



Sex differences in spatial navigation and perception in human adolescents and emerging adults[☆]

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ABSTRACT

Males typically outperform females on spatial tasks, beginning early in life and continuing into adulthood. This study aimed to characterize age and sex differences in human spatial ability using a virtual Water Maze Task (vWMT), which is based on the classic Morris water maze spatial navigation task used in rodents. Performance on the vWMT and on a task assessing visuospatial perception, Mental Rotations Test (MRT), was examined in 33 adolescents and 39 emerging adults. For the vWMT, significant effects of age and sex were observed for path length in the target region (narrower spatial sampling), and heading error, with emerging adults performing better than adolescents, and an overall male advantage. For the MRT, males scored higher than females, but only in emerging adulthood. Overall, sex differences in visuospatial perception (MRT) emerge differently from those observed on a classic navigation task, with age and sex-specific superior vWMT performance likely related to the use of more efficient strategies. Importantly, these results extend the developmental timeline of spatial ability characterization to include adolescent males and females performing a virtual version of the classic vWMT.

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1. Introduction

As early as infancy, children have the ability to localize spatial information based on the relationship between an event and environmental features (Keating et al., 1986). There are ample data available from cohorts studied in early childhood (5 years of age and younger) demonstrating the development of place learning (Hupbach et al., 2011; Ribordy et al., 2013; Sluzenski et al., 2004) and scene recognition (Chai et al., 2010) abilities. In general, the ability to process spatial and contextual information appears to mature around age eight on a variety of large-environment spatial tasks (Overman et al., 1996) and around age 9 on a computerized spatial navigation task (Laurance et al., 2003). Not surprisingly, dynamic and rapid structural and functional brain changes beyond childhood and into adolescence (Blakemore, 2012; Paus, 2005;

Spear, 2000) underlie significant improvements across a variety of cognitive domains (Casey et al., 2005; Paus, 2005), including spatial ability (Klingberg, 2006; Piper et al., 2011; Sowell et al., 2001). Results from a functional magnetic resonance imaging (fMRI) study of scene complexity demonstrated greater activation of a brain region implicated in spatial processing, the parahippocampal gyrus (PHG), for high-complexity versus low-complexity scenes in healthy participants ages 8–24 years (Chai et al., 2010). Differences in brain activation not only increased with age, but also were associated with superior memory formation.

The Morris Water Maze Task (WMT) was developed in 1981 as an alternative to the radial arm maze to study spatial learning in rodents (Wenk, 2004). The Morris WMT has since been used extensively in animal research to probe spatial memory ability (Morris, 1984), with many variants of this task being used over the past 30 years to study the neurobiology (Clark et al., 2013) and neuropharmacology (Cha et al., 2007; Markwiese et al., 1998; Swartzwelder et al., 2014) of spatial learning, as well as for developing neurobiological models of neurocognitive disorders (D'Hooge and De Deyn, 2001). Successful spatial learning in the WMT is characterized by execution of (more or less) direct trajectories to a hidden, submerged escape platform from multiple starting locations

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and persistence in searching at the platform location when it is removed for a probe trial. It is generally accepted that optimal performance in the WMT is based on the use of spatial information provided from visual environmental cues, for example, based on the fixed spatial relationship between the platform and the available visual cues (O'Keefe and Nadel, 1978) or the contributions of visual cues to the selection of trajectories to the platform location (Knierim and Hamilton, 2011). The hippocampus plays an integral role in memory function; it is critical for processing spatial and contextual information and for generating and maintaining representations utilized for navigating in space (Jarrard, 1993; O'Keefe and Nadel, 1978; Wegman et al., 2014). To this end, rodents with hippocampal lesions have been shown to exhibit deficits in spatial learning on this task, as evidenced by an inability to efficiently navigate to the hidden platform (Morris et al., 1982; Sutherland et al., 1982). Prominent sex differences also have been reported in rodents on the WMT, with adult male rats demonstrating better navigation to the hidden platform than female counterparts (Keeley et al., 2013; Perrot-Sinal et al., 1996; Roof and Stein, 1999; Saucier et al., 2008), although some studies report no differences (Bucci et al., 1995). While most examination of developmental differences in performance of the WMT in rodents has been within the context of alcohol or drug challenges (Cha et al., 2007; Markwiese et al., 1998; Sircar and Sircar, 2005), or hormone manipulations (Roof, 1993), there is some limited evidence of age-related improvements in acquisition (reduced escape latency and shorter swim distances) and retention (more time spent in goal quadrant) from adolescence to adulthood (Markwiese et al., 1998).

It has recently become possible to translate WMT findings from preclinical to clinical populations (Hamilton et al., 2009), given the development of virtual versions of the WMT (vWMT) to assess spatial ability in humans (Hamilton et al., 2009; Astur et al., 2002; Driscoll et al., 2005; Herting and Nagel, 2012; Moffat and Resnick, 2002; Newhouse et al., 2007; Sneider et al., 2011, 2013a,b; Woolley et al., 2010). Although to date no human developmental data are available to assess age-related improvements in performance on the vWMT, a cross sectional comparison of healthy volunteers across a large age span (6–67 years of age) demonstrates superior performance in adolescents and younger-adults relative to children and relative to older individuals on a variant of a spatial memory task, the Memory Island task (Piper et al., 2011). Furthermore, effects of age and sex examined in a modified version of the WMT in young adults and older adults (mid-50s) indicated that young adults performed better than older adults, again with a male advantage being evident in both age groups (Schoenfeld et al., 2010). In a virtual version of the WMT, a study of 8–10 year old prepubertal children likewise showed a male advantage in spatial ability, with boys performing better on the retention trial (probe) than girls (Newhouse et al., 2007). On the other end of the age spectrum, WMT performance declines with aging (Driscoll et al., 2005). In addition, WMT performance examined in combination with functional magnetic resonance imaging (fMRI) has been useful for elucidating underlying neurobiology associated with performance differences in healthy adults and in substance abusers, confirming that the hippocampus shows significant activation during task performance (Sneider et al., 2013b). From a translational perspective, impaired spatial navigation on the virtual WMT has been observed in patients with unilateral hippocampal resections (Astur et al., 2002) and in amnesic participants with hippocampal damage (Goodrich-Hunsaker et al., 2010), which is similar to observations found in animal hippocampal lesion studies. Thus, applications of the virtual WMT have been invaluable for investigating spatial learning and memory and for validating rodent models of neurocognitive disorders and treatments for memory disorders in humans (D'Hooge and De Deyn, 2001). While new tasks and quantitative statistical approaches for assessing place learning have

Table 1
Participant demographics.

	Adolescents (n = 33)	Young adults (n = 39)	p
Age (years)	13.6 ± 0.9 (range 12.3–15.0)	21.6 ± 1.7 (range 18.5–25.5)	<.001
Education (years)	7.5 ± 1.48	14.7 ± 1.5	<.001
SES ^a	50.1 ± 11.1	50.6 ± 11.0	.87
Handedness	28R, 4L, 1A	37R, 2L	–
Female	52%	44%	–
Ethnicity ^b	97%	97%	–
Race ^c	Non-Hispanic 85% Caucasian	non-Hispanic 64% Caucasian	–

Data represent mean values ± SD. *Abbreviations:* SES, socioeconomic status.

^a SES unavailable for n = 1 adolescent and n = 1 emerging adult.

^b Ethnicity: Hispanic vs. non-Hispanic.

^c Race: Caucasian vs. non-Caucasian (classification consisted of Asian, African American, and other).

become available and have been applied to study participants age 18 and older (Furman et al., 2014; Nardi et al., 2011), to date, the virtual WMT has been underemployed for elucidating the neurobiological role of the hippocampus during adolescence, a time when the brain is rapidly developing and when the hippocampus is particularly vulnerable to insults such as alcohol and drug use (Chin et al., 2010), and is structurally and functionally altered in adolescents with depression and other psychiatric conditions (Whittle et al., 2014).

Accordingly, the purpose of the present study is to fill a critical gap in the literature regarding healthy developmental changes in spatial ability, along with an examination of sex differences, using a virtual version of the classic WMT. Given reports that visual perception may influence spatial learning on tests such as the vWMT (Astur et al., 2004), the Mental Rotations Test (MRT) also was administered to assess visuospatial ability. Performance on mental rotation tests likewise demonstrate robust sex differences, with men demonstrating better performance than women (Astur et al., 2004; Linn and Petersen, 1985; Parsons et al., 2004), and sex differences in children as early as kindergarten, with kindergarten boys outperforming age-matched girls on rotational and translational elements of a spatial transformation task (transforming two separate halves of a shape into a whole shape) (Levine et al., 1999) and in preadolescents on house plans, mirror images and 3D object rotation tasks (Kerns and Berenbaum, 1991). Inclusion of the MRT permits an ability to dissociate whether hypothesized developmental improvements and male-related advantages in spatial ability reflect better memory-related function or better visuospatial perception, or both.

2. Method

2.1. Participants

The study sample consisted of 33 healthy adolescents (ranging in age from 12.3 to 15.0 years, mean age 13.6 ± 0.9 years) and 39 healthy emerging adults (ranging in age from 18.5 to 25.5 years, mean age 21.6 ± 1.7 years). Demographic details are provided in Table 1, including socioeconomic status (SES) (Barratt, 2006) and handedness. Participants were recruited through local advertisement and screened by telephone interview to ensure they met criteria for inclusion in the study. All aspects of the clinical research protocol were reviewed and approved by the Institutional Review Board of McLean Hospital (Belmont, MA, USA). After a complete description of the study, all participants and their parent(s) or guardian(s) (adolescent group only) provided written informed

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