Contents lists available at ScienceDirect

Intelligence

journal homepage: www.elsevier.com/locate/intell

Spatial ability as a distinct domain of human cognition: An evolutionary perspective

David C. Geary

University of Missouri, USA

ARTICLE INFO	A B S T R A C T
<i>Keywords:</i> Intelligence Spatial abilities Evolution Sex differences Cognitive abilities	Psychometric studies have consistently identified spatial abilities as a broad domain of human cognition. Spatial abilities are in fact found in species in which engagement with the physical world, as in prey capture or mate searches, influences survival or reproductive prospects and much is now known about the brain and cognitive systems that support these activities. Sex differences in spatial abilities are found in species in which one sex or the other engages the physical world in more complex ways, such as having a larger home range. Sex differences provide a unique opportunity to study the influence of evolutionary pressures on cognition, because the study of males and females from the same species controls for many aspects of evolutionary history. When there are differences in past selection pressures on males and females they are typically related to reproductive demands. The approach is illustrated here for spatial abilities and provides a blueprint for linking psychometric and evolutionary approaches to the study of human spatial and other abilities.

1. Introduction

The search for the fundamental domains of human cognition has been ongoing for well over a century (Spearman, 1904; Thomson, 1916; Thorndike, 1927; Thurstone & Thurstone, 1941) and continues to this day (e.g., Kovacs & Conway, 2016). Psychometric studies (below) have contributed greatly to these endeavors and have produced taxonomies of human abilities that capture broader (g or general intelligence) to narrower ability domains (e.g., verbal, spatial; Spearman, 1904; Thurstone & Thurstone, 1941). The evolutionary perspective on human cognition emerged independently, with the mind often cast as an amalgamation of cognitive modules that are specialized for dealing with specific recurring problems, such as detecting cheaters in reciprocal relationships (Cosmides, 1989). Evolutionists have also identified clusters of human abilities, such as language, that are universal but can be elaborated depending on social and cultural context. These are typically called folk domains and are organized around an intuitive folk psychology (systems for processing and representing social information), folk biology (systems for processing and representing information about other species), and folk physics (systems for processing and representing information about the physical world; Geary, 2005; Medin & Atran, 1999; Pinker & Bloom, 1990; Spelke, Breinlinger, Macomber, & Jacobson, 1992; Wellman & Gelman, 1992).

At one level, the evolutionary approach seems to be antithetical to some of the most replicated results in the psychometric tradition and psychology more broadly, including the positive manifold and the implication of a system of cognitive (e.g., attentional control) and biological mechanisms that span all human abilities (Warne & Burningham, 2019). Scientists in both areas have in fact largely overlooked the theoretical and empirical findings of those in the other area, but the two approaches are compatible and will eventually be integrated (Geary, 2005). Here, I illustrate the potential for integration by focusing on the relation between psychometric and evolutionary research on spatial abilities, beginning with a brief overview of psychometric studies and then moving to the evolutionary approach.

2. Psychometric taxonomies

Factor analytic studies of test performance typically identify three or four ability strata (Caemmerer, Keith, & Reynolds, 2020; Carroll, 1993; Johnson & Bouchard Jr, 2005; McGrew, 2009; Vernon, 1965). The broadest is general intelligence or *g* and most likely represents the combined effects of multiple cognitive (e.g., attentional control; Kane & Engle, 2002), brain (e.g., frontal-parietal network; Jung & Haier, 2007), and cellular (e.g., mitochondrial energy production; Geary, 2018) systems that influence learning and performance across domains.

https://doi.org/10.1016/j.intell.2021.101616

Received 8 October 2021; Received in revised form 13 December 2021; Accepted 14 December 2021 Available online 22 December 2021 0160-2896/© 2021 Elsevier Inc. All rights reserved.







^{*} Corresponding author at: Department of Psychological Sciences, University of Missouri, Columbia, MO 65211-2500, USA. *E-mail address:* GearyD@Missouri.edu.

Following Thomson (1916) and others, Kovacs and Conway (2016), in contrast, argued there are no fundamental processes that are common to all abilities, and that the positive manifold emerges from overlapping sets of processes across tasks. One task might engage processes A, B, and C, a second might engage B, D, and E, and a third C, E, and F. The result would be positive correlations among tasks, even though there is no single process that is common to all of them.

Whatever is underlying g, most psychometric studies and attendant theories have identified a second level of ability domain that captures something common across domain-specific competencies. For instance, the integration of the influential models of Cattel, Horn, and Carroll (CHC; Carroll, 1993; Cattell, 1963; Horn, 1968) results in a g factor as well as multiple broad domains of abilities, including fluid reasoning, short-term memory, and quantitative knowledge, among others (McGrew, 2009). If several spatial measures are included in the test battery, spatial ability emerges as one of these broad domains (Caemmerer et al., 2020; Carroll, 1993; Johnson & Bouchard Jr, 2005; McGrew, 2009; Vernon, 1965), although some studies suggest these can decomposed into more distinct spatial abilities (e.g., spatial relations and visualization; Johnson & Bouchard Jr, 2007; Pellegrino, Alderton, & Shute, 1984). Research in cognitive and developmental psychology also reveals a clear spatial domain that can be decomposed into several subdomains, such as visuospatial working memory and mental rotation (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006; Linn & Petersen, 1985; Voyer, Voyer, & Bryden, 1995).

A recent proposal is that spatial abilities can be understood in terms of the intrinsic-extrinsic and dynamic-static demands of the test (Uttal et al., 2013), creating four domains of spatial ability. Intrinsic and static tasks are focused on objects and relations among parts of the object (e.g., embedded figures, or mazes tests), whereas intrinsic and dynamic tasks require the mental manipulation of objects (e.g., mental rotation tasks). Extrinsic tasks focus on relations among objects, with static tasks involving judgments based on these relations (e.g., water level task) and dynamic involving changes in perspective among objects (e.g., navigating).

2.1. Spatial abilities and mathematics

Evidence for a distinct spatial domain comes from the relation between spatial abilities and students' mathematics achievement and adults' long-term accomplishments in science, technology, engineering, and mathematics (STEM) fields, controlling for intelligence (fluid abilities) or broad measures of general abilities, (Geary, Hoard, Nugent, & Scofield, 2021; Geary, Scofield, Hoard, & Nugent, 2021; Kell, Lubinski, Benbow, & Steiger, 2013). For instance, Kell et al. found that spatial abilities predicted gifted adults' STEM publication and patent records, controlling for overall SAT scores, but was unrelated to publications in the arts, humanities, and social sciences.

At the mean, there are small or no sex differences in overall mathematics achievement (Hyde, Fennema, & Lamon, 1990) but there are consistent differences, favoring boys and men, at the high end of performance (Wai, Hodges, & Makel, 2018) and in certain mathematical domains, such as on complex word problems (E. S. Johnson, 1984). Spatial abilities may contribute to sex differences at the high end of mathematics performance because these abilities appear to contribute to the ease of learning at least some types of newly introduced mathematics, controlling general intelligence (Geary, Hoard, & Nugent, 2021; Geary, Scofield, Hoard, & Nugent, 2021; Mix et al., 2016). Many of the more-specific sex differences, such as for word problems, are fully or partially mediated by boys' and men's advantages in spatial abilities (below; Casey, Nuttall, & Pezaris, 1997; Geary, Saults, Liu, & Hoard, 2000).

In all, these types of studies provide evidence for the incremental validity of psychometric measures of spatial abilities, above and beyond the contributions of intelligence or fluid reasoning, in predicting learning and performance in some mathematics domains and for longterm accomplishment in some STEM fields. The incremental validity in turn is consistent with the proposal that spatial abilities are a unique domain of human ability.

3. Evolution and spatial abilities

From an evolutionary perspective, spatial abilities are an aspect of folk physics that is supported by brain and cognitive systems that enable organisms to engage with the physical world. At the very least these include systems for moving in and representing physical space that in nonhuman species support navigating in the ecology, prey detection and tracking, prey capture, predator avoidance and other key survivalrelated behaviors (e.g., Barton & Dean, 1993; O'Keefe & Nadel, 1978). The brain (e.g., hippocampus) and cognitive (e.g., memory) systems that support ego-centric (self-referenced), and allocentric ("bird's-eye view") navigation are well understood, evolutionarily old, and found across species (e.g., Broglio et al., 2015; Byrne, Becker, & Burgess, 2007). For instance, the homologue of the hippocampus evolved in vertebrates more than 500 million years ago and enables the formation of map-like representations of the physical world that support navigation (Murray, Wise, & Graham, 2018). The basic structure of this system is conserved across present-day vertebrates, although it has become differentiated (e. g., acquired new functions) across many species.

Sex differences in males' and females' engagement with the ecology (e.g., size of home range) provide a window into how selection pressures resulted in the evolution of brain and cognitive systems for processing different aspects of visuospatial information. Examples are provided below and confirm the psychometric identification of a unique spatial domain. Before turning to this section, I note that an evolutionary perspective also provides a clear understanding of the emergence of the individual differences that ungird psychometric studies more broadly.

These individual differences follow per force from the gene mixing that occurs with sexual reproduction, which is estimated to have evolved 1.5 billion years ago and perhaps earlier (Havird, Hall, & Dowling, 2015); in this case, gene swapping in early eukaryotic (containing a nucleus) cells. The eventual evolution of two distinct sexes (one carrying sperm and the other eggs) and sexual reproduction is well understood (Beukeboom & Perrin, 2014; Parker, Baker, & Smith, 1972) and favors the creation of variation in offspring immune systems as a defense against parasites (Hamilton & Zuk, 1982) or other traits that would, for instance, reduce competition among siblings for the same ecological niches (Williams & Mitton, 1973), among other reasons (Muller, 1964). In other words, the variation that is captured by psychometric studies can, at least in part, be traced to the evolution of distinct sexes and the genetics of sexual reproduction–the evolved function of sexual reproduction is to create trait variability or individual differences.

3.1. Sexual selection

The evolution of sexual reproduction and the associated individual differences results in variation in the competitiveness and desirability of different individuals. This variation is the foundation for Darwin's (1871) sexual selection, that is, competition with members of the same sex for mates or for control of the resources (e.g., nesting sites) that mates need to reproduce (intrasexual competition) and discriminative choice of mates (intersexual choice). Sexual selection is firmly established in evolutionary biology and the results of competition and choice on the evolution and expression of sex differences have been documented in hundreds of species (Andersson, 1994; Janicke, Häderer, Lajeunesse, & Anthes, 2016; Trivers, 1972), including our own (Geary, 2021).

3.2. Sex differences in spatial abilities in nonhuman species

Scramble competition is one way in which males compete for mates and illustrates how variation in reproductive outcomes can influence the evolutionary elaboration of spatial abilities. In these cases, males search for mates that are dispersed throughout the ecology and this in turn favors males with enhanced navigational abilities and results in an evolved sex difference in this component of spatial abilities (Gaulin, 1992). Males of these species expand their range during the breeding season to search for potential mates, as illustrated by comparisons of the polygynous meadow vole (*Microtus pennsylvanicus*) and their monogamous cousins, the prairie (*Microtus ochrogaster*) and woodland (*Microtus pinetorum*) vole: The comparison of related species controls for shared evolutionary history. Male meadow voles expand their range during the breeding season to at least five times the area of females' territory, whereas male and female prairie and woodland voles share overlapping ranges of about the same size.

Range expansion and the ensuing mate searches favor males with enhanced spatial and navigational abilities, as illustrated in both laboratory (e.g., maze learning) and field (e.g., navigating from home burrow to the burrows of various females) studies. These show that male meadow voles have better spatial learning and memory than female meadow voles or male prairie and woodland voles (Gaulin & Fitzgerald, 1986). As might be expected, male meadow voles with above average spatial abilities visit more females and generally have higher reproductive success than their lower-ability peers (Spritzer, Solomon, & Meikle, 2005). The same pattern of species- and sex-differences in spatial abilities related to scramble competition has now been demonstrated with other mammals (Jašarević, Williams, Roberts, Geary, & Rosenfeld, 2012; Perdue, Snyder, Zhihe, Marr, & Maple, 2011), and in at least one species of fish (Lucon-Xiccato & Bisazza, 2017).

There is also evidence for a female advantage in spatial abilities when they have larger territories or use these territories in more complex ways than males. One example is the brown-headed cowbird (*Molothrus ater*), a brood parasite where females lay their eggs in the nests of host species and need to remember the location of these nests so they can deposit eggs at times when the unwitting host will accept them. Females of this species have a better spatial memory than males when tested in a large-scale space (Guigueno, Snow, MacDougall-Shackleton, & Sherry, 2014). Females of this species also have a larger hippocampus than males, but there is no sex difference in a related cowbird species (*Molothrus rufoaxillaris*) in which both sexes search for host nests (Reboreda, Clayton, & Kacelnik, 1996).

3.3. Human sex differences in spatial abilities

The illustrations above are not to say that ancestral men engaged in some type of scramble competition or that ancestral women were brood parasites but rather to show how sex differences in activities that have reproductive consequences will elaborate the traits that support these activities, spatial abilities in this case. In fact, comparing the sexes of the same species provides a built-in evolutionary control because most selection pressures related to survival (i.e., natural selection) will be highly similar across the sexes and thus most biological differences should be tracible to the different reproductive demands on ancestral males and females. For instance, larger and more aggressive males than females, slower male developmental, and shorter male lifespans are all consistent indicators of an evolutionary history of more intense malemale than female-female competition in primates (e.g., Leigh, 1996; Plavcan & van Schaik, 1997). These sex differences are evident in contemporary humans and sex differences in physical size are found in our ancestors dating back at least four million years (Grabowski, Hatala, Jungers, & Richmond, 2015; Plavcan, 2012).

These differences do not necessarily indicate there were ancestral sex differences in spatial abilities, only a consistent evolutionary history of physical male-male competition. The devil is in the details and the details in this case can be found in the anthropological and historical records (see Geary, 2021). These indicate high-levels of male-on-male aggression and high male mortality rates and reproductive skew (i.e., some males disproportionately reproduce; Betzig, 2012; Chagnon, 1988;

Walker & Bailey, 2013), as in other species with intense competition among males (Janicke et al., 2016). The competition included the use of blunt force (e.g., clubs) and projectile weapons (e.g., stones, spears) and larger travel ranges for men than women. The use of projectile weapons and larger travel ranges also support men's hunting but male-on-male aggression almost certainly preceded hunting as a form of male-male competition. This is because our deep ancestors (*Australopithecus*) did not appear to eat much eat (e.g., as indicated by teeth structures and wear patterns; Sponheimer & Lee-Thorp, 1999), but were very sexually dimorphic which indicates intense male-male physical competition (Grabowski et al., 2015).

Across five hunter-gatherer groups, MacDonald and Hewlett (1999) reported that men traveled roughly 2 to 4 times farther than women during their typical ranging activities, a sex difference that was also reported in the ethnographies of six other hunter-gatherer and horticultural groups and is found in modern-day urban environments (Ecuyer-Dab & Robert, 2004). A recent and extensive study of range use in another hunter-gatherer group (Hadza, Tanzania) revealed that boys and men had travel ranges that were about four times larger than those of same-age girls and women, with the range sizes beginning to diverge at about 6-years-of-age (Wood et al., 2021). These differences should select for a male advantage in the use of distal cues and allocentric representations of the ecology and result in advantages in navigation and in generating and understanding abstract representations of the ecology (e.g., map reading). Boys' and men's advantages in these areas are consistently found in Western samples and in samples of people in traditional cultures (Coluccia, Iosue, & Brandimonte, 2007; Nazareth, Huang, Voyer, & Newcombe, 2019; Vashro & Cashdan, 2015).

Hunting and ambushing human competitors should also favor the elaboration of other spatial abilities, including detection of objects obscured in a complex visual scene, detecting and tracking the movement of objects (e.g., prey, stones, spears) in physical space, and skill at behaviorally reacting to these moving objects (Law, Pellegrino, & Hunt, 1993; Peters, 1997). Indeed, boys and men have advantages in detecting the orientation of objects relative to a background and are better at seeing individual objects embedded in a complex montage. By adulthood about 7 out of 10 men outperform the average woman in these areas (Linn & Petersen, 1985; Voyer et al., 1995).

Men also show advantages in the ability to judge the velocity and trajectory of a moving object, generate visual images of a moving object, estimate when an object will hit them, and in accuracy at hitting a moving object with a thrown projectile (Peters, 1997; Schiff & Oldak, 1990). Jardine and Martin (1983) found that about 7 out of 8 adolescent boys threw more accurately at a non-moving object than did the average same-age girl, whereas 9 out of 10 of their fathers threw more accurately than their mothers. The same sex difference is found in the Hadza (Cashdan, Marlowe, Crittenden, Porter, & Wood, 2012). Peters found that 3 out of 4 men were more accurate than the average woman at hitting a close and slow-moving target, but this gap widened as the speed of the target increased. Other studies indicate that men's accuracy is related to their better estimation of the velocity of the moving target and better timing of the release of the thrown object vis-à-vis the velocity of the target (Crozier, Zhang, Park, & Sternad, 2019). Moreover, Watson and Kimura (1991) found that about 3 out of 4 men were better at blocking objects thrown at them than was the average woman, a competence that is not needed for hunting but is a core defense against projectiles hurled by other men.

At the same time, the sexual division of labor and women's gathering provide an opportunity for a female advantage in object location memory to evolve (Silverman & Eals, 1992). Pacheco-Cobos, Rosetti, Cuatianquiz and Hudson (2010) confirmed that relative to men, women in an indigenous (Mexico) community have more efficient foraging strategies, a better memory for good foraging locations, and more nuanced knowledge about the species that are likely to be found in these locations. Studies in Western samples confirm this basic sex difference (Eals & Silverman, 1994; James & Kimura, 1997), although it does not

Intelligence 90 (2022) 101616

emerge until the onset of puberty (Voyer, Postma, Brake, & Imperato-McGinley, 2007). At that time and under incidental learning conditions, at least 7 out of 10 adolescent girls and women recall more locations than does the average adolescent boy or man.

In theory, spatial and many other folk abilities have built-in skeletal perceptual and cognitive biases, but the full development of these abilities requires engagement in species-typical activities, such as social and other forms of play. For instance, infants are sensitive to relative distance and by the time they are regularly walking use distance and direction cues to locate objects or places they cannot directly see (Spelke, Lee, & Izard, 2010). In these situations, they know the relative distance and direction of where they want to go and use visual cues as they are moving to adjust their search (Newcombe, Huttenlocher, Drummey, & Wiley, 1998). By 22 months children begin to use external cues to facilitate their navigation and by 4 years use directional cues in simple maps to locate hidden objects (Huttenlocher, Newcombe, & Vasilyeva, 1999). As in other species, the development of cognitive maps of large-scale space requires active exploration of the environment, such as their neighborhood, and engagement in other spatial activities, and develops slowly during the elementary school years and into adolescence (Bullens, Iglói, Berthoz, Postma, & Rondi-Reig, 2010; Levine, Vasilyeva, Lourenco, Newcombe, & Huttenlocher, 2005; Matthews, 1992; Xiao & Zhang, 2021).

Critically, there are early sex differences in these skeletal spatial abilities and in the activities that flesh them out during development (Wilcox, Alexander, Wheeler, & Norvell, 2012). For instance, 5-monthold boys have a better intuitive understanding than girls of what objects will look like when viewed from different angles, suggesting an early advantage in some aspects of spatial ability (Moore & Johnson, 2008). Boys also engage in more of the exploratory behaviors that appear to facilitate the further development of spatial abilities and require less of these experiences, relative to same-age girls, for the development of mental representations of physical space (Munroe, Munroe, & Brasher, 1985; Newcombe, Bandura, & Taylor, 1983). Girls' developing spatial abilities also benefit from these same experiences (Moè, Jansen, & Pietsch, 2018), but may require more of them to development the same level of spatial competencies as boys (Herman & Siegel, 1978).

Overall, men's advantages in most spatial areas are consistent with the evolutionary elaboration of the perceptual, cognitive, and motor abilities that would facilitate navigation in large-scale space and the use of projectile weapons, as well as defenses against projectile weapons. Women can engage in many of the same activities because these are dependent on evolutionarily conserved visuospatial systems that are found across vertebrate species (Murray et al., 2018). The sex differences in reproductive activities result in the elaboration and refinement of these conserved systems and the well-studied human sex differences in spatial abilities (for more detail see Geary, 2021). The point here is that these sex differences help us to understand the evolutionary function of spatial abilities and provide evidence that these evolved independently of other core abilities, such as fluid reasoning, that have emerged in psychometric studies (Geary, 2005).

4. Discussion

The merging of comparative (across species) studies, anthropological research, and evolutionary theory provides a well-vetted means of studying sex differences and in this case illustrates the adaptive advantages of spatial abilities. Organisms that need to move and track other organisms in physical space have brain and cognitive systems that have evolved to support these activities (Broglio et al., 2015; O'Keefe & Nadel, 1978). The associated systems can become more elaborated in one species or another or in one sex or the other if there are differences in engagement with physical space (Murray et al., 2018). Most sex differences should be traceable to differences in the reproductive demands on males and females (Andersson, 1994; Darwin, 1871) and if these demands involve differences in engagement with the physical world, sex

differences in spatial abilities will evolve.

The anthropological and historical records clearly show sex differences in human reproductive demands, one of which is intense malemale competition for status and resource control. As described, some of the associated activities involve spatial abilities that in theory should have resulted in the evolution of sex differences, although the full expression of these differences will be dependent on species-typical developmental experiences. Indeed, sex differences in spatial abilities are well documented in various cognitive tasks and on psychometric measures. The next step in integrating these diverse literatures is to map men's spatial-related activities in natural contexts to the spatial competencies assessed by various spatial measures used in psychometric studies. Performance on some measures, such as map reading, navigating by dead reckoning, and performance in virtual mazes follow directly from the spatial systems that support navigation in large-scale space.

Although less certain, embedded figures tests might reflect an evolved ability to detect prey or people hiding in foliage, whereas mental rotation measures may support the mechanical reasoning that contributes to tool construction (Hegarty, 2004), which is largely a male activity in traditional contexts (Daly & Wilson, 1983). Whatever the details, the approach outlined here provides a potentially useful blueprint for thinking about how broad ability domains identified across more than a century of psychometric studies can be reconciled with an evolutionary perspective on cognition.

The approach also provides a means to conceptualize how schooldependent, evolutionarily recent abilities, such as reading and writing and quantitative knowledge (McGrew, 2009), that have been identified in psychometric studies can be understood from an evolutionary perspective. These are abilities that are built upon folk domains (Geary, 1995), but only with organized formal instruction. Reading and writing involve the integration of basic systems for visual processing (Schlaggar & McCandliss, 2007), with the evolved language (Price, 2000) and theory of mind (for understanding the motives of characters in stories) systems to build evolutionarily novel abilities. Similarly, some aspects of the visual spatial system, an intuitive sense of approximate quantity, and the ability to reason logically (part of fluid ability) are integrated during instruction to build a system of quantitative knowledge (Casey & Ganley, 2021; Feigenson, Dehaene, & Spelke, 2004; Geary, Scofield, Hoard, & Nugent, 2021). These domains are only expected to emerge in developed nations with modern school systems, whereas a spatial ability domain is expected to be universal (see Cashdan et al., 2012).

References

- Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.
- Barton, R. A., & Dean, P. (1993). Comparative evidence indicating neural specialization for predatory behaviour in mammals. Proceedings of the Royal Society of London B: Biological Sciences, 254, 63–68. https://doi.org/10.1098/rspb.1993.0127
- Betzig, L. (2012). Means, variances, and ranges in reproductive success: Comparative evidence. *Evolution and Human Behavior*, 33, 309–317. https://doi.org/10.1016/j. evolhumbehav.2011.10.008
- Beukeboom, L. W., & Perrin, N. (2014). The evolution of sex determination. Oxford, UK: Oxford University Press.
- Broglio, C., Martín-Monzón, I., Ocaña, F. M., Gómez, A., Durán, E., Salas, C., & Rodríguez, F. (2015). Hippocampal pallium and map-like memories through vertebrate evolution. *Journal of Behavioral and Brain Science*, 5, 54939. https://doi. org/10.4236/jbbs.2015.53011
- Bullens, J., Iglói, K., Berthoz, A., Postma, A., & Rondi-Reig, L. (2010). Developmental time course of the acquisition of sequential egocentric and allocentric navigation strategies. *Journal of Experimental Child Psychology*, 107, 337–350. https://doi.org/ 10.1016/j.jecp.2010.05.010
- Byrne, P., Becker, S., & Burgess, N. (2007). Remembering the past and imagining the future: A neural model of spatial memory and imagery. *Psychological Review*, 114, 340–375. https://doi.org/10.1037/0033-295X.114.2.340
- Caemmerer, J. M., Keith, T. Z., & Reynolds, M. R. (2020). Beyond individual intelligence tests: Application of Cattell-Horn-Carroll theory. *Intelligence*, 79, Article 101433. https://doi.org/10.1016/j.intell.2020.101433
- Carroll, J. B. (1993). Human cognitive abilities: A survey of factor-analytic studies. New York: Cambridge University Press. https://doi.org/10.1017/CB09780511571312
- Casey, B. M., & Ganley, C. M. (2021). An examination of gender differences in spatial skills and math attitudes in relation to mathematics success: A bio-psycho-social

D.C. Geary

model. Developmental Review, 60, Article 100963. https://doi.org/10.1016/j. dr.2021.100963

- Casey, M. B., Nuttall, R. L., & Pezaris, E. (1997). Mediators of gender differences in mathematics college entrance test scores: A comparison of spatial skills with internalized beliefs and anxieties. *Developmental Psychology*, 33, 669–680. https:// doi.org/10.1037/0012-1649.33.4.669
- Cashdan, E., Marlowe, F. W., Crittenden, A., Porter, C., & Wood, B. M. (2012). Sex differences in spatial cognition among Hadza foragers. *Evolution and Human Behavior*, 33, 274–284. https://doi.org/10.1016/j.evolhumbehav.2011.10.005
- Cattell, R. B. (1963). Theory of fluid and crystallized intelligence: A critical experiment. Journal of Educational Psychology, 54, 1–22. https://doi.org/10.1037/h0046743
 Chagnon, N. A. (1988 February 26). Life histories, blood revenge, and warfare in a tribal
- population. *Science*, 239, 985–992. https://doi.org/10.1126/science.239.4843.985 Coluccia, E., Iosue, G., & Brandimonte, M. A. (2007). The relationship between map
- drawing and spatial orientation abilities: A study of gender differences. *Journal of Environmental Psychology*, 27, 135–144. https://doi.org/10.1016/j.jenvp.2006.12.005
- Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187–276. https://doi.org/10.1016/0010-0277(89)90023-1
- Crozier, D., Zhang, Z., Park, S. W., & Sternad, D. (2019). Gender differences in throwing revisited: Sensorimotor coordination in a virtual ball aiming task. *Frontiers in Human Neuroscience*, 13, 231. https://doi.org/10.3389/fnhum.2019.00231
- Daly, M., & Wilson, M. (1983). Sex, evolution and behavior (2nd. ed.). Boston, MA: Willard Grant.
- Darwin, C. (1871). The descent of man, and selection in relation to sex. London: John Murray.
- Eals, M., & Silverman, I. (1994). The hunter-gatherer theory of spatial sex differences: Proximate factors mediating the female advantage in recall of object arrays. *Ethology* and Sociobiology, 15, 95–105. https://doi.org/10.1016/0162-3095(94)90020-5
- Ecuyer-Dab, I., & Robert, M. (2004). Spatial ability and home-range size: Examining the relationship in Western men and women (*Homo sapiens*). Journal of Comparative Psychology, 118, 217–231. https://doi.org/10.1037/0735-7036.118.2.217
- Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. Trends in Cognitive Sciences, 8, 307–314. https://doi.org/10.1016/j.tics.2004.05.002 Gaulin, S. J. C. (1992). Evolution of sex differences in spatial ability. Yearbook of Physical
- Anthropology, 35, 125–151. https://doi.org/10.1002/ajpa.1330350606
- Gaulin, S. J. C., & Fitzgerald, R. W. (1986). Sex differences in spatial ability: An evolutionary hypothesis and test. *The American Naturalist*, 127, 74–88. https://www. jstor.org/stable/2461648.
- Geary, D. C. (1995). Reflections of evolution and culture in children's cognition: Implications for mathematical development and instruction. *American Psychologist*, 50, 24–37. https://doi.org/10.1037/0003-066X.50.1.24
- Geary, D. C. (2005). The origin of mind: Evolution of brain, cognition, and general intelligence. Washington, DC: American Psychological Association. https://doi.org/ 10.1037/10871-000
- Geary, D. C. (2018). Efficiency of mitochondrial functioning as the fundamental biological mechanism of general intelligence (g). *Psychological Review*, 125, 1028–1050. https://doi.org/10.1037/rev0000124
- Geary, D. C. (2021). Male, female: The evolution of human sex differences (3rd ed.). Washington, DC: American Psychological Association.
- Geary, D. C., Hoard, M. K., & Nugent, L. (2021). Boys' visuospatial abilities compensate for their relatively poor in-class attentive behavior in learning mathematics. *Journal* of *Experimental Child Psychology*, 211, 10522. https://doi.org/10.1016/j. jecp.2021.105222
- Geary, D. C., Hoard, M. K., Nugent, L., & Scofield, J. E. (2021). In-class attentive behavior, spatial ability, and mathematics anxiety predict across-grade gains in adolescents' mathematics achievement. *Journal of Educational Psychology*, 113, 754–769. https://doi.org/10.1037/edu0000487
- Geary, D. C., Saults, S. J., Liu, F., & Hoard, M. K. (2000). Sex differences in spatial cognition, computational fluency, and arithmetical reasoning. *Journal of Experimental Child Psychology*, 77, 337–353. https://doi.org/10.1006/ jecp.2000.2594
- Geary, D. C., Scofield, J. E., Hoard, M. K., & Nugent, L. (2021). Boys' advantage on the fractions number line is mediated by visuospatial attention: Evidence for a parietalspatial contribution to number line learning. *Developmental Science*, 24, Article e13063. https://doi.org/10.1111/desc.13063
- Grabowski, M., Hatala, K. G., Jungers, W. L., & Richmond, B. G. (2015). Body mass estimates of hominin fossils and the evolution of human body size. *Journal of Human Evolution*, 85, 75–93. https://doi.org/10.1016/j.jhevol.2015.05.005
- Guigueno, M. F., Snow, D. A., MacDougall-Shackleton, S. A., & Sherry, D. F. (2014). Female cowbirds have more accurate spatial memory than males. *Biology Letters*, 10, 20140026. https://doi.org/10.1098/rsbl.2014.0026
- Hamilton, W. D., & Zuk, M. (1982 October 22). Heritable true fitness and bright birds: A role for parasites? *Science*, 218, 384–387. https://doi.org/10.1126/science.7123238
- Havird, J. C., Hall, M. D., & Dowling, D. K. (2015). The evolution of sex: A new hypothesis based on mitochondrial mutational erosion. *Bioessays*, 37, 951–958. https://doi.org/10.1002/bies.201500057
- Hegarty, M. (2004). Mechanical reasoning by mental simulation. Trends in Cognitive Sciences, 8, 280–285. https://doi.org/10.1016/j.tics.2004.04.001
- Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: Individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, 34, 151–176. https://doi.org/ 10.1016/j.intell.2005.09.005

- Herman, J. F., & Siegel, A. W. (1978). The development of cognitive mapping of the large-scale environment. *Journal of Experimental Child Psychology*, 26, 389–406. https://doi.org/10.1016/0022-0965(78)90120-0
- Horn, J. L. (1968). Organization of abilities and the development of intelligence. *Psychological Review*, 75, 242–259. https://doi.org/10.1037/h0025662
- Huttenlocher, J., Newcombe, N., & Vasilyeva, M. (1999). Spatial scaling in young children. Psychological Science, 10, 393–398. https://doi.org/10.1111/1467-9280.00175
- Hyde, J. S., Fennema, E., & Lamon, S. (1990). Gender differences in mathematics performance: A meta-analysis. Psychological Bulletin, 107, 139–155. https://doi.org/ 10.1037/0033-2909.107.2.139
- James, T. W., & Kimura, D. (1997). Sex differences in remembering the locations of objects in an array: Location-shifts versus local exchanges. *Evolution and Human Behavior*, 18, 155–163. https://doi.org/10.1016/S1090-5138(97)00004-4
- Janicke, T., Häderer, I. K., Lajeunesse, M. J., & Anthes, N. (2016). Darwinian sex roles confirmed across the animal kingdom. *Science Advances*, 2, Article e1500983. https://doi.org/10.1126/sciadv.1500983
- Jardine, R., & Martin, N. G. (1983). Spatial ability and throwing accuracy. Behavior Genetics, 13, 331–340. https://doi.org/10.1007/BF01065771
- Jašarević, E., Williams, S. A., Roberts, R. M., Geary, D. C., & Rosenfeld, C. S. (2012). Spatial navigation strategies in *Peromyscus*: A comparative study. *Animal Behaviour*, 84, 1141–1149. https://doi.org/10.1016/j.anbehav.2012.08.015
- Johnson, E. S. (1984). Sex differences in problem solving. Journal of Educational Psychology, 76, 1359–1371. https://doi.org/10.1037/0022-0663.76.6.1359
- Johnson, W., & Bouchard, T. J., Jr. (2005). The structure of human intelligence: It is verbal, perceptual, and image rotation (VPR), not fluid and crystallized. *Intelligence*, 33, 393–416. https://doi.org/10.1016/j.intell.2004.12.002
- Johnson, W., & Bouchard, T. J., Jr. (2007). Sex differences in mental abilities: G masks the dimensions on which they lie. Intelligence, 35, 23–39. https://doi.org/10.1016/j. intell.2006.03.012
- Jung, R. E., & Haier, R. J. (2007). The Parieto-frontal integration theory (P-FIT) of intelligence: Converging neuroimaging evidence. *Behavioral and Brain Sciences*, 30, 135–154. https://doi.org/10.1017/s0140525x07001185
- Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individualdifferences perspective. *Psychonomic Bulletin & Review*, 9, 637–671. https://doi.org/ 10.3758/BF03196323
- Kell, H. J., Lubinski, D., Benbow, C. P., & Steiger, J. H. (2013). Creativity and technical innovation: Spatial ability's unique role. *Psychological Science*, 24, 1831–1836. https://doi.org/10.1177/0956797613478615
- Kovacs, K., & Conway, A. R. (2016). Process overlap theory: A unified account of the general factor of intelligence. *Psychological Inquiry*, 27, 151–177. https://doi.org/ 10.1080/1047840X.2016.1153946
- Law, D. J., Pellegrino, J. W., & Hunt, E. B. (1993). Comparing the tortoise and the hare: Gender differences and experience in dynamic spatial reasoning tasks. *Psychological Science*, 4, 35–40. https://doi.org/10.1111/j.1467-9280.1993.tb00553.x
- Leigh, S. R. (1996). Evolution of human growth spurts. American Journal of Physical Anthropology, 101, 455–474. https://doi.org/10.1002/(SICI)1096-8644(199612) 101:4<455: AID-AJPA2>3.0.CO;2-V
- Levine, S. C., Vasilyeva, M., Lourenco, S. F., Newcombe, N., & Huttenlocher, J. (2005). Socioeconomic status modifies the sex differences in spatial skill. *Psychological Science*, 16, 841–845. https://doi.org/10.1111/j.1467-9280.2005.01623.x
- Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial abilities: A meta-analysis. *Child Development*, 56, 1479–1498. https://doi. org/10.2307/1130467
- Lucon-Xiccato, T., & Bisazza, A. (2017). Sex differences in spatial abilities and cognitive flexibility in the guppy. *Animal Behaviour*, 123, 53–60. https://doi.org/10.1016/j. anbehav.2016.10.026
- MacDonald, D. H., & Hewlett, B. S. (1999). Reproductive interests and forager mobility. *Current Anthropology*, 40, 501–523. https://doi.org/10.1086/200047
- Matthews, M. H. (1992). Making sense of place: Children's understanding of large-scale environments. Savage, MD: Barnes & Noble Books.
- McGrew, K. S. (2009). CHC theory and the human cognitive abilities project: Standing on the shoulders of the giants of psychometric intelligence research. *Intelligence*, 37, 1–10. https://doi.org/10.1016/j.intell.2008.08.004
- Medin, D. L., & Atran, S. (Eds.). (1999). Folkbiology. Cambridge, MA: MIT Press/Bradford Book.
- Mix, K. S., Levine, S. C., Cheng, Y. L., Young, C., Hambrick, D. Z., Ping, R., & Konstantopoulos, S. (2016). Separate but correlated: The latent structure of space and mathematics across development. *Journal of Experimental Psychology: General*, 145, 1206–1227. https://doi.org/10.1037/xge0000182
- Moè, A., Jansen, P., & Pietsch, S. (2018). Childhood preference for spatial toys. Gender differences and relationships with mental rotation in STEM and non-STEM students. *Learning and Individual Differences*, 68, 108–115. https://doi.org/10.1016/j. lindif.2018.10.003
- Moore, D. S., & Johnson, S. P. (2008). Mental rotation in human infants: A sex difference. Psychological Science, 19, 1063–1066. https://doi.org/10.1111/j.1467-9280.2008.02200
- Muller, H. J. (1964). The relation of recombination to mutational advance. *Mutation Research*, 1, 2–9. https://doi.org/10.1016/0027-5107(64)90047-8
- Munroe, R. H., Munroe, R. L., & Brasher, A. (1985). Precursors of spatial ability: A longitudinal study among the Logoli of Kenya. *The Journal of Social Psychology*, 125, 23–33. https://doi.org/10.1080/00224545.1985.9713505
- Murray, E. A., Wise, S. P., & Graham, K. S. (2018). Representational specializations of the hippocampus in phylogenetic perspective. *Neuroscience Letters*, 680, 4–12. https:// doi.org/10.1016/j.neulet.2017.04.065

Nazareth, A., Huang, X., Voyer, D., & Newcombe, N. (2019). A meta-analysis of sex differences in human navigation skills. *Psychonomic Bulletin & Review, 26*, 1503–1528. https://doi.org/10.3758/s13423-019-01633-6

- Newcombe, N., Huttenlocher, J., Drummey, A. B., & Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. *Cognitive Development*, 13, 185–200. https://doi.org/ 10.1016/S0885-2014(98)90038-7
- Newcombe, N. S., Bandura, M. M., & Taylor, D. C. (1983). Sex differences in spatial ability and spatial activities. Sex Roles, 9, 377–386. https://doi.org/10.1007/ BF00289672
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* New York: Oxford University Press.
- Parker, G. A., Baker, R. R., & Smith, V. G. F. (1972). The origin and evolution of gamete dimorphism and the male-female phenomenon. *Journal of Theoretical Biology*, 36, 529–553. https://doi.org/10.1016/0022-5193(72)90007-0
- Pellegrino, J. W., Alderton, D. L., & Shute, V. J. (1984). Understanding spatial ability. Educational Psychologist, 19, 239–253. https://doi.org/10.1080/ 00461528409529300
- Perdue, B. M., Snyder, R. J., Zhihe, Z., Marr, M. J., & Maple, T. L. (2011). Sex differences in spatial ability: A test of the range size hypothesis in the order *Carnivora. Biology Letters*, 7, 380–383. https://doi.org/10.1098/rsbl.2010.1116
- Peters, M. (1997). Gender differences in intercepting a moving target. Journal of Motor Behavior, 29, 290–296. https://doi.org/10.1080/00222899709600016
- Pinker, S., & Bloom, P. (1990). Natural language and natural selection. Behavioral and Brain Sciences, 13, 707–784. https://doi.org/10.1017/S0140525X00081061
- Plavcan, J. M. (2012). Body size, size variation, and sexual size dimorphism in early Homo Current Anthropology. 53 pp. S409–S423). https://doi.org/10.1086/667605
- Plavcan, J. M., & van Schaik, C. P. (1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 103, 37–68. https://doi.org/10.1002/(SICI)1096-8644(199705)103:1<37:AID-AJPA4>3.0.CO:2-A
- Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *The Journal of Anatomy*, 197, 335–359. https://doi.org/10.1046/ j.1469-7580.2000.19730335.x
- Reboreda, J. C., Clayton, N. S., & Kacelnik, A. (1996). Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *Neuroreport*, 7, 505–508. https://doi.org/10.1097/00001756-199601310-00031
- Schiff, W., & Oldak, R. (1990). Accuracy of judging time to arrival: Effects of modality, trajectory, and gender. Journal of Experimental Psychology: Human Perception and Performance, 16, 303–316. https://doi.org/10.1037/0096-1523.16.2.303
- Schlaggar, B. L., & McCandliss, B. D. (2007). Development of neural systems for reading. Annual Review of Neuroscience, 30, 475–503. https://doi.org/10.1146/annurev. neuro.28.061604.135645
- Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 533–549). New York: Oxford University Press.
- Spearman, C. (1904). "General intelligence," objectively determined and measured. The American Journal of Psychology, 15, 201–292. https://doi.org/10.2307/1412107
- Spelke, E., Lee, S. A., & Izard, V. (2010). Beyond core knowledge: Natural geometry. Cognitive Science, 34, 863–884. https://doi.org/10.1111/j.1551-6709.2010.01110.x
- Spelke, E. S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. Psychological Review, 99, 605–632. https://doi.org/10.1037/0033-295X.99.4.605
- Sponheimer, M., & Lee-Thorp, J. A. (1999). Isotopic evidence for the diet of an early hominid, Australopithecus africanus. *Science*, 283, 368–370. https://doi.org/ 10.1126/science.283.5400.368

- Spritzer, M. D., Solomon, N. G., & Meikle, D. B. (2005). Influence of scramble competition for mates upon the spatial ability of male meadow voles. *Animal Behaviour*, 69, 375–386. https://doi.org/10.1016/j.anbehav.2004.03.015
- Thomson, G. H. (1916). A hierarchy without a general factor. British Journal of Psychology, 8, 271–281. https://doi.org/10.1111/j.2044-8295.1916.tb00133.x
- Thorndike, R. L. (1927). The measurement of intelligence. New York: Teachers College. https://doi.org/10.1037/11240-000
- Thurstone, L. L., & Thurstone, T. G. (1941). Factorial studies of intelligence. *PsychometricMonographs, No.* 2, whole.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), Sexual selection and the descent of man 1871–1971 (pp. 136–179). Chicago, IL: Aldine Publishing.
- Uttal, D. H., Meadow, N. G., Tipton, E., Hand, L. L., Alden, A. R., Warren, C., & Newcombe, N. S. (2013). The malleability of spatial skills: A meta-analysis of training studies. *Psychological Bulletin*, 139, 352–402. https://doi.org/10.1037/ a0028446
- Vashro, L., & Cashdan, E. (2015). Spatial cognition, mobility, and reproductive success in northwestern Namibia. *Evolution and Human Behavior*, 36, 123–129. https://doi.org/ 10.1016/j.evolhumbehav.2014.09.009
- Vernon, P. E. (1965). Ability factors and environmental influences. American Psychologist, 20, 723–733. https://doi.org/10.1037/h0021472
- Voyer, D., Postma, A., Brake, B., & Imperato-McGinley, J. (2007). Gender differences in object location memory: A meta-analysis. Psychonomic Bulletin & Review, 14, 23–38. https://doi.org/10.3758/BF03194024
- Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration and consideration of critical variables. *Psychological Bulletin*, 117, 250–270. https://doi.org/10.1037/0033-2909.117.2.250
- Wai, J., Holges, J., & Makel, M. C. (2018). Sex differences in ability tilt in the right tail of cognitive abilities: A 35-year examination. *Intelligence*, 67, 76–83. https://doi.org/ 10.1016/j.intell.2018.02.003
- Walker, R. S., & Bailey, D. H. (2013). Body counts in lowland south American violence. Evolution and Human Behavior, 34, 29–34. https://doi.org/10.1016/j. evolhumbehav.2012.08.003
- Warne, R. T., & Burningham, C. (2019). Spearman's g found in 31 non-Western nations: Strong evidence that g is a universal phenomenon. *Psychological Bulletin*, 145, 237–272. https://doi.org/10.1037/bul0000184
- Watson, N. V., & Kimura, D. (1991). Nontrivial sex differences in throwing and intercepting: Relation to psychometrically-defined spatial functions. *Personality and Individual Differences*, 12, 375–385. https://doi.org/10.1016/0191-8869(91)90053-F
- Wellman, H. M., & Gelman, S. A. (1992). Cognitive development: Foundational theories of core domains. *Annual Review of Psychology*, 43, 337–375. https://doi.org/ 10.1146/annurev.ps.43.020192.002005
- Wilcox, T., Alexander, G. M., Wheeler, L., & Norvell, J. M. (2012). Sex differences during visual scanning of occlusion events in infants. *Developmental Psychology*, 48, 1091–1105. https://doi.org/10.1037/a0026529
- Williams, G. C., & Mitton, J. B. (1973). Why reproduce sexually? Journal of Theoretical Biology, 39, 545–554. https://doi.org/10.1016/0022-5193(73)90067-2
- Wood, B. M., Harris, J. A., Raichlen, D. A., Pontzer, H., Sayre, K., Sancilio, A., & Jones, J. H. (2021). Gendered movement ecology and landscape use in Hadza hunter-gatherers. *Nature Human Behaviour*, 5, 436–446. https://doi.org/10.1038/ s41562-020-01002-7
- Xiao, N., & Zhang, X. (2021). Interest in spatial activities predicts young children's spatial ability development: A two-year longitudinal study. *Contemporary Educational Psychology*, 64, Article 101943. https://doi.org/10.1016/j.cedpsych.2021.101943