Neurobiology of Learning and Memory 132 (2016) 1–8

Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

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

Not all anxious individuals get lost: Trait anxiety and mental rotation ability interact to explain performance in map-based route learning in men

John C. Thoresen [a], Rebecca Francelet [a], Arzu Coltekin [b], Kai-Florian Richter [b], Sara I. Fabrikant [b], Carmen Sandi [a,*]

[a] Laboratory of Behavioural Genetics, Brain Mind Institute, Ecole Polytechnique Fédérale de Lausanne (EPFL), CH-1015 Lausanne, Switzerland
[b] Department of Geography, University of Zurich, Switzerland

ARTICLE INFO

Article history:
Received 25 February 2016
Revised 6 April 2016
Accepted 20 April 2016
Available online 22 April 2016

Keywords:
Spatial learning
Anxiety
Mental rotation ability
Navigation
Working memory
Arousal

ABSTRACT

Navigation through an environment is a fundamental human activity. Although group differences in navigational ability are documented (e.g., gender), little is known about traits that predict these abilities. Apart from a well-established link between mental rotational abilities and navigational learning abilities, recent studies point to an influence of trait anxiety on the formation of internal cognitive spatial representations. However, it is unknown whether trait anxiety affects the processing of information obtained through externalized representations such as maps. Here, we addressed this question by taking into account emerging evidence indicating impaired performance in executive tasks by high trait anxiety specifically in individuals with lower executive capacities. For this purpose, we tested 104 male participants, previously characterised on trait anxiety and mental rotation ability, on a newly-designed map-based route learning task, where participants matched routes presented dynamically on a city map to one presented immediately before (same/different judgments). We predicted an interaction between trait anxiety and mental rotation ability, specifically that performance in the route learning task would be negatively affected by anxiety in participants with low mental rotation ability. Importantly, and as predicted, an interaction between anxiety and mental rotation ability was observed: trait anxiety negatively affected participants with low—but not high—mental rotation ability. Our study reveals a detrimental role of trait anxiety in map-based route learning and specifies a disadvantage in the processing of map representations for high-anxious individuals with low mental rotation abilities.

1. Introduction

Navigation is important in many day-to-day tasks, be it planning a driving route to a new location, or finding your way within a building. Navigation activities can rely on internal representations derived from sensory experience and on externalized representations such as maps or diagrams (Wolbers & Hegarty, 2010). Although humans greatly differ in their navigational abilities (Wolbers & Hegarty, 2010), the factors that explain these differences are not well understood.

Most of the early efforts to characterise inter-individual variability in navigational abilities highlighted the existence of important group differences, especially related to gender (Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005; Lawton, 1994; Montello, Lovelace, Golledge, & Self, 1999) and age (Driscoll et al., 2005; Head & Isom, 2010; Wilkniss, Jones, Korol, Gold, & Manning, 1997). Although much less is known about factors that define large individual differences in navigational abilities that exist within the same gender and age groups, variance in spatial aptitude seems to play a prominent role (Malinowski, 2001; Shah & Miyake, 1996). Using performance measures in the Vandenberg and Kuse (1978) mental rotation test (MRT) as a proxy of spatial aptitude, several studies have shown that individual differences in mental rotational abilities correlate with participants' learning abilities to navigate in virtual mazes (Moffat, Hampson, & Hatzipantelis, 1998) and performance in map-based route learning tasks (Galea & Kimura, 1993).

Aside from spatial aptitude, emerging evidence in animals and humans suggest that trait anxiety contributes to the variance in navigational abilities. Trait anxiety—a personality characteristic related to the degree to which the world in general is perceived

* Corresponding author.
E-mail address: carmen.sandi@epfl.ch (C. Sandi).

http://dx.doi.org/10.1016/j.nlm.2016.04.008
1074-7427/

as threatening by the individual (Spielberger, 1972)—is known to be related to cognitive functioning in different domains (e.g., Bishop, 2009; Bishop, Duncan, Brett, & Lawrence, 2004; Eysenck & Calvo, 1992; Robinson & Petchenik, 1976; Sandi & Richter-Levin, 2009). Specifically, when trained in a spatial learning task, high-anxious rats displayed a slower learning rate than low-anxious rats (Herrero, Sandi, & Venero, 2006). In humans, existing evidence was obtained using virtual environments through which individuals were exposed to different trajectories and subsequently asked to draw a map (Viaud-Delmon, Berthoz, & Jouvent, 2002) or to locate landmarks on an aerial view of the previously seen environment (Burles et al., 2014). High-anxious individuals were impaired in both tasks (Burles et al., 2014; Viaud-Delmon et al., 2002) but their performance did not differ from low-anxious individuals when they had to reproduce a learned trajectory with their own movements during the exposure to the virtual scenario (Viaud-Delmon et al., 2002). These data are in line with a reported preference in high-anxious individuals for the use of an egocentric—as opposed to allocentric—strategy for spatial orientation (Viaud-Delmon, Siegler, Israël, Jouvent, & Berthoz, 2000; Viaud-Delmon et al., 2002). These studies link trait anxiety with individuals' capability to rely on internal representations in order to construct global representations of space (i.e. to form cognitive maps). However, at this time, it is not known whether trait anxiety affects the processing of information obtained through externalized representations such as maps.

In order to address this question, we investigated the link between trait anxiety and a map-based route-learning task. For this purpose, we invited 104 male individuals to perform a navigation task, in which they were shown computer animations of specific routes on a map and asked whether they matched a route that had been shown to them shortly before. The response time had a limit of 4 s. Thus, in each trial, participants had to process spatial information about a particular trajectory in a newly presented map, to hold it briefly in memory, and to then assess whether a subsequently displayed trajectory presented at a faster rate than originally matched the former route.

Gender differences are frequently reported both in performance (Burles et al., 2014; Driscoll et al., 2005; Vandenberg & Kuse, 1978), strategies (Galea & Kimura, 1993; Lawton, 1994) and confidence in spatial tasks (Nardi, Newcombe, & Shipley, 2012), and sex hormones have been shown to influence mental rotation ability (Hausmann, Slabbekoorn, Van Goozen, Cohen-Kettenis, & Güntürkün, 2000; Schöning et al., 2007). For this reason, we chose to conduct the experiment only with male participants.

First, and in order to validate this task in the context of the related literature (Fields & Shelton, 2006; Galea & Kimura, 1993; Moffat et al., 1998; Pazzaglia & De Beni, 2001; Tom & Tversky, 2012), we aimed to evaluate the link between mental rotation ability, using the MRT, and navigation performance in the map-based route learning task. Second, we assessed the potential contribution of trait anxiety in navigation performance. Furthermore, given that trait anxiety affects behaviour, and cognitive function does not fully explain inter-individual variation (e.g., Castro et al., 2012; Salehi, Cordero, & Sandi, 2010), we predicted that navigation performance would be modulated by the interaction between individuals' mental rotation ability and their level of trait anxiety. Specifically, we hypothesized that trait anxiety would play a detrimental role in participants with low, but not high, MRT scores. This prediction stems from the following converging lines of evidence: (i) our task involves a working memory component and, in males, performance in the MRT has been shown to strongly correlate with spatial—but not verbal—working memory performance (Christie et al., 2013; Shah & Miyake, 1996); (ii) substantial evidence and theoretical approaches to anxiety (e.g., the Attentional Control Theory; Eysenck, Derakshan, Santos, & Calvo, 2007) propose that anxiety disrupts working memory processes (Bishop, 2009; Eysenck & Calvo, 1992; Eysenck et al., 2007); (iii) an interaction between trait anxiety and working memory capacity was recently reported to explain a large amount of variance in cognitive performance in tasks involving executive function: whereas anxiety did not have an influence in individuals with average working memory capacity, it was negatively related to test performance in individuals with low working memory capacity (Edwards, Moore, Champion, & Edwards, 2015; Johnson & Gronlund, 2009; Owens, Stevenson, Hadwin, & Norgate, 2014).

As the impact of trait anxiety in behavioural and cognitive performance is strengthened under arousing conditions (e.g., Goette, Bendahan, Thoresen, Hollis, & Sandi, 2015; Herrero et al., 2006; Salehi et al., 2010), we tested participants under slight time constraint and in groups of four. Moreover, given that monetary motivation has been shown to be effective in inducing mild stress in individuals (Buckert, Schwieren, Kudielka, & Fiebach, 2015), we primed participants during recruitment indicating that test performance could affect their final payoff. Prior to the experimental session, participants were assessed on online versions of the State-Trait Anxiety Inventory, trait subscale (STAI-T; Spielberger, 1983) and the Vandenberg and Kuse (1978) mental rotation task (MRT). During the experimental session, state anxiety was measured through the State subscale of the STAI questionnaire and saliva samples were collected to measure cortisol. Given the reported link between trait anxiety and confidence (Goette et al., 2015), we also obtained confidence ratings in individual judgments.

2. Materials and methods

2.1. Participants

A total of 120 male, French-speaking students of the Ecole Polytechnique Fédérale de Lausanne (EPFL) and the University of Lausanne took part in the study. Due to a computer problem, some of the participants could not complete the whole experiment, and their data were therefore excluded from the analyses. The analysed sample consists thus of 104 participants (mean age = 20.8 years, *SD* = 2.6).

During recruitment, participants were told that their total reimbursement could depend on their test performance during the experimental session. Specifically, they were told that in addition to a guaranteed reimbursement of CHF 25 (1 CHF = 1.10 USD), one participant in each group of four would win a further bonus ranging between CHF 5 and CHF 30, and that this person would either be selected randomly or based on their performance in the task. This study was approved by the Brain Mind Institute (BMI) Ethics Committee for Human Behavioural Research of the EPFL.

2.2. General procedure

The experimental procedure is outlined in Fig. 1. Participants completed questionnaires individually, administered using the online platform *www.qualtrics.com*. This included demographics questionnaires, a French version of the *State-Trait Anxiety Inventory* (STAI; Spielberger, 1983), and a French version of the *Vandenberg and Kuse Mental Rotations task* (Albaret & Aubert, 1996; Vandenberg & Kuse, 1978). In the Mental Rotations Task (MRT), the participant is shown a line drawing of a block figure. Participants have to match two out of four additional block images to the target. These two represent rotated versions of the target; the other two are either mirror images or novel configurations of blocks. Two blocks of ten trials were used, and a time limit of 3 min was imposed on each block. Three days after completing

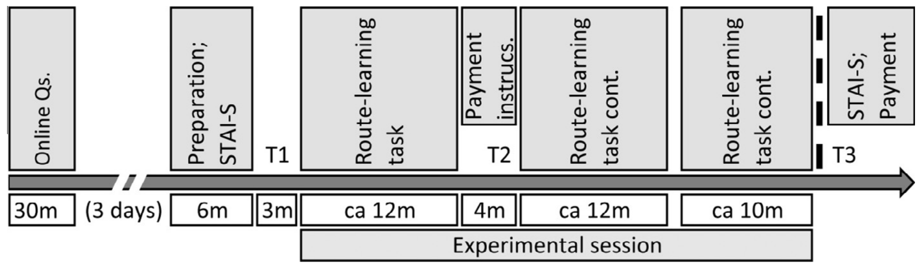

Fig. 1. Experimental procedure. *Note*. Online Qs. = online questionnaires, consisting of demographics, STAI-T (Spielberger, 1983) and MRT (Vandenberg & Kuse, 1978). T1, T2 and T3 = saliva sampling points, taken together with subjective stress measures.

the online questionnaires, participants came to the lab to perform the experiments.

Testing was performed in groups of four in order to create an arousing situation. Participants completed the state-subscale of the STAI inventory (STAI-S; Spielberger, 1983) both before and after the route-learning task. Furthermore, we measured cortisol throughout the experiment by means of Oral Swab saliva collection devices (Salimetrics, Newmarket, Suffolk, United Kingdom): participants placed a small swab under the tongue for 90 s and subsequently transferred it to a holder tube. The first saliva sample was taken at the very beginning of the experiment, the second during the first break in the route-learning task, and the third at the end of the experiment (see Fig. 1). To control for the circadian rhythm of cortisol, all experimental sessions were scheduled after 2 PM. Subjective stress levels were also obtained at each saliva sampling point by asking participants to indicate their perceived level of stress on a scale of 0 (not at all stressed/anxious) to 4 (very stressed/anxious).

2.3. Map stimuli

Forty-eight maps with similar route density were created using Google Static Maps API (*https://developers.google.com/maps*). An area of 0.9 km^2 was shown, and a pixel resolution of 640 $\times$ 640 was used. Half the maps were cartographic road maps and half were satellite maps with roads superimposed; see Fig. 2 for example stimuli with trajectories. No analysis of the influence of map type was intended or performed for this article but can be accessed elsewhere (Francelet, Coltekin, Richter, Thoresen, & Fabrikant, submitted for publication).

2.4. Map-based route learning task

A map-based route learning task was created and displayed using the software E-prime (version 2.0; Psychology Software Tools, Pittsburgh, PA). Participants viewed animations on individual 17-in. LCD computer screens showing a red dot following a set route with the instruction to learn the trajectory of the route. At the end of the trajectory, the red dot remained static for 2000 ms. On the subsequent slide, the question "Is this the same route as before?" appeared in French for 1000 ms, and was directly accompanied with a second animation. The animation was shown in the same format, but speed was doubled and map size was reduced by 27%. The response trajectory was either congruent or incongruent to the learning trajectory; evenly distributed between trials and fully randomised. Response trajectories always used the same starting and ending point as the original, whether congruent or incongruent. The trajectory was shown twice, after which the

Fig. 2. Example trajectories shown on the two map types used in the study: road map (left) and satellite map (right). *Note*. The dot marks the start position and the triangles mark the end position of the trajectory. The red dot moved twice along the red trajectory during the learning phase. In the following trial phase, the red dot again moved twice along the trajectory in the same direction but at double the speed, either congruently (i.e. along the red-dotted lines) or incongruently (along the blue-dotted lines). The dotted lines were not visible during the trials. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

red dot remained static for 4000 ms. Participants could respond as soon as the second trajectory appeared, but were told that after viewing the repeated trajectory they had 4 s to answer, and were prompted to give their response ("same" or "different") using predefined keys of a standard keyboard. At the end of each trial, participants additionally answered the question 'How sure are you of your answer?' to assess their response confidence on a 6-point Likert scale.

The map-route-learning task consisted of 72 trials, separated by two breaks: during the first break half the participants were told that their bonus payoff would depend on their performance; the other half were told nothing. The first break lasted approximately 4 min, the second approximately 2 min. Four practice trials were included but responses to these were not recorded; this procedure was repeated after each break. The learning animation had a duration of 17 s, while the response trajectory had a duration of 13 s; after the second break, speed was increased by 40%, to respectively 12 s for the learning animation and 8.4 s for the second animation.

2.5. Cortisol assessment

Following each session, saliva samples were stored at −20 °C until processed. Samples were then centrifuged at 3000 rpm for 15 min at room temperature and salivary cortisol concentrations measured by enzyme immunoassay (Salimetrics, Newmarket, Suffolk, United Kingdom) according to the manufacturer's instructions.

2.6. Statistical analyses

Mean percentages of hits and false alarms were calculated across all trials in order to calculate the sensitivity parameter d' for each participant. A cortisol increase index was also obtained for each participant, in order to check whether any effect of anxiety on performance was due to the personality trait and not to stress per se. The cortisol increase index measures the activation of the endocrine system from baseline and was defined as the maximum value of the last two saliva samples minus the value of first sample. In addition, a cortisol area-under-the-curve parameter (AUC) was calculated for each participant. Data were analysed using ANCOVAs, treating anxiety and mental rotation ability dichotomously, parametric correlations, and repeated-measures ANOVAS. All analyses were performed using SPSS (IBM SPSS Statistics, Version 21). Analyses include partial η^2 ($\eta_p{}^2$) as an estimation of effect size where appropriate. A probability of .05 was set as the required significance level, α, for all tests (two-tailed).

3. Results

3.1. Main results

Three participants obtained negative d' measures, with accuracy levels under 50%. We considered that they were not engaged in the actual task and, since they were the only participants scoring below chance, their data were excluded from the analyses. Group classification of trait anxiety and mental rotation ability was based on median-splits on the STAI-T and MRT scores, excluding the median (STAI-T = 40; MRT = 24). See Table 1 for demographics of the participants, with a comparison of low versus high trait groups.

A 2 (mental rotation ability) by 2 (trait anxiety) ANCOVA was carried out, with cortisol-increase entered as a covariate and average d' as the dependent variable. This model explained a significant amount of variance [$F(4,84) = 4.6$, $p < .01$, $\eta_p{}^2 = .18$]. As expected, an interaction between mental rotation ability and trait anxiety was observed [$F(1,84) = 4.0$, $p = .05$, $\eta_p{}^2 = .05$]. A main effect was found for mental rotation ability [$F(1,84) = 12.42$, $p < .001$, $\eta_p{}^2 = .13$] but not for trait anxiety [$F(1,84) = 2.20$, $p = .14$, $\eta_p{}^2 = .03$]. No effect was found for cortisol increase ($p = .66$). This was further validated in zero-order correlation analyses, which saw no link between performance in the map-based route learning task and cortisol increase or other absolute cortisol measurements (see Supplemental Information). Sidak-corrected post hoc analyses showed a detrimental effect of anxiety on map-based route learning performance for low-MRT participants [$F(1,84) = 6.01$, $p = .02$, $\eta_p{}^2 = .07$] but not for high-MRT participants [$F(1,84) = 0.1$, $p = .75$, $\eta_p{}^2 < .01$]; see Fig. 3.

A second 2 (mental rotation ability) by 2 (trait anxiety) ANCOVA was carried out for average confidence rating; in addition to the cortisol increase index, d' was included as a covariate due to the inherent link between accuracy and confidence. The model explained a significant amount of variance [$F(5,83) = 2.9$, $p = .02$, $\eta_p{}^2 = .15$]. Confidence was found to be explained by mental rotation ability [$F(1,83) = 4.31$, $p = .04$, $\eta_p{}^2 = .05$]. However, there was no significant difference between the trait anxiety groups in their confidence ratings [$F(1,83) = 2.42$, $p = .12$, $\eta_p{}^2 = .03$], as can be seen in Fig. 4. No other effects were found (all Fs < 2.2, all ps > .13).

3.2. Assessment of arousal

A 2 (time) by 2 (trait-anxiety) by 2 (mental rotation ability) by 2 (incentive type) repeated-measures ANOVA was carried out, with STAI-S as the dependent variable. Incentive type (monetary or random) was included to assess whether the instructions given regarding reimbursement after the first break had an impact on arousal. Importantly, a significant main effect of time was found [$F(1,81) = 4.74$, $p = .03$, $\eta_p{}^2 = .06$]. A post hoc paired-sample t-test confirmed that participants' state-anxiety level was higher after ($M = 32.5$, $SD = 6.7$) than before ($M = 31.1$, $SD = 5.8$) the experiment [$t(100) = 3.1$, $p < .01$]. As expected, participants previously categorised as high on trait-anxiety showed higher state-anxiety scores throughout, as shown by a significant main effect of trait-anxiety [$F(1,81) = 18.68$, $p < .001$, $\eta_p{}^2 = .19$]. See also Fig. 5. No other main effects or interaction effects were found (all ps > .22), indicating that mental rotation ability did not predict or modulate state anxiety during the experiment.

Subjective stress levels were entered into a 3 (time) × 2 (incentive type) × 2 (trait-anxiety) by 2 (mental rotation ability) repeated-measures ANOVA. This analysis too revealed a main effect of time [$F(2,168) = 8.50$, $p < .001$, $\eta_p{}^2 = .09$], which post hoc analyses showed to be quadratic [$F(1,81) = 11.86$, $p < .001$, $\eta_p{}^2 = .13$]. A main effect was found for both trait-anxiety [$F(1,81) = 5.68$, $p = .02$, $\eta_p{}^2 = .07$] and for mental rotation ability [$F(1,81) = 4.01$, $p = .05$, $\eta_p{}^2 = .05$]. No other significant interaction effects or main effects were found (all ps > .12).

Finally, cortisol values were entered into a 3 (time) × 2 (incentive type) × 2 (trait-anxiety) by 2 (mental rotation ability) repeated-measures ANOVA. A filter was first applied, removing participants whose initial cortisol sample exceeded two standard deviations of the mean (12.90 nMol/L; $n = 7$). A main effect of time was found [$F(2,150) = 10.30$, $p < .001$, $\eta_p{}^2 = .12$]. As expected, an interaction between trait-anxiety and time was found [$F(2,150) = 3.10$, $p = .05$, $\eta_p{}^2 = .04$]. No other main effects or interaction effects were found (all ps > .19). Mental rotation ability did not modulate the impact of trait anxiety on cortisol, neither overall ($p = .82$) or its interaction with time ($p = .37$), lending no support to individual differences in hormone profiles underlying the interaction between STAI-T and MRT in map-based route learning (see Section 3.1).

Further repeated-measures ANOVAs run separately on the anxiety groups showed a significant linear effect of time in the low-anxiety group [$F(1,40) = 13.50$, $p < .001$, $\eta_p{}^2 = .25$] and a significant

Table 1
Participant demographics in function of mental rotation ability and trait anxiety.

Attribute	Mental rotation ability (MRT)			Anxiety level (STAI-T)		
	Low MRT (*n* = 47)	High MRT (*n* = 48)	Student's *t*-test (*p*)	Low anxious (*n* = 47)	High anxious (*n* = 48)	Student's *t*-test (*p*)
MRT	17.0 (5.3)	29.9 (3.7)	**13.9*****	23.4 (7.7)	23.6 (7.6)	0.1 (.90)
Age	21.5 (2.6)	20.2 (2.1)	**2.6** (.01)	20.9 (2.4)	20.8 (2.6)	0.1 (.94)
STAI-T	40.8 (8.3)	40.2 (6.5)	0.4 (.66)	34.4 (3.5)	46.6 (5.3)	**13.1*****
STAI-S1	31.7 (6.3)	30.4 (4.8)	1.1 (.29)	28.4 (4.1)	34.0 (6.2)	**5.2*****
STAI-S2	32.7 (5.9)	31.8 (6.4)	0.7 (.47)	29.9 (5.1)	35.1 (7.3)	**4.1*****

Note. The two first columns in each trait section represent means (standard deviation in brackets). The third column represents absolute *t* values from Student's *t*-tests comparing the two groups (*p*-value in brackets); boldface indicates significant difference at the .05 level. MRT = Mental Rotation Test; STAI = State-Trait Anxiety Inventory; STAI-T = Trait subscale obtained prior to the experimental session; STAI-S = State subscale obtained immediately before (S1) or after (S2) the experimental session.
*** $p < .001$.

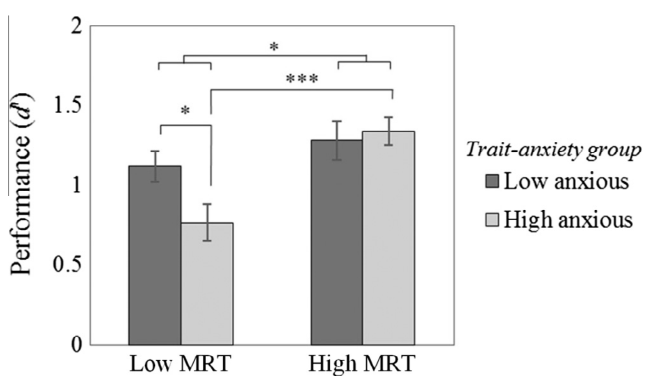

Fig. 3. Map-based route learning performance (d') in function of participants' mental rotation ability (MRT) and trait anxiety (STAI-T). *Note*. ANCOVA with cortisol increase as a covariate revealed a significant interaction effect between trait anxiety and mental rotation ability. Asterisks are from Sidak-corrected post hoc analyses. * $p < .05$, *** $p < .001$.

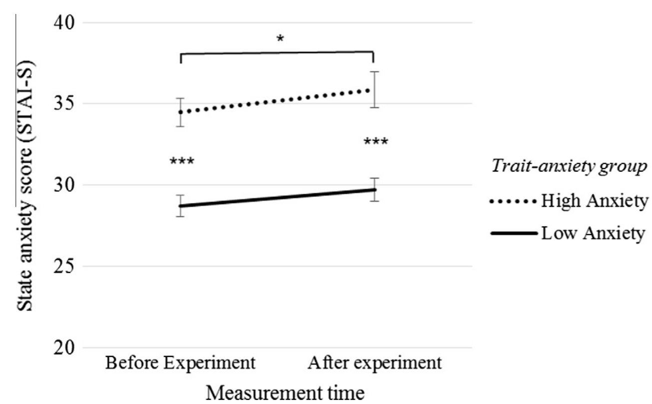

Fig. 5. State anxiety scores (STAI-S) depending on trait anxiety group (STAI-T). *Note*. STAI-S scores were obtained on the day of the experimental session whereas STAI-T scores were obtained three days prior. A repeated-measures ANOVA confirmed that participants were more anxious after than before the experiment, and showed a significant main effect of trait anxiety. Error bars represent one *SEM*. Between-group asterisks represent significance levels from independent-samples *t*-tests. * $p < .05$; *** $p < .001$.

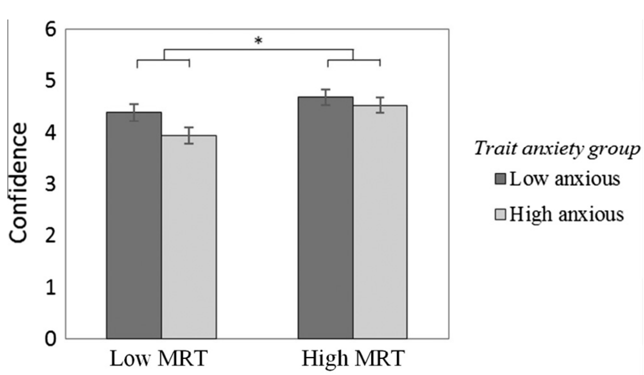

Fig. 4. Confidence in individual judgements, in function of participants' mental rotation ability (MRT) and trait anxiety (STAI-T). *Note*. Represented statistical test is an ANCOVA with cortisol increase and d' as covariates. * $p < .05$.

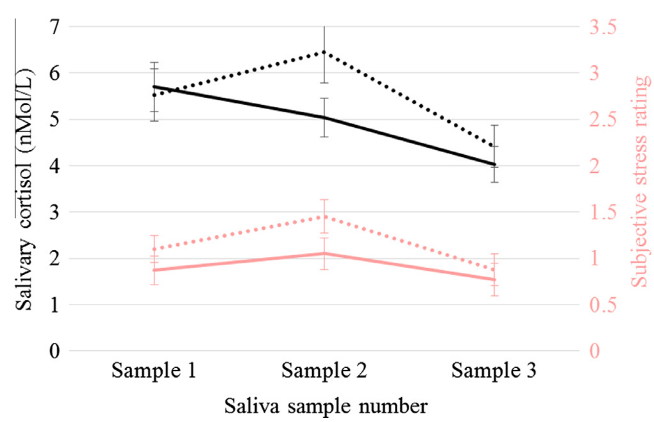

Fig. 6. Cortisol and subjective stress measures for low trait-anxiety group (solid lines) and high trait-anxiety group (dotted lines). *Note*. Black lines represent average salivary cortisol; pink/grey lines represent subjective stress ratings. Error bars represent one *SEM*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

quadratic effect of time in the high-anxiety group [$F(1,41) = 9.91$, $p < .01$, $\eta_p^2 = .20$], indicating a steady decline in cortisol in low-anxious individuals throughout the experiment, and a strong stress-response followed by recovery in the high-anxious individuals. This can also be seen in Fig. 6.

Taken together, these results indicate that the setting in which the experiment was held was arousing in nature and more so for participants of high trait anxiety compared to those of low trait anxiety. The differential instructions regarding monetary incentive given during the actual experiment did not appear to impact on the arousal levels.

4. Discussion

This study set out to answer whether performance in a map-based route learning task is related to trait anxiety and, more specifically, whether trait anxiety and mental rotation ability interact in map-based route learning. To this end, we conducted an experiment in which participants gave same/different judgements to routes presented dynamically on road maps. In agreement with our predictions, we found a significant interaction between trait anxiety and mental rotation ability. Our study reveals a role for trait anxiety in map-based route learning, and specifies a disadvantage in the processing of map representations for high-anxious individuals with low mental rotation abilities. Trait anxiety negatively affected performance in participants with low—but not high—mental rotation ability.

As we developed the map-based route-learning task in-house, we performed a first validation in the framework of the existing literature. A large body of evidence relates spatial navigation performance with performance in the Vandenberg and Kuse (1978) as a proxy of mental rotation ability (e.g., Pazzaglia & De Beni, 2006; Smallman & Cook, 2011; Wilkening & Fabrikant, 2011), including route-learning in maps (Fields & Shelton, 2006; Galea & Kimura, 1993; Tom & Tversky, 2012). In support of this prior research, participants with high MRT scores in our study performed significantly better than those with low MRT scores. Our results give additional support for the Vandenberg and Kuse's (1978) MRT to predict performance in a map-based route learning task. As we classify our sample for differences in performance in the MRT, it is important to indicate that, together with spatial perception and spatial visualization, mental rotation ability is considered one of three factors underlying general spatial ability (Johnson & Bouchard, 2005; Linn & Petersen, 1985). The MRT is one instrument mapping onto the mental rotation factor, and involves abstract reasoning relying on working memory and executive functioning. Importantly, performance in the MRT correlates with fluid intelligence and spatial working memory, but not with verbal working memory (Mackintosh & Bennett, 2003).

As predicted, we found a detrimental effect for trait anxiety on performance in the map-based route learning task. Although substantial evidence links trait anxiety with performance in different cognitive domains, including attention (Bishop, 2009; Bishop et al., 2004) and concentration (Kessler et al., 2009; Vytal, Cornwell, Letkiewicz, Arkin, & Grillon, 2013), the results in the literature are mixed regarding the direction of the effect: whereas many studies indicate detrimental effects of high trait anxiety on selective attention (Bishop, 2009; Eriksen & Hoffman, 1973; Fox, 1993) and spatial attention (Caparos & Linnell, 2012), others have reported positive effects (Berggren, Blonievsky, & Derakshan, 2015; Derryberry & Reed, 1998; Murray & Janelle, 2003). According to the postulates from the influential Attentional Control Theory (ACT; Eysenck et al., 2007), these discrepancies might be partially explained by differences in cognitive load, either related to differences in task demands or in individuals' capacities. The ACT proposes that high anxiety exhausts resources within the limited working memory capacity, as highly anxious individuals devote resources not only to task-relevant but also to task-irrelevant cues. Accordingly, in some occasions, high-anxious individuals might perform well by increasing their efforts, needing more time or mental effort to reach the same result as low-anxious individuals (Eysenck & Calvo, 1992). When auxiliary resources are not available (for example, under high time constraints), performance of anxious individuals would be impaired in both, efficiency and effectiveness. However, in our study, the disadvantage of high-anxious individuals was evident for the d' parameter, which is a reliable index for response accuracy without taking into account response time. In fact, we did not find differences in response time (data not reported), which might have been partially due to the response time window masking potential inter-individual variability.

In any case, the interaction effect between mental rotation ability and trait anxiety—indicating that the detrimental effect of anxiety was specific to participants with low mental rotation ability—favours the view that the effects of anxiety are revealed under compromised cognitive resources. Our task involves a working memory component and, as indicated above, performance in the MRT in male individuals is linked to spatial working memory performance and fluid intelligence (Christie et al., 2013; Miyake, Friedman, Rettinger, Shah, & Hegarty, 2001; Shah & Miyake, 1996). Our findings thus add to emerging evidence that high trait anxiety is predictive of detrimental cognitive effects in executive tasks specifically at lower, but not higher, working memory capacity (Edwards et al., 2015; Johnson & Gronlund, 2009; MacLeod & Donnellan, 1993; Owens et al., 2014). Importantly, our findings further reveal that the interaction with mental rotation capabilities – and therefore most probably with fluid intelligence and spatial working memory – is also of high relevance to explain the effects of trait anxiety in map-based route learning.

Animal (Cordero, Just, Poirier, & Sandi, 2016; Hollis et al., 2015; Jennings et al., 2013; Kim et al., 2013; Sandi et al., 2008) and human (Berggren & Derakshan, 2013; Bishop, 2009; Etkin et al., 2004; Klumpp et al., 2011; Taylor & Whalen, 2015) studies have implicated different brain areas in the behavioural and cognitive effects of anxiety. Although many of those studies point at the amygdala as critically implicated in anxiety, emerging evidence highlight the amygdala-medial prefrontal circuitry as particularly involved in the behavioural and cognitive effects of anxiety (Blackmon et al., 2011; Eden et al., 2015; Kim & Whalen, 2009; Kim et al., 2011; Taylor & Whalen, 2015). Reductions in corticolimbic grey matter, particularly within the hippocampus and medial prefrontal cortex (mPFC) (Eden et al., 2015; Gorka, Hanson, Radtke, & Hariri, 2014), as well as functional differences in the activation of these structures (Bishop, 2009; Satpute, Mumford, Naliboff, & Poldrack, 2012) have also been found to be associated with adult trait anxiety. While some studies indicate enhanced mPFC activity in high anxious participants (for a review, see Berggren & Derakshan, 2013), others have found decreased activity (Bishop, 2009) and proposed that high anxiety leads to insufficient recruitment of cognitive resources. Given these imaging findings and the crucial role played by the hippocampus and mPFC in spatial working memory (Jin & Maren, 2015; Spellman et al., 2015), it is tempting to speculate that structural and functional differences in the hippocampus and mPFC could account for the interaction between trait anxiety and mental rotation abilities reported in our study.

Stressful experimental conditions are sometimes required in order to reveal behavioural differences between individuals low- and high in trait anxiety (Goette et al., 2015). For this reason, our study included several arousing experiments. Notably, participants knew that their total earnings could depend on their performance; experimental sessions were run in groups of four; and a response time limit was imposed. In agreement with evidence that individuals with higher trait anxiety tend to have higher state anxiety scores when challenged (Horikawa & Yagi, 2012), we found that high trait anxiety individuals showed higher state anxiety than those low in trait anxiety. However, state anxiety did not depend on mental rotation ability: also trait-anxious individuals with high mental rotation ability—and whose task performance was spared—showed high state anxiety during the experiment. Salivary cortisol levels did not differ between groups, which is in agreement with a lack of effect for trait anxiety in this hormonal parameter recently reported in a similar population sample (Goette et al., 2015).

Regarding confidence ratings, we found that participants' self-assessment of skills was somewhat accurate. Low-MRT participants reported less confidence than did high-MRT participants—in line with their performance—suggesting that high and low spatial people are equally capable of accurate self-assessment. However, the fact that there was no effect of trait anxiety, and particularly no interaction between trait anxiety and mental rotation ability for confidence in this task reveals a mismatch between the poorer performance observed in high trait anxiety and low mental rotation ability individuals and their capacity to judge their failure, which further supports their inferior performance.

Our study reveals, for the first time, a particular difficulty for high trait anxiety and low mental rotation ability individuals to deal with route learning in maps. However, our findings have a few important limitations that should be noted. We tested male participants only and, therefore, future studies should address potential gender differences. Moreover, our task does not allow us to disentangle whether the detected difficulty in map-based route learning is specific to the quality of information (animated depiction of a route in a map) or illustrates a broader domain-unspecific deficit of high trait anxious and low mental rotation ability individuals. Similarly, our study does not allow us to discern whether the nature of the deficit relies on the involvement of working memory demands in the task or whether a deficit could already exist at the information processing and attentional levels.

In summary, we identify here an important interaction between trait anxiety and mental rotation ability in explaining individual differences in performance in a map-based route-learning task and, thus, contribute with critical information to the fields of learning and memory, individual differences and navigation.

Acknowledgments

We thank Olivia Zanoletti for her assistance in performing the cortisol assays. We gratefully acknowledge support from the Swiss National Science Foundation (grant SNSF CR10I3-146431), the NCCR Synapsy and intramural funding from the EPFL. The funding sources had no further role in the study, including design, the collection, analysis or interpretation of data, or publication decisions.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.nlm.2016.04.008.

References

Albaret, J. M., & Aubert, E. (1996). Etalonnage 15–19 ans du test de rotation mentale de Vandenberg. *Evolutions Psychomotrices*, 206–209.

Berggren, N., Blonievsky, T., & Derakshan, N. (2015). Enhanced visual detection in trait anxiety. *Emotion, 15*(4), 477–483. http://dx.doi.org/10.1037/a0039449.

Berggren, N., & Derakshan, N. (2013). Attentional control deficits in trait anxiety: Why you see them and why you don't. *Biological Psychology, 92*(3), 440–446. http://dx.doi.org/10.1016/j.biopsycho.2012.03.007.

Bishop, S. J. (2009). Trait anxiety and impoverished prefrontal control of attention. *Nature Neuroscience, 12*(1), 92–98. http://dx.doi.org/10.1038/nn.2242.

Bishop, S. J., Duncan, J., Brett, M., & Lawrence, A. D. (2004). Prefrontal cortical function and anxiety: Controlling attention to threat-related stimuli. *Nature Neuroscience, 7*(2), 184–188. http://dx.doi.org/10.1038/nn1173.

Blackmon, K., Barr, W. B., Carlson, C., Devinsky, O., DuBois, J., Pogash, D., ... Thesen, T. (2011). Structural evidence for involvement of a left amygdala-orbitofrontal network in subclinical anxiety. *Psychiatry Research: Neuroimaging, 194*(3), 296–303. http://dx.doi.org/10.1016/j.pscychresns.2011.05.007.

Buckert, M., Schwieren, C., Kudielka, B. M., & Fiebach, C. J. (2015). *How stressful are economic competitions in the lab? An investigation with physiological measures.* . urn:nbn:de:bsz:16-heidok-187487.

Burles, F., Guadagni, V., Hoey, F., Arnold, A. E., Levy, R. M., O'Neill, T., & Iaria, G. (2014). Neuroticism and self-evaluation measures are related to the ability to form cognitive maps critical for spatial orientation. *Behavioural Brain Research, 271*, 154–159. http://dx.doi.org/10.1016/j.bbr.2014.06.002.

Caparos, S., & Linnell, K. J. (2012). Trait anxiety focuses spatial attention. *Emotion, 12*(1), 8. http://dx.doi.org/10.1037/a0026310.

Castro, J. E., Diessler, S., Varea, E., Márquez, C., Larsen, M. H., Cordero, M. I., & Sandi, C. (2012). Personality traits in rats predict vulnerability and resilience to developing stress-induced depression-like behaviors, HPA axis hyper-reactivity and brain changes in pERK1/2 activity. *Psychoneuroendocrinology, 37*(8), 1209–1223. http://dx.doi.org/10.1016/j.psyneuen.2011.12.014.

Christie, G. J., Cook, C. M., Ward, B. J., Tata, M. S., Sutherland, J., Sutherland, R. J., & Saucier, D. M. (2013). Mental rotational ability is correlated with spatial but not verbal working memory performance and P300 amplitude in males. *PLoS ONE, 8*(2), e57390. http://dx.doi.org/10.1371/journal.pone.0057390.

Cordero, M. I., Just, N., Poirier, G. L., & Sandi, C. (2016). Effects of paternal and peripubertal stress on aggression, anxiety, and metabolic alterations in the lateral septum. *European Neuropsychopharmacology, 26*(2), 357–367. http://dx.doi.org/10.1016/j.euroneuro.2015.11.017.

Derryberry, D., & Reed, M. A. (1998). Anxiety and attentional focusing: Trait, state and hemispheric influences. *Personality and Individual Differences, 25*(4), 745–761. http://dx.doi.org/10.1016/S0191-8869(98)00117-2.

Driscoll, I., Hamilton, D. A., Yeo, R. A., Brooks, W. M., & Sutherland, R. J. (2005). Virtual navigation in humans: The impact of age, sex, and hormones on place learning. *Hormones and Behavior, 47*(3), 326–335. http://dx.doi.org/10.1016/j.yhbeh.2004.11.013.

Eden, A. S., Schreiber, J., Anwander, A., Keuper, K., Laeger, I., Zwanzger, P., ... Dobel, C. (2015). Emotion regulation and trait anxiety are predicted by the microstructure of fibers between amygdala and prefrontal cortex. *The Journal of Neuroscience, 35*(15), 6020–6027. http://dx.doi.org/10.1523/JNEUROSCI.3659-14.2015.

Edwards, M. S., Moore, P., Champion, J. C., & Edwards, E. J. (2015). Effects of trait anxiety and situational stress on attentional shifting are buffered by working memory capacity. *Anxiety, Stress, & Coping, 28*(1), 1–16. http://dx.doi.org/10.1080/10615806.2014.911846.

Eriksen, C. W., & Hoffman, J. E. (1973). The extent of processing of noise elements during selective encoding from visual displays. *Perception and Psychophysics, 14*(1), 155–160. http://dx.doi.org/10.3758/bf03198630.

Etkin, A., Klemenhagen, K. C., Dudman, J. T., Rogan, M. T., Hen, R., Kandel, E. R., & Hirsch, J. (2004). Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. *Neuron, 44*(6), 1043–1055. http://dx.doi.org/10.1016/j.neuron.2004.12.006.

Eysenck, M. W., & Calvo, M. G. (1992). Anxiety and performance: The processing efficiency theory. *Cognition and Emotion, 6*(6), 409–434. http://dx.doi.org/10.1080/02699939208409696.

Eysenck, M. W., Derakshan, N., Santos, R., & Calvo, M. G. (2007). Anxiety and cognitive performance: Attentional control theory. *Emotion, 7*(2), 336. http://dx.doi.org/10.1037/1528-3542.7.2.336.

Fields, A. W., & Shelton, A. L. (2006). Individual skill differences and large-scale environmental learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 32*(3), 506–515. http://dx.doi.org/10.1037/0278-7393.32.3.506.

Fox, E. (1993). Attentional bias in anxiety: Selective or not? *Behaviour Research and Therapy, 31*(5), 487–493. http://dx.doi.org/10.1016/0005-7967(93)90129-I.

Francelet, R., Coltekin, A., Richter, K.-F., Thoresen, J. C., & Fabrikant, S. I. (ancelet et al., submitted for publication). *An empirical study on the effect of realism and abstraction on map-based route learning.* (submitted for publication).

Galea, L. A. M., & Kimura, D. (1993). Sex differences in route-learning. *Personality and Individual Differences, 14*(1), 53–65. http://dx.doi.org/10.1016/0191-8869(93)90174-2.

Goette, L., Bendahan, S., Thoresen, J., Hollis, F., & Sandi, C. (2015). Stress pulls us apart: Anxiety leads to differences in competitive confidence under stress. *Psychoneuroendocrinology, 54*, 115–123. http://dx.doi.org/10.1016/j.psyneuen.2015.01.019.

Gorka, A. X., Hanson, J. L., Radtke, S. R., & Hariri, A. R. (2014). Reduced hippocampal and medial prefrontal gray matter mediate the association between reported childhood maltreatment and trait anxiety in adulthood and predict sensitivity to future life stress. *Biology of Mood & Anxiety Disorders, 4*(1), 1–10. http://dx.doi.org/10.1186/2045-5380-4-12.

Hausmann, M., Slabbekoorn, D., Van Goozen, S. H., Cohen-Kettenis, P. T., & Güntürkün, O. (2000). Sex hormones affect spatial abilities during the menstrual cycle. *Behavioral Neuroscience, 114*(6), 1245–1250. http://dx.doi.org/10.1037/0735-7044.114.6.1245.

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research, 209*(1), 49–58. http://dx.doi.org/10.1016/j.bbr.2010.01.012.

Herrero, A. I., Sandi, C., & Venero, C. (2006). Individual differences in anxiety trait are related to spatial learning abilities and hippocampal expression of mineralocorticoid receptors. *Neurobiology of Learning and Memory, 86*(2), 150–159. http://dx.doi.org/10.1016/j.nlm.2006.02.001.

Hollis, F., van der Kooij, M. A., Zanoletti, O., Lozano, L., Cantó, C., & Sandi, C. (2015). Mitochondrial function in the brain links anxiety with social subordination. *Proceedings of the National Academy of Sciences, 112*(50), 15486–15491. http://dx.doi.org/10.1073/pnas.1512653112.

Horikawa, M., & Yagi, A. (2012). The relationships among trait anxiety, state anxiety and the goal performance of penalty shoot-out by university soccer players. *PLoS ONE, 7*(4), e35727. http://dx.doi.org/10.1371/journal.pone.0035727.

Jennings, J. H., Sparta, D. R., Stamatakis, A. M., Ung, R. L., Pleil, K. E., Kash, T. L., & Stuber, G. D. (2013). Distinct extended amygdala circuits for divergent motivational states. *Nature, 496*(7444), 224–228. http://dx.doi.org/10.1038/nature12041.

Jin, J., & Maren, S. (2015). Prefrontal-hippocampal interactions in memory and emotion. *Frontiers in Systems Neuroscience, 9*, 170. http://dx.doi.org/10.3389/fnsys.2015.00170.

Johnson, W., & Bouchard, T. J. Jr, (2005). The structure of human intelligence: It is verbal, perceptual, and image rotation (VPR), not fluid and crystallized. *Intelligence, 33*(4), 393–416. http://dx.doi.org/10.1016/j.intell.2004.12.002.

Johnson, D. R., & Gronlund, S. D. (2009). Individuals lower in working memory capacity are particularly vulnerable to anxiety's disruptive effect on performance. *Anxiety, Stress, & Coping, 22*(2), 201–213. http://dx.doi.org/10.1080/10615800802291277.

Kessler, R. C., Aguilar-Gaxiola, S., Alonso, J., Chatterji, S., Lee, S., Ormel, J., ... Wang, P. S. (2009). The global burden of mental disorders: An update from the WHO World Mental Health (WMH) surveys. *Epidemiologia e Psichiatria Sociale, 18*(01), 23–33. http://dx.doi.org/10.1017/S1121189X00001421.

Kim, S.-Y., Adhikari, A., Lee, S. Y., Marshel, J. H., Kim, C. K., Mallory, C. S., ... Deisseroth, K. (2013). Diverging neural pathways assemble a behavioural state from separable features in anxiety. *Nature, 496*(7444), 219–223. http://dx.doi.org/10.1038/nature12018.

Kim, M. J., Loucks, R. A., Palmer, A. L., Brown, A. C., Solomon, K. M., Marchante, A. N., & Whalen, P. J. (2011). The structural and functional connectivity of the amygdala: From normal emotion to pathological anxiety. *Behavioural Brain Research, 223*(2), 403–410. http://dx.doi.org/10.1016/j.bbr.2011.04.025.

Kim, M. J., & Whalen, P. J. (2009). The structural integrity of an amygdala–prefrontal pathway predicts trait anxiety. *The Journal of Neuroscience, 29*(37), 11614–11618. http://dx.doi.org/10.1523/JNEUROSCI.2335-09.2009.

Klumpp, H., Ho, S. S., Taylor, S. F., Phan, K. L., Abelson, J. L., & Liberzon, I. (2011). Trait anxiety modulates anterior cingulate activation to threat interference. *Depression and Anxiety, 28*(3), 194–201. http://dx.doi.org/10.1002/da.20802.

Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. *Sex Roles, 30*(11–12), 765–779. http://dx.doi.org/10.1007/bf01544230.

Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development, 56*(6), 1479–1498. http://dx.doi.org/10.2307/1130467.

Mackintosh, N. J., & Bennett, E. S. (2003). The fractionation of working memory maps onto different components of intelligence. *Intelligence, 31*(6), 519–531. http://dx.doi.org/10.1016/S0160-2896(03)00052-7.

MacLeod, C., & Donnellan, A. M. (1993). Individual differences in anxiety and the restriction of working memory capacity. *Personality and Individual Differences, 15*(2), 163–173. http://dx.doi.org/10.1016/0191-8869(93)90023-V.

Malinowski, J. C. (2001). Mental rotation and real-world wayfinding. *Perceptual and Motor Skills, 92*(1), 19–30. http://dx.doi.org/10.2466/pms.2001.92.1.19.

Miyake, A., Friedman, N. P., Rettinger, D. A., Shah, P., & Hegarty, M. (2001). How are visuospatial working memory, executive functioning, and spatial abilities related? A latent-variable analysis. *Journal of Experimental Psychology: General, 130*(4), 621–640. http://dx.doi.org/10.1037/0096-3445.130.4.621.

Moffat, S. D., Hampson, E., & Hatzipantelis, M. (1998). Navigation in a "virtual" maze: Sex differences and correlation with psychometric measures of spatial ability in humans. *Evolution and Human Behavior, 19*(2), 73–87. http://dx.doi.org/10.1016/S1090-5138(97)00104-9.

Montello, D. R., Lovelace, K. L., Golledge, R. G., & Self, C. M. (1999). Sex-related differences and similarities in geographic and environmental spatial abilities. *Annals of the Association of American Geographers, 89*(3), 515–534. http://dx.doi.org/10.1111/0004-5608.00160.

Murray, N. P., & Janelle, C. M. (2003). Anxiety and performance: A visual search examination of the processing efficiency theory. *Journal of Sport and Exercise Psychology, 25*(2), 171–187.

Nardi, D., Newcombe, N. S., & Shipley, T. F. (2012). Reorienting with terrain slope and landmarks. *Memory and Cognition, 41*(2), 214–228. http://dx.doi.org/10.3758/s13421-012-0254-9.

Owens, M., Stevenson, J., Hadwin, J. A., & Norgate, R. (2014). When does anxiety help or hinder cognitive test performance? The role of working memory capacity. *British Journal of Psychology, 105*(1), 92–101. http://dx.doi.org/10.1111/bjop.12009.

Pazzaglia, F., & De Beni, R. (2001). Strategies of processing spatial information in survey and landmark-centred individuals. *European Journal of Cognitive Psychology, 13*(4), 493–508. http://dx.doi.org/10.1080/09541440125778.

Pazzaglia, F., & De Beni, R. (2006). Are people with high and low mental rotation abilities differently susceptible to the alignment effect? *Perception, 35*(3), 369–383. http://dx.doi.org/10.1068/p5465.

Robinson, A. H., & Petchenik, B. B. (1976). *The nature of maps: Essays toward understanding maps and mapping.*Chicago: University of Chicago Press.

Salehi, B., Cordero, M. I., & Sandi, C. (2010). Learning under stress: The inverted-U-shape function revisited. *Learning & Memory, 17*(10), 522–530. http://dx.doi.org/10.1101/lm.1914110.

Sandi, C., Cordero, M. I., Ugolini, A., Varea, E., Caberlotto, L., & Large, C. H. (2008). Chronic stress-induced alterations in amygdala responsiveness and behavior – Modulation by trait anxiety and corticotropin-releasing factor systems. *European Journal of Neuroscience, 28*(9), 1836–1848. http://dx.doi.org/10.1111/j.1460-9568.2008.06451.x.

Sandi, C., & Richter-Levin, G. (2009). From high anxiety trait to depression: A neurocognitive hypothesis. *Trends in Neurosciences, 32*(6), 312–320. http://dx.doi.org/10.1016/j.tins.2009.02.004.

Satpute, A. B., Mumford, J. A., Naliboff, B. D., & Poldrack, R. A. (2012). Human anterior and posterior hippocampus respond distinctly to state and trait anxiety. *Emotion, 12*, 56–68. http://dx.doi.org/10.1037/a0026517.

Schöning, S., Engelien, A., Kugel, H., Schäfer, S., Schiffbauer, H., Zwitserlood, P., ... Konrad, C. (2007). Functional anatomy of visuo-spatial working memory during mental rotation is influenced by sex, menstrual cycle, and sex steroid hormones. *Neuropsychologia, 45*(14), 3203–3214. http://dx.doi.org/10.1016/j.neuropsychologia.2007.06.011.

Shah, P., & Miyake, A. (1996). The separability of working memory resources for spatial thinking and language processing: An individual differences approach. *Journal of Experimental Psychology: General, 125*(1), 4–27. http://dx.doi.org/10.1037/0096-3445.125.1.4.

Smallman, H. S., & Cook, M. B. (2011). Naïve realism: Folk fallacies in the design and use of visual displays. *Topics in Cognitive Science, 3*(3), 579–608. http://dx.doi.org/10.1111/j.1756-8765.2010.01114.x.

Spellman, T., Rigotti, M., Ahmari, S. E., Fusi, S., Gogos, J. A., & Gordon, J. A. (2015). Hippocampal-prefrontal input supports spatial encoding in working memory. *Nature, 522*(7556), 309–314. http://dx.doi.org/10.1038/nature14445.

Spielberger, C. D. (1972). *Anxiety: Current trends in theory and research* (Vol. 1)New York: Academic Press.

Spielberger, C. D. (1983). *Manual for the State-Trait Anxiety Inventory STAI.* .

Taylor, J. M., & Whalen, P. J. (2015). Neuroimaging and anxiety: The neural substrates of pathological and non-pathological anxiety. *Current Psychiatry Reports, 17*(6), 1–10. http://dx.doi.org/10.1007/s11920-015-0586-9.

Tom, A. C., & Tversky, B. (2012). Remembering routes: Streets and landmarks. *Applied Cognitive Psychology, 26*(2), 182–193. http://dx.doi.org/10.1002/acp.1805.

Vandenberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills, 47*(2), 599–604. http://dx.doi.org/10.2466/pms.1978.47.2.599.

Viaud-Delmon, I., Berthoz, A., & Jouvent, R. (2002). Multisensory integration for spatial orientation in trait anxiety subjects: Absence of visual dependence. *European Psychiatry, 17*(4), 194–199. http://dx.doi.org/10.1016/S0924-9338(02)00667-3.

Viaud-Delmon, I., Siegler, I., Israël, I., Jouvent, R., & Berthoz, A. (2000). Eye deviation during rotation in darkness in trait anxiety: An early expression of perceptual avoidance? *Biological Psychiatry, 47*(2), 112–118. http://dx.doi.org/10.1016/S0006-3223(99)00111-0.

Vytal, K. E., Cornwell, B. R., Letkiewicz, A. M., Arkin, N. E., & Grillon, C. (2013). The complex interaction between anxiety and cognition: Insight from spatial and verbal working memory. *Frontiers in Human Neuroscience, 7*, 1–11. http://dx.doi.org/10.3389/fnhum.2013.00093.

Wilkening, J., & Fabrikant, S. I. (2011). The effect of gender and spatial abilities on map use preferences and performance in road selection tasks. *Paper presented at the proceedings of the international cartographic conference*.

Wilkniss, S. M., Jones, M. G., Korol, D. L., Gold, P. E., & Manning, C. A. (1997). Age-related differences in an ecologically based study of route learning. *Psychology and Aging, 12*(2), 372–375. http://dx.doi.org/10.1037/0882-7974.12.2.372.

Wolbers, T., & Hegarty, M. (2010). What determines our navigational abilities? *Trends in Cognitive Sciences, 14*(3), 138–146. http://dx.doi.org/10.1016/j.tics.2010.01.001.