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Cognitive and Affective Aspects of Thigmotaxis Strategy in Humans

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The present article describes the cognitive and emotional aspects of human thigmotaxis (a wall-following spatial strategy) during exploration of virtual and physical spaces. The authors assessed 106 participants with spatial and nonspatial performance-based learning–memory tasks and with fear and anxiety questionnaires. The results demonstrate that thigmotaxis plays a distinct role at different phases of spatial learning. The 1st phase shows a positive correlation between thigmotaxis and general phobic avoidance, whereas there is no association between thigmotaxis and general phobic avoidance during later phases of learning. Furthermore, participants who underperformed in working memory tests and in a spatial construction task exhibited greater thigmotaxis and a higher potential for fear response. Findings are interpreted in the framework of interactions among emotion-, action-, and knowledge-controlled spatial learning theories.

Keywords: thigmotaxis, spatial exploration, cognitive map, fear, anxiety

Research on the analysis of spatial strategies draws a distinction between action- and knowledge-based spatial orientation (Hartley, Maguire, Spiers, & Burgess, 2003). *Thigmotaxis*, the way in which an organism organizes behavior relative to tactile stimuli, is a phylogenetically old and energetically inexpensive exploratory strategy that embodies both action- and knowledge-based explorations (Creed & Miller, 1990; Fraenkel & Gunn, 1961). As such, thigmotaxis provides an opportunity to examine relations among emotion, action, knowledge, and the temporal dynamics of spatial learning.

Stimulus–Response Route Following

Action-based route-following strategies involve a behavioral sequence based on an egocentric frame of reference that—through reinforcement, punishment, or extinction—associates cues with actions in a place and time. In guidance-based navigation (O'Keefe & Nadel, 1978), spatial orientation is composed of actions acquired during an experiential learning history, beginning at a defined start position (usually identified by the presence of a local landmark), which triggers a specific response sequence leading from the start position to a goal (Reid & Staddon, 1998).

Within this system, generalized goal-relevant actions include appropriate responses to a localized stimulus cue and the sequential use of navigational landmarks associated with the action. Although learning obviously occurs, the organism does not integrate these local landmarks into a system that includes spatial relations; instead, it encodes only sequential associations between cues and actions.

Models examining route following do not explain how an organism acquires spatial knowledge; instead, they describe specific action sequences. These models explain why numerous spatial errors occur during route following (e.g., Reid & Reid, 2005; Wang & Spelke, 2004). Generally, these models claim that such errors are due to limited memory capacity for successive action patterns occurring under novel circumstances at different times and in different contexts.

Egocentric models of route following (e.g., Gallistel, 1990; Hartley et al., 2003; Wang & Spelke, 2004) rely on distinct mechanisms to account for spatial-orientation errors that occur mainly in large scale spaces. First, the models invoke a dynamic updating of previously visited landmarks and completed actions. Second, the models propose that, during updating, the occurrence of integration error between the selected path and action patterns is necessary (Gallistel, 1990; Whishaw, Hines, & Wallace, 2001).

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In these models, the temporal organization of successive events organizes behavior. Hence, these models adequately describe the acquisition and execution of a path (route) in restricted and familiar space, but they do not describe how an organism orients in a new space, finds short cuts, or finds alternative routes when new obstacles arise along the path route (Reid & Reid, 2005).

Cognitive Exploration

In contrast, knowledge-based models of spatial behavior postulate the existence of a mental construction that serves to mediate interactions among behavior, goals, and an integrated system of navigational objects (cues and/or landmarks). Theoretically, this mental construction aids in the organization of a coherent view of space and relates that view to sets of latent behavioral strategies, each of which might be used to search the space or to locate and/or relocate places (e.g., goals) in that space. This mental construction consists of either a viewer-dependent apperception of the geometric properties of the environment (e.g., Cheng, 1986) or of a viewer-independent abstract knowledge system built from various cognitive modules that construct and upload coherent spatial information (O'Keefe & Nadel, 1978). Hence, these approaches describe an abstract mental system that builds up contextual information over time but limits the importance of temporal information itself. This context-specific spatial knowledge may serve as a navigational guide by providing detailed information about the location of relevant goals within a coherent system of related salient navigational landmarks. Nevertheless, it is currently a matter of intense theoretical debate regarding how context-specific spatial knowledge translates into coherent spatial navigation (Wang & Spelke, 2004). Thigmotaxis, an automatic, biologically primitive strategy for exploring space, may provide a lens through which the nature of this dynamic processing in humans' spatial learning may be revealed.

Thigmotaxis

Although thigmotaxis is a well-characterized behavioral tactic commonly observed in nonhuman animals, its role in human navigation is yet to be explained. Etymologically, the term thigmotaxis is based on the Greek word *thigma*, meaning contact with an object. The expression *taxis* refers to the reaction of an organism to external stimuli by movement in a specific direction. When an animal initially explores an enclosed place, it tends to stay in close contact with the perimeter of that space (Barnett, 1968). One may quantify the tendency to avoid the inner zone of an open field by measuring either the time or the path length that an organism spends in close contact with the wall. This behavior is sometimes known as wall-following, wall-touching, or centrophobic behavior (Besson & Martin, 2004; Creed & Miller, 1990; Fraenkel & Gunn, 1961). Thigmotaxis is especially prominent on the initial encounter of a novel space, is a dominant factor early in the exploration of an enclosed space, and is not associated with the rate of acquisition or quality of retrieval of spatial knowledge (Choleris, Thomas, Kavaliers, & Prato, 2001). Instead, thigmotaxis appears to help an organism define the boundary of an enclosed space and serves as a "home base" from which the construction of a spatial map may occur. Obviously, thigmotaxis permits the organism to determine the boundaries of an enclosed space; its continued use, however, prevents other spatial strategies that permit the formation of a cognitive map of an environment. Hence, the continued use of thigmotaxis prohibits an organism from locating or relocating an escape platform during the middle and later phases of spatial learning in a Morris-type maze task (Graziano, Petrosini, & Bartoletti, 2003; Kallai, Makany, Karadi, & Jacobs, 2005).

Damage to the lateral caudate putamen influences many of the exploratory strategies exhibited by participants in spatial learning experiments (McDonald & White, 1994), yet a primary effect is a dramatic increase in thigmotaxis. Specific lesions to these dorsomedial striatal areas result in an impairment of acquisition and expression of learned responses to spatial cues (Devan, McDonald, & White, 1999).

Thigmotaxis is frequently found in highly anxious animals (Jeanson et al., 2003; Ohl, Sillaber, Binder, Keck, & Holsboer, 2001; Pellow & File, 1986). Laboratory investigations studying the effects of anxiolytic drugs reveal that thigmotaxis is one manifestation of a biologically prepared fear reaction and that it plays an important role in the formation of anxiety-induced avoidance behavior and cognition. Some argue it may serve as a model for the analysis of human anxiety disorders (Treit & Fundytus, 1988).

Thigmotaxis as defined above is a primordial, genetically grounded type of behavior and an ecologically important strategy used by humans and other animals for spatial exploration (Creed & Miller, 1990; Jeanson et al., 2003; Kallai et al., 2005; Simon, Dupuius, & Constentin, 1994) mainly in open-field and arena–maze experiments. Although studies with nonhuman animals describe thigmotaxis behaviorally, its relationship to human cognitive or affectively driven performance remains to be determined.

Current research in animals and humans stresses that novel spatial situations trigger thigmotaxis. It is typically manifested when searching boundaries of an enclosed space to find a starting point (home base) for further spatial exploration. Its presence also necessarily delays or inhibits the exploration of the central zone of a novel space until the organism identifies salient or relevant cues (Besson & Martin, 2004; Kallai et al., 2005). Once identified, these salient or relevant cues serve as elements of a spatial or cognitive map. In the early phase of map construction, the salient or relevant cues are not integrated into a cognitive map; instead, they are only cues with emotional significance for approach or avoidance.

Although measures of thigmotaxis taken during the first phase of exploration do not predict the eventual success of spatial learning (Lipp & Wolfer, 1998), thigmotaxis may serve as an essential element in the control of the dynamics of spatial learning. The major transient point of a series of learning trials that can predict the success of spatial acquisition occurs during the middle trials when a home base has been established, egocentric space calibration has occurred, and the acquisition of the structure of Euclidean space has begun (Kallai et al., 2005).

Fear and Anxiety

The strategies that an organism uses to explore a novel environment are guided by behavior economy and factors related to individual differences in spatial neophobia, the organism's perceived ability to escape from novel environments, and the organism's tolerance for ambiguous situations. Spatial anxiety (Lawton, 1994), sometimes known as spatial neophobia, and the fear of losing one's way (Kozlowski & Bryant, 1997) differ fundamentally from anxiety in humans. Fear and neophobia are related to low fear-response threshold in fear-provoking situations, originating from inborn escape-reaction sensitivity (Kagan et al., 1990; Klein, 1981). The appearance of these types of fear (some might call it caution) is marked by elevated safety-seeking strategies that influence (a) actual behavioral sequences (Jeanson et al., 2003), (b) tactics used to explore unfamiliar places (Bryant, 1997), (c) the maintenance of attentive focus on the geometrical features of the environment (Kozlowski & Bryant, 1997), (d) the ability to memorize spatial locations (Evans, Skorpanich, Gänling, Bryant, & Bresolini, 1984), (e) the speed and fluency of the navigation movements and the mobilization of configuration knowledge (Schmitz, 1997), and (f) the integration of ego-allocentric-based spatial information (Jacobs & Nadel, 1999; Kallai, Kosztolanyi, Osvath, & Jacobs, 1999).

In light of several methodological complexities, we assessed a carefully selected sample of participants with different levels of fear and anxiety. Our purpose was to examine cognitive and emotional factors that may underpin thigmotaxis in virtual and physical arena mazes and in different spatial and nonspatial learning and memory tasks. First, because thigmotaxis plays different roles in the various phases of spatial learning in humans, our aim was to identify emotional and cognitive factors underlying the use of thigmotaxis during different phases of spatial learning. Second, we attempted to determine the statistical relations among measures of the identified emotional and cognitive factors and of the manifestation of thigmotaxis. Finally, we characterized the role thigmotaxis plays in human orientation and way finding in a novel environment.

Method

Participants

A total of 106 participants took part in the present study. Thirty-nine male participants, ranging in age from 19 to 26 years, with a mean age of 21.41 years (*SD* = 1.8), and 67 female participants, ranging in age from 19 to 26 years, with a mean age of 21.40 years (*SD* = 1.5), were recruited through advertisements and received compensation for participating. The experimenter described the experimental procedures as a part of the informed consent procedure. No participant had previous psychiatric illnesses or physical disabilities that could interfere with the completion of the computer-based or physical spatial tasks. Anticipating a possible distortion coming from individual differences of computer gaming experience (Waller, 2000), participants with self-reported computer game playing time exceeding 30 min/week were ineligible for the study. The study procedures met or exceeded standards established by the Helsinki Declaration of 1975, as revised in 1983.

Apparatus

Computer-generated arena (CGA). A desktop-based computer program was used to record and measure search strategies that participants used to locate and relocate a specific place in a computer-generated space (for details see Jacobs, 1997; Jacobs, Laurance, & Thomas, 1997).

The participants viewed a monitor, attached to a standard PC, which displayed a circular arena located within a square room. Each wall in the room had a distinctive texture and contained local icons consisting of windows or arches, which provided means by which participants could orient themselves within the virtual space. The participants viewed the arena from a first-person perspective as though standing or moving on the floor of the arena.

Real arena maze (RAM). A large-scale physical environment was used to record and measure exploration strategies. This RAM was built to model the Morris-type maze task (Morris, 1984) in humans. The RAM task was first developed and described by Kallai et al. (2005; see Figure 1 for a picture and see http://www.aok.pte.hu/spacelab/ for further details).

The RAM apparatus consisted of a large, circular timber wall arena (6.5 m in diameter, 2.0 m in height, 33.0 m^2 in floor space, with an inner temperature of 20 ± 5 °C). Inside the arena, eight navigation objects were placed on 1-m high shafts. Each object had different fixed geometric cues that were unique in shape but equal in size and surface.

Three starting positions (A, B, C) were located equidistant around the edge of the west and south wall of the arena. A round target platform disc (50 cm in diameter) was placed in a fixed location within the northeast quadrant of the maze floor and at an equal distance from the three starting positions. The target was equipped with pressure-sensitive detectors. When the participant stepped on the target platform, a 60-dB tone was emitted. The participants received no other feedback on their performance. The location of the navigation cues and the target remained fixed across trials.

The RAM was equipped with doors on the west and south walls. The doors served as an entrance or an exit on a pseudorandom schedule. Before entering the RAM, participants were fitted with opaque swimming glasses, so that they could not obtain any visual

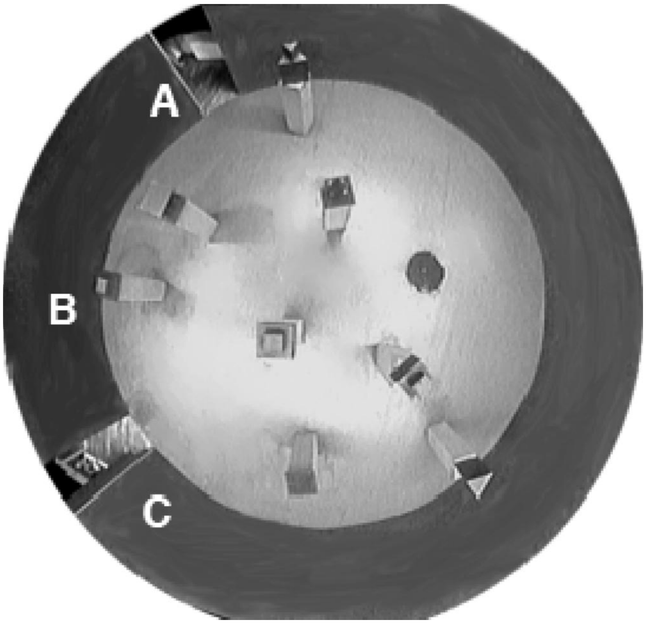

Figure 1. A bird’s-eye view perspective image taken from the real arena maze depicting the entrance and exit doors, the eight navigation objects, and the circular platform (target) on the floor. The three starting positions are indicated with white letters (A, B, C).

information on the layout that might have helped them to locate landmarks or the target. Spatial performance was recorded and scored by the EthoVision 3.0 video tracking system (Noldus, Spink, & Tegelenbosch, 2001).

Procedure

CGA. The experimenter seated participants in front of a 17-in. (43.18-cm) super video graphics array monitor, a pair of stereo speakers, and a joystick controlled by a standard desktop PC and read a set of standardized instructions (see Appendix). The CGA software displayed two types of rooms. The first was a practice room with no objects or platforms in it. The purpose of this room was to familiarize participants with the virtual environment and practice virtual locomotion in that environment. After becoming familiar with a virtual environment, the participants were teleported to the test room. The test room consisted of a circular arena within a bigger square room. The room had a floor with an irregular texture and a gray ceiling. Distal objects were placed on the walls. A blue rectangular target appeared on the floor (see Table 1 for a description of the parameters used in the practice and test rooms).

The target was visible in the first two probe trials (Probe 1 and Probe 2). In the test phase from Trial 1 to Trial 8, the target was invisible, though it remained in the same fixed location. The participants' task was to locate and relocate the target as quickly as possible on each trial. The position of the textured walls and the distal objects on them remained constant across all trials.

Recorded movement in CGA. The CGA software recorded movement in the virtual environment as a set of binary variables (vector coordinates) sampled at a rate of 35 frames/s. Hence, the software recorded virtual motion as a change in these coordinates across time. The CGA also calculated the latency to locate the target, the path length from the start position to contact with the target, and the path maps, which could be presented in a bitmap format from the full set of vector coordinates generated within each trial. These CGA calculations served as the basis of the statistical analyses.

Table 1
The Computer-Generated Arena (CGA) Structural and Motion Parameters

Parameter	Measurement
Room	
Room dimensions	512 × 512 × 128
Arena wall radius	50
Arena wall height	3.5
Target dimensions	10 × 10
Participant	
Participant eye height[a]	2.0
Field of view	50°
Motion[b]	
Move quantum	0.80
Turn quantum	1

Note. Unless otherwise indicated, all measurements are in Arena Units. The reader may consider an Arena Unit as the equivalent of a virtual meter.
[a] The PC monitor displays all views of the arena from a first-person perspective and as if the eyes of the participant are a certain user-defined distance (an "eye height") from the floor of the CGA rooms.
[b] The move quantum describes the shift in the participant's view of the CGA with each stroke of the up or down arrow. Similarly, the turn quantum describes the shift in the participant's view of the CGA with each stroke of the right or left.

Identifying thigmotaxis. Thigmotaxis, in the present context, is the portion of the path map that represents movement close to the arena wall (see Figure 2A). This is a summed value of every such motion pattern in the actual trial. In many cases, thigmotaxis reoccurred at the same section of the arena wall, so the final summed value may exceed 360° (the total circle of the arena wall). We measured thigmotaxis navigation strategies (represented in the following equations as CGATHIGM) in degrees and then transformed the value into Arena Units (virtual meters; vm). We calculated vm using the following formula:

$$\mathrm{CGATHIGM} = \frac{\pi}{180} * wall^\circ * r_{CGA}$$

where $wall^\circ$ is the degree of the measured overall distance between the initial wall touch and the terminal wall touch, and r_{CGA} is the radius of the CGA in Arena Units (50 Arena Units in this experiment).

To investigate temporal dynamics of thigmotaxis, we determined four different measures by collapsing individual trials into blocks. These blocks were as follows: first trial (Trial 1), early phase (the mean of Trials 2, 3, and 4), middle phase (the mean of Trials 5 and 6), and late phase (the mean of Trials 7 and 8). Furthermore, an overall measure was also calculated as the mean of the scores from all the trials (overall CGA thigmotaxis).

RAM. An assistant guided the participants into the RAM via a pseudorandomly chosen entrance door to either of the three starting positions (see Figure 1). The assistant instructed the participants to locate the target using the tactile navigational cues, which would help them find and learn the shortest route towards the platform. The assistant also instructed the participants to pay particular attention to the spatial relations among the landmarks after locating the escape platform and to remember the spatial relations among the navigation cues.

Each acquisition trial lasted a maximum of 300 s. If the participant failed to locate the target within 300 s, then a new trial was started. If the participant managed to locate the target, then an extra 15 s were given to provide time to explore the surrounding environment. There were seven consecutive acquisition trials with 2-min intertrial intervals. After completing the trial, an assistant guided the vision-occluded participant out of the maze.

RAM data collection. The variables included a measure of the contact with the arena wall in meters from trial to trial (RAMTHIGM). Following the CGATHIGM calculation described above, RAMTHIGM was transformed into meters for each trial. The participants' performance on each trial was recorded by a video camera fixed above the center of the arena. Two independent raters assessed thigmotaxis manually. Following the participants' path along with contact of the wall, the raters used a protractor to score thigmotaxis (see Figure 2B). The RAMTHIGM for each trial was transformed into meters using the formula:

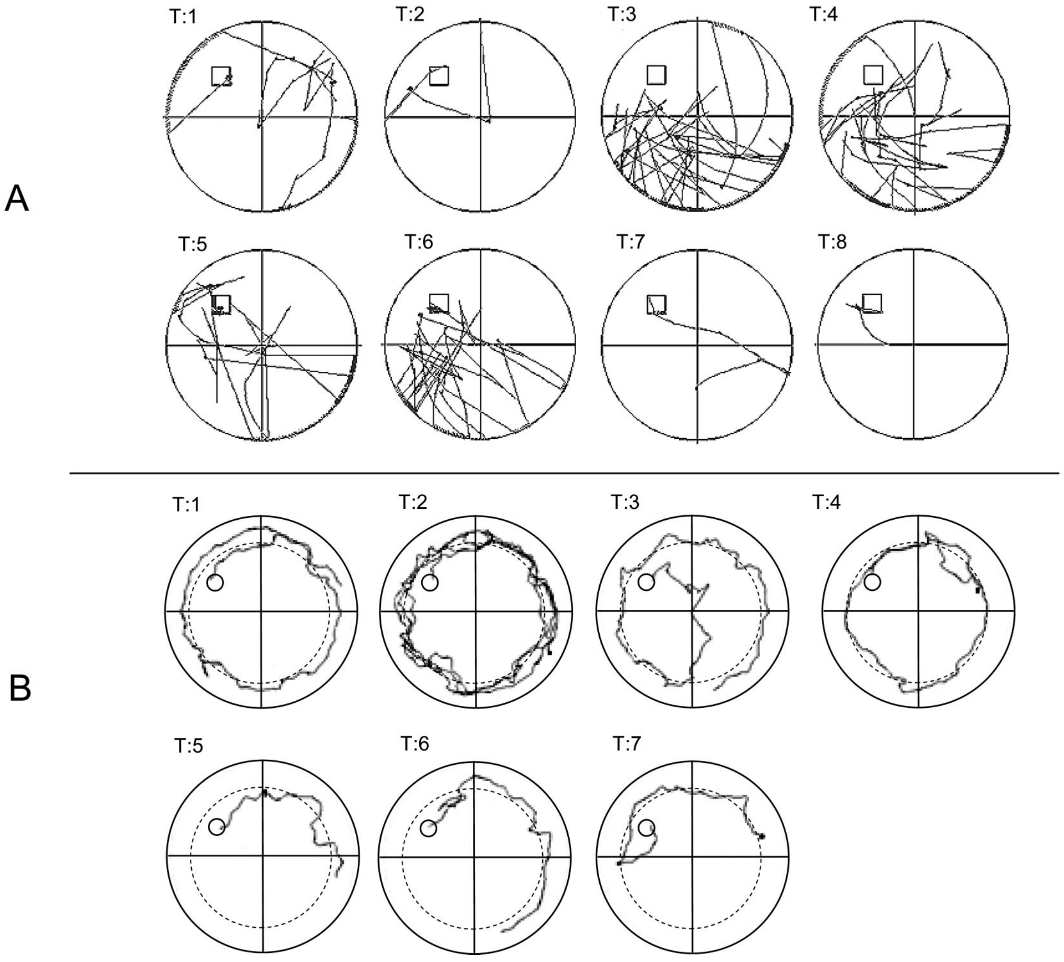

Figure 2. A: The circular computer-generated arena (CGA) is shown in a plane view with an imaginary division into four quadrants. The location of the platform is indicated on these maps as a square, and the navigation path is indicated with a continuous line. B: The circular real arena maze is shown in a plane view with the same imaginary divisions into the four quadrants as in the CGA. The division of inner and outer zones is shown with dotted lines. The navigation search path is indicated with a continuous line. T:1–T:8 = Trials 1–8.

$$\mathrm{RAMTHIGM} = \frac{\pi}{180} * wall^{\circ} * r_{RAM}$$

where $r_{RAM} = 3.25$ m, which was the radius of the RAM.

For analyzing the temporal dynamics of thigmotaxis in the RAM, we used the same four phases as described in the case of the CGA. The phases were first trial (Trial 1), early phase (the mean of Trials 2, 3, and 4), middle phase (the mean of Trials 5 and 6), and late phase (Trial 7). Furthermore, an overall measure was also calculated as the mean of the scores from all the trials (overall RAM thigmotaxis).

Map construction posttest. After leaving the RAM, the participants were asked to construct a 3:1 scaled-down model of the RAM on a round table. The participants were provided with eight miniature navigation cues similar to those that were used in the RAM and with eight distractor objects with small shape differences from the original cues. They were asked to select the appropriate cues and construct an accurate model of the RAM and to mark the place of the target. The set of miniature geometric objects provided no information on the spatial order of the RAM.

A relative distance of the target from its correct location (platform deviation) on the scaled-down posttest arena was scored with the following method: The placement of the escape platform was fitted in an *x, y* coordinate system, and the distance from the proper location (measured in the same *x, y* coordinate system) was used as an error score.

Fear and anxiety. A self-reported test battery including the Fear Survey Schedule (FSS; Arrindell, 1993) with Social Fear, Agoraphobia, Fear from Sexual and Aggressive Scenes, Fear of Illness subscales and the overall fear-driven Avoiding Behavior Activity (Overall Fear) score was used. The participants' anxiety levels were assessed by the anxiety scale of the Spielberger's State–Trait Anxiety Inventory (STAI; Sipos, 1978; Spielberger, Gorsuch, & Lushene, 1970). See Table 2 for a summary of these scales and the main scores. Gender-related differences in the scores are indicated and discussed.

Table 2

Descriptive Statistics and Independent Samples t-test Statistics for the Gender Split of the Fear Survey Schedule (Arrindell, 1993) and the Spielberger's State–Trait Anxiety Inventory's Anxiety Scale (Sipos, 1978; Spielberger, Gorsuch, & Lushene, 1970)

	Male		Female		*t* test	
Questionnaire and subscale	*M*	*SD*	*M*	*SD*	*t*	*df*
Fear Survey Schedule						
Social Fear	14.82	9.70	22.31	9.31	3.94^{**}	104
Agoraphobic Fear	6.54	4.78	15.85	6.42	7.87^{**}	104
Fear from Sexuality	4.26	3.45	9.11	4.69	5.63^{**}	104
Fear from Illness	9.79	5.76	11.79	9.02	1.24	104
Overall Fear	4.15	4.57	9.78	5.88	5.13^{**}	104
Spielberger's State–Trait Anxiety Inventory	42.05	7.59	46.84	0.84	3.07^{*}	104

$^{*}p < .05$. $^{**}p < .001$.

Measurement of cognitive functions. The subscales of the Hungarian version of the Wechsler Adult Intelligence Scale (WAIS–H; Kun & Szegedi, 1971; based on Wechsler, 1997) were used to assess the participants' cognitive functions. The WAIS–H standard scores were calculated from raw scores according to the standards of the Hungarian manual (Kun & Szegedi, 1971). There are 10 subtests in the WAIS–H: Information (general knowledge recall), Comprehension (adaptation to everyday situations), Digit Span (numerical working memory), Arithmetic (arithmetic skills), Similarities (abstract reasoning), Digit–Symbol (perceptuo–motor skills), Picture Arrangement (understanding social interactions), Picture Completion (closure and goodness of gestalt formation), Block Design (spatial construction skills), and Object Assembly (spatial integration skills).

Results

We performed two main analyses to examine the relationship of affective and cognitive components with the occurrence of thigmotaxis strategy in each trial of the CGA and RAM tasks. A preparatory examination on the data with independent-sample *t* tests indicated a significant gender effect in the self-reported questionnaires, as women scored higher than men on all subscales except for Fear from Illness (see Table 2). Consequently, all further analyses considered gender differences.

Analysis of the Affective Components (Fear and Anxiety)

An analysis using partial correlation coefficients was carried out to examine the relationship between affective components (fear and anxiety) and thigmotaxis in the two test environments (CGA and RAM). Gender was used as a controlling variable in all cases. See Table 3 for a summary of the findings.

CGA. The measure of Overall Fear correlated with thigmotaxis in the early phase of CGA, $r(104) = .22$, $p < .05$. The other phases were not associated with fear. In addition, Overall Anxiety did not correlate significantly with any of the CGA thigmotaxis scores.

RAM. Overall Fear correlated with thigmotaxis in the first trial of RAM, $r(103) = .26$, $p < .05$. However, other phases did not show significant associations with the measure of fear. Similarly, as in the case of CGA, there was no correlation between Overall Anxiety and RAM thigmotaxis.

Taken together, it appears that the psychometrically assessed level of fear correlated with high rates of thigmotaxis in the initial phases of place learning but that the anxiety scores do not correlate with measured thigmotaxis at any point in learning.

Analysis of the Cognitive Components

A second analysis focused on how cognitive factors might influence the occurrence of thigmotaxis strategy in different

Table 3

Summary of the Partial Correlations Between the Overall Affective Components (Fear and Anxiety) and the Thigmotaxis Measured in the Two Environments (CGA and RAM)

	CGA					RAM				
Component	First trial	Early phase	Middle phase	Late phase	Overall	First trial	Early phase	Middle phase	Late phase	Overall
Fear	.00	$.22^{*}$	.13	.11	.17	$.26^{*}$	.11	−.15	−.08	.13
Anxiety	.11	.15	.14	.08	.16	.12	.00	−.03	−.05	.04

Note. Results are controlled for gender. CGA = computer-generated arena; RAM = real arena maze.
$^{*}p < .05$.

phases of spatial learning. Categorical grouping variables were created on the basis of the 33rd and 66th percentiles of the 10 subtests from the WAIS–H and of the platform deviation measure of the map construction posttest. These grouping variables were used as independent variables. Furthermore, gender was included as a covariate factor to control for sex differences. Two multivariate general linear models were used to examine the effects of the independent variables on the occurrence of thigmotaxis strategy as a dependent variable within the two environments (CGA and RAM).

CGA. Participants with extensive thigmotaxis usage (M = 107.59 vm, SE = 18.62) in the early phases had scored significantly lower (≤14 points) on the Information subtest than did the participants who showed less thigmotaxis (M = 44.04 vm, SE = 24.97) but had higher Information scores (≥16 points). The effect was significant, $F(2, 105) = 3.49$, $p < .05$. Similarly, in the Block Design subtest, the higher scoring (≥15 points) participants used less thigmotaxis (M = 38.14 vm, SE = 19.07) in the early phase than did the lowest scoring group of participants (≤14 points) with intense thigmotaxis (M = 110.92 vm, SE = 22.26). This was also a significant effect, $F(2, 105) = 3.50$, $p < .05$. Early phase and overall thigmotaxis were also significantly different in the three categorical groups of platform deviation, $F(2, 105) = 6.40$, and, $F(2, 105) = 4.81$, respectively (both ps < .05). In the early phase, participants with good platform-position-recall ability ($M \leq .98$ cm) had less thigmotaxis (M = 55.54 vm, SE = 17.31), whereas participants with higher platform deviations ($M \geq 13.96$ cm) had more thigmotaxis (M = 116.96 vm, SE = 18.52). Similarly, participants with high overall thigmotaxis (M = 725.25 vm, SE = 108.31) showed more platform displacement in the posttest than did participants with low overall thigmotaxis (M = 377.61 vm, SE = 101.24) who were more precise with remembering the location of the platform.

RAM. Participants who used thigmotaxis extensively (M = 13.84 m, SE = 2.86) in the early phase of spatial learning scored higher (≥16 points) on the Information subtest than did those who used less thigmotaxis (M = 6.58 m, SE = 2.07; ≤14 points on the Information subtest). This effect was significant, $F(2, 105) = 3.76$, $p < .05$. Reversely, participants with low scores on the Block Design subtest (≤14 points) had extensive thigmotaxis (M = 2.96 m, SE = 1.44) in the middle phase, whereas those with high scores (≥15 points) had low thigmotaxis (M = .593 m, SE = 1.24). This effect was also significant, $F(2, 105) = 3.27$, $p < .05$. Although all the cognitive ability variables were included in each model, for the sake of clarity we only present the significant variables in Table 4.

The final data analysis examined the relationships between the affective and cognitive measures. A regression analysis demonstrated that overall fear could be moderately predicted by the working memory dependent platform deviation variable, $R^2 = .210$, $F(11, 104) = 2.25$, beta = .277, $t(105) = 2.70$, $p < .05$. However, the same relationship was not found in the case of anxiety.

Table 4

Summary of the F Values for the Information, Block Design, and Platform Deviation Scores on the Thigmotaxis Measures

Phase	Information Subtest	Block Design Subtest	Platform deviation
	CGA, $F(2, 105)$		
First phase	0.28	1.23	1.66
Early phase	3.49*	3.50*	6.40*
Middle phase	1.04	0.53	0.93
Late phase	0.57	0.93	1.88
Overall	1.00	2.18	4.81*
	RAM, $F(2, 105)$		
First phase	1.65	1.41	1.77
Early phase	3.76*	0.39	0.78
Middle phase	0.41	3.27*	0.75
Late phase	0.76	0.33	0.47
Overall	2.79	1.10	1.19

Note. Gender was used as a covariate. All values without asterisks are nonsignificant. CGA = computer-generated arena; RAM = real arena maze.
* $p < .05$.

Discussion

Studies with mammals, insects, and worms indicate that thigmotaxis is a strategy used by organisms seeking safety (Besson & Martin, 2004; Choleris et al., 2001; Creed & Miller, 1990; Treit & Fundytus, 1988). This safety-seeking strategy appears in the early phases of exploration in new and potentially dangerous situations. The present study investigated differences in thigmotaxis activity in a visually dominated CGA and a perceptuo–motor-guided RAM during the first, early, middle, and late phases of spatial learning in humans. The data analyses suggest several principles.

First, humans who use egocentric thigmotaxis strategy during the early trials of virtual or real mazes also exhibit high levels of psychometric fear and avoidance bias for fear-mobilizing situations. This suggests that human thigmotaxis, the tendency to refrain from exploring the inner zone of novel places, is similar to that exhibited by other animals (Besson & Martin, 2004; Treit & Fundytus, 1988)—its presence indicates a general bias to cautious, safety-seeking phobic behavior.

Second, limits in working memory and gross mapping errors are parts of an enhanced use of thigmotaxis. We suggest that a deficit in general spatial integration plays a significant role in maintaining thigmotaxis activity, principally during the early to middle phases of spatial learning. This means that humans with spatial integration difficulties are cautious navigators; they use thigmotaxis more extensively in the early and middle phases of place learning. They also tend to avoid the central zone of an enclosed space and prefer to stay close to the border for a longer period of time.

Third, the results of the analysis of the RAM data revealed a pattern showing that, similar to the CGA task, deficits in spatial integration and an extensive use of thigmotaxis are related during the early and middle phases of spatial learning. These results support the proposal that the capacity to form gestalts plays a role in switching from egocentric navigation to allocentric-based map construction. Consequently, deficits in spatial gestalt construction increase the likelihood of egocentric-based thigmotaxis behavior.

The question that arises is as follows: How do phase and mechanism tip the balance between avoiding and embracing exploration? We suggest that the individual differences in this point vary because of the ability of the participants to construct and complete the basic structure of the current surroundings. If a good gestalt of a given space is not constructed, then thigmotaxis remains active and the basic egocentric spatial definition prevails. The main condition for the switch between egocentric and allocentric representations would be whether the individual forms an intelligible gestalt (cognitive map) of the surroundings or not.

Fourth, participants with a high level of thigmotaxis activity manifest a low rate of spatial-map-formation ability and large relocation errors during the early and middle phases of learning to relocate the hidden platform. Large relocation errors on the miniature map model of the RAM indicated that participants with a high thigmotaxis score estimated the distance from the arena wall to the hidden platform to be greater than it is in reality. This bias in distance estimation appears with extensive use of CGA thigmotaxis during the early phase of spatial learning.

The regression model demonstrated that placement error correlated positively with measures of phobic avoidance but not with high levels of anxiety. Our results support previous propositions (e.g., Kagan et al., 1990; Klein, 1981; Öhman & Mineka, 2001) and are consistent with the suggestion that fear and human thigmotaxis are closely related. Individuals with high measured levels of fear overestimated the distance from the target to the border of the space. Consequently, fearful people have difficulty with identifying the location of the target accurately. On the surface, it appears that the presence of fear and the accompanying thigmotaxis disrupts either the formation or use of the spatial representation of the current environment.

Although it seems to be plausible that thigmotaxis is a defensive strategy, it is less likely that thigmotaxis prevents the participant from learning the location of the target. Instead, we would argue that fear, related to an encounter with an enclosed spatial environment, triggers a specific exploratory strategy such as thigmotaxis, which plays an essential preparatory role in the first phase of spatial learning. The use of thigmotaxis helps the individual define the borders of an enclosed space and identify escape routes from that space. Thigmotaxis also provides the individual with the elements of an egocentric frame of reference. With the elements of that frame of reference in hand, the organism can begin to construct a cognitive map.

By this view, thigmotaxis impairs spatial learning only when its use is prolonged. If prolonged use is related to behavioral inflexibility or an inability to switch to an appropriate search strategy, then and only then will spatial learning be disrupted. One might then consider behavioral rigidity as being at least partially related to a low fear threshold. Once the critical level of fear is reached, gestalt learning will be disrupted by inadequate emotional and perceptual signals.

Thigmotaxis has two functions, each of which relates to different neuronal structures. During the first phase of learning, the organism calibrates an enclosed space by using thigmotaxis as an exploratory strategy. Functionally, this defines the borders of the space and identifies escape routes. In addition, the organism uses the strategy to gather necessary information for an egocentric frame of reference that provides a context for additional learning. Several authors (e.g., Fanselow, 2000; O'Reilly & Rudy, 2001) have described the dynamics of a transformation from the initial encoding of fragmented, contextual stimulus elements into a unified or gestalt representation and, notably in this context, have described the role of the dorsal hippocampus and the prefrontal cortex in this transformation. Our results demonstrate that prolonged thigmotaxis indicates a longer preparation to learn the context in a novel environment and that this prolonged activity is associated with reduced working memory and a reduced capacity to form a general spatial gestalt in normal humans.

Finally, our results are consistent with some neurobehavioral findings demonstrating that the hippocampus, in both vertebrate and invertebrate animals, is involved in thigmotaxis (Belzung, 1992; Besson & Martin, 2004; Kallai et al., in press; Simon et al., 1994). However, the exact neural mechanisms have not been yet fully understood.

Spatial ability is not a single unitary skill; instead, it consists of subcomponents. Its main parts are spatial visualization, spatial orientation, and the collection and recognition of spatial relations among proximal or distal cues. Although some researchers (Stumpf & Eliot, 1995) suggest that the different spatial functions may be categorized as a general spatial factor, recent (Quasier-Pohl, Lehmann, & Eid, 2004) and earlier (Siegel, 1981) data suggest that spatial ability and the spatial cognition of environment (cognitive map construction) are independent. Performance on simple paper-and-pencil tasks does not provide data leading to a resolution of such topics. For a deeper understanding of spatial cognition, the field needs experimental tasks that require people to use spatial cognition itself. The investigation on spatial orientations through the use of a computer-generated virtual environment and digitally recorded and analyzed experiments in large-scale real spaces (e.g., Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Thomas, Hsu, Laurance, Nadel, & Jacobs, 2001; Wilson, Foreman, & Stanton, 1997) provides successful empirical approaches for this problem.

The present study analyzed the role of thigmotaxis in spatial orientation in both real and virtual environments. We suggest that thigmotaxis is a basic element of spatial cognition and emotionally guided, safety-seeking behavior. On the basis of our results, we suggest that humans do not only learn the location of objects but that they gradually develop an economic and individual structure of the current environment, one that contains further subjective elements. The environment and the person then function as a unit. Acquisition of a mental map involves spatial knowledge as well as orientations, strategies, cue usage, and abstract and perceptuo–motor processes. A cognitive map is classically defined as a representation of a set of connected places systematically related to each other by a group of spatial transformation rules (O'Keefe & Nadel, 1978). Our results demonstrated how one part of this system, the thigmotaxis strategy, might be able to cooperate with the whole.

Human thigmotaxis, which appears when exploring a novel enclosed space, seems to be related to subjective levels of fear. Functionally, thigmotaxis appears to permit the organism to learn the borders of the space and to detect escape routes. Thigmotaxis also appears to provide information that can be used as a frame of reference in which spatial mapping might occur. This takes place during the first phases of place learning. In the middle phases of place learning, action and knowledge systems appear to work together to produce a relatively coherent map or gestalt of the space. This occurs when the individual uploads landmark-based route information to a knowledge-based map and, conversely, translates map knowledge into movement of the head and trunk. This translation process requires broad working memory capacity. If the capacity of working memory is overloaded, thigmotaxis may remain uninhibited and learning may be thereby disrupted.

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Appendix

Arena Instruction

In this experiment, your task is to find a target on the floor of a computer-generated room. You will be transported into two different computer-generated rooms, a practice room and an experimental room. Both rooms contain circular arenas inside large square rooms.

You will start in a practice room. It has brightly colored walls, a white ceiling, a red arena wall, and a gray floor. In this room, all you need to do is practice moving around using a joystick.

Moving and Looking

To go forward, push the joystick forward.

To go backward, pull the joystick backward.

To turn to the right, push the joystick right.

To turn to the left, push the joystick left.

Remember: pushing the joystick left or right will turn you in the corresponding direction, but will not move you sideways.

When you have mastered moving and looking, press the space bar on the keyboard and you will be transported to the experimental room.

In the experimental room, your task is to search for, find, and stand on a large blue target. The first two trials of the experiment have visible targets. With a visible target, simply move to it as quickly as you can. You will know you are on the target when you hear a drum. Once you're on the target, you won't be able to get off, so just hit the space bar to teleport to the waiting room.

The next 8 trials of the experiment will have an *invisible* target. With the invisible target, you should search the room to find it. The invisible target is **always in the same place,** so you should take a **GOOD LOOK** around the room when you find it. When you have taken a good look around, press the space bar to go back to the waiting room.

There will be a trial with a visible target at the end of the experiment. Again, for the visible target, move to it as quickly as you can.

On each trial, you will have limited time to find the target. If you go over this time you will be automatically transported back to the practice room.

Remember: the *visible* targets will be in different places, but the ***invisible*** target will always in the same place, so take a good look around when you first find the invisible target.

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