labor resulted in selection for and maintenance of sexual dimorphism across a wide range of characteristics, including body size, hormonal physiology, behavior, and perhaps spatial abilities. In laboratory tasks among undergraduates there is a general male advantage for navigational and mental-rotation tasks, whereas studies find female advantage for remembering item locations in complex arrays and the locations of plant foods. Adaptive explanations of sex differences in these spatial abilities have focused on patterns of differential mate search and routine participation in distinct subsistence behaviors. The few studies to date of spatial ability in nonindustrial populations practicing subsistence lifestyles, or across a wider age range, find inconsistent results. Here we examine sex- and age-based variation in one kind of spatial ability related to navigation, dead-reckoning, among Tsimane forager horticulturalists living in lowland Bolivia. Seventy-three participants (38 male) aged 6–82 years pointed a handheld global positioning system (GPS) unit toward the two nearest communities and the more distant market town. We find no evidence of sex differences in dead reckoning ($p=0.47$), nor do we find any evidence of age-related decline in dead-reckoning accuracy ($p=0.28$). Participants were significantly more accurate at pointing toward the market town than toward the two nearest villages despite its being significantly farther away than the two nearest communities. Although Tsimane do show sexual

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dimorphism in foraging tasks, Tsimane women have extensive daily and lifetime travel, and the local environment lacks directional cues that typically enhance male navigation. This study raises the possibility that greater similarity in mobility patterns because of overlapping subsistence strategies and activities may result in convergence of some male and female navigation abilities.

Keywords Spatial ability · Navigation · Sexual dimorphism · Tsimane · Dead reckoning

Throughout human evolution, males and females have engaged in sexually dimorphic reproductive and economic strategies (Gurven et al. 2009). These different strategies resulted in sexual dimorphism in a number of traits, from body size and muscle mass to hormonal physiology, behavior, and mortality (Estalrrich and Rosas 2015; Gurven et al. 2009; Hurtado et al. 1985; Kruger and Nesse 2006; Lassek and Gaulin 2009; Plavcan 2012; Ruff 2002; Washburn and Lancaster 1968). Sex differences in spatial cognition, especially with regard to laboratory tasks such as mental rotation, are well established (Cutmore et al. 2000; Maccoby and Jacklin 1974; Rosenthal and Rubin 1982; Voyer et al. 1995). There is debate over the selective pressures that could have produced such cognitive sex differences, with some arguing that a sexual division of foraging labor—where women concentrated on immobile plant foods while men focused their efforts on targeting mobile animal prey—would have resulted in male bias in mental rotation owing to the cognitive demands of returning home after pursuing game (Silverman and Eals 1992). Other lines of research have used cross-species comparisons to show that males in polygynous species have larger range sizes owing to greater mate searching (Gaulin 1992; Gaulin and FitzGerald 1988; Geary 1995). Evidence suggests that sex differences on some spatial/navigational tasks are not restricted to humans and, across species, have a shared, hormonally mediated developmental basis (Clint et al. 2012; Gaulin 1992; Geary 1995; Williams and Meck 1991). Since nonhuman species lack the hunter-gatherer division of labor, a shared mammalian developmental basis for this sex difference argues for the sexual-selection hypothesis.

Laboratory tasks among undergraduates show a general male advantage on a variety of navigational tasks, including distance estimation and Euclidean orientation strategies involving cardinal directions (Coluccia and Louse 2004; Dabbs et al. 1998; Jones et al. 2003; Silverman et al. 2000). Self-report studies indicate that males are more likely to use Euclidian orientation strategies that rely on room geometry (on indoor tasks) or distant geomorphological and topographic cues (on outdoor tasks), whereas female strategies rely on proximate landmarks that indicate specific turning points (Coluccia and Louse 2004; Saucier et al. 2002; Schug 2015). Among university undergraduates, real-world navigation tasks show either a male advantage (Kirasic et al. 1984; Malinowski and Gillespie 2001; Saucier et al. 2002; Silverman et al. 2000)—though these often have no controls or manipulations for cue type—or no sex difference (Kirasic et al. 1984; Montello and Pick 1993). No studies report a female advantage in real-world navigation (Coluccia and Louse 2004).

From an evolutionary perspective, the sexual division of foraging labor as well as divergent reproductive strategies could have driven selective pressures on male and female spatial abilities. The relatively sparse data suggest that, across industrial (Bagley and Mokhtarian 2002) and foraging populations (Cashdan et al. 2012; MacDonald and

Hewlett 1999; Vashro and Cashdan 2015; Vashro et al. 2015), males have larger home ranges. In several cases, these larger home ranges are associated with better dead-reckoning ability (Cashdan et al. 2012; Vashro and Cashdan 2015; Vashro et al. 2015), though exceptions are known (Cashdan et al. 2012, 2015). Among Tsimane forager-horticulturalists, adolescent males engage in significantly more inter-village travel than age-matched females, but only one of four measures of lifetime home range indicates that males cover more territory (Miner et al. 2014).

Although the preponderance of the literature strongly suggests an overall male advantage on spatial tasks (for a meta-analysis see Voyer et al. 1995), there is a significant female advantage on certain spatial tasks, arguably related to the demands of foraging for such immobile resources as plants, including recognizing position changes in arrays (Silverman and Eals 1992), locating specific plants in arrays (Neave et al. 2005), dead-reckoning in relation to previously revealed food locations (New et al. 2007), and remembering the location of plant foods (but not other categories of items) in digitally presented arrays (Krasnow et al. 2011). Prior cross-cultural work suggests that the sex differences in spatial ability may not develop in all contexts. For example, Berry (1966, 1971, 1976) found the “typical” Western sex difference in spatial ability among West African Temne agriculturalists, who live in a spatially differentiated environment in which women in particular do not travel far from home. In contrast, he found no such sex difference among Baffin Island Inuit hunters, where both sexes have large ranges in a relatively featureless environment. In other words, a wide range of influences—including developmental effects of local environments (e.g., Inuit vs. Temne), natural selection acting differently on men and women (e.g., foragers vs. hunters), or sexual selection for mate-seekers vs. parents—might simultaneously be acting on the cognitive abilities collectively called “spatial.”

A wide range of variation in male and female tasks is seen even in hunter-gatherer ecologies with marked division of labor. Ache men often engage in stationary palm larvae harvesting, and Ache women travel long distances through the forest while moving camp each day (Hurtado et al. 1985). Although female hunting is generally rare cross-culturally, hunting with dogs is reported among some Agta women (Estioko-Griffin 1986), and net hunting is not uncommon among Aka women (Noss and Hewlett 2001). Thus populations in environments where there is greater overlap in male and female travel patterns may result in more similar male and female navigational abilities.

The Present Study

Here we examine sex- and age-based variation in navigational ability, in particular dead-reckoning performance, among Tsimane forager horticulturalists living in lowland Bolivia. Dead reckoning is operationalized here as the ability to point toward an unseen location; accuracy at this task can be assessed by measuring an individual’s accuracy in pointing in terms of deviation from the true bearing to that location.

The Tsimane practice a relatively traditional lifestyle with more than 90% of calories generated by small-scale horticulture, hunting, fishing, and foraging (Gurven 2004; Gurven et al. 2009; Martin et al. 2012). Given that the Tsimane occupy nearly 100 communities, there is significant variation in micro-environment, topography, and landscape, but all five of the communities that contributed participants to this study are in a lowland area with high canopy tree cover and no line of sight to mountains or other large-scale landscape cues to cardinal directions. The river is serpentine; thus its local orientation is also an unreliable cue to cardinal directions. Many footpaths follow a winding course along the river.

Tsimane men have significantly higher rates of travel during adolescence but do not differ from women in terms of travel in childhood or after marriage (Miner et al. 2014). Tsimane women have extensive lifetime travel ranges, with an average minimum convex polygon (MCP) range of 939 km^2. Although men's lifetime MCP ranges do significantly exceed women's, male and female Tsimane do not significantly differ in three other measures of lifetime range: half range, kernel utilization distance, and exploration range (Miner et al. 2014).

Is There a Sex Difference in Dead-Reckoning Ability?

The Tsimane manifest the typical forager sexual division of labor, with hunting activity largely restricted to males. Miner et al.'s (2014) study implies stronger sexual selection for male spatial abilities because only male ranges expand during the key period of mate search and because only female ranges contract with increasing numbers of dependent young. Thus, based both on sex differences in mate search (Gaulin 1992) and on sexual division of labor (Silverman and Eals 1992), results of prior work would predict some sexual dimorphism in spatial ability among the Tsimane. However, mortality from losing one's way is a strong selection pressure that impacts every forager leaving his/her home community regardless of age or sex (e.g., Berry 1966, 1971), especially in areas with significant predation risk (Hill and Hurtado 1996; Hill et al. 2007). Among the Tsimane, Ache, Hiwi, and !Kung, deaths from being lost or separated from a group are noted causes of accidental mortality (Blurton Jones et al. 1994; Gurven et al. 2007; Hill and Hurtado 1996; Hill et al. 2007; Sugiyama et al. 2011). This is important to note given the generally similar magnitude of lifetime range size among Tsimane men and women. In addition, although the kinds of local-landmark cues prioritized by female navigation strategies (Saucier et al. 2002) may be abundant, the male-preferred large-scale topographic features that provide Euclidean orientation are largely absent for the Tsimane participants in this study, a situation that could differentially compromise male navigational abilities. Thus the sexual-selection and division-of-labor models both predict sex differences in spatial ability among the Tsimane, whereas the mortality-selection model does not. Moreover, given sex-typical spatial cue preferences, males are relatively cue-deprived among the Tsimane, which should also tend to lessen any male advantage in measured spatial ability.

Sun Compass: Does a Clear Line of Sight to the Sun Improve Dead-Reckoning Accuracy?

Although we remain agnostic as to the cognitive cues or mechanisms that mediate dead-reckoning ability, we test one specific type of directional sense ability—the use of a sun compass. Species across many taxa, including insects (Heinze and Reppert 2011), fish (Quinn 1980), and mammals including humans (Finney 1995), use sun-based navigational cues. No experimental studies have specifically examined the role of solar visibility in terrestrial orientation among nonindustrial populations. Anecdotally, Tsimane hunters report using sun-based cues while hunting, even under a relatively dense jungle canopy. In order to test the potential importance of solar visibility (the use of a sun compass) in aiding dead-reckoning ability, individuals were asked to point to the two nearest communities, one from inside their home and the other from outside their home.

Does Resource Value Affect Dead-Reckoning Ability?

Previous research suggests that men and women are both more accurate at dead reckoning to locations with high-quality resources (New et al. 2007). Thus we hypothesize that Tsimane males and females will be more accurate when pointing toward the market town, San Borja (population ~25,000) as opposed to the nearest up- and downriver communities, despite San Borja's greater distance.

Does Dead-Reckoning Ability Decline with Age?

Many aspects of cognitive performance decline with age in industrial and foraging populations (Barrett-Connor et al. 1999; Cashdan et al. 2012; Singh-Manoux et al. 2012; Trumble et al. 2014b). Declining physical ability in older ages also limits travel as well as hunting and foraging away from the home (Gurven et al. 2006; Stieglitz et al. 2014). As selective pressures decline with age, and travel is limited at older age by physical ability, dead-reckoning ability may also decline with age.

Methods

The study was conducted with 73 participants from five riverine communities ($n=38$ males), mean±SD age 33.01±22.60 (range 6–82) years (Table 1). Participants pointed a handheld GPS receiver (Garmin International Inc., Olathe, KS) to indicate their dead-reckoned estimate of the bearing to each of three locations, (*a*) the central schoolhouse of the nearest upriver community, (*b*) the central school house of the nearest down-river community, and (*c*) the city center (*plaza central*) of the market town of San Borja. Participants were randomized as to whether they pointed to the nearest upriver or downriver community first; San Borja was always the final target location.

Half of the participants were randomly assigned to point first while under the roof of their house, and the other half pointed first outside of their house; participants then

Table 1 Deviation between participant's heading and actual heading for 73 Tsimane participants

	Mean deviation±SD	Median deviation	Mean (range) distance to target	Median last time visited
First Village	32.8°±30.6°	26.5°	5.5 (2.0–13.6) km	118.5 days
Second Village	34.4°±30.3°	26.8°	5.5 (1.1–13.1) km	79.0 days
Market Town	25.1°±17.83°	22.1°	10.1 (2.7–22.4) km	21.6 days

switched and pointed to the next location (up- or downriver) from the opposite roof condition. Thus when pointing to the two nearest communities, each person pointed once from under their roof and once while outside their home. When pointing toward San Borja, participants were always outside.

As a covariate, participants were asked how recently they had visited each of the two closest communities and San Borja.

In ArcGIS, the coordinates of the participants' homes (or just outside their homes, depending on the condition) and the coordinates of the target locations were jointly used to compute true bearings. These true bearings were used to establish dead-reckoning accuracy by subtracting the participant's dead-reckoned estimate and taking the absolute value of the difference. Euclidean distances between individual homes and the schoolhouses of the nearest up- and downriver communities, as well as the central plaza for San Borja, were also established in ArcGIS. Because participants were clustered across five communities, linear mixed-effects models were used to ensure proper control for village-level effects.

Statistical Methods

To foster a full review of the data, statistical analyses were conducted at two levels. First, for each of the three target locations, individual linear mixed-effects models examined the associations between dead-reckoning accuracy and the four independent variables—age, sex, distance to target, and the time interval since the target location was last visited—with community of residence as a random effect (Table 2). Second, all data were aggregated into a single linear mixed-effects model to examine the associations between dead-reckoning accuracy and five independent variables—age, sex, a dummy variable indicating whether target location was a village or the market town, distance to target, and the time interval since the target location was last visited—with individual as a random effect to deal with the non-independence of each individual pointing to three locations (Table 3).

Table 2 Multivariate linear mixed-effects models for each target community examining covariates influencing deviations in pointing accuracy (in degrees) for 73 Tsimane men and women, with community of residence as a random effect

	First Village		Second Village		Market Town	
	ß	p	ß	p	ß	p
Last time visited target (days)	−0.03	0.11	−0.01	0.5	−0.01	0.90
Distance to target community (km)	**0.01**	**<0.001**	**0.01**	**0.01**	0.001	0.64
Age (yrs)	**−0.78**	**0.004**	0.07	0.78	−0.05	0.51
Sex (1=male)	14.7	0.19	−3.49	0.78	−1.03	0.76

Bold values are significant

Each column is a separate analysis of an individual target location. A positive beta indicates worse performance (more degrees off target)

Table 3 Aggregate mixed-effects models examining covariates associated with pointing accuracy (in degrees) with individuals as a random effect

	β	p
Market town vs. Village (1=town)	**−9.23**	**0.038**
Last time visited target (days)	0.002	0.72
Distance to target community (km)	0.02	0.596
Age (yrs)	−0.11	0.227
Sex (1=male)	2.95	0.468

Bold values are significant

A negative beta indicates better accuracy (closer to true heading)

Treatment of Outliers

In several cases individuals performed poorly when pointing to community A (n=5) or community B (n=6), with poor performance defined as a deviation of more than 90° from the target (Cashdan et al. 2012). For the market town, in five cases participants were more than three standard deviations away from mean accuracy. Running all models without these 16 outlier data points had no impact on the sign or significance of any of the results. The results presented below include all data points.

Results

Overall Results

The mean dead-reckoning errors (degrees off target) for the two closest communities were 32.8° and 34.4°, which are not statistically different (t=−0.33). Individuals were significantly more accurate when pointing to San Borja (mean=25.1° off-target) than to the two closest communities (t=1.92 and 2.43; Table 1, Fig. 2). On average, San Borja is nearly twice as far away as either of the neighboring communities, but it was visited much more recently than either (t=4.33 and 4.04; Table 1). Considering just the two neighboring communities, dead-reckoning error increases with intercommunity distance (β=0.01, p<0.001 and β=0.01, p=0.01, respectively) and is unrelated to days since last visit (all p>0.11; Table 2).

Predictors of Dead-Reckoning Accuracy

All data were aggregated into a single mixed-effects model to determine which factors reliably impact dead-reckoning accuracy. Results indicates that individuals were 9.2° more accurate (closer to the true heading) when pointing to San Borja (p=0.038) compared with the other two villages; no other covariates were significant (Table 3).

Performance by Sex

No significant difference was found between male and female dead-reckoning accuracy when we controlled for age, distance to target, or last time individuals visited the target for any single target location (Tables 2 and 3; Figs. 1 and 2), nor for all communities combined (Table 3). There was a trend toward better male accuracy for the market town (Table 2, Fig. 2), though this did not hold for both villages, nor in the overall model (Tables 2 and 3). Controlling for age, we found a consistent male bias toward more recent visitation to all three locations; males were significantly more likely to have recently visited the nearest upriver and downriver communities ($p=0.006$; both locations combined). Males had also visited San Borja more recently, though this sex difference was not significant ($p=0.133$). San Borja is upriver from these communities, and individuals mainly travel downriver to hunt or fish, activities that are conducted more often by males (Gurven et al. 2009; Trumble et al. 2014a).

Sun Compass: Is Dead Reckoning Aided by Solar Navigation Cues?

There was no statistically significant difference in dead-reckoning accuracy for the two nearest villages when participants were pointing from inside their homes versus from outside their homes, after we controlled for age, sex, distance to target, and the last time the participant visited the target location (all p values >0.12). However, the number of walls in participants' homes varied, with 16% of homes having no walls and 63% having four walls. Thus, shadows could have provided important cues to the sun's direction. Also, the cane walls of most homes let in varying amounts of light, which could also have given cues to the location of the sun. When individuals who had

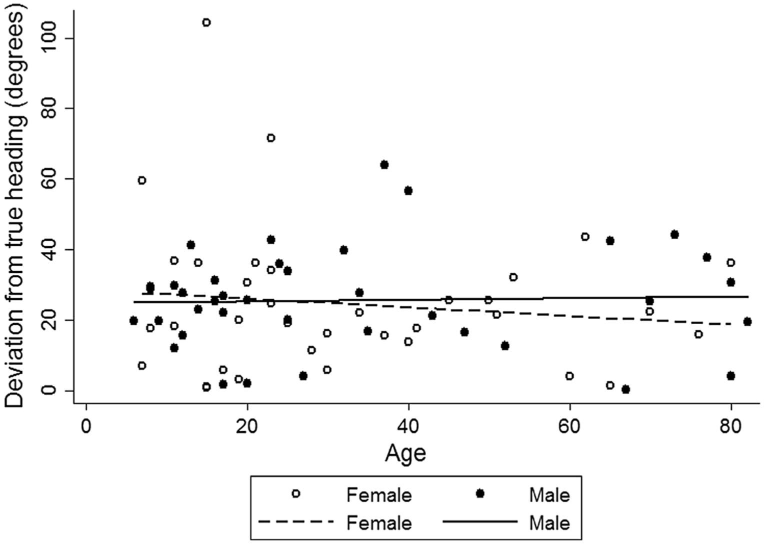

Fig. 1 Deviation from true heading (in degrees) for 73 male (*dark circle*, *solid line*) and female (*open circle*, *dashed line*) participants pointing toward San Borja. There is no statistically significant difference for male or female pointing accuracy. The elimination of five outliers did not change the significance nor associations shown here for age or sex

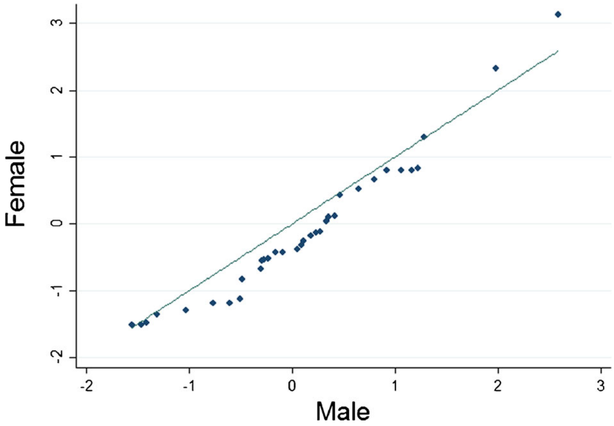

Fig. 2 Quantile-Quantile plot comparing male and female *z* scores for pointing accuracy toward San Borja showing no statistically significant difference. Unlike in Tables 2 and 3, these values have been standardized, and thus positive values indicate more accurate dead reckoning (in *z* scores), whereas negative scores indicate less accurate dead reckoning. Points on the male side of the 1:1 line indicate better male performance

pointed from inside homes with no walls were grouped with individuals who pointed from outside their homes, there was still no significant disadvantage to pointing from inside a house with walls ($\beta=3.89$, $p=0.194$). Additional models examined just individuals pointing from inside a home with four walls versus those who pointed from outside or from homes with fewer than four walls, and again there was no significant difference in pointing accuracy for either of these conditions ($p=0.849$).

San Borja

Individuals were significantly more accurate at pointing toward the market town of San Borja than to the two nearest villages ($p=0.003$ and $p=0.009$, respectively), despite the fact that San Borja is significantly farther away than the two nearest communities (all p values <0.001) (Tables 1, 2, and 3 and Fig. 3). However, individuals were more likely to have visited the market town more recently than they had their nearest neighboring communities ($p<0.001$). When the accuracy of individuals pointing toward San Borja was examined by itself, neither distance from the individual's home to San Borja, age, sex, nor recency of last visit significantly impacted dead-reckoning accuracy (Table 2).

Age

In the aggregate mixed-effects model, age was not associated with dead reckoning ability ($p=0.227$; see Table 3). When each target location was examined independently, age was not associated with accuracy in pointing toward San Borja ($p=0.51$), whereas older individuals pointed more accurately than younger people toward one of the nearby communities ($\beta=-0.78$, $p=0.004$), though not the other ($p=0.78$; see Table 2).

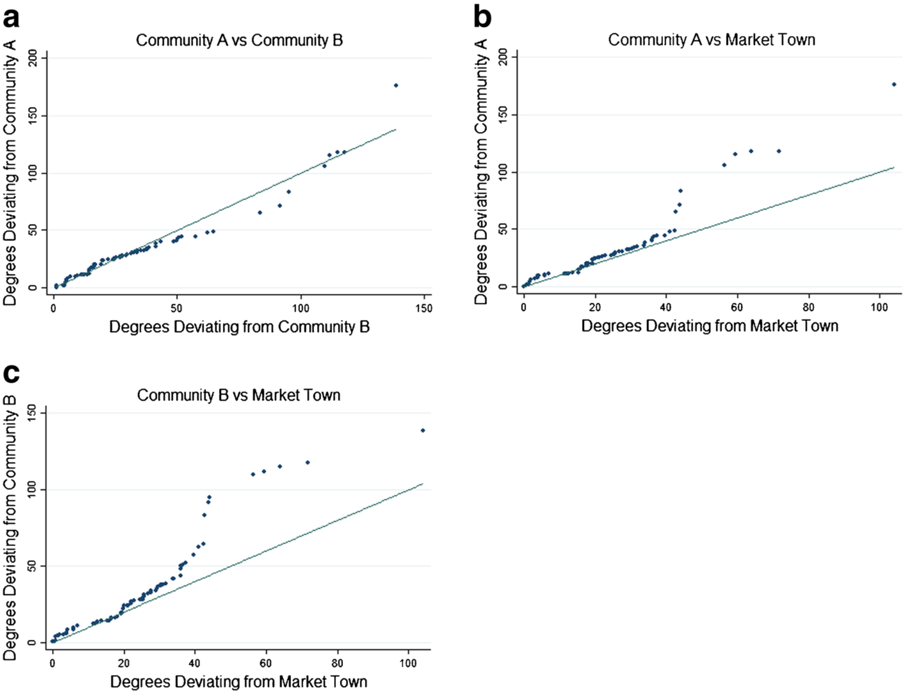

Fig. 3 Quantile-Quantile plots comparing all three target locations. Participants were significantly more accurate when pointing towards San Borja than pointing towards either Tsimane community (see b and c). Participants did not significantly differ in their accuracy for the first two communities they pointed toward, but were more accurate in pointing toward San Borja than the other communities ($p=0.03$ and 0.009, respectively). For reference, the solid line slows a slope of 1

Discussion

This study examined age and sex differences in dead-reckoning ability among Tsimane forager-horticulturalists. We find no evidence of sex differences in dead-reckoning, nor do we find any evidence of any age-related decline in dead-reckoning accuracy. In fact, with respect to nearby communities, accuracy may increase with age. Despite a greater distance to the market town of San Borja, individuals were significantly more accurate when pointing to San Borja than they were when pointing to nearby communities, and this difference was not explained by the recency of visits to this market town.

No Evidence of Sex Differences

In industrial populations, there is extensive evidence of male-biased spatial ability in a number of cognitive domains (Cutmore et al. 2000; Gagnon et al. 2015; Gaulin 1992; Geary 1995; Voyer et al. 1995). Fewer studies have been undertaken among subsistence populations where individuals actively travel away from their communities while hunting, foraging, or visiting kin, and where mortality while separated from the group could be a significant selective force (e.g., Hill and Hurtado 1996). Previous studies examining dead-reckoning in subsistence populations have taken place in relatively open environments, without heavy forest cover (Cashdan et al. 2012; Vashro and

Cashdan 2015). Among the Hadza, sex differences in dead-reckoning were noted in a more acculturated settled community but not in bush villages, where both sexes still actively engaged in foraging (Cashdan et al. 2012). Controlling for number of locations individuals had visited in the last year, they found no significant sex difference in pointing accuracy among the Hadza. Among the Twe and Tjimba of Namibia, individuals who had traveled to more locations performed better on several spatial tests (Vashro and Cashdan 2015). Populations may differ in the extent to which male and female travel patterns and opportunities for spatial learning diverge. For example, Berry (1966) contrasted Temne agriculturalists, where only males leave home to engage in agriculture, with Inuit populations, where men and women both engage in long-distance foraging, and found evidence of male-biased navigational abilities only among the Temne. Among the Tsimane, it is not uncommon for both men and women to travel several kilometers through the jungle to work in agricultural fields, forage for fruit and honey, fish, and search for medicinal plants, firewood, and materials for house construction. Similarly, evidence from a variety of cognitive tasks in industrial populations supports the notion that sex differences in mathematical performance are smaller in countries with more gender equality (Miller and Halpern 2014; Reilly 2012). Thus, while there is consistent evidence of male bias in some aspects of spatial ability in the United States, the United States also has the largest gaps in male and female science and math ability compared with other industrialized populations (Reilly 2012).

There are a number of hypotheses regarding the evolutionary bases of male-biased spatial ability. For humans, it has been argued that the selection pressures arising out of a sexual division of labor—with males pursuing game wherever it might lead and then needing to find their way home—have put a greater premium on navigational skills for males than for females, who could follow more regularized foraging routes (Silverman and Eals 1992; Silverman et al. 2000). Nevertheless, there is evidence of male advantage in a variety of cognitive tasks across many taxa where there is no sex difference in foraging (Clint et al. 2012). Although variance in male home ranges resulting from mate search patterns explains sex differences in certain spatial abilities (e.g., maze performance) across several species (Gaulin 1992; Vashro and Cashdan 2014), it may not be relevant in some species or populations where there is no sex difference in home range (Clint et al. 2012). Others have contended that these sex differences are the results of proximate differences in sexually dimorphic hormone levels—in particular, androgens (Clint et al. 2012) and estrogens (Cashdan et al. 2012; Duff and Hampson 2000). Although hormonal data are not available for the Tsimane men and women in the present study, there is evidence that Tsimane men have significantly lower levels of testosterone than age-matched US males (Trumble et al. 2012), and that testosterone is positively associated with several domains of cognitive performance, including aspects of spatial ability, in industrial populations as well as among the Tsimane (Sherry and Hampson 1997; Trumble et al. 2014b).

Finally, studies suggest that the sexes tend to differ on navigational cue use, with females exploiting route-proximate landmarks whereas males rely more heavily on distal landscape, terrain, and geometric cues (Saucier et al. 2002). This latter class of cues was conspicuously absent for the Tsimane participants in this study, and that absence might differentially disadvantage male navigation strategies in this population. Similar results have been reported in studies using virtual landscapes; although men are generally better than women at directional finding in virtual landscapes, smaller sex differences were observed when the virtual landscape had only route-proximal pinpoint landmarks and no distal landmarks (Chai and Jacobs 2009). The male advantage on this same task increased when only distal, directional (landscape) cues were available (Chai and Jacobs 2009).

No Evidence of Age-Related Decline

Whereas previous cognitive tests among the Tsimane show significant age-related declines in several cognitive domains (Trumble et al. 2014b), we find no evidence here of any parallel decline in dead-reckoning ability with age. We had expected to find a significant decline in this ability at older ages as travel becomes more difficult. One possibility is that dead-reckoning ability may approximate semantic memory, which remains relatively stable across the lifespan in most industrial populations and can even increase with age (Hartshorne and Germine 2015; Salthouse 2010). Just as semantic memory increases with age, knowledge of local geography, including the locations of nearby communities and the market town of San Borja, likely remain stable or increase as individuals visit the locations and become more familiar with the surrounding geography over the course of their life. Among the Tsimane, we see no age-related decline in one aspect of semantic memory, category fluency, in which participants are asked to name all of the animals and fish they can in a two-minute period.[1] Most spatial navigation studies have been focused on young, college-age participants, which precludes analysis of age-related changes in navigational ability.

No Effect of Solar Cues

We found no evidence that the ability to see the sun impacted dead-reckoning accuracy. However, 37% of homes did not have four walls, and thus although individuals could not directly see the sun (all homes had roofs) it was possible to see shadows, or other solar cues. Even in homes that have four walls, light is still let in through gaps in building materials. That said, we may not see an effect because individuals may have enough prior knowledge that they do not need cues from the sun. Future studies will have participants dead reckon their homes from their distant horticultural plots, or while hunting, where they would not have as much experience with the location and might rely more on sun-based locational cues. Although dead reckoning in our study did not appear to be aided by the use of a solar compass, this does not mean that the solar compass plays no role in human navigation.

Market Town

Although distance from target was associated with poorer dead-reckoning accuracy for the two closest communities, individuals were significantly more accurate when pointing to the much more distant market town of San Borja. Other research suggests that participants have better navigational accuracy for high-value resources (New et al. 2007), and the market town contains many high-value resources, including

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[1] The subject of a forthcoming publication by Fuerstenberg et al., to which some of the coauthors in the current article are contributing.

opportunities to buy (or sell) crops, meat, clothes, household goods, medicines, and other important resources, such as health clinics and the local hospital. In addition to calories and material goods and services, San Borja also offers the opportunity for some men to engage in extra-pair sexual encounters (Stieglitz et al. 2012). Thus the accuracy in pointing to San Borja is consistent with both the hunter-gatherer theory of spatial cognition (New et al. 2007; Silverman et al. 2000) as well as the mate-search models (Gaulin 1992).

Limitations

This study included a relatively small sample of Tsimane from a restricted portion of their geographic range, and a single measure of spatial ability was used—though it is arguably one with a high degree of ecological validity. Working with a mobile population who continue to engage in subsistence foraging is vital to understanding the evolution of navigational skills in a population without GPS or maps, but comparability to studies of US undergrads may be low, especially given the generally restricted age range of most undergraduate populations.

Follow-up studies are needed to better parse potential sex differences in spatial ability, and the underlying socioecological variables that impact any dimorphism (or lack thereof). We see three logical extensions of this study to help elucidate and better understand spatial ability in this population. First, any sex differences in dead reckoning may be diminished when pointing from home, an area of extreme familiarity for both males and females. An alternative design would be to have individuals point toward their homes from a distant location with which they are not overwhelmingly familiar, such as San Borja. A second design would be to have participants engage in a vector summing task while walking through an unfamiliar area of the forest. In vector summing tasks, participants follow a convoluted route that involves numerous twists and turns, and then after following a set course participants are asked to dead reckon back to the starting point. This type of task could obscure familiarity of the home environment and give a more direct view of individual direction sense, though it still may not uncover high levels of sexual dimorphism because the flat landscape and jungle canopy mask any potential distal geographic landmarks (which typically enhance male spatial ability), while still providing local route-proximal landmarks (which typically enhance female spatial ability) (Chai and Jacobs 2009). A third test of sexual dimorphism in spatial ability would be the use of one of the most commonly employed laboratory tasks that consistently demonstrates sexual dimorphism in performance—mental rotation (Voyer et al. 1995). Examining these other aspects of spatial ability will be an important next step in determining whether the pattern we report here extends to other aspects of spatial ability or is limited to a single domain owing to ecological circumstance or artifacts of study design.

Conclusion

These data add to a growing body of evidence suggesting that sex differences in navigational ability noted in many industrial populations may not be universal in subsistence populations (Berry 1966; Cashdan et al. 2012). More acculturated groups with less female foraging (e.g., the Temne, or the settled Hadza in Mangola) show male-biased advantages, whereas populations whose females engage in more extensive foraging (e.g., mobile Hadza, Inuit, Tsimane) do not show sex differences in navigational ability. If this pattern holds across other hunting and foraging groups, it suggests that evolved navigational algorithms are developmentally sensitive to experience and cue availability, and that a fuller specification of those inputs will be needed to accurately predict the presence or absence of sex differences in various navigational abilities. Human evolution occurred in a mosaic of environments that resulted in a number of localized subsistence strategies, and variation in the magnitude of sexual division of labor and travel. More overlap in subsistence strategy and daily activities is likely to result in convergence of male and female navigation performance.

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