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ABSTRACT
Increased cortisol may differentially impact navigation strategies. Three within-subjects experiments investigated how the Trier Social Stress Test (TSST), the Cold Pressor Test (CPT), and a prolonged bout of physical exercise (PE), all known to increase cortisol, affect navigation strategy and efficiency. Participants learned an environment, were stressed, and then navigated. Cortisol was higher in all stress sessions relative to a no-stress control session. TSST and CPT did not affect strategy or efficiency, while PE increased shortcut use. Results suggest navigation strategies are resilient to cortisol-based stress however questions remain as to how strategy shifts occur.

KEYWORDS
Navigation; strategy; cortisol; individual differences; stress

As we navigate in our environment from one place to another, we experience various cognitive and physiological states. Some situations, such as navigating to our place of work, can be mundane and typical, while others, such as navigating in a novel or dangerous environment, can be stressful. In humans, stress can activate two systems. The first is the sympathetic adrenal medulla (SAM) axis, leading to the immediate release of catecholamines to prepare the body for action. The second system is the hypothalamic pituitary adrenal (HPA) axis which is comparatively slower. This system releases glucocorticoids, such as cortisol, which peaks 20–40 minutes after the stressor and then dissipates, returning to the baseline by 60 minutes after the stressor (Gagnon & Wagner, 2016). Here, we study the effects of the HPA axis (i.e., the release of cortisol) on navigation strategy and efficiency.

People use different navigation strategies, notably following familiar routes and taking shortcuts, supported by memory systems and brain regions that are differentially implicated in the stress response system. Following well-learned routes is supported by stimulus-response learning associated with the caudate

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nucleus, whereas shortcutting is supported by a spatial place-based, cognitive system supported by the hippocampus (Furman et al., 2014; Iaria et al., 2003; Maguire et al., 1998; Marchette et al., 2011; O'Keefe & Nadel, 1978; Packard & McGaugh, 1996). Notably, cortisol binds more in the hippocampus than the caudate and may impede the use of shortcuts, causing people to fall back on learned routes. Here, we investigated the effects of three different acute stressors (known to elicit cortisol response) on navigation strategy, to test the hypothesis that acute stress would impede shortcut-based navigation and cause people to shift to navigate based on familiar routes.

2. Navigation strategy and the brain

Navigation refers to the set of cognitive processes involved in both locomotion and wayfinding (Montello, 2005). There are large individual differences in navigation abilities, such as the ability to learn the layout of a new environment (Hegarty et al., 2006; Ishikawa & Montello, 2006; Weisberg & Newcombe, 2016), and the strategy used to navigate a familiar environment (Furman et al., 2014; Lawton et al., 1996; Marchette et al., 2011).

A wealth of evidence from animal and human neuroscience and behavioral studies suggests that there are two primary navigation strategies supported by different memory systems and brain structures: a place-based strategy and a response-based strategy (Furman et al., 2014; Iaria et al., 2003; Maguire et al., 1998; Marchette et al., 2011; O'Keefe & Nadel, 1978; Packard & McGaugh, 1996). The *place-based strategy* relies on an internal representation of the layout of the environment and is characterized by flexible spatial reasoning, enabling navigators to point to unseen locations accurately and take shortcuts to goal locations (Kozlowski & Bryant, 1977). This strategy is largely dependent upon the hippocampus (Morris et al., 1982; Sutherland et al., 1982), including hippocampal place cells (O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978). The *response strategy* is characterized by reliance upon a sequence of stimulus response actions made at choice points in the environment during learning (i.e. a learned route). This strategy is less flexible, but also less demanding of cognitive resources. In human fMRI studies, the caudate nucleus is active when this strategy is used (Iaria et al., 2003; Marchette et al., 2011).

Human and animal neuroscience studies have generally supported these strategy distinctions. Specifically, the hippocampus is activated to a greater extent when navigators use spatial strategies compared to those that use non-spatial strategies (Iaria et al., 2003; Kumaran & Maguire, 2005; Maguire et al., 1998; Maguire et al., 2006; Schinazi et al., 2013) and the caudate nucleus is more active for those navigating by response-based strategies (Bohbot et al., 2007; Iaria et al., 2003). Importantly, in animal studies, chemical inactivation or lesions of the hippocampus leads to more response-like navigation, while inactivation of the caudate nucleus leads to more place-like navigation (Packard & McGaugh, 1996), indicating that in the absence of one system, the second system is engaged to enable the animal to achieve navigation goals.

Building on work in the rodent literature, Marchette et al. (2011) developed a "Dual Solution Task (DSP)" to study the interplay between these two navigation strategies in humans. They showed participants a video of a path through an enclosed desktop virtual environment (the learned route) along which landmark objects were placed. After learning this route (by viewing the video several times), participants were placed in different locations on the learned route and asked to navigate to other landmarks in the environment. They were free to navigate using any strategy. Trials were categorized as either shortcuts or learned routes by a winner-takes-all strategy of number of steps on each route. Marchette et al. (2011) found that some people took all learned routes while others took all shortcuts, and many used a mix of strategies. Critically, fMRI analysis indicated that participants who used spatial strategies and took shortcuts showed greater activation in the hippocampus when they learned the maze compared to those who used response strategies. In contrast, participants using more response-based strategies showed greater activation in the caudate nucleus during learning compared to those who use spatial strategies. More recently, Boone et al. (2018) found similar patterns regarding individual differences in strategy in the DSP. However, in addition to taking shortcuts and learned routes, participants sometimes reversed their learned route or wandered in the environment until they found the goal. Further, Boone et al. (2019) found that repeated exposures to the task led to a small but significant increase in shortcutting behavior.

2.1. Assessing effect of acute stressors on navigation strategy and efficiency

After a stressful event, glucocorticoids are released from the adrenal cortex. In one rodent study, McEwen et al. (1968) injected rats with corticosteroids (similar to cortisol in humans) to understand where they are retained within the brain. Across the six tested locations across the brain, they found that the largest concentrations of this hormone were in the septum and the hippocampus (McEwen et al., 1968). Stress has a range of effects on declarative memory systems, which are dependent on the hippocampus. Stress can either enhance or impair learning and memory consolidation, depending on the temporal placement of the stressor and the level of stress (Andreano & Cahill, 2006; Kirschbaum et al., 1996) but generally impedes memory retrieval (de Quervain et al., 1998, 2000; Gagnon & Wagner, 2016). Moreover, both animal and human studies suggest that acute stress causes a shift from a reliance on flexible hippocampal-dependent memory and learning systems to more rigid habit-based systems, supported by striatal brain regions (Schwabe & Wolf, 2013; Schwabe et al., 2007).

Studies of human spatial memory have manipulated stress either *before* participants learned the layout of an environment, measuring the effects of stress on learning, or *after* people learned the layout of the environment and before testing, measuring the effects of stress on retrieval. In these studies, stress is typically induced using the Trier Social Stress Task (TSST; Kirschbaum et al., 1993), or the Cold Pressor Test (CPT), a measure of physical stress (Hines & Brown, 1932; Lamotte et al., 2021). The TSST is a well-validated social stress manipulation that requires a participant to prepare a speech, then present it to a critical peer group, followed by a difficult mental arithmetic task. This task reliably increases cortisol over baseline due to the social-evaluative nature of the task representing a threat to the social self (Dickerson & Kemeny, 2004). In the CPT, participants immerse a limb in cold water for several minutes. This procedure induces pain and a variety of physiological responses, including elevated heart rate, blood pressure, and cortisol (Bullock et al., 2023; Larra et al., 2015).

Studies of the effects of different stressors on learning have shown mixed effects. In studies of virtual navigation tasks modeled on the Morris Water maze, Duncko et al. (2007) found that inducing stress via the CPT led to better performance, Thomas et al. (2010) found that the TSST impaired performance in female but not male participants, van Gerven et al. (2016) found no effect of the TSST and Klopp et al. (2012) found that a stressful mental arithmetic task biased people to use an allocentric rather than an egocentric strategy, but did not affect overall task performance. In studies that required learning the layout of virtual environments, stress induced by a frustrating mirror star tracing task slowed performance but did not affect accuracy (Richardson & VanderKaay Tomasulo, 2011), while the socially evaluated cold pressor task (Richardson & VanderKaay Tomasulo, 2022) and time pressure (Credé et al., 2019) showed no effects. These varied results might reflect differences in the nature of the stressors, the level of stress induced, variations in the timing of stressors relative to learning and testing, or task differences (including difficulty, goals, and strategy demands).

The present study is concerned with the effects of stress on wayfinding strategies, that is, how people navigate to goal locations based on previously acquired knowledge. Two previous studies have manipulated stress after people learned the layout of a virtual environment and while they were performing wayfinding trials based on their knowledge. Brunyé et al. (2016) used time pressure to induce stress and found that people were more likely to follow learned routes than more efficient shortcuts, but they did not objectively measure stress. Brown et al. (2020) examined the effects of the threat of cutaneous shock on strategies in a dual solution task similar to that of Marchette et al. (2011). After learning inefficient routes through virtual environments, participants had to plan and then execute routes to locations in the virtual environments. Participants were more likely to take the learned routes than available shortcuts, and navigated less efficiently while under stress (which was accompanied by higher levels of cortisol). Moreover, these effects were mediated by decreased neural activity in hippocampal circuits involved in memory retrieval and mental simulation of potential paths. This was the first demonstration in humans that cortisol can affect strategy choice in a dual solution task by impeding access to hippocampal circuits underlying place-based navigation. It is consistent with studies suggesting a shift from spatial to stimulus response strategies with stress (Schwabe & Wolf, 2013; Schwabe et al., 2007). In related research, Bohbot et al. (2011) found that participants with lower basal levels of cortisol were less likely to use spatial strategies in a virtual maze navigation task, contrary to prediction, and suggested that the effects of stress conformed to an inverted U-shaped function.

These previous studies raise questions about which types of stressors, timing of stress relative to learning, and levels of stress can affect navigation. Extant studies differed in their methods of inducing stress, navigation task studied, and timing of stress relative to navigation, making it difficult to discern which factors are responsible for the seeming discrepancies across studies. Here, we study the effects of three different stressors on the same task, the Dual Solution Task (Marchette et al., 2011). In a series of three studies, stress was induced after participants learned the layout of a spatial environment and before they were tested. Each participant completed navigation trials both under stress and in a control condition, on two separate days. Experiment 1 employed the Trier Social Stress Test (TSST; Kirschbaum et al., 1993). Experiment 2 employed a variant of the Cold Pressor Test (CPT; Hines & Brown, 1932 Larra et al., 2015). In Experiment 3, stress was induced by an extended bout of physical exercise (cycling on a stationary bike for 120 minutes) which dramatically increases cortisol over baseline values (Bullock & Giesbrecht, 2014; O'Connor & Corrigan, 1987) but has not been implemented in studies of stress and navigation to date. While stress is induced by psychosocial threat in the case of the TSST, noxious stimulation in the case of the CPT and prolonged physical exercise in the case of biking, the stressors were selected because each is known to increase cortisol. Our goal was not to directly compare the effects of these stressors but to establish the effects of three different stressors (known to increase cortisol) on navigation. Based on the previous literature suggesting that stress generally impedes retrieval of hippocampal-based memories (Gagnon & Wagner, 2016), and causes a shift from reliance on flexible hippocampal-dependent memory systems to more rigid habit-based systems (Brown et al., 2020; Brunyé et al., 2016; Schwabe & Wolf, 2013), we predicted that navigation would be less flexible under stress (when induced by either the TSST, CPT, or physical exercise and evidenced by an increase in cortisol) than in control conditions. Specifically, we predicted that when asked to navigate in a learned environment, participants would take fewer shortcuts and fall back on well-learned routes when under stress, leading to less efficient navigation in stressful conditions when compared to control conditions.

3. Experiment 1: social evaluative stress

Experiment 1 examined the effects of social evaluative stress (the Trier Social Stress Task) on DSP performance. Social evaluative stressors are the most reliable methods of increasing cortisol relative to baseline measures in laboratory studies (Dickerson & Kemeny, 2004). The TSST (Birkett, 2011; Kirschbaum et al., 1993) requires participants to give a speech to a critical peer group, followed by a difficult mental arithmetic task, and shows four-fold increases in cortisol release relative to baseline (Dickerson & Kemeny, 2004). This task is also associated with hippocampal deactivation for participants with higher cortisol reactivity (Pruessner et al., 2008). As a control task, we use a non-evaluative version of the TSST which is devoid of the negative aspects of the standard TSST and does not show an increase in cortisol relative to baseline (Dickerson et al., 2008; Het et al., 2009; Wiemers et al., 2013). Three previous studies have investigated the effects of the TSST on learning spatial layout (Klopp et al., 2012; Thomas et al., 2010; van Gerven et al., 2016) finding inconsistent results, as reviewed above. To date, no study has examined the effects of this stressor on retrieval of spatial memories or navigation strategy, as we do here.

In Experiment 1 navigation strategy was measured using the DSP in two sessions. In one session, participants were stressed by performing the TSST after learning and before the wayfinding (retrieval) trials. In a second session, they performed an active control version of the TSST after learning and before testing. We predicted that place-based navigation strategies would be disrupted in the full TSST stress condition such that participants would take fewer shortcuts and navigate less efficiently than in the active control condition, and that this disruption would be mediated by increased levels of cortisol in the stress condition.

4. Method

4.1. Participants

Participants were 40 University of California, Santa Barbara students (20 females) who were compensated at a rate of $20 per hour. One female participant was unable to complete the trials due to motion sickness and was removed from analysis.

4.2. Design

A 2 (stress condition: Stress vs. Active Control) × 2 (order: Control first vs. Stress first) design was used. Stress was manipulated within subjects, and order of conditions was manipulated between subjects.

4.3. Materials and apparatus

4.3.1. Overall study

An Asus VS278 27-inch monitor, with a resolution of 1920 × 1080 and a refresh rate of 60 Hz, was used to present stimuli. The viewing distance was approximately 1350 mm. Thermo cryotubes (Thermo Fisher Scientific, Waltham, MA) were used to collect saliva at regular intervals across the testing sessions. After the collection, cryotubes were placed into a freezer at a temperature of −80°C. Saliva samples were shipped on dry ice and assayed at the University of California Davis Clinical Endocrinology Lab using standard ELISA cortisol assay kits (Salimetrics, Inc., State College, PA). Experimental sessions were conducted in the morning or the afternoon, and the experimental and control sessions were always conducted at the same time day for each participant. Physiological, EEG, eye tracking, and thermal imaging recordings were collected as part of a larger study and are described in Supplementary Materials.

4.3.2. Trier social stress test (TSST)

An 8 × 10 ft room divider was used to create a speech preparation room section and a panelist section in a large room (approximately 30 × 30 ft). Three female panelists wearing white lab coats sat in a row facing the participant approximately 8 ft away. One panelist used a stopwatch to record speech timing and another conducted the session by reading a script printed on paper.

4.3.3. Dual solution mazes

Two mazes used in previous research (Boone et al., 2019), which differed in visual appearance (red brick vs. white brick) but were similar in complexity (they were mirror images of each other and had different starting locations), were used in the present study (see Figure 1). The equivalent difficulty of these mazes was established in a pilot study (see Supplementary Materials). The pairing of maze (red brick vs. white brick) with stressor was counterbalanced across subjects.

4.4. Procedure

This experiment was conducted in the context of a larger study that examined the effects of stress on several cognitive tasks. A description of the overall procedure for the study can be found in the Supplementary Materials (Figure SM1).

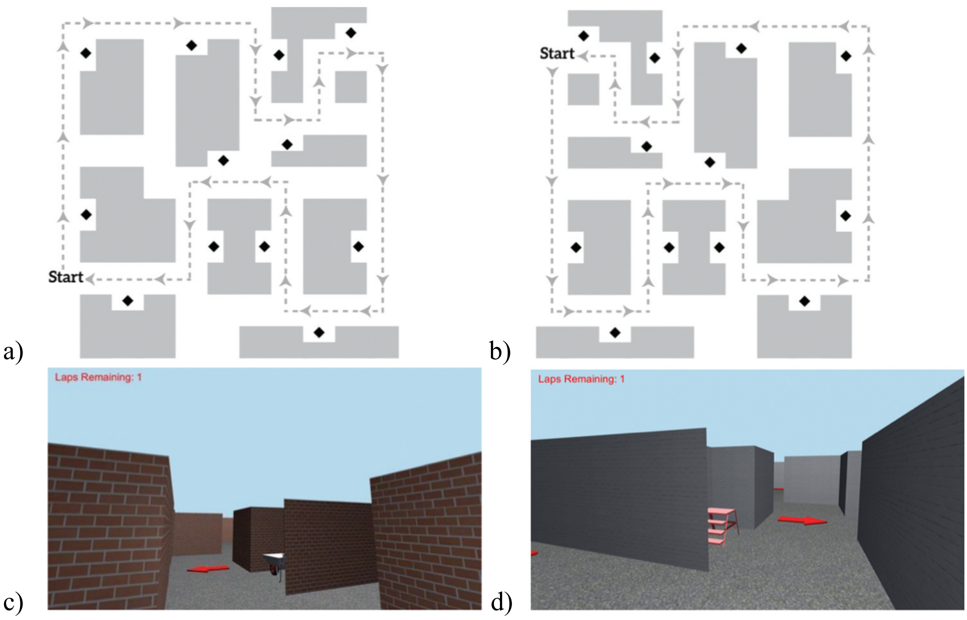

Figure 1. Maze layouts used in this experiment representing the learned route (dashed line) and environmental view from the participant's perspective. Participants learned only this route in each maze. a) Red brick maze schematic structure modeled after Marchette et al. (2011), b) gray brick maze schematic mirroring the red brick maze, c) participant view of red brick maze and d) gray brick maze during the learning phase taken from the same viewpoint. *Note*. Black diamonds represent local landmark locations. Participants walk this route five total times in first person perspective on a desktop computer in the learning phase. In the red brick maze, the order of the objects presented in alcoves along the learning tour was as follows: brown desk chair, blue U.S. Post Office mail drop box, telescope, potted plant, picnic table, stove, piano, trashcan, empty bookshelf, wheelbarrow, harp, and a wooden wishing well. In the gray brick maze, the order of the objects was as follows: desk, water cooler, streetlamp, red stepladder, refrigerator, bicycle, lion statue, couch, phone booth, wooden swing, grandfather clock, and a television. All objects were downloaded from TurboSquid.com or through the Unity asset store.

4.4.1. Dual solution paradigm task (DSP)

Participants learned a specific route through the first maze by traversing the route five times using keyboard and mouse controls. Then, they performed 20 trials in which they were placed at one object in the maze and asked to navigate to another object. For each trial, there was a clear shortcut, but participants were free to navigate by any strategy. Trials were coded as shortcut or "other strategy" (taking the learned route, reversing the learned route, or wandering). Figure 2 shows examples of these categories.

4.4.2. Trier social stress task and active control

Figure 3 (first panel) shows the sequence of events in the stress and control sessions. The order of control and stress conditions was counterbalanced across participants. A generalized procedure will be described for both

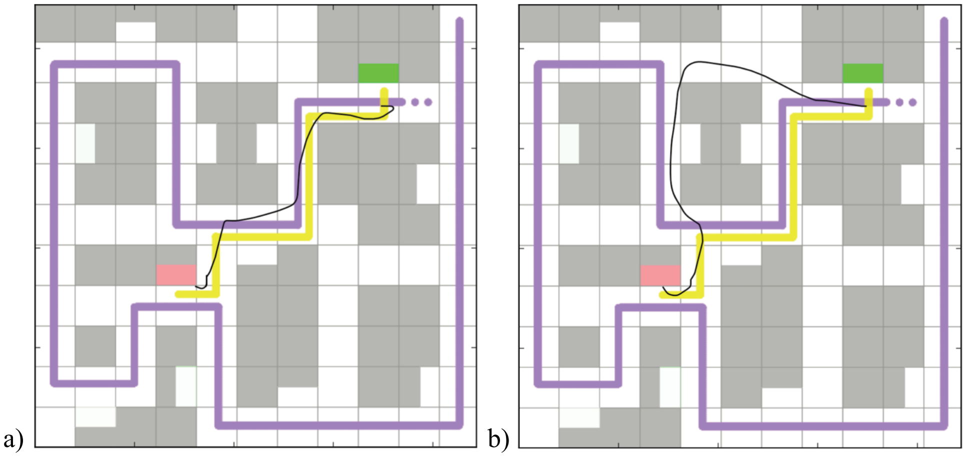

Figure 2. Representative examples of a) a direct shortcut and b) a shortcut with a slight deviation. The purple line indicates the entire learned path. The yellow line indicates the shortcut path on this specific trial. The black line represents the navigation path of the participant. The green and red rectangles represent the start and end location on this trial, respectively. Participants did not see the colored start or end colored squares.

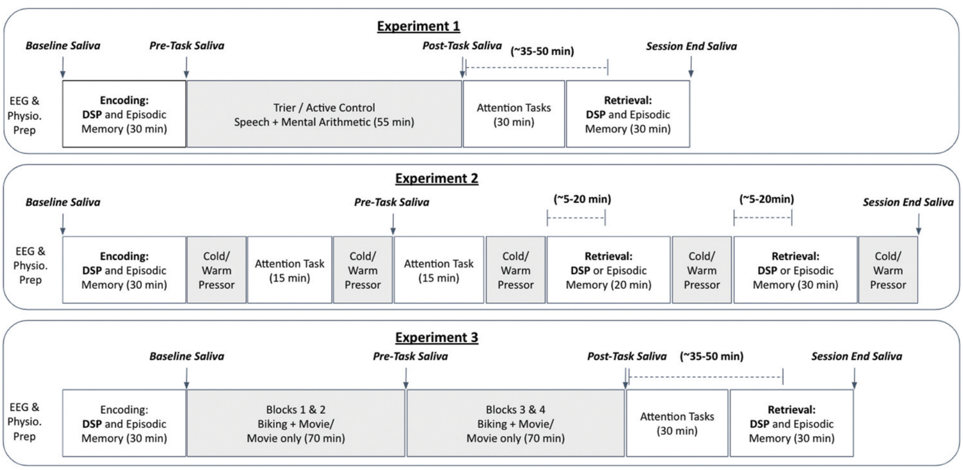

Figure 3. Procedure for each stressor experiment, indicating the timing of tasks. Stressors are indicated in gray and cognitive tasks in white rectangles. The navigation trials were started approximately 35–50 minutes after the mental arithmetic task in experiment 1, 5–20 minutes after the preceding foot submersion in experiment 2, and 35–50 minutes after the final biking/movie task in experiment 3. Note that control and experimental sessions were conducted at the same time of day (morning or afternoon) for each subject.

sessions. In each session, participants were fitted with instrumentation (see supplementary materials), provided the first saliva sample and then relaxed while a 3-minute baseline physiological recording was administered. Next, they completed the learning phases for two tasks: they learned the maze route in the DSP and encoded a sequence of natural scenes images (for a separate recognition memory task not reported here). After this, participants provided a second saliva sample and were relocated by the experimenter to a large room that was set up for the TSST or matched control.

In the TSST (modeled after Birkett, 2011) after a short baseline period, participants were instructed by the lead experimenter that they would be given 10 minutes to prepare a five-minute speech on why they would be the ideal candidate for their dream job. They were told they would be recorded on video and audio and were given the opportunity to ask questions before the preparation time began. After 10 minutes, the room divider was removed, revealing three female panelists matched roughly in age to the participant. The participant was then told to deliver their speech to the panelists for 5 minutes. If the participant stopped speaking for 20 seconds consecutively, they were instructed by the lead panelist (seated at the center of the desk) to continue. After 5 minutes had elapsed, the lead panelist instructed the participant to stop speaking, and that they would next complete a math task in which they must consecutively subtract 13 starting from 1022 for a period of 5 minutes. If the participant made a mistake, a panelist interrupted them with the message "That is incorrect, please start over at 1022" and the participant restarted the subtraction task.

In the active control condition, participants were given a similar set of instructions by the lead experimenter. To avoid emotionally evocative talking points (Dickerson et al., 2008; Het et al., 2009), participants gave a speech about their everyday lives while facing the room divider. The lead experimenter was in the room but did not pay attention to their speech, except to ensure that they spoke for the entire time. Next, participants were instructed to complete a simple addition task; they were required to start at zero and count up by fives for 5 minutes (e.g. 0, 5, 10, 15 …). Finally, in both conditions, after all TSST components were completed, participants were allowed to rest for 5 minutes and were moved back to the testing room where they self-reported their stress level on a 0–100 scale and provided the third saliva sample.

Participants performed a series of unrelated tasks (see supplementary materials and Figure 3) before collection of the fourth saliva sample. Then, participants performed the test trials of the navigation task (DSP) and the memory recall task (with order of these tasks counterbalanced between participants). In the DSP, participants had 40 seconds to complete each of the 20 trials. Participants then performed another unrelated task (see supplementary materials) and provided the final saliva sample.

4.4.3. Coding and analysis

All protocols were approved by Western IRB. The same analysis approach was used for each of the following experiments. The cortisol data for each condition was assessed for normality per (Miller & Plessow, 2013) (see also Box &

Cox, 1964). All theta values fell within confidence interval ranges. Therefore, all samples were subsequently log transformed. The main method of analysis utilizes ANOVA to examine the effects of stress/control conditions on navigation performance, strategy, and efficiency. Greenhouse–Geisser corrections for the degrees of freedom were used for violations of sphericity. The Bayes factors R package (Morey & Rouder, 2022) is used to examine null effects of stress where appropriate.

The coding system for the DSP was established in earlier research (see Boone et al., 2019) and used in all three experiments reported here. Navigation success (task performance) was the number of trials in which a participant reached the goal within the 40 seconds time limit. Trials were coded individually as shortcuts or other categories (the learned route, reversal of the learned route, or wandering). We computed a single, solution index measure (SI) equal to the number of shortcut trials divided by the number of successful trials (Furman et al., 2014; Marchette et al., 2011). This formula produces a number on a scale of 0 (indicating no shortcuts) to 1 (indicating all successful trials were shortcuts). Path efficiency, as previously described in Boone et al. (2019), was computed by dividing the distance traveled in each trial by the optimal (i.e., shortest) distance between the two locations and then averaging over trials. This metric expresses the path length traveled in relation to the shortest path, where larger numbers indicate *less* efficient travel (e.g., an average path efficiency of two indicates that the participant traveled twice as far as the shortest path across trials).

5. Results

Manipulation Checks. Participants rated their stress level as much higher in the stress condition ($M = 61.68$ on a scale from 0 to 100, $SD = 26.13$) than in the control condition ($M = 27.18$, $SD = 21.82$), $t(32) = 9.03$, $p < .001$, $d = 1.43$. Log-transformed cortisol values across sessions and samples (used in the analyses) are shown in Figure 4 (left panel), and raw data means are shown in Table 1. The first (baseline) cortisol sample of each session was never different between conditions in any of the experiments and will not be discussed further. A 2 (condition: stress vs control) × 3 (time of cortisol samples: pre-stress, post-stress, final) ANOVA indicated a significant effect of condition, $F(1, 38) = 5.01$, $p = .03$, $\eta_p^2 = .12$, with higher values in the stress condition ($M = .80$, $SD = .23$) than the control condition ($M = .75$, $SD = .25$). There was also a significant effect of time of cortisol sample, $F(1.82, 69.06) = 22.62$, $p < .001$, $\eta_p^2 = .37$, with highest levels of cortisol in the third (post-stress) sample, as expected, and an interaction of condition and time, $F(1.54, 58.51) = 5.30$, $p = .01$, $\eta_p^2 = .12$. Critically, simple effects analyses indicated no differences between conditions on the second (pre-stressor) sample, $F(1, 38) = .41$, $p = .74$, and a significant difference between

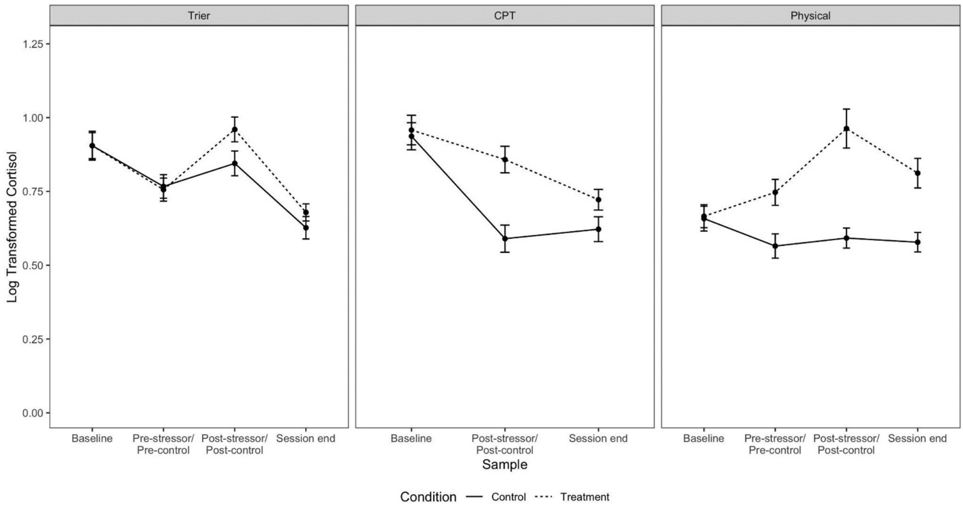

Figure 4. Average log-transformed cortisol values for salivary collection sample in each experiment. Error bars represent ± 1 SEM.

Table 1. Mean levels of cortisol (nmol/l) observed in the control and stress conditions at different stages of experiments 1 through 3. Levels of cortisol observed after inducing stress are shown in bold font.

	Experiment 1 (Trier)		Experiment 2 (CPT)		Experiment 3 (Biking)	
	Control	Stressor	Control	Stressor	Control	Stressor
Baseline sample	10.40 (8.35)	9.76 (6.78)	10.89 (7.32)	12.23 (10.11)	5.56 (4.13)	5.55 (4.92)
Pre-stressor sample	6.89 (4.16)	6.82 (5.08)	–	–	4.47 (3.03)	6.71 (4.16)
Post-stressor sample	8.40 (5.42)	**10.79 (6.00)**	5.35 (7.15)	**9.03 (6.32)**	4.23 (2.19)	**13.85 (13.70)**
Final sample	5.11 (4.35)	5.22 (2.43)	5.49 (6.55)	6.22 (4.33)	4.26 (2.15)	8.80 (9.93)

conditions on the third (post-stressor) sample, $F(1, 38) = 9.59$, $p = .004$, $\eta_p^2 = .20$. However, no difference was found between conditions in the fourth (post task) sample, $F(1, 38) = 4.16$, $p = .05$, $\eta_p^2 = .10$. In sum, participants subjectively experienced more stress and had higher cortisol after the stress manipulation than after the active control condition.

5.1. Navigation success

Participants navigated successfully, as seen in the left panel of Figure 5, to the goal location on most trials ($M = 17.64$, $SD = 2.05$ control trials and $M = 17.92$, $SD = 1.92$ stress trials) within the 40-second time limit (*Mean time* = 22.74 s, $SD = 9.57$ s) as is typical for this task (Boone et al., 2018, 2019). There was no effect of stress, $F(1, 37) = .72$, $p = .40$, $BF = .42$, trial order, $F(1, 37) = .88$, $p = .36$, $BF = .28$, nor their interaction on this measure of performance, F(1, 37) = .72, $p = .40$, $BF = .28$, in all cases and the Bayes factor for the main effect of stress indicated anecdotal to moderate evidence for the null hypothesis.

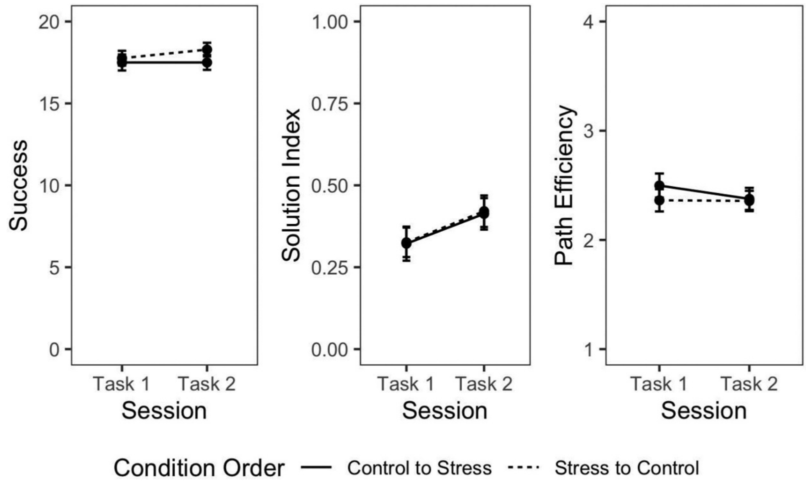

Figure 5. Each main dependent variable of the DSP assessed after the trier social stress test. Success was the count of successful trials. Solution index was measured by dividing the number of shortcuts taken out of 20 trials. Path efficiency was measured as the average distance traveled compared to the shortest route, where 1 would be the shortest path and 2 would be twice the distance of the shortcut. Error bars represent ± 1 SEM.

5.2. Navigation strategy

We predicted less shortcutting in the stress condition compared to the control condition. The raw strategy counts can be found in Table 2. The center panel of Figure 5 shows navigation strategy (Solution Index) across tasks. Contrary to prediction, a 2 (stressor condition) × 2 (task order) ANOVA using solution index as the dependent variable indicated no main effect of stress, $F(1, 37) = .01$, $p = .92$, $BF = .24$, indicating moderate evidence for the null hypothesis. A total of 33.7% trials in the control condition and 33.1% trials in the stress condition were coded as shortcuts. There was no effect of task order, $F(1, 37) = .01$, $p = .92$, BF = .24, indicating moderate evidence for the null hypothesis. There was a significant interaction of condition by task order, $F(1, 37) = 14.49$, $p = .001$, $\eta_p^2 = .28$, BF = 1.22, such that participants took more shortcuts in their second session, regardless of stress condition, suggesting a practice effect (consistent with Boone et al., 2019). The Bayes factor of the interaction indicates anecdotal evidence for the alternate hypothesis. Importantly, there

Table 2. Count of each strategy for each experiment by condition.

	Experiment 1 (Trier)		Experiment 2 (Cold Pressor)		Experiment 3 (Biking)	
	Control	Stressor	Control	Stressor	Control	Stressor
Shortcut	6.74 (4.40)	6.62 (4.04)	8.35 (4.31)	8.69 (4.16)	8.08 (4.36)	8.10 (4.09)
Learned	5.38 (4.56)	6.00 (4.50)	4.73 (4.49)	4.83 (4.56)	4.78 (3.82)	4.70 (4.17)
Reversal	2.33 (1.84)	2.36 (1.81)	2.04 (1.52)	1.73 (1.38)	2.43 (1.69)	2.35 (1.37)
Uncodable	2.69 (1.92)	2.67 (1.81)	2.77 (2.00)	2.79 (1.79)	2.73 (1.81)	2.55 (1.93)
Wandering	0.49 (.88)	0.28 (.51)	0.42 (.74)	0.63 (.89)	0.35 (.62)	0.53 (.68)

was a strong positive correlation between solution indices for the two conditions, $r(38) = .82$, $p < .001$, indicating that participants typically used the same strategies in the stress and control conditions.

5.3. Navigation efficiency

The right panel of Figure 5 presents the navigation efficiency across tasks and conditions. Again, contrary to prediction, a 2 (stressor condition) × 2 (order) ANOVA indicated no main effects of condition, $F(1, 37) = .65$, $p = .43$, $BF = .26$, order, $F(1, 37) = .29$, $p = .59$, $BF = .28$, nor an interaction of these factors, $F(1, 46) = .93$, $p = .34$, $BF = .27$, on efficiency. Bayes factors indicated moderate evidence for the null hypothesis in all cases.

5.4. Individual differences in stress response

Participants varied in their response to the social stressor. To determine whether cortisol expression was related to navigation performance, participants' cortisol levels in the TSST stress condition were regressed on their control day cortisol values and residuals from this analysis were used as a measure of stress response (with higher positive values indicating more reaction to the stressor). Nineteen participants were categorized as high responders and 20 were categorized as low responders based on a median split on the residuals. A 2 (condition) by stress response (high vs low) repeated measures ANOVA was conducted on solution index and navigation efficiency. No main effects nor interactions were significant, all $F(1, 37) \leq 2.97$, all $p \geq .09$.

6. Discussion

The TSST was successful in elevating cortisol levels in the stress compared to the control condition and produced a large difference in subjective ratings of stress. However, while the amount of cortisol elicited by the TSST (10.79 nmol/l) in this experiment is similar to levels observed in previous studies (Kirschbaum et al., 1993; Schwabe et al., 2007) it is notable that cortisol was also elevated in the active control condition (see Figure 4 left panel and Table 1). Moreover, differences in cortisol seem to have dissipated by the end of the experimental procedure. Altogether, these results suggest that the TSST did elevate cortisol levels, although not as strongly as expected from previous studies.

In general, navigation success, strategy, and efficiency were unaffected by stress manipulation; in all cases, Bayes factors indicated anecdotal to moderate evidence for the null hypothesis. Contrary to prediction, participants were less inclined to navigate via learned routes when under stress. Moreover, post-hoc comparisons of high- and low-cortisol responders did not indicate the predicted changes in navigation performance, strategy, or efficiency. It is therefore possible that the differences in cortisol levels between the stress and control conditions were not large enough to differentially affect the hippocampal circuits underlying place-based navigation strategy. As in previous work on using the Dual Solution Paradigm, there was a sizable practice effect (Boone et al., 2019) such that participants were more likely to take shortcuts in the second session, regardless of stress condition

7. Experiment 2: cold pressor test

Physiological stressors are stressors that produce a threat to the body, in contrast to psychosocial stressors, which represent a threat to the social self. Both stressor types elicit cortisol, although the threat posed by each stressor differs in how it is evaluated. The cold pressor task (CPT) used here is a physiological stressor task that reliably stresses participants above baseline. The CPT traditionally requires participants to submerge a hand or forearm in an ice water bath between 0° and 4° C for a period of up to 3 minutes. Recent research has shown larger effects on cortisol when participants are required to place both feet in the water (~10 nmol/l on average; Larra et al., 2015), and this method was applied here (Bullock et al., 2023; Kumar et al., 2021). It has the added advantage that hands and fingers are not made cold or immobile by the ice bath and can be used for immediate subsequent tasks. A previous study found that the CPT enhanced performance on a virtual Morris water maze task (Duncko et al., 2007) but no study to date has examined the effects of this stressor on retrieval of spatial knowledge or wayfinding strategy.

Experiment 2 used the same design as Experiment 1 except that the CPT replaced the TSST as the stressor. In the stress session, participants performed the DSP wayfinding trials after placing their feet in an ice bath, and in the control condition, they did so after placing their feet in warm water. The session order was counterbalanced across participants. As the stressor took only 90 seconds in this task, stress was induced several times over the course of the session, ensuring that participants were stressed during navigation trials. We predicted that place-based navigation strategies would be disrupted in the CPT stress condition, but not in the control condition, such that participants would take fewer shortcuts and navigate less efficiently, and that this disruption would be mediated by increased levels of cortisol in the stress condition.

8. Methods

8.1. Participants

Participants consisted of 48 University of California, Santa Barbara students (22 females) who were paid $20 per hour. Two participants were dropped from analyses due to motion sickness.

8.2. Design

A 2 (Stress vs Control) × (order: Control – Stressor vs. Stressor-Control) design was used. Session and maze type were manipulated within subjects, and order of sessions was manipulated between subjects.

8.3. Materials and apparatus

All materials used in Experiment 2 were the same as in Experiment 1 except for the substitution of the CPT for the TSST. A large, oval-shaped metal wash basin was used for the pressor tests, filled approximately 60% with water. For the stress condition, ice was added to maintain a temperature between 0°C and 4°C. For the control condition, the water was warmed to between 30°C and 38°C by introducing warm water heated through an electric tea kettle. The temperature was continuously monitored with a Zacro digital thermometer (Shenzhen, China).

8.4. Procedure

The general protocol for Experiment 2 follows that of Experiment 1 with exceptions during the stress and control sessions. Figure 3 (center panel) shows the sequence of events in sessions four and five, in which the navigation task was performed. In these sessions, the order of tasks and procedures was the same except that during one session warm water was used for all submersions (active control), while in the other session, cold water was always used (stress). Participants completed the same tasks as in Experiment 1, with the foot dips interleaved, as seen in Figure 3. The participants kept their feet in the water for 90 seconds while remaining as still as possible, after which they removed them from the water. Saliva samples were taken before the first set of cognitive tasks, after the second bout of foot dips, and after the fifth and final dip. After each water dip, the participants rated their level of stress on a 0–100-point scale.

8.4.1. Dual solution paradigm procedure

The same general procedure for this task was used as in Experiment 1, except that approximately 1 hour elapsed between learning and testing.

9. Results

9.1. Manipulation checks

Participants rated the cold pressor stress condition as much more stressful ($M = 67.87$ on a scale of 1 to 100, $SD = 18.30$) than the warm pressor control condition task ($M = 2.93$, $SD = 10.61$), $t(46) = 23.26$, $p < .001$, $d = 4.31$. Log-transformed cortisol values across sessions and samples (used in the analyses) are shown in Figure 4 (middle panel), and raw data means are shown in Table 1. A 2 (stressor condition) × 3 (timing of sample: pre-stress sample, post-stress sample, final sample) ANOVA on log-transformed cortisol levels indicated a significant effect of condition on cortisol, $F(1, 46) = 21.63$, $p < .001$, $\eta_p^2 = .32$, such that the cold pressor stress condition ($M = .85$, $SD = .31$) showed higher cortisol values than the warm pressor control condition ($M = .72$, $SD = .31$). There was also an effect of time of cortisol sample, $F(1.47, 67.41) = 41.64$, $p < .001$, $\eta_p^2 = .48$, and an interaction, $F(2, 75.20) = 16.94$, $p < .001$, $\eta_p^2 = .27$. Critically, simple effects analyses of cortisol samples across conditions indicated no differences between sessions on the baseline sample, $F(1, 45) = .29$, $p = .59$, and higher cortisol levels in the stress condition for the post-stressor/control task, $F(1, 45) = 57.84$, $p < .001$, $\eta_p^2 = .56$, and in a third sample taken at the end of the session, $F(1, 45) = 7.22$, $p = .01$, $\eta_p^2 = .14$. Given that the navigation task was temporally placed between these two cortisol samples, this analysis confirms that participants were navigating under higher cortisol levels in the stress condition than in the control condition.

9.2. Navigation success

As in Experiment 1, participants were generally successful in navigating to the goal location ($M = 18.31$, $SD = 1.65$ control trials and $M = 18.69$, $SD = 1.68$ stress trials), within the time limit ($M = 21.06$ sec, $SD = 9.30$). A 2 (stressor condition) × 2 (order) ANOVA indicated no significant effects of stress, $F(1,46) = 2.08$, $p = .15$, $BF = .37$, order, $F(1,46) = .000$, $p = 1.00$, $BF = .21$, nor their interaction $F(1, 46) = .35$, $p = .56$, $BF = .24$, on navigation success (see left panel of Figure 6). In all cases, Bayes factors indicated anecdotal to moderate evidence for the null hypothesis.

9.3. Navigation strategy

The raw strategy counts can be found in Table 2. A 2 (stressor condition) × 2 (order) ANOVA with solution index as the dependent variable indicated no main effect of stress condition, $F(1, 46) = .13$, $p = .72$, $BF = .22$, on solution index. A total of 41.8% control trials and 43.5% stress trials were coded as shortcuts. There was also no significant effect of order, $F(1, 46) = .29$, $p = .59$, $BF = .26$. However, there was a trending interaction of condition and order, F

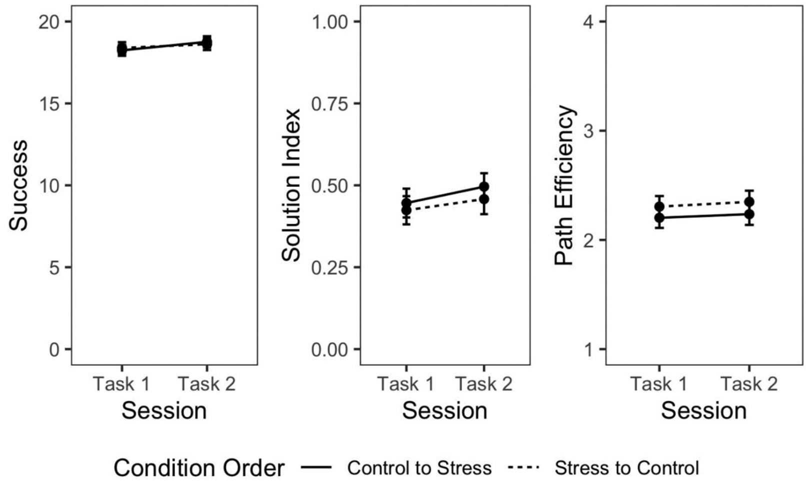

Figure 6. Each main dependent variable of the DSP assessed after the CPT. Success was the count of successful trials. Solution index was measured by dividing the number of shortcuts taken out of 20 trials. Path efficiency was measured as the average distance traveled compared to the shortest route, where 1 would be the shortest path and 2 would be twice the distance of the shortcut. Error bars represent ± 1 SEM.

(1, 46) = 3.57, $p = .07$, $\eta_p^2 = .07$, $BF = .33$. Again, all Bayes factors indicated anecdotal to moderate evidence for the null hypothesis. As seen in the center panel of Figure 6, participants were marginally more likely to take a shortcut on the second task they performed, but the gain from session 1 to 2 was larger in the control-stress condition. There was a strong positive correlation between SI in the stress and control conditions, $r(46) = .72$, $p < .001$, indicating participants typically used the same strategy in the two conditions.

9.4. Navigation efficiency

As can be seen in the right panel of Figure 6, a 2 (stressor condition) × 2 (order) ANOVA using path efficiency data as the dependent variable indicated no main effects of stress, $F(1, 46) = .44$, $p = .51$, $BF = .23$, order, $F(1, 46) = .75$, $p = .39$, $BF = .37$, and no interaction of these factors, $F(1, 46) = .01$, $p = .93$, $BF = .21$. All Bayes factors indicated anecdotal to moderate evidence in favor of the null hypothesis.

9.5. Individual differences in stress response

As in Experiment 1, there were large individual differences in cortisol expression within condition, and participants were categorized as high or low responders as in Experiment 1. Twenty-four participants were categorized as high responders and 24 were categorized as low responders. Using those groupings, a 2 (stress condition) by residual median split (high vs. low) repeated measures ANOVA was conducted on each measure of interest in the DSP (performance, solution index, and efficiency measures). No main effects nor interactions were significant, all $F(1, 46) \leq 2.53$, all $p \geq .12$.

10. Discussion

The cold pressor task was successful in elevating cortisol levels more in the stress condition than in the control condition; cortisol remained elevated during the experimental trials. The amount of cortisol elicited by the cold pressor ($M = 9.03$ nmol/l, $SD = 6.32$) is consistent with the previous literature (Larra et al., 2015). Moreover, self reports of stress were much higher in the cold pressor conditions. These results confirm that stress, via cortisol, was successfully elicited. The results from the navigation task, however, indicated that navigation strategy and efficiency are resilient to these stress and cortisol levels with Bayes factors in both cases indicating anecdotal or moderate evidence for the null hypothesis. Contrary to prediction, participants were no less likely to navigate by shortcuts in the stress (ice water) condition relative to the control (warm water) condition. Moreover, a post-hoc comparison between high and low cortisol responders did not show differences between the stress and control conditions in any of the measures of navigation. The usual practice effect from the first to the second session was marginal. Overall, these results suggest that the levels of stress induced by the cold pressor task have little influence on navigation performance, strategy, or efficiency.

11. Experiment 3: prolonged physical exercise

Acute physical exercises, such as stationary biking, of sufficient duration and intensity can be associated with fatigue and exhaustion (Ament & Verkerke, 2009) and can drive large increases in cortisol (Bullock & Giesbrecht, 2014; O'Connor & Corrigan, 1987). To an extent, the stress induced by physical exercise may overlap with the two previous stressors discussed in this manuscript (CPT and TSST), such that exercise can cause acute physical discomfort and anxiety, which may be partly responsible for the cortisol response. However, physical exercise also requires that the body mobilize sufficient metabolic resources to sustain movement for the duration of the bout, so the elevated cortisol levels are also part of the body's adaptive response to ensure the muscles are provided with sufficient energy. To our knowledge, no studies have examined the effects of physical exercise on navigation. In Experiment 3, participants completed the DSP testing session either after spending 2 hours total cycling on a stationary bike (stress) or after a 2 hour period of physical inactivity (control).

The main hypothesis, as outlined above, was that participants would take fewer shortcuts in the stress condition, because stress raises cortisol levels, which in turn impede hippocampal processing, on which the place-based strategy that allows for shortcutting depends (Brown et al., 2020). A potential explanation for the null effect in Experiments 1 and 2 is that the stressors in those conditions (social stress and noxious stimulation) do not impact navigation as they do not interfere with the physiological resources that would be required to successfully navigate in a real-world environment. This raises the possibility that a stress manipulation that taxes physiological resources may be more likely to impact navigation performance. Given that strenuous cycling (the manipulation used here) increases cortisol levels, we might expect it to inhibit the hippocampal brain system underlying place-based navigation so that people are more likely to take learned routes following this manipulation.

However, it is also possible that fatigue due to extended physical exercise might induce more shortcutting, reflecting a tradeoff between physical and cognitive effort in the Dual Solution task (Hegarty et al., 2022). That is, following bouts of prolonged physical exercise, participants may be more motivated to take shortcuts to reduce physical effort. In fact, a recent meta-analysis indicated that acute exercise can improve both short and long term cognitive processes (Roig et al., 2013) by way of noradrenergic activation (Segal et al., 2012). Therefore, participants may take more shortcuts in the face of a physical stressor that depletes bioenergetic resources.

12. Method

12.1. Participants

Participants were 40 University of California, Santa Barbara students (19 females) who were paid $20 per hour.

12.2. Design

A 2 (Stress vs. Active Control) × (order: Control – Stress vs. Stress-Control) design was used. Session and maze type were manipulated within subjects, and order of conditions was manipulated between subjects.

12.3. Materials and apparatus

A Viasprint 150p stationary bike and Vyntus CPX metabolic cart (Vyaire Medical, Yorba Linda, CA, USA) were used in both the stress and control conditions.

12.4. Procedure

All general procedures for Experiment 3 were the same as in Experiments 1 and 2 (see the lower third panel of Figure 3). After EEG prep, participants began the encoding tasks including learning the DSP navigation maze route and gave the first saliva sample. After all encoding trials, participants were positioned on a stationary bike in front of a television screen and were allowed to select a movie of their choice. In the stress condition, they then completed a total of 2 hours of cycling (split into four 30 m blocks with 5-minute breaks between each block) while simultaneously viewing the movie.

Each block began with a three-minute warm up at 40 watt resistance. Then, resistance was gradually increased so that the participant was exercising at ~60% of their aerobic capacity (determined in an earlier session by having each participant complete a maximal VO2 test). Exercise workload was determined during the initial 3 minutes of cycling by monitoring oxygen uptake via a mouthpiece connected to the metabolic cart and increasing or decreasing resistance to meet the 60% workload requirement. The mouthpiece was removed from the participant's mouth after 3 minutes to avoid participant discomfort but was briefly reinserted at 15 minute and 25 minute to check that the 60% workload requirement was being maintained. Resistance adjustments were made at 15 minute and 25 minute if the workload was not at 60%. Finally, at 28 minutes, resistance was decreased to 40 W for 2 minutes to allow the participant to cool down before cessation of cycling. The participant was then allowed to dismount from the stationary bike to avoid discomfort from the bike seat.

A five-minute rest period was allowed between blocks. Saliva samples were collected during the rest period after blocks two and four (see Figure 3). During each block, the participant was allowed to view the movie from 5 minutes to 25 minutes. In the control condition, the protocol was identical except that participants were positioned on a stationary bike and were not required to cycle. In both sessions, the final saliva sample was collected at the end of the whole session. In both conditions, after about 90 minutes of the session, participants were asked to rate their aversion to continuing the session on a 1–100 scale. Finally, at about 120 minutes, participants were asked to rate their level of fatigue on a 1–100 scale.

12.4.1. Dual solution paradigm procedure

The same general procedure for this task was used as in Experiments 1 and 2. Two and a half to 3 hours elapsed between learning and testing.

13. Results

13.1. Manipulation checks

At 90 minutes, participants rated their aversion to continuing the task and rated the stress condition as significantly more aversive ($M = 39.40$, $SD = 31.84$ on a scale of 1 to 100) than the control condition ($M = 9.77$, $SD = 21.29$), $t(34) = 6.61$, $p < .001$, $d = 1.09$. Further, after 120 minutes, biking was rated as more fatiguing ($M = 66.77$, $SD = 20.94$) than the control task ($M = 7.89$, $SD = 10.20$), $t(34) = 16.64$, $p < .001$, $d = 3.58$. Log-transformed cortisol values across sessions and samples (used in the analyses) are shown in Figure 4 (right panel). A 2 (stress vs. control) × 4 (timing of samples: pre-stress sample, intra-stress sample, post-stress sample, final sample) ANOVA on log cortisol values indicated that cortisol was significantly more elevated in the stress compared to the control condition, $F(1, 36) = 48.27$, $p < .001$, $\eta_p^2 = .57$. There was a significant effect of timing of sample, F $(2.16, 78.29) = 3.54$, $p = .02$, $\eta_p^2 = .09$, and of the interaction between stress condition and time, $F(2.20, 79.24) = 20.044$, $p < .002$, $\eta_p^2 = .36$. Critically, the last three samples in the stress condition (after cycling) were significantly more elevated than the control condition (all three comparisons, $p < .001$), while there was no difference between conditions in the first (baseline) sample ($p = .83$). In sum, we were successful in elevating cortisol more in the stress condition. Given that the navigation task was temporally placed between the third and fourth cortisol samples, this analysis confirms that participants were navigating under higher cortisol levels in the stress condition (1.59 times higher, see Table 1) than in the control condition.

13.2. Navigation success

As in Experiments 1 and 2, participants were generally successful navigating to the goal ($M = 18.35$, $SD = 1.73$ in control trials, $M = 18.23$, $SD = 1.70$ in stress trials) within the 40-sec time limit (*Mean* = 22.74, $SD = 9.57$) as seen in the left panel of Figure 7. A 2 (stress condition) × 2 (order) ANOVA on the number of successful trials indicated no main effect of stress condition, $F(1, 38) = .18$, $p = .68$, $BF = .24$. There was a main effect of order, $F(1, 38) = 24.78$, $p < .001$, $BF > 100$, such that participants in the stress-control order were more successful (95.50%) than those in the control-stress order (86.5%). There was no interaction of condition and order, $F(1, 38) = .02$ $p = .90$, $BF = .24$, indicating anecdotal evidence for the null hypothesis.

13.3. Navigation strategy

The raw strategy counts can be found in Table 2. A 2 (stress condition) × 2 (task order) ANOVA showed no main effect of stress on solution index, $F(1, 38) = .48$, $p = .50$, $BF = .24$, indicating anecdotal evidence for the null hypothesis. A total of 40.3% control trials and a total of 40.5% stress trials were coded as shortcuts. There was a main effect of task order, $F(1, 38) = 7.58$, $p = .01$ $\eta_p^2 = .17$, $BF = 38.85$, such that participants in the stress-control order took more shortcuts than participants in the control-stress order, with the Bayes factor indicating very strong evidence for the alternative hypothesis. Finally, there was also a significant interaction of condition and order, $F(1, 38) = 8.61$, p

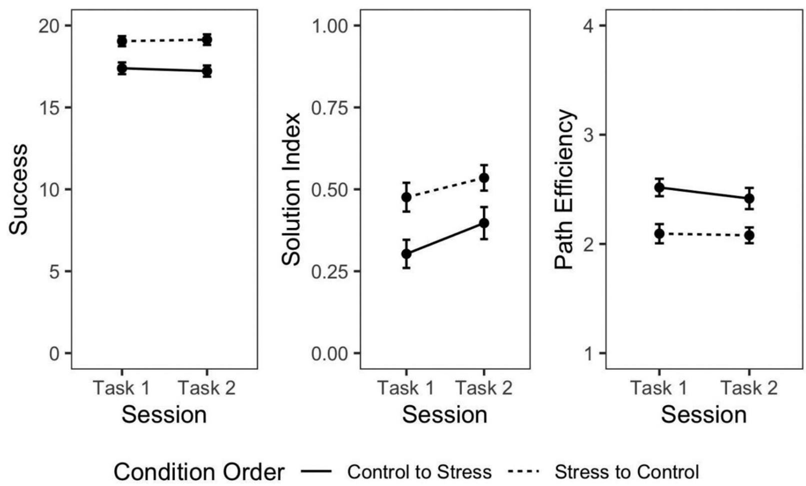

Figure 7. Each main dependent variable of the DSP assessed after extended physical exercise (biking). Success was the count of successful trials. Solution index was measured by dividing the number of shortcuts taken out of 20 trials. Path efficiency was measured as the average distance traveled compared to the shortest route, where 1 would be the shortest path and 2 would be twice the distance of the shortcut. Error bars represent ± 1 SEM.

= .005, $\eta_p^2 = .18$, $BF = .70$ (see Figure 7, center panel). Simple effects analyses indicated that there was a significant increase in the solution index from the first to the second session for those in the control-stress order, $F(1, 38) = 5.97$, $p = .02$, $\eta_p^2 = .14$, but not in the stress-control order, $F(1, 38) = 2.80$, $p = .10$. As in Experiments 1 and 2, participants took more shortcuts in the second session. There was a strong positive correlation between the solution indices for the stress and control conditions, $r(38) = .64$, $p < .001$, indicating participants typically used the same strategy in both sessions.

13.4. Navigation efficiency

A 2 (stress) × 2 (order) ANOVA indicated no main effects of stress on path efficiency, $F(1, 38) = .67$, $p = .42$, $BF = .25$, and no interaction, $F(1, 38) = 1.19$, $p = .28$, $BF = .27$. Bayes factors for both effects indicated anecdotal evidence for the null hypothesis. However, there was a significant effect of order, $F(1, 38) = 12.50$, $p = .001$, $\eta_p^2 = .25$, $BF > 100$, such that participants in the stress-control order were more efficient across both sessions (see the right panel of Figure 7).

13.4.1. Individual differences in stress response

As in Experiments 1 and 2, there were large individual differences in cortisol expression within condition. Participants were again grouped by their log transformed cortisol reaction via a regression of their cortisol level in the stress condition cortisol against that in the control condition. Participants with a positive residual were considered high responders, and those with negative residuals were classified as low responders. A 2 (stress condition) by residual median split (high vs. low stress response) repeated measures ANOVA indicated no main effects nor interactions for navigation success (successful trials), all $F(1, 35) \leq .59$, all $p \geq .45$, solution index, all $F(1, 35) \leq 1.66$, all $p \geq .21$, nor path efficiency, all $F(1, 35) \leq 2.71$, all $p \geq .11$. This analysis provides no evidence that those with a greater stress response had different navigation behaviors to those with a more reduced stress response.

14. Discussion

The **prolonged** physical exercise task used in Experiment 3 was successful in elevating cortisol levels more in the stress condition than in the control condition, more than the TSST and CPT stressors in Experiments 1 and 2, and similar to the levels of cortisol induced by biking in a previous study (Bullock & Giesbrecht, 2014). Participants also self-reported the biking condition as being more fatiguing and aversive relative to the control condition. Despite this, the stress condition did not overtly impact navigation strategy and efficiency. Further, participants took more shortcuts and navigated more efficiently in their second DSP session than their first, as in Experiments 1 and 2 and in previous research (Boone et al., 2019). However, the condition order indicated intriguing results. Contrary to predictions based on the stress hypothesis, but consistent with a tradeoff between physical and cognitive effort, participants were more inclined to navigate via shortcuts in both sessions when the stress condition was first than when the control condition was first. Participants with greater or lesser stress responses across conditions did not show differences in any of the measures of navigation performance, strategy, or efficiency in either the stress or control conditions. Overall, these results suggest that fatigue due to extended physical exercise may have shifted the navigation strategies toward a more flexible and efficient shortcut strategy, perhaps reflecting a tradeoff between physical and cognitive effort or due to more arousal during the testing session.

15. General discussion

Three experiments were conducted to examine the influence of different types of stressors (psychosocial, noxious stimulation, and an extended bout of physical exercise) on navigation success, strategy, and efficiency in the Dual Solution Paradigm (Marchette et al., 2011). Participants learned a maze layout from a first-person perspective on a desktop computer. After learning, they were exposed to one of the stressors or an active control in counterbalanced order. The main hypothesis was that participants would show more response-based strategies compared to place-based strategies while under stress, assuming that stress, via cortisol, inhibits the place-based navigation strategy by blocking hippocampal place cell and cognitive map access, necessary for this place-based, shortcutting strategy. An alternative hypothesis, considered in Experiment 3, was that fatigue due to an extended bout of physical exercise might increase use of the shortcut strategy, due to a tradeoff between cognitive and physical resources. In general, stress was successfully induced, as indexed by higher cortisol and higher self-reported stress in all stressor conditions when compared to their respective active control conditions.

Contrary to prediction, across all three experiments the stress conditions did not cause participants to shift from more place-based to more response-based strategies (Bayes factors showed anecdotal to moderate evidence for the null hypothesis). There were strong correlations between measures of navigation strategy across the stress and control conditions, suggesting that people were consistent in the strategy they used across conditions. We also found evidence of practice effects such that most participants took more shortcuts in their second testing session regardless of condition, although they were navigating in a different environment. Interestingly, in Experiment 3, a different pattern was observed. In Experiment 3, the stressor (physical exercise) seemed to increase rather than decrease use of the shortcut strategy when it was experienced first, such that participants in the stress-first order were significantly more likely to take shortcuts than those in the control-first condition.

Given the large individual differences in reaction to stress, post-hoc analyses were conducted comparing participants whose cortisol value increased with stress versus those who did not show such an increase. Overall, these analyses indicated little influence of the size of the cortisol reaction (to stress) on navigation performance, strategy, or efficiency. That is, those with a large stress response performed similarly to those with little or no stress response.

The results of these experiments indicate that stress, at least at the levels induced by the stressors in these studies, does not produce shifts toward more response-like and less efficient navigation. Further, physical exercise produced an effect on performance that was contrary to the main prediction presented here and in the literature. There are several possible reasons, explored below, for the lack of an effect of stress on navigation strategy in two of our three experiments.

16. Level of stress induced

First, it is possible that the levels of stress induced in this set of studies were not sufficiently high to affect navigation strategy. Comparing the raw levels of cortisol produced in each condition across experiments (shown in Table 1) can inform this question. The cortisol increase in the Trier Social Stress Task (TSST) was in the range typically found for this task (Kirschbaum et al., 1993). However, contrary to previous studies (Dickerson et al., 2008; Het et al., 2009), there was also a relatively large increase in cortisol in the control condition, so that the difference in stress induced in the experimental and control conditions in Experiment 1 may not have been large. In terms of the cold pressor task (CPT) used in Experiment 2, the levels of circulating cortisol were similar to those documented previously (Larra et al., 2015) and clearly different in the stress and the active control conditions wherein the cortisol declined more in the control condition compared to the stressor condition. Finally, the physical exercise task used in Experiment 3 showed a difference between stress and control conditions that was larger than that induced by the TSST and CPT and similar to recent work using a similar biking stressor (Bullock & Giesbrecht, 2014). Notably, in Experiments 1 and 2, baseline cortisol levels were elevated, likely arising from the instrumentation activities at the start of each experimental session (e.g., biophysical lead application, EEG capping). However, this pattern was not observed in Experiment 3 wherein participants provided the baseline saliva sample after the encoding phase of the protocol and therefore had more time to achieve baseline levels. In Experiments 1 and 2, however, a greater reduction in salivary cortisol is seen in the control condition relative to the stressor condition, indicating that participants were carrying stress effects throughout the stressor conditions.

It is notable that the changes in cortisol from baseline in our studies were smaller than those induced by Brown et al. (2020), who used anticipation of shock as a stressor, observed an increase in cortisol of 13.75 nmol/l in the stress condition, and found evidence for a switch from place based (shortcutting) to response based (learned route) strategies. Interestingly, however, only the first trial showed this response, suggesting that this effect is tightly coupled to the exposure of the stressor. It has been proposed that the effects of stress on navigation strategies conform to an inverted-U-shaped function (Bohbot et al., 2011; Gagnon & Wagner, 2016) with intermediate levels of cortisol leading to more place-based strategies but higher levels associated with more response-based strategies. It is possible that the levels induced here fell between intermediate and high levels. Future studies need to address not just the presence of a stress response (i.e. a significant difference in cortisol levels), but also the absolute level of cortisol and amount of increase in cortisol (effect size) that is associated with a shift in navigation strategy.

Is Spatial Learning Special? Most studies of the effects of stress on human memory retrieval (reviewed by de Quervain et al., 2000; Gagnon & Wagner, 2016; Het et al., 2005; Shields et al., 2017) were conducted with verbal stimuli. We are just beginning to study the effects of stress on navigation processes. It is possible that spatial memories created in the context of the Dual Solution paradigm (DSP) are stronger than those created in verbal memory tasks, and thus more resistant to the effects of stress. In the DSP, as one navigates the maze on wayfinding (test) trials, many cues, including landmarks and environmental geometry, are present to influence local decision-making processes such as which turns to take within the maze. These cues provide a richer context in which to navigate and arrive at a goal, and as such may provide a safeguard to the effects of stress during navigation which may be similar to the type of retrieval practice that staves off stress effects in word learning tasks (Smith et al., 2016). While Brown et al. (2020) found that stress biased participants toward learned routes, one difference between their study and ours is that their participants had to plan each route in advance of executing it, so they did not have access to the rich retrieval cues in the environment while planning. A question remains as to whether spatial memories or retrieval cues may be stronger than other types of declarative memories.

Decontextualized stress? Another possible explanation for the non-effects in our studies is that the stressors were unrelated to the navigation task. In the animal model of navigation under stress, the stressors are extremely aversive (e.g., foot shocks, restraints, fear of drowning in the Morris Water Maze). Those stressors are related to the navigation task (e.g., the animal must run away or navigate home) and occur simultaneously with the navigation task. The social threat from the TSST and the noxious stimulation from the CPT are unrelated to navigation, and this may explain their failure to affect navigation strategy. In contrast, biking is more related to navigation in that both involve physical movements through an environment and might lead us to consider the energetic cost of navigational options more thoroughly. This could be similar to how people judge distances as longer when carrying heavy loads (Proffitt et al., 2003). In this case, the addition of stress via cortisol may engage the body to make more strategically effective decisions while navigating in order to preserve resources. Further, it is important to note that cortisol released during exercise is also metabolized and used by the body during that exercise (Hackney, 2006; Viru & Viru, 2004). Although the effect of biking on navigation strategies in Experiment 3 was not mediated by cortisol, the effect could be due to other endocrine processes related to cortisol or arousal states during testing after the biking task.

16.1. Future directions

By timing the stressor before the wayfinding trials, our work focused on the relatively sluggish hypothalamic pituitary adrenal (HPA) axis (i.e., cortisol release). Other work with stressors that occur during the spatial tasks such as the threat of shock (Brown et al., 2020) or the use of a countdown timer (Brunyé et al., 2016) suggests that the effects of stress on navigation strategy may also activate the more immediate sympathetic adrenal medulla (SAM) axis. Future research is needed to understand the separate and combined effects of these two systems on navigation. This will involve collecting both physiological measures of the immediate cardiovascular response and the delayed cortisol response to understand their dynamical interactions in relation to navigation tasks. In the future work on the HPA response, it will also be important to more precisely control the timing of the stressor relative to performance, as the present research may have captured the effects of stress during consolidation of spatial memories in addition to retrieval. Finally, it will be important to systematically vary the intensity of the stressor and observe its effects to learn what levels on the proposed inverted U function have the greatest effects on navigation strategy.

17. Conclusion

Navigation under stress was tested with three different stress manipulations: psychosocial stress, noxious stimulation, and extended physical exercise. Despite large effects of these stressors on cortisol release and self reports, stress did not affect navigation performance, strategy, or efficiency. In fact, more use of shortcuts and greater efficiency were observed following physical exercise. While navigation strategy and efficiency were generally resilient to the effects of stress in this study, these results raise important questions about factors that affect both retrieval of spatial memories and consequent shifts in navigation strategy, including levels and types of stress, timing, and relevance of the stressor to the navigation task. Overall, although we face acute stressors in our daily lives, this research indicates that our navigation strategies are largely resilient to that stress.

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