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RESEARCH REPORT

Error detection and error memory in spatial navigation as reflected by electrodermal activity

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Abstract The study investigated spatial navigation by means of electrodermal activity (EDA). Two groups of healthy subjects (group 1, age <38; group 2, age ≥38) were recorded during navigation through two 3-D virtual mazes differing in difficulty, that is, Maze Simple (MazeS) and Maze Complex (MazeC). Our results show (1) an effect of difficulty, that is, larger skin conductance responses (SCRs) and slower velocity profiles while navigating through MazeC as compared to MazeS. (2) An effect of age, that is, larger SCRs and faster velocity profiles in younger subjects (group 1) compared to older subjects (group 2). (3) An effect of maze region, that is, SCRs increased when subjects entered dead ends with group 1 (young group) decreasing in velocity, whereas group 2 (old group) increased in velocity. (4) And an error memory effect, that is, subjects who remembered an error at a given decision point (crossroads preceding dead ends in MazeC) from previous trials, and then if they did not repeat that error, elicited decreased SCRs as compared to subjects who did not remember and subsequently repeated an error. The latter aspect is the most impactful as it shows that EDA is able to reflect error detection and memory during spatial navigation. Our data designate EDA as suitable monitoring tool for identification and differentiation of the affective correlates underlying spatial navigation, which has recently attracted researchers' attention due to its increased use in 3-D virtual environments.

Keywords Electrodermal activity (EDA) · Skin conductance response (SCR) · Autonomic nervous system (ANS) · Virtual reality maze · Spatial navigation · Error detection · Error memory · Age

Introduction

Research on spatial navigation and spatial memory in humans focuses on how information from past and present is represented in behavioral, physiological, cognitive and neural correlates and how this information is used for making complex navigational decisions (for reviews see Humphries and Prescott 2010; Lew 2011; Wolbers and Hegarty 2010). As recently summarized by Wolbers and Hegarty (2010), the ability to find one's way in complex everyday environments represents one of the most fundamental human cognitive functions. Involving perceptual and memory-related processes as well as visuo-spatial associative learning, navigation is particularly complex because it is a multisensory process in which information needs to be integrated and manipulated over time and space. Successful navigation through complex environments is thereby facilitated by the presence, identification and remembering of environmental spatial cues, among which individuals are required to distinguish between those placed at navigationally relevant (decision points, such as crossroads before dead ends) or irrelevant locations (non-decision points, such as normal straight-line paths) (Janzen et al. 2007). Based on this knowledge, spatial navigation has recently attracted researchers' attention due to its relevance in the development of 3-D virtual reality

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environments. Patel and Vij (2010) considered the navigation process one of the most challenging and complex tasks when working with virtual worlds. The use of virtual environments has made it possible to explore effects of environment layout and content on human way-finding performance and how the interdependent human systems mentioned above make different contributions to behavior.

Wolbers and Hegarty (2010) considered three interdependent domains relevant to navigational abilities: cognitive and perceptual factors, neural information processing and variability in brain microstructure. Recent research on neural networks supporting navigation has been notable for our increased understanding of the factors affecting human navigation (Maguire et al. 1999) using methods such as functional magnetic resonance imaging (fMRI), for example, (Head and Isom 2010; Marsh et al. 2010; Rodriguez 2010; Simon and Daw 2011; Viard et al. 2011; Weniger et al. 2010), electroencephalography (EEG), for example, (Chiu et al. 2012; Friedrich et al. 2011; Gramann et al. 2009; Jaiswal et al. 2010; Kober and Neuper 2011; Watrous et al. 2011), magnetoencephalography (MEG) (Cornwell et al. 2008), positron emission tomography (PET) (Ghaem et al. 1997) or functional near-infrared spectroscopy (fNIRS) (Ayaz et al. 2011a, b, 2012a, b).

In addition to these three components relevant for navigational abilities, affective states elicited by the autonomic nervous system (ANS) have been shown to contribute to navigational decision-making by modulating cue utilization, attentional focus and memory (Gardony and Taylor 2011). Affective states are typically assessed using electrodermal activity (EDA). EDA-derived skin conductance responses (SCRs) are an indirect psychophysiological index of changes in the ANS associated with human affect, emotion, cognition and attention (Colbert et al. 2011; Critchley 2002; Critchley et al. 2000; Sequeira et al. 2009) and decision-making functions (Figner and Murphy 2010). However, so far only few studies evaluated the affective processes reflected by SCRs during spatial navigation (Duncko et al. 2007; Gould et al. 2009; Murty et al. 2011). In particular, Murty et al. (2011) investigated the effect of motivation on declarative spatial learning during navigation through a virtual navigation Morris water task (VNMWT). SCR analysis indicated a critical and selective role of affective aspects in determining how reinforcement influences goal-oriented learning. Duncko et al. (2007) investigated effects of acute stress exposure in terms of a cold pressor test (CPT) on learning performance in a VNMWT. Analysis revealed enhanced SCR activity in spatial learning indicating a response to acute exposure to stress. Gould et al. (2009) compared mental workload and performance in two simulated high-speed ship navigation systems, an electronic and a conventional system. SCR results indicated higher workload in conventional navigation, but the differences between groups were not significant.

Extending these previous works, the present study aimed to focus on one specific navigation ability, that is, the detection and memory of errors. Spatial navigation is an excellent tool to study human error behavior. Error detection and error memory in spatial navigation has been shown in numerous studies to be influenced by age (for review see Gazova et al. 2012). As recently summarized by Carelli et al. (2011), age-related differences in cognitive functioning refer to the ability to pay attention and infer information from the world, learn and memorize, solve problems and make decisions. Although the various components of spatial error memory do not suffer a homogeneous decline, normal age-related cognitive decline mainly affects the speed of information processing, the ability to inhibit irrelevant or distracting information and the capacity of error memory. As a consequence, age differences emerge when demanding storage and processing of information are simultaneously required (Craik and Salthouse 2000). So far, error detection and error memory during spatial navigation has not been studied using EDA. However, few studies have used EDA in other tasks involving error processing behavior. These studies showed that EDA is indeed sensitive to the internal detection of errors, such as in a reaction task (Hajcak et al. 2003), a Stroop task (Hajcak et al. 2004), a stop signal task (Zhang et al. 2012) or a logical reasoning task (Spiess et al. 2007). Although the results are not entirely consistent, these studies revealed that error detection measured by EDA is typically reflected by an increase in SCRs. Here, we aimed to test whether error detection and error memory in spatial navigation would elicit the same responses as described in these previous studies. To test this approach, we compared two 3-D virtual mazes differing in difficulty, a simple maze (MazeS) and a complex maze (MazeC). While MazeS only contained normal straight-line paths, in MazeC we implemented several critical decision points, that is, crossroads, that either led to a normal straight-line path or to a dead end. Decision-making at these crossroads therefore required subjects to decide about the direction and consequently to remember in the next trial whether the previous decision was an error or not.

Taken together, the present study aimed to investigate characteristics of affective correlates as assessed by EDA in response to spatial navigation in virtual 3-D mazes. Our study was motivated by the questions (1) whether SCRs could be utilized during spatial navigation performance to differentiate between the critical decision points in complex virtual environments and simple virtual environments without decision points (MazeC vs. MazeS), (2) whether younger as compared to older subjects would elicit differential SCRs in response to these task conditions, and

(3) whether SCRs would reflect error detection and error memory in these spatial navigation environments. Using this approach, we aimed to test the potential of EDA in monitoring affective signals as complementary information to behavioral responses that might provide additional layers of information on affective processing.

Materials and methods

Subjects

Thirteen subjects [five females, mean age (±STD) 32.6 ± 12.7] were included in the study. Subjects were assigned to two groups based on a cutoff age of 38 years (Bosco and Coluccia 2003; Reuter-Lorenz et al. 2000; Salthouse et al. 1989), with group 1 (age <38; $N = 7$; two females; mean age 22 ± 2.7) and group 2 (age ≥38; $N = 6$; three females; mean age 45 ± 5.3). All subjects were right-handed (mean laterality quotient (LQ ± STD) = 89.3 ± 12.4; group 1 = 88 ± 12.1; group 2 = 91 ± 13.8) according to the Edinburgh Handedness Inventory (Oldfield 1971). Exclusion criteria were any history of visual, neurological or psychiatric disorder or any current medication; all subjects had normal or corrected-to-normal vision. All subjects gave written informed consent. The study was approved by the ethic committee of the Canton Zurich and in accordance with the latest version of the Helsinki declaration.

Experimental protocol

In each session, the setup consisted of a subject sitting in front of a PC screen on a table. The experimental protocol consisted of subjects navigating through virtual 3-D mazes displayed on the screen. Two mazes were created using MazeSuite (Ayaz et al. 2008). MazeSuite is a complete toolset to prepare, present and analyze navigational and spatial experiments. The editor application for constructing maze environments (MazeMaker) can be used to construct, design and edit virtual 3-D environments, track subjects' behavioral performance within the virtual environment and synchronize behavior with external devices. Two navigation conditions were studied differing in difficulty level:

- Condition 1: Maze Simple (MazeS) represented a simple maze consisting of only straight-line paths (Fig. 1, left).
- Condition 2: Maze Complex (MazeC) was characterized by a richly textured series of interconnected paths, some leading to straight line and others leading to dead ends in the environment. Compared to MazeS, this maze represented an enhanced level of difficulty, due to an increased path length and a number of dead ends (Fig. 1, right). This maze was adapted from a previous study by Ayaz et al. (Maze 1 with permission by Ayaz et al. 2011b).

Three trials of each navigation condition were performed. The order of the conditions and trials was randomized between subjects. In both conditions, the visualization/rendering module (MazeWalker) of MazeSuite was used to display the subjects' view through the 3-D mazes. Each maze contained a start and an end point, the latter signalized by the sign "exit." Subjects were asked to use their right hand to navigate through the mazes using the keyboard arrow keys. Subjects were able to control the direction of navigation [up arrow (forward), down arrow (backwards), left and right arrows] as well as the speed of navigation (faster by pressing the keys continuously, slower or stopping by pressing the keys

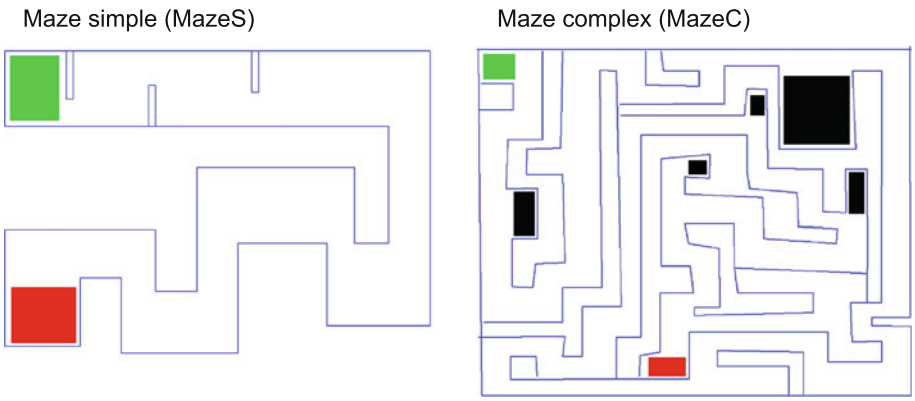

Fig. 1 3-D mazes used for spatial navigation. (*Left*) Maze Simple (MazeS) represented a simple maze consisting of only straight-line paths. This maze was designed by the authors using the MazeMaker included in MazeSuite. (*Right*) in contrast to MazeS, difficulty was enhanced in Maze Complex (MazeC) both by increasing the path length of the maze and by introducing a number of dead ends. This maze was taken from a previous study with permission by Ayaz et al. (Maze 1 described by Ayaz et al. 2011b). The regions and their boundaries that were considered for analysis are indicated, that is, the start of maze (ST, *green*) and the end of maze (EN, *red*) as well as the five dead ends (DE, *black*)

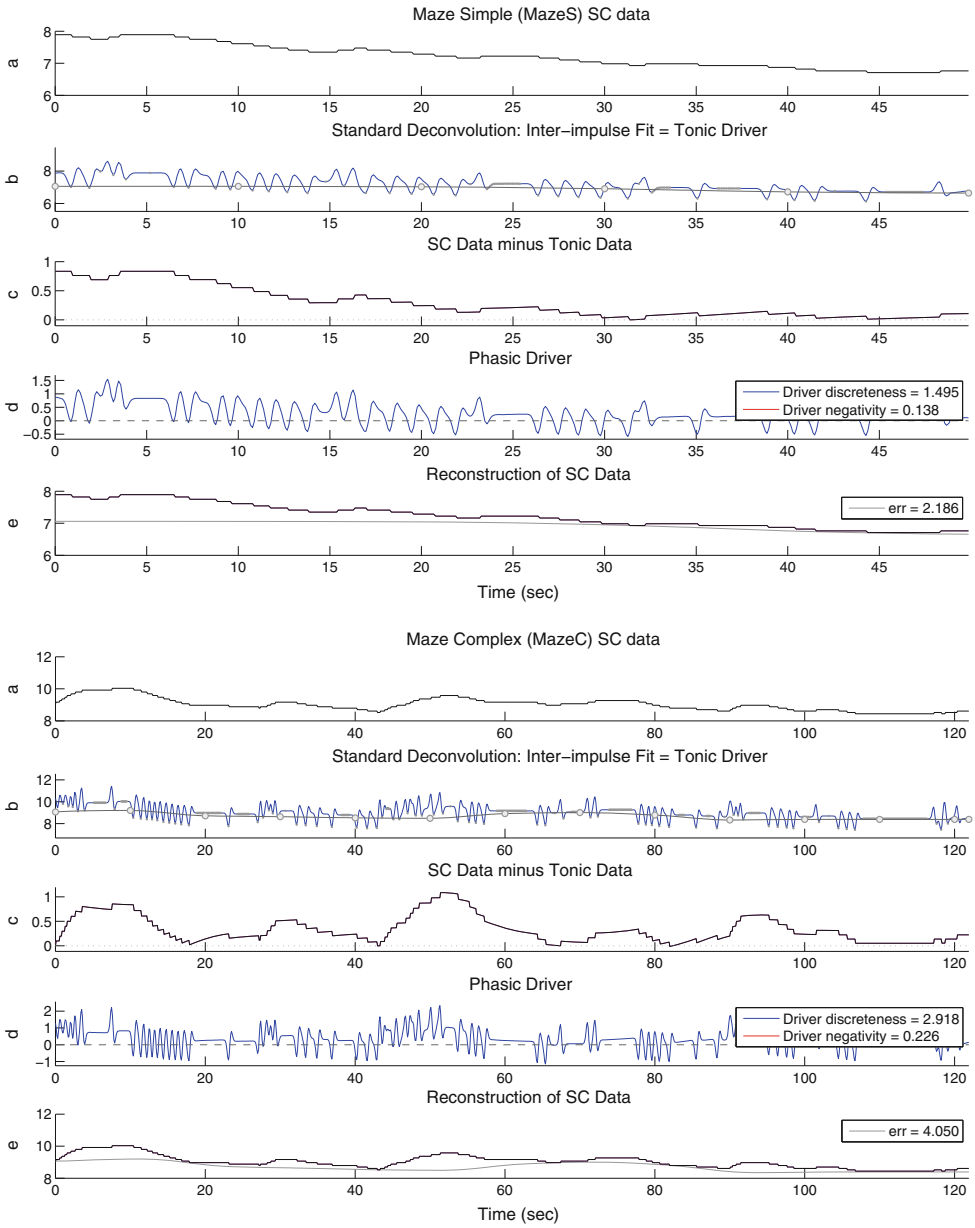

Fig. 2 Decomposition procedure of skin conductance (SC) data. Sample analysis plots for Maze Simple (MazeS) (*Top*) and Maze Complex (MazeC) (*Bottom*). Shown are the four steps involved in the continuous decomposition analysis (CDA) performed by Ledalab software for an example subject and trial. **a** Raw SC data [μS]. **b** Tonic SC activity is estimated based on inter-impulse data detected in the standard deconvolution of the raw SC data [μS]. **c** Continuous deconvolution is applied to the phasic SC data [μS] (original SC data minus tonic SC activity) and single impulses and **d** corresponding pore opening components are identified by means of segmentation of driver and remainder signal [μS]. **e** The original SC data are finally reconstructed by superposition of its tonic and phasic [μS] (*err* = error)

intermittently). Subjects were instructed to navigate through the mazes by reaching the end point as fast and straight as possible. Behavioral data were sampled at 60 Hz and contained information about navigation performance within the 3-D environment concerning the path a subject travelled as well as subject's view vector.

Electrodermal activity (EDA) instrumentation

A wired EDA system (Mind-Reflection, VERIM® Audio-Strobe® Molinis, 16 Bit resolution, max 8 samples/s and range from 10 kΩ to 4.5 MΩ) was used for recording SCRs throughout both navigation conditions (MazeS and MazeC). The system allowed for the acquisition of completely raw, unfiltered EDA data sampled at 10 Hz. EDA was measured using two grounded flat electrodes attached to the distal phalange of the index and middle fingers of the left, non-dominant hand. A custom-made MATLAB® interface was used to display and event-mark the psychophysiological data. Electrodes were attached prior to beginning the measurement, in order to allow subjects to adapt to the recording equipment, and to allow EDA levels to stabilize (Fowles et al. 1981). It was made sure that the electrodes were attached tight enough to the skin to prevent movement artifacts but still allow blood to circulate freely. Prior to the two navigation conditions, a baseline, that is, baseline EDA activity, of at least 120 s was recorded in each subject.

Data analysis

Behavioral data

For each navigation condition, MazeS and MazeC, behavioral data were processed using the analysis and mapping tool (MazeAnalyzer). Each maze performed was visualized using the subjects' path through a given maze (x, y, z coordinates). The following navigational performance parameter was extracted as cursory behavioral measures: the time profile (mean and total time spent per maze/trial [s]), the path length profile (mean and total path length per maze/trial in maze units [v]) and the velocity profile (mean and total maze velocity per maze/trial [μ/s]).

Based on the two maze configurations, MazeS and MazeC (Fig. 1), five maze regions were defined. MazeS contained regions 1, 2 and 5, whereas MazeC contained all regions 1–5.

- Region 1 = start of maze (ST): initial position when entering the maze.
- Region 2 = normal paths (N): all paths that allowed for straight-line navigation.
- Region 3 = crossroads (CX): paths that were characterized by path junctions where two or three paths met (straight line, right and/or left); crossroads represented the critical decision points which required subjects to make an effort in decision-making in order to choose the correct path and to avoid dead ends.
- Region 4 = dead ends (DE): paths with no exit or way through; dead ends required subjects to detect the incorrect path choice, to subsequently return to the previous crossroad and to choose another path. For analysis, we only considered five dead ends (out of the total of nine dead ends as marked in Fig. 1, Right) that were actually entered by the subjects in this study; the remaining dead ends (and the corresponding crossroads) not entered by our subjects were not considered for analysis.
- Region 5 = end of maze (EN): last position before completing the maze.

Electrodermal activity (EDA) decomposition procedure

Skin conductance (SC) data derived from EDA measures are usually characterized by a sequence of overlapping phasic SCRs overlying a tonic component. For full decomposition of SC data into tonic and phasic components, we used the analysis software Ledalab (V3.x) written in MATLAB®, which has previously been described by Benedek and Kaernbach (2010a, b). In particular, we applied the continuous decomposition analysis (CDA), that is, the extraction of the continuous phasic and tonic activity. The continuous decomposition procedure involves four steps as illustrated in Fig. 2 for an example subject: estimation of the tonic component, non-negative deconvolution of phasic SC data, segmentation of driver and remainder and reconstruction of SC data.

For further statistical analysis, we focused on the phasic SCR (average phasic driver (CDA.SCR [μS])); this score is thought to represent phasic activity within response window most accurately, but does not fall back on classic SCR amplitudes. We do not report results obtained of the tonic activity as it did not reveal additional relevant information. In particular, event-related SCR activity of the regions defined above based on a response window of 1–4 s after the event (entry in the region) and a minimum amplitude criterion of 0.05 μS were used as suggested by (Dawson et al. 2007; Levinson and Edelberg 1985). Examples of the SCRs time course during navigation through MazeS and MazeC are given in Fig. 3.

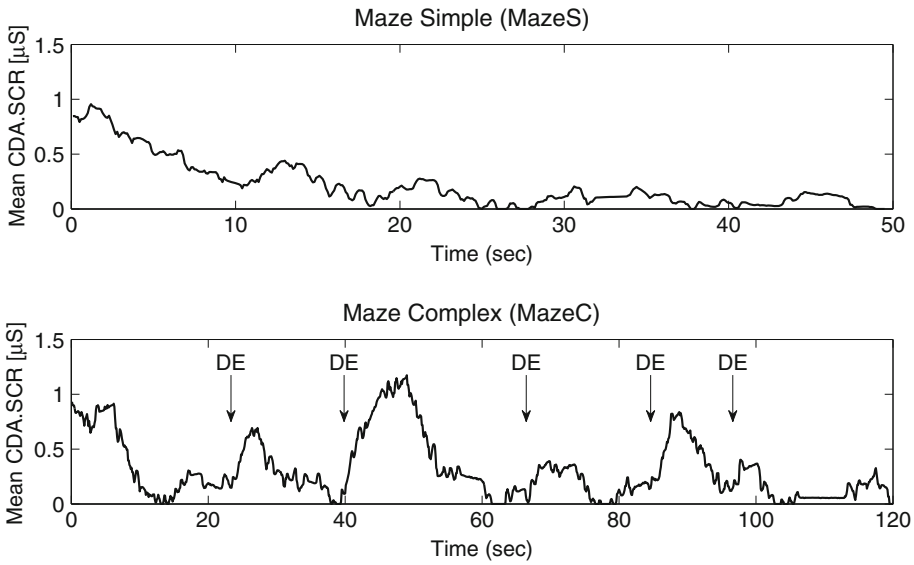

Fig. 3 Phasic skin conductance response (SCR): sample signal time course for Maze Simple (MazeS) and Maze Complex (MazeC). Shown are examples of the time course of the SCR (average phasic driver per region (CDA.SCR [μS])) during navigation through MazeS and MazeC for an example subject and trial. In MazeC, the SCR signal peaks elicited after the subject entered a dead end (DE) are indicated by *arrows*

Statistical analysis

Multivariate ANOVA analyses using SPSS® (Version 17) were performed using SCRs as dependent variable (average phasic driver per region (CDA.SCR [μS])) reflecting affective correlates. Time, path length and velocity profiles were taken as additional dependent variables reflecting the behavioral performance. Bonferroni correction was used for pair-wise comparison of means. The following five fixed factors were tested for main effects:

- Factor "Maze" (MazeS vs. MazeC): the difference in difficulty level between the two mazes.
- Factor "Group" (group 1–2): age group assignment based on the cutoff point of 38 years.
- Factor "Trial" (trial 1–3): the order of the trials 1–3 performed per maze.
- Factor "Region" (region 1–5): see definitions given for the regions in the section "Behavioral data".
- Factor "Error Memory" (no vs. yes): error memory determined whether subjects were able to detect that they made an error in choosing the correct maze path in a previous trial and to subsequently remember that error in order to adapt decision-making at crossroads in the following trial whether or not to enter a dead end again. This factor was only applied to MazeC. No = subject did not remember the error made in previous trials and subsequently entered the same dead end again; yes = subject did remember the error made in previous trials and subsequently avoided that given dead end.

Results

Behavioral data

Main findings of behavioral data during spatial navigation performance using multivariate ANOVA were that subjects spent significantly more time per region ($F_1 = 100.331$, $p \leq 0.001$) and the path taken was significantly longer ($F_1 = 182.531$, $p = 0.004$) while navigating through MazeC as compared to MazeS. For both mazes, we further found a significant effect of the factor "Group" indicating that group 2 (old group) spent significantly more time per region as compared to group 1 (young group) (MazeS $F_1 = 10.344, p \leq 0.001$, MazeC $F_1 = 33.158, p \leq 0.001$). There was no difference in path length between groups. Moreover, for both mazes, a significant effect of the factor "Trial" was observed. This effect was only significant in group 2 (MazeS $F_1 = 7.063$, $p \leq 0.001$, MazeC $F_1 = 5.225$, $p \leq 0.001$), indicating that older subjects spent significantly more time per region in trial 1 as compared to trial 2 and trial 3 (post hoc comparisons MazeS: trial 1 vs. 2 $p = 0.009$, trial 1 vs. 3 $p = 0.004$, MazeC: trial 1 vs. 2 $p = 0.044$, trial 1 vs. 3 $p = 0.004$). Group 1 did not show differences between trials neither in time nor in path length.

Spatial navigation performance as reflected in SCRs and velocity profiles

Multivariate ANOVA using the fixed factors "Maze" (MazeS vs. MazeC), "Group" (group 1–2), "Trial" (trial 1–3) and "Region" (region 1–5) for the two parameters SCRs and velocity profiles revealed the following main findings (Table 1; Figs. 4, 5; see supplementary material for post hoc comparisons):

First, a main effect of the factor "Maze" was found for both SCRs and velocity profiles, although differing in direction. Significant larger SCRs and significant slower velocity profiles were observed during navigation through MazeC compared to MazeS.

Second, separate analyses for each maze difficulty level, MazeS and MazeC, showed main effects of the factor "Group" (Fig. 4). In particular, navigation through both mazes revealed significant larger SCRs and significant faster velocity profiles for the younger group 1 as compared to the older group 2.

Third, separate analyses for each group 1–2 presented main effects of the factor "Region" on both SCRs and velocity profiles (Fig. 4). While navigating from the start position toward the end position of the mazes, similar SCRs pattern was found for MazeS and MazeC, that is, subjects in both groups 1–2 revealed a decrease in SCRs accompanied by an increase in velocity (non-significant for MazeC). These findings are in line with previous studies describing that the magnitude of SCRs typically decreases with number of repetitions in terms of habituation (Frankenhaeuser et al. 1967; Hagdahl et al. 1967).

Fourth, related to the previous point, both difficulty levels were characterized by a main effect of the factor "Trial" on the velocity profiles (Fig. 5). In particular, significant faster velocity profiles were managed by the subjects in the last trial as compared to the first trial; this effect was consistent in both groups. No effect of the factor "Trial" was documented for the SCR data in the ANOVA.

Fifth, while navigating through MazeC, both groups 1–2 showed a significant increase in SCRs after entering dead ends (as compared to normal paths). However, the velocity profiles differed at these points between groups as illustrated in Fig. 4; while group 1 (young group) showed a significant decrease in velocity when entering dead ends, group 2 (old group) significantly increased its velocity after entering dead ends (as compared to normal paths).

Table 1 Multivariate ANOVA for phasic skin conductance response (SCR) and velocity profiles: Maze Simple (MazeS) and Maze Complex (MazeC)

Multivariate ANOVA: CDA.SCR (μS)/velocity (μ/s)								
	df	MazeS versus MazeC		MazeS: group 1 versus group 2		MazeC: group 1 versus group 2		
		F	Sig.	*F*	Sig.	*F*	Sig.	
CDA.SCR	1	5.500	0.020*	21.219	0.001**	31.472	0.001**	
Velocity	1	8.400	0.004**	6.252	0.013*	13.010	0.001**	
			df	Group 1		Group 2		
				F	Sig.	*F*	Sig.	
MazeS	CDA.SCR	Trial	2	2.441	0.089	0.110	0.896	
	Velocity		2	4.709	0.010**	9.758	0.001**	
	CDA.SCR	Region	2/4	14.518	0.001**	7.712	0.001**	
	Velocity		2/4	7.015	0.001**	10.789	0.001**	
MazeC	CDA.SCR	Trial	2	4.171	0.016*	0.129	0.879	
	Velocity		2	6.839	0.001**	3.742	0.024*	
	CDA.SCR	Region	2/4	21.200	0.001**	4.517	0.001**	
	Velocity		2/4	15.703	0.001**	2.511	0.020*	

Results are shown for the analysis examining the SCR (average phasic driver per region (CDA.SCR [μS])) and the velocity profile (mean maze velocity per region [μ/s]) using the fixed factors "Maze" (MazeS vs. MazeC), "Group" (group 1–2), "Trial" (trial 1–3) and "Region" (region 1–5). Shown are *F*-statistics with degree of freedom (F_x) and significant *p* values ($p \leq 0.05$) are highlighted (*). Regions 1–5: *ST* start of maze, *N* normal path, *CX* crossroad, *DE* dead end, *EN* end of maze. Please see supplementary material for post hoc comparisons

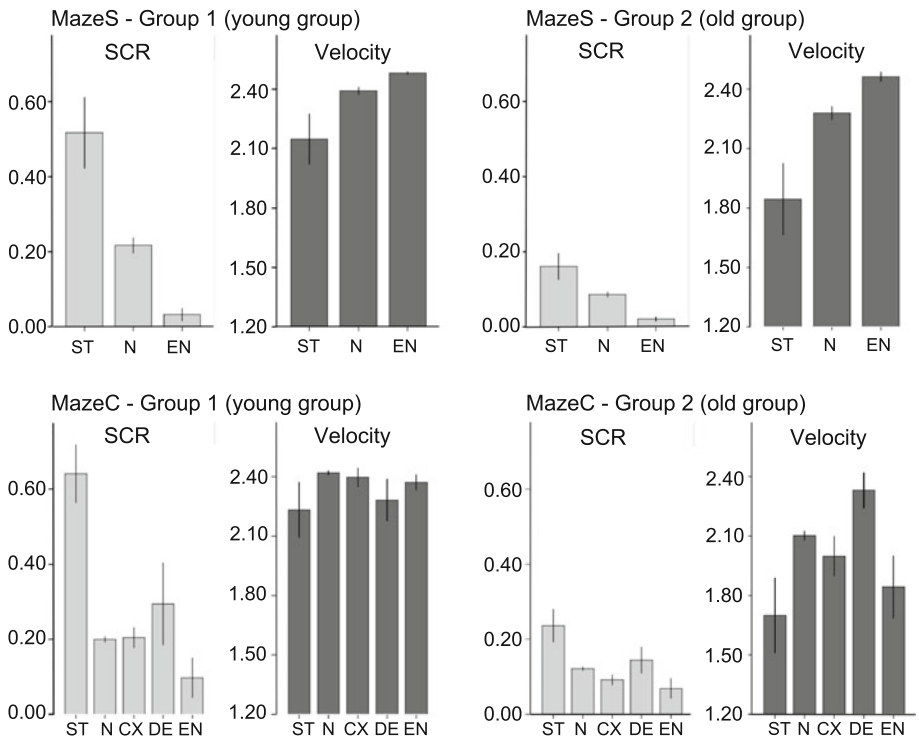

Fig. 4 Main effects of "Group" and "Region" on phasic skin conductance response (SCR) and velocity profiles: Maze Simple (MazeS) and Maze Complex (MazeC). Shown are histograms of the SCR (average phasic driver per region (CDA.SCR [μS] ± SE)) and the velocity (mean maze velocity per region [μ/s] ± SE) for the fixed factors "Maze" (MazeS vs. MazeC), "Group" (group 1–2) and "Region" (region 1–5) over all trials 1–3. Regions 1–5: *ST* start of maze, *N* normal path, *CX* crossroad, *DE* dead end, *EN* end of maze. The corresponding analysis is shown in Table 1

Error memory reflected in SCRs

Last, we evaluated whether subjects detected and remembered errors made during spatial navigation performance. In particular, we investigated subjects' SCRs and velocity profiles at the crossroads, that is, the decision points, from trial 1 to trial 3. Crossroads represented the critical points during maze navigation where subjects were required to

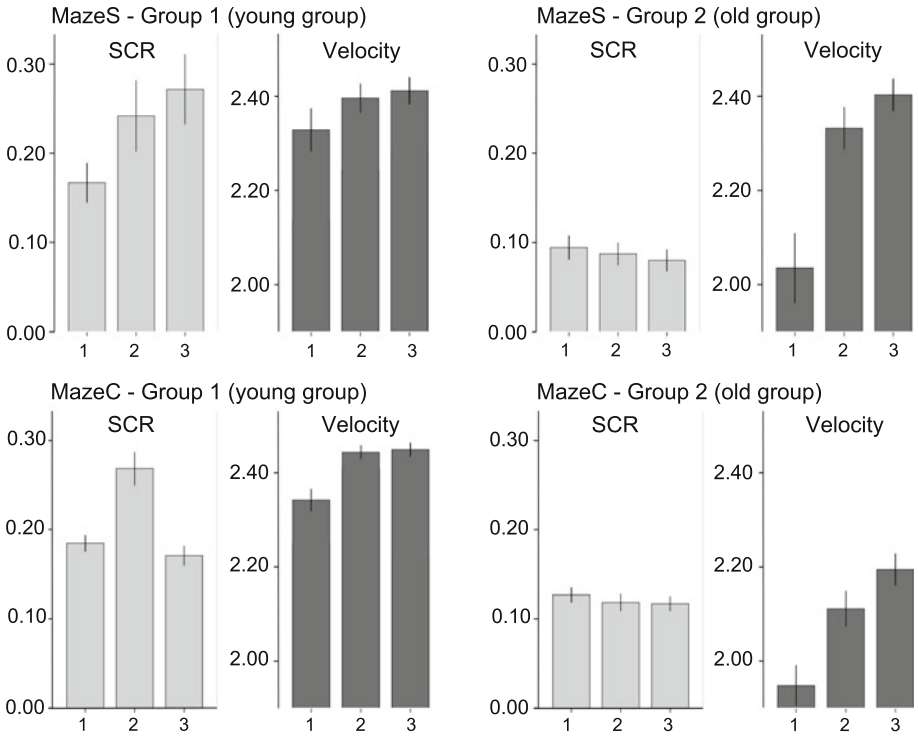

Fig. 5 Main effects of "Trial" (1–3) on phasic skin conductance response (SCR) and velocity profiles: Maze Simple (MazeS) and Maze Complex (MazeC). Shown are histograms of the SCR (average phasic driver per region (CDA.SCR [μS] ± SE)) and the velocity (mean maze velocity per region [μ/s] ± SE) for the fixed factor "Maze" (MazeS vs. MazeC), "Group" (group 1–2) and "Trial" (1–3). Corresponding analysis is shown in Table 1

make a decision on which path to choose next thereby avoiding dead ends. This analysis was performed only for MazeC, since MazeS did not contain dead ends.

Based on the identified five dead ends in MazeC that were actually entered by the subjects, overall percentages for each trial for the fixed factors "Error Memory" (no vs. yes) and "Group" (group 1–2) were calculated (Table 2). These data revealed an error memory effect on spatial navigation, that is, the number of subjects who remembered an error increased from trial 2 to trial 3 (21.54 vs. 32.31 %) and accordingly the number of subjects who did not remembered an error decreased from trial 2 to trial 3 (30.77 vs. 26.15 %).

To quantify the reflection of the error memory effect in the SCR data and the velocity profiles, multivariate ANOVA using the fixed factor "Error Memory" (no vs. yes) was performed (Fig. 6). While no effects were found for the transition from trial 1 to trial 2, results revealed a significant effect on SCRs for the transition from trial 2 to the last trial 3 (overall subjects $F_2 = 4.996$, $p = 0.011$, group 1 $F_2 = 6.505$, $p = 0.006$, group 2 $F_2 = 0.212$, $p = 0.811$). This finding indicated that in subjects who detected and remembered an error (1) SCRs decreased from trial 2 to the last trial 3 and (2) within the last trial 3, SCRs were significantly smaller compared to those who did not remember an error. In addition, the last trial 3 presented an effect of the factor "Group" on SCRs indicating that subjects who did not remember an error elicited significant larger SCRs in group 1 (young group) as compared to group 2 (old group) (post hoc comparisons, overall subjects $p = 0.016$, group 1 $p = 0.006$, group 2 $p = 1.000$). Subjects who never enter a given dead end elicited relatively stable, non-different magnitudes of SCRs from trial-to-trial transition (from trial 1 to trial 3) while navigating through the corresponding crossroads. No effect was found for the velocity profiles.

Discussion

We present behavioral and EDA data recorded in two groups of healthy subjects, that is, a younger group 1 (<38 years of age) and an older group 2 (≥38 years of age), during spatial navigation through two virtual 3-D mazes differing in difficulty level. Referring to our questions stated in the introduction, our study showed (1) that SCRs recorded during spatial navigation were able to differentiate the difficulty level between the complex maze (MazeC) as compared to the simple maze (MazeS), (2) that younger as compared to older subjects elicited significant differential SCRs in response to these task conditions and (3) that SCRs reflected a significant effect of error memory on spatial virtual navigation identified at the critical decision points in MazeC. The latter aspect is the most impactful as it shows that EDA is able to reflect error detection and memory during spatial navigation. In the following sections, we discuss our key findings and their relevance in the light of the current literature on EDA and error processing behavior.

Table 2 Error memory effect: crossroads (CX) regions of Maze Complex (MazeC)

	Percentages of "Error Memory"					
	Overall		Group 1		Group 2	
Trial 2						
No	$N = 20$	30.77 %	$N = 11$	16.92 %	$N = 9$	13.85 %
Yes	$N = 14$	21.54 %	$N = 8$	12.31 %	$N = 6$	9.23 %
Trial 3						
No	$N = 17$	26.15 %	$N = 10$	15.38 %	$N = 7$	10.77 %
Yes	$N = 21$	32.31 %	$N = 13$	20.00 %	$N = 8$	12.31 %

Overall percentages for the fixed factor "Error Memory" (no vs. yes) calculated for each trial. Analysis was based on the identified five dead ends that were actually entered by the subjects

Behavioral data

Results of spatial navigation performance confirmed the suitability of our experimental mazes, MazeS and MazeC (Fig. 1). The difference in difficulty levels was significantly reflected both in the longer time spent and the longer path taken while navigating through MazeC as compared to MazeS. Additionally, behavioral data showed age-related differences between groups in both mazes, that is, older subjects (group 2) took significantly longer to navigate as compared to our younger subjects (group 1). Finally, behavioral data showed some kind of learning effect in the older subject (group 2) as indicated by a decrease in the time taken for completing both mazes that became apparent in the last trial 3 as compared to the first trial 1.

Spatial navigation performance as reflected in SCRs and velocity profiles

Effect of difficulty on SCRs and velocity profiles

To address our first question, we compared SCRs with the behavioral parameter, that is, the velocity profiles (Table 1; Figs. 4, 5). The difficulty level between mazes was reflected in both groups, that is, subjects elicited smaller SCRs and faster velocity profiles while navigating through MazeS as compared to MazeC. These findings are in line with previous studies reporting that SCRs can reflect different levels of cognitive complexity. For example, SCRs have been shown to exhibit a positive linear relationship with simple versus complex stimuli ranging from auditory stimuli (Bradley et al. 2007; Hagdahl et al. 1967; Seppänen et al. 2009; Zimmer 1992), visual stimuli (Bradley et al. 2007; Fredrikson and Öhman 1979), psychophysiological states in post-stroke upper extremity rehabilitation (Novak et al. 2010), visual and cognitive demand on driving performance (Engström et al. 2005; Mehler et al. 2010; Reimer et al. 2009), solving anagrams (Pecchinenda 1996) or spatial navigation (Gould et al. 2009). It has been further reported that such complexity-related SCRs correlate with the neural response associated with affective stimuli detected in the human brain (Critchley 2002; Laine et al. 2009; Nagai et al. 2004; Sequeira et al. 2009).

Effect of age on SCRs and velocity profiles

Second, an effect of age was found, that is, younger subjects (group 1) elicited larger SCRs and faster velocity profiles as compared to the older subjects (group 2) during navigation through both mazes, MazeS and MazeC. Generally, empirical studies to date clearly identify navigation as an aspect of cognitive function that is vulnerable to the aging process. Our data reflect previous studies that have shown that EDA is able to differentiate age-related differences in cognitive tasks and that the associated SCRs typically correlate negatively with age, that is, SCRs decrease with increasing age (Barontini et al. 1997; Figner et al. 2009; Gavazzeni et al. 2008; Mehler et al. 2010; Shmavonian et al. 1968; Venables and Mitchell 1996).

Moreover, another effect of age has been observed related to the behavior within dead ends. Subjects in both groups elicited increased SCRs after entering the dead ends in MazeC. However, within dead ends, the velocity profiles differed at these points between groups; while younger subjects (group 1) decreased their velocity, the older subjects (group 2) showed an increase in velocity. As recently summarized by Notebaert et al. (2009), it is generally assumed that post-error slowing is a cognitive control effect reflecting a more careful response strategy after errors. Cognitive control is responsible for adjusting our information processing network to context demands and goal settings. Cognitive control theories attribute these post-error slowing to adaptive control mechanisms that induce more deliberate behavior to reduce the probability of error commission (Botvinick et al. 2001). According to these theories, one of the most replicable effects is the observation that responses are slower after an error than after a correct trial. As a result, post-error trials are predicted to be slower and more accurate. Based on these assumptions, our findings might therefore be interpreted as a kind of stress reaction in the older subjects induced by the situation in the dead end; by increasing their velocity, older subjects might have tried to fix the error and recoup the time lost by returning to the crossroad as fast as possible. In contrast, younger subjects might have reacted more deliberate in order to carefully consider the best path to choose next. Together, these age effects on SCRs and velocity observed reflect an excellent example of age-related deterioration in spatial performance associated with differences both in navigation strategies and degrees of fluidity in navigation.

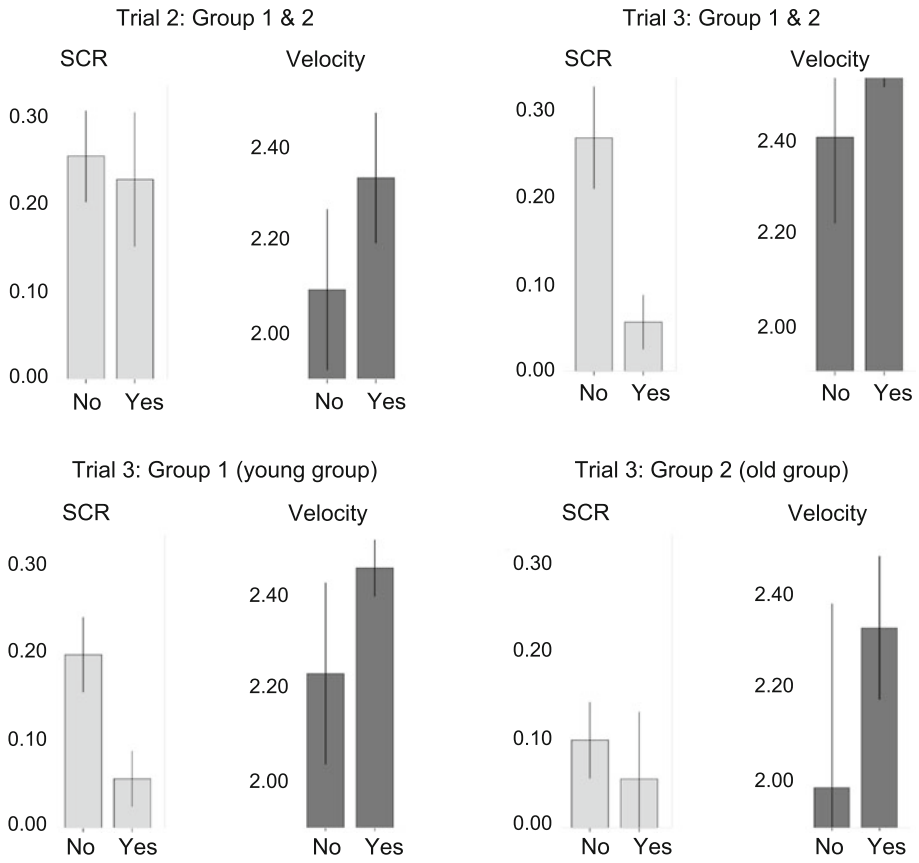

Fig. 6 Error memory effect reflected in phasic skin conductance response (SCR): Histograms for Maze Complex (MazeC) of the crossroads (CX) regions. Shown are SCRs (average phasic driver per region (CDA.SCR [μS] ± SE)) and velocity profiles (mean maze velocity per region [μ/s] ± SE) using the fixed factors "Error Memory" (no vs. yes) and "Group" (group 1–2) for trial 3. No = subject did not remember the error made in previous trials and subsequently entered the same dead end again; yes = subject did remember the error made in previous trials and subsequently avoided that given dead end

Error memory reflected in SCRs

Last, we found an error memory effect that was significantly reflected in EDA data. To uncover the error memory effect, we exclusively examined the navigational decision points, that is, the crossroads in MazeC, which preceded the identified five dead ends (Table 2; Fig. 1, right). Our findings indicated that in subjects who detected and remembered an error (1) SCRs decreased from trial-to-trial and (2) within the last trial, SCRs were significantly smaller compared to those who did not remember an error. Separate analyses per group verified the error memory effect in both younger and older subjects. However, younger subjects who did not show an error memory effect elicited a significant higher affective response reflected by larger SCRs as compared to the older group. This observation overlapped with our findings on age-related SCR differences in response to spatial navigation as discussed in section "Effect of age on SCRs and velocity profiles". These data thereby show that younger subjects not only exhibited significantly larger SCRs as compared to older subjects during navigation performance, but that this relationship can also be detected when extending the evaluation of affective responses to critical navigational decision points and hence, to the differentiation between subjects able versus unable to integrate error detection in subsequent error correction.

Errors are common in all realms of human cognition. Within the domain of memory, errors include failures of information retrieval (misses), as well as the erroneous retrieval and endorsement of false information (intrusions and false alarms). Considering the term error memory in terms of spatial memory, that is, the ability to remember the location in which something is perceived and to recall a series of visited locations (Vandierendonck and Szmalec 2011), we observed two cases. First, in cases where error memory effects took place, subjects were able to refer to their experience from the last trial(s) and subsequently correctly avoided a given dead end; in contrast, in cases where subjects did not remember from previous trials, they subsequently erroneously decided to enter a dead end again. We suggest that these two cases were reflected in our SCR results. Subjects, who entered a given dead end in the first trial 1 and subsequently transferred their navigational knowledge of the location of a given dead end to the next trials 2 and 3, elicited a significant decrease in SCRs in the last trial 3. Hence, these subjects with a successful error memory obviously experienced a low degree of arousal due to the fact that they were able to remember the correct path. On the other hand, subjects who entered a

given dead end in the first trial 1, but subsequently did not show an error memory effect in the next trials 2 and 3, elicited a significant increase in their SCRs in trial 2 that remained high in trial 3. We suggest that these subjects who failed to transfer their navigational knowledge experienced a high arousal response triggered by the unpleasant realization of being unable to remember the correct path in trials 2 and 3. This unsuccessful exploration of the maze environment might be similar to what has been previously described in mice (Miller and Eilam 2011). While being unable to remember the correct path, our subjects might have undertaken several explorative actions in order to facilitate the decision-making at crossroads, such as exploring sections of traversed paths repetitively, turning sideways or rotating on the spot to visually scan the path junction at the crossroads, or even turning back to retrace their path upon the first arrival at each crossroad. This in turn might have resulted in the large affective response reflecting the stress-induced experience. Taken together, we therefore suggest that our results illustrate how SCRs can provide information about the affective response that occurs in response of successful versus unsuccessful error integration of tangible entities (crossroads, paths) when acquiring an abstract representation (map) of the maze. These findings showed that detecting and remembering navigationally relevant error is differentiable using EDA. Monitoring EDA might therefore be suitable to catch certain subtle phenomena that other measures might not catch, thereby offering additional layers of information that could augment other methods, such as neurophysiological or neuroimaging methods.

Conclusion

The present study investigated the affective correlates during spatial navigation by means of EDA. Navigation performance through virtual mazes revealed that phasic SCRs and subjects' velocity profiles significantly reflected effects of difficulty level, age group and error memory. Our data designate EDA as suitable monitoring tool for identification and differentiation of the affective correlates underlying spatial navigation. It is suggested that EDA might provide an additional layer of information on cognitive and affective processing that has so far not been considered sufficiently using other neurophysiological or neuroimaging methods. These findings may have potential implications for further development navigation tools for studying difficulty levels, age differences and error memory effects in spatial navigation, such as currently frequently applied in the development of virtual environments.

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