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ORIGINAL PAPER

Threat impairs flexible use of a cognitive map

Brian Silston[1] · Kevin N. Ochsner[1] · Mariam Aly[1]

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Abstract

Goal-directed behavior requires adaptive systems that respond to environmental demands. In the absence of threat (or presence of reward), individuals can explore many behavioral trajectories, effectively interrogating the environment across multiple dimensions. This leads to flexible, relational memory encoding and retrieval. In the presence of danger, motivation shifts to an imperative state characterized by a narrow focus of attention on threatening information. This impairs flexible, relational memory. We test how these motivational shifts affect behavioral flexibility in an ecologically valid setting. Participants learned the structure of maze-like environments and navigated to the location of objects in both safe and threatening contexts. The latter contained a predator that could 'capture' participants, leading to electric shock. After learning, the path to some objects was unpredictably blocked, forcing a detour for which one route was significantly shorter. We predicted that threat would push participants toward an imperative state, leading to less efficient and less flexible navigation. Threat caused participants to take longer paths to goal objects and less efficient detours when obstacles were encountered. Threat-related impairments in detour navigation persisted after controlling for non-detour navigation performance, and non-detour navigation was not a reliable predictor of detour navigation. This suggests a specific impairment in flexible navigation during detours, an impairment unlikely to be explained by more general processes like predator avoidance or divided attention that may be present during non-detour navigation. These results provide ecologically valid evidence that dynamic, observable threats reduce flexible use of cognitive maps to guide behavior.

Keywords Motivational states · Motivation · Navigation · Memory · Cognitive flexibility · Behavioral flexibility · Decision-making · Threat · Stress

Introduction

Whether tracking and avoiding moving shadows when walking home alone at night, avoiding a bear sighted in the distance on a hike, or scampering through corridors to avoid an active shooter, dynamic threats affect what we pay attention to, learn, and remember. Such real-world dangers represent evolving threats that require real-time decisions and actions to mitigate conflict or prevent contact. How do such visible, dynamic threats that wax and wane over time and space affect the flexible, online use of memory in the service of navigational goals? This question is significant because adaptive goal-directed behavior in the real world requires shifts in motivational states that are flexible, timely, and appropriate (vis-a-vis changing environmental demands). While a considerable body of work has investigated how stress, anxiety, and threat affect learning, performance, navigation, and memory, most studies use tasks that do not adequately capture the dynamic experience of natural threats (e.g. Goodman et al., 2020), and sometimes collect measures of learning and memory only post-facto (e.g., Weymar et al., 2013). The focus of work that has deployed more ecologically valid threats (e.g., dynamic predators, bombs, gunfire) has traditionally been phenomena such as contextual fear conditioning and extinction (see Dunsmoor et al., 2014; Faul et al., 2020; Marusak et al., 2017), as opposed to investigation of navigation and recognition memory; and those that examine navigation assess limited outcomes such as threat-free navigation after threat-based route learning (e.g., Courtney et al., 2013).

Models such as the Survival Optimization System (SOS; Mobbs et al., 2015) propose that activation and suppression of defensive brain circuits governed by threat imminence

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✉ Brian Silston
bs2684@columbia.edu

[1] Department of Psychology, Columbia University, New York, NY 10027, USA

gates access to specific information and particular behavioral repertoires. In particular, activation of defensive brain circuits may reduce access to, and use of, flexible cognitive representations. This provides a mechanism to account for how motivational states linked to threat avoidance may impair real-time behaviors that require flexible cognition. Consistent with this, studies that manipulate stress and threat with unpredictable electric shocks (Brown et al., 2020) or shocks for navigating to incorrect locations (Murty et al. 2011) have found that such threats impair the efficiency (i.e., path lengths) and accuracy of navigation. However, because the threat in these studies was unpredictable and invisible, it is not clear how knowledge of threat imminence may affect behavior. Navigational impairments may be exacerbated when an active, agentic threat is visible, allowing continuous monitoring of danger. In these cases, attention may narrowly focus on the threat, at the expense of forming a flexible cognitive map of the environment (Murty & Adcock, 2017). Alternatively, navigational impairments may be *reduced* when a threat is visible, because at any given time individuals may be aware of relative safety vs danger based on the threat's distance and heading direction; moments of safety may reduce anxiety compared to situations in which threat is invisible and hence completely unpredictable. Here, we sought to determine whether navigational impairments observed with invisible threat (e.g., Brown et al., 2020; Goodman et al., 2020; Murty et al., 2011) replicate when a threat is visible and dynamic—an important bridge to ecologically valid settings.

Our aims are (1) to extend prior work on how stress and threat affect navigational efficiency and flexibility (e.g., Brown et al., 2020; Goodman et al., 2020; Murty et al., 2011) by examining how continuously present, visible, dynamic threats affect flexible goal-directed navigation; (2) test whether threat-related spatial memory impairments are pervasive, lasting even after the threat is removed, or are specific to acute stages of threat; and (3) explore how threat affects the ability of individuals to rapidly reconfigure their behavior online, as may occur if individuals suddenly come upon an obstacle, e.g., a locked door through which they expected to escape (for non-threat obstacles, see also Javadi et al., 2019; Spiers & Gilbert, 2015)). To these ends, we measure behavior both online during active threats and with traditional post-task memory tests in the absence of threat. This enables us to test how motivational states affect the online use of spatial memories to guide navigation, and whether such memories are differentially accessible when the threat is removed. Such data may help explain the moment-to-moment, transient effects of threat and stress: why at times we cannot think under pressure at work, lose our way on familiar routes, or fail to perform to our standards or potential while under threatening circumstances—and yet, can seemingly recollect a great deal about such situations later on. Further, addressing these questions would provide a bridge from laboratory studies of how threat affects navigation to real-world scenarios in which threats can be dynamic and behavior has to be rapidly updated.

Our work is inspired by, and builds on, research exploring how motivation affects learning and memory. Such research has shown that motivational states inform the goals we pursue, the way we approach them, and the memories that we form. For example, orienting individuals toward threatening (relative to non-threatening) information prior to a visit of an art gallery disrupts the links between exploration and subsequent memory (Chiew et al., 2018). Motivational states associated with monetary rewards and other incentives tend to prioritize memory for steps, decisions, items, or other information related to reward acquisition (Shohamy & Adcock, 2010; Spaniol et al., 2014; Wittmann et al., 2011). To the extent that motivation engages the hippocampus—which is critical for linking items together in memory (Eichenbaum et al., 1994)—learning and memory will reflect the multi-dimensional nature of experience, integrating multiple elements into a rich, relational memory and enabling flexible use of information in new domains (Kumaran & McClelland, 2012; Murty & Adcock, 2017). In contrast, external stimuli that are threatening or generate anxiety prioritize visuospatial attention and working memory, directing focus and search towards the physical environment for salient information (Bolton & Robinson, 2017). For example, delayed memory recall for a real-world haunted house experience was biased towards perceptual details over event details (Reisman et al., 2021). Furthermore, the presence of emotionally arousing images can impair memory for background perceptual details (Mather et al., 2009; Mather & Sutherland, 2011).

These types of studies have largely supported a distinction between *interrogative* and *imperative* motivational states (Murty & Adcock, 2017). Interrogative—or exploratory—states facilitate unconstrained sampling and are characterized by broad attentional processing. Conversely, imperative—or hyper-focused—states limit sampling, and typically narrow attention to salient features in the service of proximal, often defensive, goals (Murty & Adcock, 2017)); also see (Murty & Dickerson, 2016). Interrogative states are proposed to promote flexible, relational memories dependent on the hippocampus and its input from the dopaminergic ventral tegmental area (Murty & Adcock, 2017; Murty et al., 2012; Wise, 1998). Conversely, imperative states, particularly states induced by threat, often recruit survival system circuitry (e.g., the periaqueductal gray, anterior insula, the amygdala and its connections to parahippocampal and orbitofrontal areas) (Meyer et al., 2019; Murty et al., 2012). This leads to the prioritization of automatic, heuristic responses (Mobbs et al., 2015) and promotes memory for item-based information at the expense of flexible behavior and relational memories (Bisby & Burgess, 2014). In that way, imperative states impede forward planning, information integration, and flexible access to memories (Brown et al., 2020; Niv et al., 2006), and increase reliance on familiar, previously learned, or rote strategies (Brunye et al., 2017).

Here, we test how imperative vs interrogative states influence flexible navigation and memory for relational and item-based information. We sought converging evidence from three studies that used a within-participant design (Table 1). Participants performed a navigation task to find objects that were located in consistent positions in a virtual reality maze environment. Navigation efficiency (path length) was compared in contexts with and without a dynamic threat: a villain that roved through the maze in an attempt to 'capture' participants, with capture leading to electric shock. To assess behavioral flexibility, we introduced obstacles on some trials, forcing participants to navigate to an obstructed goal object by taking one of two available detours, one of which was always shorter than the other. Path lengths following detours indexed whether participants were able to flexibly retrieve and use cognitive maps when well-known paths were unavailable. Across Studies 1–3, we compared navigation contexts that varied in motivational incentives: Study 1 compared a threatening context to one associated with reward incentives. Study 2 compared the threat and reward contexts with a neutral context. Finally, Study 3 was similar to Study 1 except that the reward context also included an actively navigating agent (a 'hiker') to control for the presence of a social agent in the threat condition (the "predator").

After navigation, a sequence of tests was conducted—in the absence of threat—to assess how broadly threat may have affected memory representations. These tests included assessments of map recognition memory, object-in-place memory, and memory for incidental paintings. Because performance on these memory tests was generally poor and hence inconclusive, the results are shown in Supplementary Information.

Together, these studies allowed us to test how item-based and relational memory, and navigation, were affected by the presence of a dynamic threat.

Study 1

Overview

Study 1 examined the effect of threat and reward on the ability to form and use cognitive maps in the service of navigational goals. Participants learned the layout of two (2) fixed environments, along with the locations of six (6) everyday objects in each. One environment was assigned to the Threat condition and the other to the Reward condition. In the Threat condition, we induced shifts to imperative motivational states by introducing a dynamic, waxing and waning threat represented by a virtual predator. Capture by the predator resulted in electric shock, and collection of goal objects resulted in temporary immunity to the predator. To encourage interrogative motivational states in the Reward condition, participants earned coins and points upon collection of goal objects.

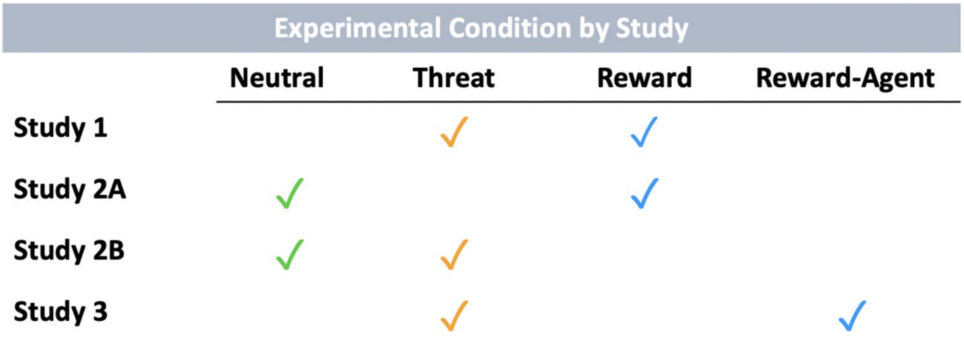
Methods

Materials referenced herein may be made available upon request. We report how we determined our sample sizes, all data exclusions (if any), all manipulations, and all measures in the studies.

Participants

We aimed to meet or exceed the sample size of similar studies that have used virtual navigation tasks (Brown et al., 2020; Brunyé et al., 2012; Brunye et al., 2017; Goodman et al., 2020; Graves et al., 2020; Hahm et al., 2007; Murty et al., 2011; Plancher et al., 2018; Sauzéon et al., 2016). 40 (25 female; mean age = 22) participants were recruited and

Table 1 Experimental conditions by study



Experimental Condition by Study	Neutral	Threat	Reward	Reward-Agent
Study 1		✓	✓	
Study 2A	✓		✓	
Study 2B	✓	✓		
Study 3		✓		✓

For each study, two conditions were tested separately on different maps. Each study used a within-participant design paid $20 for completion of the tasks. Nine (9) participants were unable to complete the task due to motion sickness or discomfort during the navigation portion of the studies. Motion sickness can occur during first-person video games, even without immersive virtual reality (Kennedy & Shapiro, 2009; Lubeck et al., 2015). These participants are excluded from data presentation, resulting in 31 participants. All individuals consented to participate per requirements of the Columbia University Institutional Review Board.

We note that it is possible that study drop-out is not random (as is true for any study); in particular, it is possible that participants who withdrew from the study were particularly averse to shock. However, we believe this should have only hurt our ability to detect condition differences: If participants who withdrew are those that are most averse to shock, that would indicate that those who remain may not find shock particularly aversive—which would in turn hurt our ability to see impairment due to the threat of shock.

Prior to the task, participants were instructed that certain conditions utilized electric shock (those that contained a virtual predator). Electric stimulation and threat thereof have been shown to elicit ecologically valid anxiety states (Mobbs et al., 2007; Robinson et al., 2013). Shock intensity was calibrated for each participant. This was done by administering shocks that increased in intensity until finding a level of shock that was tolerable for the participant but still aversive. That level of shock was then used throughout the Threat condition for that participant. This method is analogous to methods using heat to induce pain (Atlas et al., 2014). Average shock intensity was 5.7 (on an objective shock-strength scale from 10 to 0, where 0 represents the strongest shock available), with a standard deviation of 2.75.

Stimuli

Map environments Map layouts used for first-person navigation were created using custom software and rendered into 3D environments with the Unity gaming platform (Fig. 1). Two map layouts were presented to each participant, with map-to-condition (Threat or Reward) assignments counterbalanced across participants. The layouts were open enough to facilitate swift learning, while large enough such that successful (vs unsuccessful) learning would result in significantly shorter path lengths, on average. Each map was 13 tiles × 13 tiles and contained six (6) goal objects, which remained in the same place throughout the task and were each collected on every trial (Fig. 1). Object identities were specific to the map layout (i.e., not repeated across maps). Each goal object was strategically placed such that the path to it could be blocked from any direction, forcing a detour for which one route was always shorter. Some wall sections on each map contained unique textures to assist participants in orienting to the environment. Additionally, each map contained a number of paintings that could appear on predetermined walls. The participant could view up to a maximum of eight (8) paintings per trial, depending on whether

Fig. 1 Map layouts. Depiction of the two semi-open map layouts navigated by each participant. Dark brown squares represent locations of walls. Goal objects appear superimposed on black squares with bags of money underneath (money only appeared in the Reward and Reward-Agent conditions). The small scene images embedded in the walls represent paintings that could appear at that location based on the participant's heading direction (see text for details). The squares containing blue arrows represent the starting location of the participant for the upcoming trial

they navigate to and face the walls selected to display the paintings. Each painting could be viewed only once, for a maximum of six (6) seconds.

Paintings Paintings were selected from the Google Arts & Culture platform and placed into the map environments. Paintings included abstract works, portraits, and landscapes. Eight unique (8) paintings were potentially presented on each of the six (6) trials in each of the two (2) conditions for each participant. They appeared on designated walls only if the participant navigated to and was facing the wall. Painting locations and display times (maximum 6 s) were the same across participants, but paintings were typically not viewed for the maximum allotted time, i.e., because the participant navigated away. Across studies, images were viewed for an average of 1.49 s (SD = 0.28 s), with no statistically significant differences between conditions in any study (all ps > 0.08).

Software

Map layouts were generated using a custom map editor created in Adobe and stored as .json files. The 3D environment was rendered in Unity. Map files were called into Unity via configuration files generated using the MATLAB platform. Memory tasks were administered using PsychoPy 2. Questionnaires were completed in the Qualtrics platform.

Procedure

Navigation task All tasks were run on a desktop computer. Participants completed the Reward and Threat conditions shown in Fig. 2, with condition order counterbalanced across participants. Six (6) trials with six (6) goal items each were completed for each condition. Thus, 36 objects were collected in each condition. On each trial, participants first rated their current anxiety level by answering the question "How anxious do you feel right now?" on a continuous scale with values from zero (0) to seven (7). The trial then proceeded with a partially obscured overhead view of the map indicating the starting position for the upcoming navigation trial. This view obscured all but 1.5 tiles, making it an ineffective way of learning the 13 × 13 tile map layout. Instead, learning the map layout required participants to remember their navigation experience.

Starting positions varied on a trial-by-trial basis. The starting positions were constrained such that: (1) no two locations could be repeated; (2) starting locations were always on the outer edge of the map, forcing navigation inward; and (3) starting locations were equally spaced along the outer edge of the map. Thus, each trial started with a unique perspective, starting locations were distributed along the outer boundary of the map, and together the varied starting locations required participants to explore the entire map layout.

After being cued with their starting position, the participant was placed in the first-person 3D environment. After an unconstrained exploratory period of eight (8) seconds, a goal item appeared on the top of the screen indicating that the participant should search for it. Concurrent with the goal message, the actual item appeared in the environment. Goal item locations were stable across the task, such that once participants learned the location of an item, navigation efficiency could be improved based on the acquisition of spatial knowledge and item locations. Participants had to collect all six (6) goal items during a given trial, with eight (8) seconds of free exploration time between collecting one object and being cued with the next. The order of goal items for a given trial was selected with an algorithm that first (1) randomly selected one of the six items; then (2) if that item had already been navigated to, selected a different item; and finally (3) if that item was within 8 tiles of the participant's current location, the algorithm was run again until a non-collected object at least 8 tiles away was selected. This ensured that participants had to navigate to each item.

After navigating to all six (6) goal objects three (3) times each over the course of three (3) trials, the paths to some objects could be blocked by an obstacle, forcing the participant to find an alternative route (Detour objects). One of the detour routes was always shorter than the other. Importantly, the obstacle blocking the goal object appeared only after the goal object had been located but not yet collected. Thus, participants had to rapidly plan a detour when an obstacle blocked an object just prior to its collection.

The first three (3) trials (six (6) objects each, thus eighteen (18) objects in total) on each map were always Non-Detour trials, in which participants sequentially collected goal items and no Detours occurred. This was done so that participants had the opportunity to learn the map layout (over 10–15 min) before they had to rapidly plan alternative routes online. In each of the subsequent three (3) trials (with six (6) objects each), two (2) objects featured an obstacle for which a detour route was required, while the other four (4) objects were collected in the same manner as during the first three (3) trials. Detours were probabilistic so that participants would be less likely to plan for them, and instead had to adapt online once an obstacle was encountered. Each object required a detour only once.

For the Reward condition, participants received gold coins for securing objects, the amount of which depended on navigation efficiency. The maximum reward was 100 points per object. Reward amount decayed down to a minimum of 50 points as time passed before the object was collected. Point totals were always displayed on the screen. Upon collection of an object, an animation with gold coins was displayed on the screen with the specific reward amount

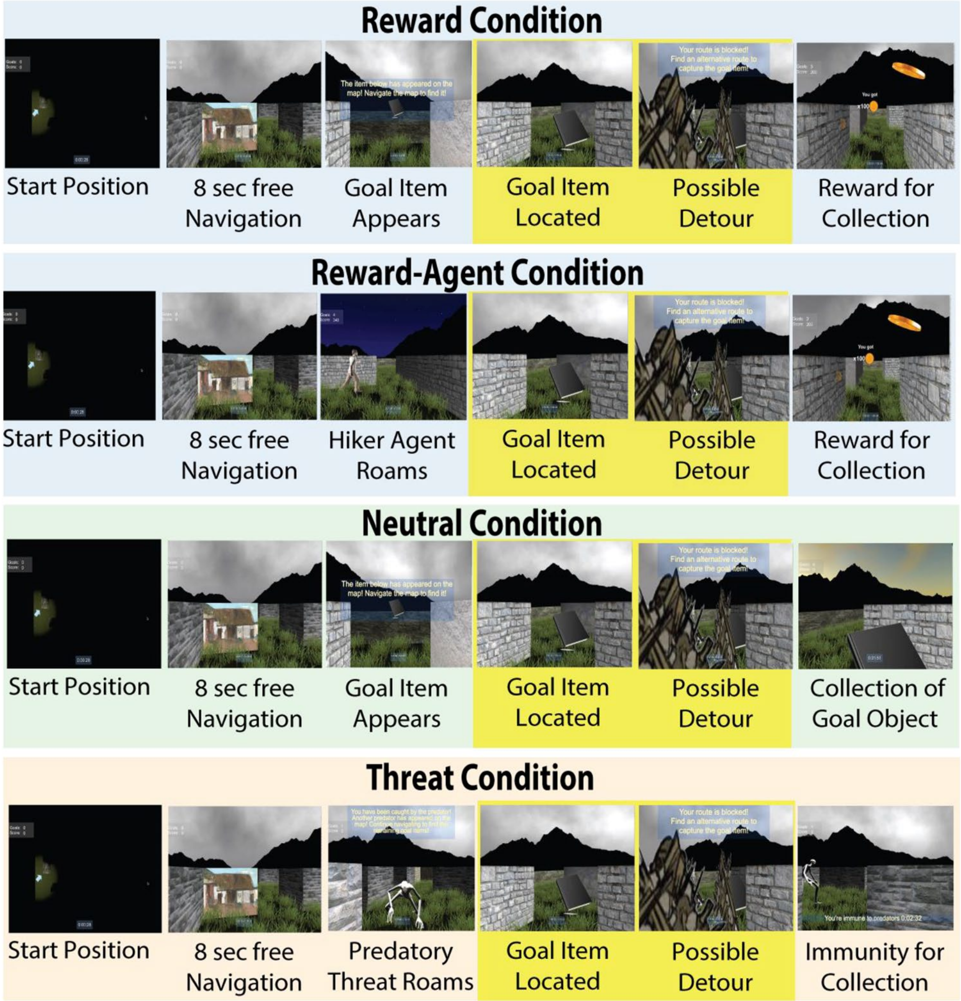


Fig. 2 Trial structure. Temporal sequence of events in each experimental condition. At the beginning of each trial, participants were shown an overhead view of a partially occluded map depicting the starting location and heading direction for the upcoming trial. Participants were then placed into the first-person, 3D environment and were provided eight (8) seconds of free exploration time (no goal requirements). A goal item then appeared on the map with accompanying text instructing the participant to search for and collect the item. After three (3) trials with six (6) goal objects each, the path to a goal item could be obstructed when the object was found and just prior to its collection, forcing a detour path. Upon collection of the goal object, participants were granted a coin reward (Reward and Reward-Agent conditions), nothing (Neutral condition), or short-term immunity from the roaming predator (Threat condition). During the Threat condition, a predator began roaming the environment at the start of each trial, and could find and capture the participant, resulting in electric shock. After a capture event, the predator reappeared at a new, randomly selected location within the environment. In the Reward-Agent condition, a hiker roamed the environment, moving through it in the same way as the predator. If the participant encountered the hiker, the hiker provided a greeting (no electric shock was delivered), and then reappeared at a new, randomly selected location

(i.e., points) indicated. Participants were told that rewards collected would determine the amount of incentive pay received, up to $20. All participants did well enough to be rewarded the maximum amount.

In the Threat condition, a zombie-like predator roamed the environment as the participant navigated. The predator appeared at a random location at least 10 tiles in distance from the player at the start of each Threat trial. If the predator was facing and within 4.5 tiles of the participant, the predator would actively attempt to capture the participant. If the participant was caught, they received an electric shock to the underside of the left wrist. After capture, the predator would then appear elsewhere in the maze, with the constraint that the location had to be at least 10 tiles away. Collecting objects in the Threat condition provided short-term immunity from capture by the predator. Maximum immunity was 8 s, and it decayed to a minimum of 4 s as time passed before the object was collected (Fig. 2). A counter on the screen showed participants how much immunity time they had remaining.

Memory tasks After completing both navigation tasks (i.e., both the Reward and Threat conditions), participants were tested on item recognition and relational, spatial memory. Participants were not told about these memory tests in advance: they received instructions about these tests only after the navigation portion was completed. Relational memory was probed using a forced-choice map identification task and a map drawing task. Item recognition memory was tested by asking participants to discriminate between paintings that were viewed during navigation and those that were never presented. Seen and not seen paintings were presented one at a time, and recognition memory judgments were made. Across our Studies, these memory tests were inconclusive because of poor behavioral performance and/or inconsistent results. For these reasons, they are not discussed in detail in the main manuscript. Interested readers can find further details and results in Supplementary Information.

Questionnaires Individual difference measures were collected after the navigation and memory tasks, including the State Trait Anxiety Inventory (STAI), Behavioral Activation/Inhibition Scale (BIS/BAS), and the Stress Mindset Measure (SMM). Additionally, questions about the participants' experience with the task, including strategy use, were administered. Questionnaires were administered via Qualtrics. These data were collected for potential use in future exploratory and descriptive analyses. They are not discussed further in the current study because we do not have sufficient power for individual differences analyses (for which a sample size of 190 is needed to detect a typical medium-sized effect (Gignac & Szodorai, 2016).

Sensitivity power analysis

Our sample size was selected based on prior studies, which have the potential of being under-powered. We therefore report sensitivity power analyses for our main analyses. This approach requires specifying a desired level of power, an alpha level, and the available sample size to determine the minimum effect size that can be reliably detected (Bloom, 1995; Faul et al., 2009; Perugini et al., 2018).

To conduct these analyses, we used G*Power 3.1 and the freeware offered by Psychometrica.de. We report sensitivity power analyses based on 80% power and an alpha of 0.05 (two-tailed when applicable). For t-tests, minimum effect sizes from the sensitivity analyses are reported as Cohen's dz, which can be directly compared to our observed Cohen's dz values. For ANCOVA results, minimum effect sizes from the sensitivity analyses are reported as partial eta-squared (η_p^2) and Cohen's F, which can be directly compared to the corresponding observed values.

These sensitivity power analyses confirmed that almost all of our critical effects were larger than the minimum effect that could be reliably detected. Two effects of interest were slightly under the effect size estimated by the sensitivity analysis, but those effects nevertheless replicated in our other Studies.

Results

Manipulation checks

To ensure that our threat manipulation was successful, we compared participants' mean anxiety ratings between conditions. As expected, participants reported significantly more anxiety in the Threat condition vs the Reward condition (Reward: $M = 1.79$, SD = 1.51; Threat: $M = 3.47$, SD = 1.67; $t(30) = 7.85$, $p < 0.001$, 95% CI [1.24, 2.12], Cohen's dz = 1.41, 95% CI [0.92, 1.93]).

We also examined how often participants were captured by the predator in the Threat condition, leading to electric shock. Participants were captured (and shocked) an average of 17 times (SD = 13.5). This amounts to approximately three (3) shocks per trial (where a trial requires collection of six (6) objects and lasts roughly five (5) minutes).

As a final manipulation check, we tested whether navigation showed improvement by examining whether path lengths to goal objects became progressively shorter over the course of the task. For each participant, we examined path length as a function of object number, separately by condition and separately for Detour and Non-Detour objects. This yielded one learning slope per participant for each condition and object type (Detour or Non-Detour). We then tested whether there was a significant negative slope across participants with a t-test.

Indeed, participants showed such a learning effect for Non-Detour objects in the Reward condition ($t(30) = 3.46$, $p = 0.0017$, 95% CI [0.11, 0.42]). They also showed numerical improvement for Non-Detour objects in the Threat condition but this effect was not statistically reliable ($t(30) = 1.61$, $p = 0.12$, 95% CI [− 0.28, 0.034]). Nevertheless, there was no significant difference between conditions in the slope of the path length reduction over Non-Detour objects ($t(30) = 1.54$, $p = 0.13$, 95% CI [− 0.32, 0.045]). This confirms that participants generally learned about the layout of the environment and improved at navigating.

In contrast, participants did not show shorter path lengths as a function of Detour object number (Reward: $t(30) = 1.23$, $p = 0.23$, 95% CI [− 0.39, 0.097]; Threat: $t(30) = 0.12$, $p = 0.90$, 95% CI [− 0.46, 0.41]; Reward vs. Threat: $t(30) = 0.48$, $p = 0.63$, 95% CI [− 0.64, 0.40]). This was expected because (1) a given object was only obstructed once; and (2) Detours were rare and unpredictable, making it unlikely that participants would plan for them. However, there were only 6 Detours per condition; thus it is possible that learning would have been evident with more trials (and therefore more statistical power).

Navigation performance

Non-detour navigation

We hypothesized that threat would induce an imperative motivational state, leading to less efficient navigation, as measured by longer path lengths to goal objects. To test this prediction, we first compared travel distances, in tiles traversed, for the Threat and Reward conditions for objects that did not require a detour. Participants took longer paths overall to find objects in the Threat vs. the Reward condition (Fig. 3A) (Reward: $M = 29.94$, SD = 11.33; Threat: $M = 38.65$, SD = 13.76; $t(30) = 4.18$, $p < 0.005$, 95% CI [4.45, 12.96]; Cohen's dz = 0.75, 95% CI [0.35, 1.17]; sensitivity power analysis: Cohen's dz = 0.52).

We conducted an exploratory analysis to determine if navigation differences for Non-Detour objects in the Threat vs. Reward conditions differed based on whether the Threat condition was navigated first or second. We subtracted the mean path length in the Threat condition from the mean path length in the Reward condition to calculate a difference score for each participant. We then compared these difference scores as a function of condition order using Welch's two sample t-test, with the Welch-Satterthwaite correction for degrees of freedom. Participants who navigated the Threat condition first (vs. second) showed greater navigational impairment in the Threat vs. Reward condition ($t(24.94) = 3.38$, $p = 0.0024$, 95% CI [4.76, 19.68]). This difference was driven by worse performance in the Threat condition when Threat occurred first vs. second, as measured by average path length ($t(21.28) = 2.66$, $p = 0.014$, 95% CI [2.68, 21.70]). There was no difference in performance in

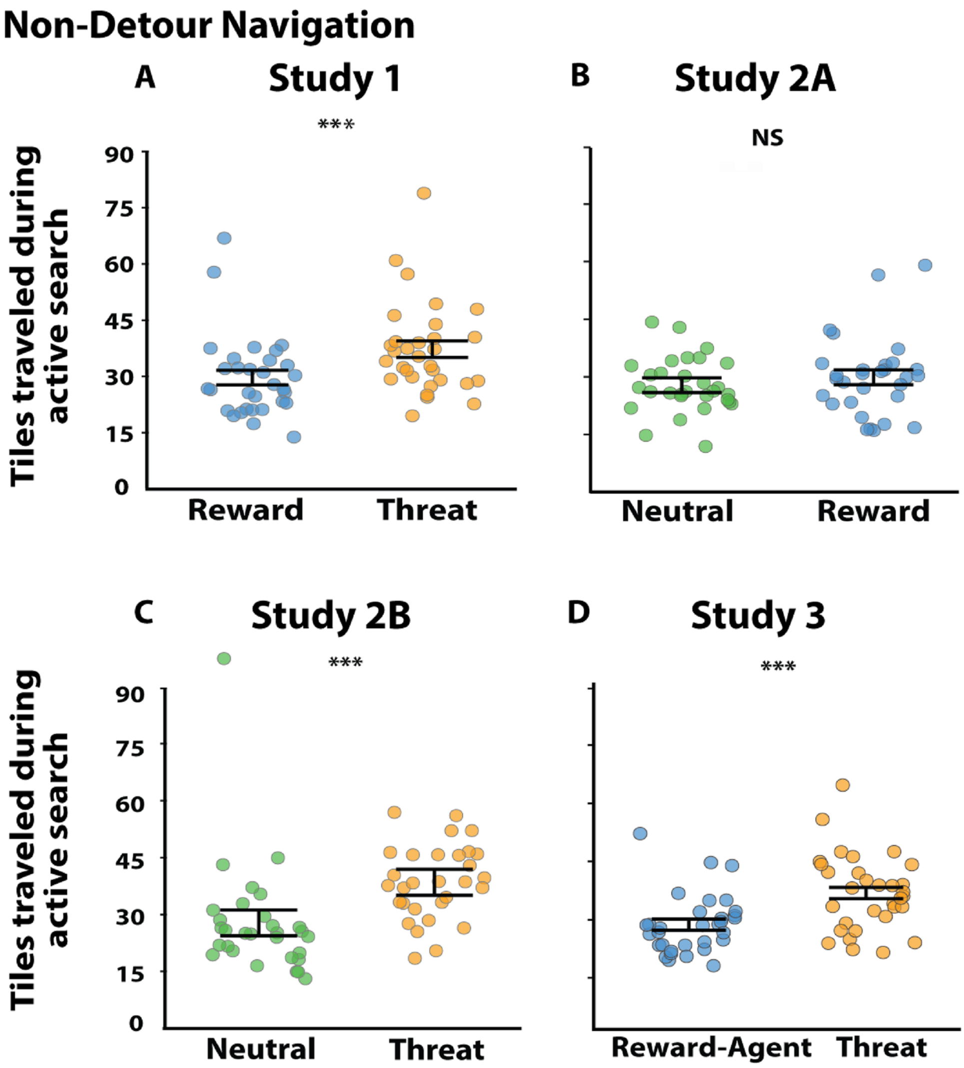


Fig. 3 Non-detour navigation. **A** In Study 1, path lengths for Non-Detour objects were longer in the Threat vs. Reward condition. **B** In Study 2A, no differences in path length were observed between the Neutral and Reward conditions. **C** In Study 2B, path lengths were longer in the Threat vs. Neutral condition. **D** Finally, in Study 3, path lengths were longer in the Threat vs. Reward-Agent condition. Error bars represent ± standard error of the within-participant condition difference. *NS* not statistically significant. ***$p < 0.005$

the Reward condition when it was navigated first vs. second (t(27.73) = 0.0082, $p = 0.99$, 95% CI [− 8.51, 8.58]). Thus, these results are not consistent with general practice effects; instead, performance in the Threat condition was disproportionately worse (vs. the Reward condition) when Threat was navigated first vs. second. This suggests that practice navigating in a safe context, even if in a different map, may reduce threat-related impairments in Non-Detour navigation.

Thus, we found that navigational performance for Non-Detour objects was worse in the Threat vs. Reward condition. These results may be due to impairments in attention, the ability to actively represent or retrieve previously learned information, the ability to operate on retrieved representations, or a desire to avoid the predator. To narrow down these possibilities, we examined performance for Detour objects.

Detour navigation

We next examined navigation performance for Detour objects—those in which the participant's path to the item was blocked, forcing a detour for which the possible routes were always different distances. We found significant differences in route length, such that path lengths for the Threat condition were greater than those for the Reward condition (Fig. 4A) (Reward: $M = 12.13$, SD = 1.30; Threat: $M = 13.39$, SD = 2.19; t(30) = 3.04, $p = 0.005$, 95% CI [0.41, 2.10]; Cohen's dz = 0.55, 95% CI [0.17, 0.93]; sensitivity power analysis: Cohen's dz = 0.52).

As for Non-Detour objects, we conducted an exploratory analysis to determine if differences in path length for Detour objects in the Threat vs. Reward conditions varied based on whether Threat was navigated first or second. Unlike for Non-Detour objects, no condition order effects were observed (t(28.54) = 0.68, $p = 0.50$, 95% CI [− 1.14, 2.27]).

To determine if the differences in Detour navigation between the Threat and Reward conditions remained over and above those due to performance on the Non-Detour objects, we ran an Analysis of Covariance (ANCOVA). The model included the mean number of tiles traversed (i.e., path length) for Detour objects as the dependent variable; the

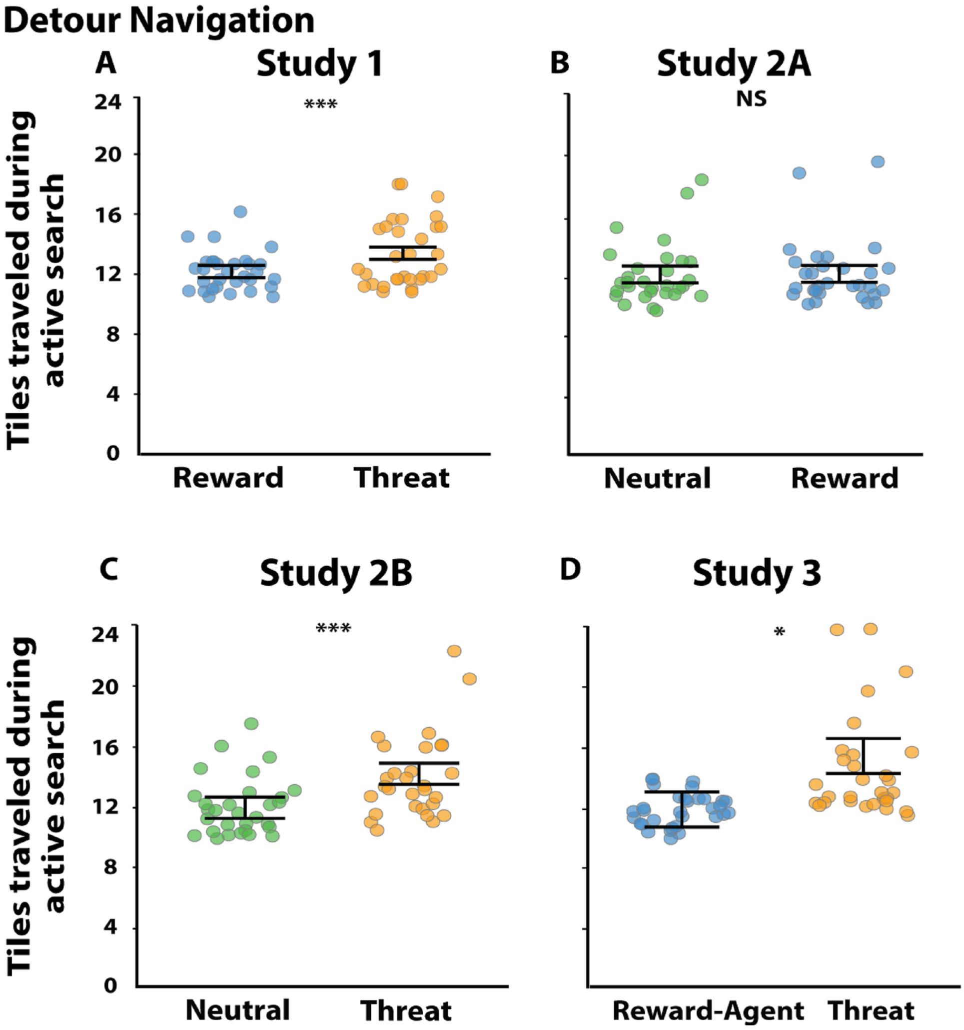


Fig. 4 Detour navigation. **A** In Study 1, path lengths for Detour objects were longer in the Threat vs. Reward condition. **B** In Study 2A, no differences in path lengths were observed between the Neutral and Reward conditions. **C** In Study 2B, path lengths were longer in the Threat vs. Neutral condition. **D** Finally, in Study 3, path lengths were longer in the Threat vs. Reward-Agent condition. Error bars represent ± standard error of the within-participant condition difference. *NS* not statistically significant. $^{*}p < 0.05$, $^{***}p < 0.005$

independent variables were condition (Threat or Reward), condition order (Threat condition navigated first vs. second; this is a between-participants variable), condition by condition order interaction, and the mean number of tiles traversed (i.e., path length) for Non-Detour objects (separately for the Threat and Reward conditions), as the critical control. The model formula was therefore:

$$\text{mean\_detour\_tiles} \sim \text{condition} + \text{condition Order} + \text{condition} * \text{conditionOrder} + \text{mean\_nondetour\_tiles} + \text{error(participant)}$$

This model was run with the 'aov' function from the R stats package; statistical details were obtained using the function 'anova_stats' from the sjstats package.

The model indicated additional impairments in performance for Detour objects in the Threat vs Reward condition, signaled by a main effect of condition ($F(1, 28) = 8.90$, $p = 0.006$, $\eta_p{}^2 = 0.24$, Cohen's $F = 0.564$; sensitivity power analysis: $\eta_p{}^2 = 0.24$, Cohen's $F = 0.523$). There was no main effect of condition order, i.e., Threat first or Reward first ($F(1, 28) = 0.002$, $p = 0.97$, $\eta_p{}^2 = 0.00$) nor a condition order by condition interaction ($F(1, 28) = 0.039$, $p = 0.85$, $\eta_p{}^2 = 0.001$). The main effect of path length for Non-Detour objects was also not significant ($F(1, 28) = 0.88$, $p = 0.36$, $\eta_p{}^2 = 0.0311$).

The main effect of condition in this critical analysis suggests that performance for Detour objects was impaired due to reasons above and beyond the processes that produced impairment for Non-Detour objects. Thus, this threat-related impairment for Detour objects is unlikely to be due to predator avoidance, divided attention due to monitoring the predator, or more general cognitive impairments; if so, it should not have survived controlling for performance on Non-Detour objects, for which predator avoidance and predator monitoring should be a goal. We therefore interpret this additional impairment as one due to the need to *flexibly* use a cognitive map when well-known paths are no longer available.

Discussion

Study 1 demonstrated impairments in navigation efficiency, measured by path length, for the Threat condition. This impairment was present for both Detour and Non-Detour objects; however, the impairment for Detour objects was above and beyond that expected based on Non-Detour objects. We speculate that this additional impairment is due to the demand for *flexible* navigation for Detour objects, because familiar paths were no longer available. In particular, to the extent that heuristics, or narrow rule-based strategies, are used in the presence of threat (Brown et al., 2020; Goodman et al., 2020), any event that disrupts the usefulness of such strategies (e.g., an obstacle) will require executive control of memory systems to be able to engage in adaptive, flexible behavior. For example, path trajectory must be reassessed, which occurs through active representation of the environment from memory and simulation of possible routes. Because threat can activate survival circuits, which in turn can inhibit circuits associated with cognitive control of emotion and behavior (Mobbs et al., 2015), access to certain kinds of representations may be blocked or impoverished. This can in turn produce impairments in real-time integration and simulation. The inability to perform these cognitive operations is likely to impact both the formation or use of relational memories and hence affect behavioral flexibility (Olton, 1979).

Critically, navigational impairment for Detour objects is unlikely to be due to predator avoidance or divided attention due to monitoring the predator. Although individuals may be trying to avoid the predator or dividing their attention between navigation and monitoring the predator's location during Non-Detour navigation, examining Detour navigation in a model with Non-Detour navigation performance as a covariate controls for these general cognitive effects. However, the impairment for Detour objects remained after controlling for performance on Non-Detour objects (and, indeed, navigation performance for Non-Detour objects was not a reliable predictor of performance for Detour objects). This suggests that the impairment for Detour objects may be driven by a specific disruption of flexible navigation when a detour is required under threat, rather than more general cognitive processes. Furthermore, the disruption of flexible navigation echoes findings from studies using unpredictable and invisible electric shock (Brown et al., 2020; Goodman et al., 2020), suggesting that the impairment observed in the current study is unlikely to be purely driven by the visual appearance of the predator and attempts to avoid it.

Study 1 therefore demonstrated that threat impacts the ability to retrieve and/or use relational memories online during navigation. In Study 2, we sought to replicate our findings with a design that addressed limitations of Study 1.

Study 2

Overview

Study 1 investigated navigational performance and memory in rewarded and dynamic threat conditions, finding differences in path efficiency when unexpected obstacles blocked planned routes. However, the results could have been obtained due to reward *enhancing* performance as opposed to threat *impairing* performance. Study 2 addressed this issue by including a neutral condition. Participants were randomly assigned to complete one of two condition pairings (see Table 1): Neutral and Reward or Neutral and Threat. These pairings enable comparison of incentive and threat effects on both navigation efficiency and memory outcomes.

We predicted that threat would account for the negative effects, seen in Study 1, on navigational efficiency. That is, we expected path length for both Detour and Non-Detour objects to be worse in the Threat condition vs the Neutral condition. We had no strong predictions about whether performance in the Reward condition would be significantly different from that in the Neutral condition. On the one hand, reward can promote an interrogative state (Murty & Adcock, 2017) and as a result enhance relational memory and navigation. On the other hand, the reward manipulation (coins for fast object collection, and knowledge that more coins lead to more pay) may not have been as strongly positive as the threat and shock were negative (Ito et al., 1998; Norris, 2021; Vaish et al., 2008).

Methods

Participants

74 (49 female; mean age = 25) participants were recruited and paid $20 for completion of the tasks. We aimed to roughly double the sample size of Study 1 because Study 2 consisted of two sub-experiments in two different groups of participants. 14 participants were unable to complete the task due to motion sickness or discomfort during the navigation portion of the studies. These participants are excluded from data presentation, resulting in net participation of 60 individuals.

Procedure

Stimuli, software, and procedures were identical to Study 1 with the following exceptions: (1) the Study 2 cohort was divided into two groups, one of which received the Neutral and Reward conditions (Study 2A, 30 participants, condition order counterbalanced); the other received the Neutral and Threat conditions (Study 2B, 30 participants, condition order counterbalanced) (see below for condition descriptions); and (2) the Map Drawing Task was replaced with the Object Placement Task (see below for description). Two map layouts were used in the Neutral/Reward condition and the same two map layouts were used in the Neutral/Threat condition. Condition-to-map assignments were counterbalanced. Thus, a given map could be viewed in either the Neutral condition, the Reward condition, or the Threat condition across participants. As before, shock was calibrated for each participant who took part in the Threat condition; average shock intensity was 6.9 (on a scale from 10 to 0, where zero (0) was the strongest shock available), with a standard deviation of 1.7.

Navigation task

The Reward condition was identical to that in Study 1: participants were rewarded with coins for collecting goal items. Faster navigation resulted in greater coin rewards. Participants were told that rewards collected would determine the amount of incentive pay received, up to $20. All participants did well enough to be rewarded the maximum amount.

The Threat condition was also identical to that in Study 1: participants navigated as a predator roamed the environment. When sufficiently close to the participant, the predator entered ‘chase mode’ and pursued the participant. If the participant was caught, they received an electric shock to the underside of the left wrist. Instead of receiving rewards for collection of goal objects, the participant was granted immunity from capture for a period of time.

The new Neutral condition was identical to the Reward condition, except that participants were not provided with coin rewards (or points) upon collection of goal items.

As in Study 1, post-navigation memory tests were conducted; these are further described in Supplementary Information.

Results

Manipulation checks

As in Study 1, we compared participants' mean anxiety ratings between conditions to make sure that our threat manipulation was successful. Indeed, participants reported significantly more anxiety in the Threat condition vs the Neutral condition (Neutral: $M = 1.66$, SD = 1.25; Threat: $M = 3.39$, SD = 1.52; $t(29) = 5.87$, $p < 0.001$, 95% CI [1.13, 2.34]; Cohen’s dz = 1.07, 95% CI [0.63, 1.54]). Anxiety ratings did not differ between the Reward and Neutral conditions (Neutral: $M = 1.41$, SD = 1.27; Reward: $M = 1.33$, SD = 1.28; $t(29) = 0.92$, $p = 0.37$, 95% CI [− 0.28, 0.11]; Cohen’s dz = 0.17, 95% CI [− 0.54, 0.20]).

We also examined how often participants were captured by the predator in the Threat condition, leading to electric shock. Participants were captured (and shocked) an average of 17.4 times (SD = 9.5).

As in Study 1, we also tested if navigation improved with experience by examining whether path lengths to goal objects became progressively shorter over the course of the task. Participants showed such a learning effect for Non-Detour objects in all conditions, and the slope of this learning effect did not differ between conditions in either Study 2A (Reward: *t*(29) = 3.91, *p* = 0.0005, 95% CI [0.12, 0.39]; Neutral: *t*(29) = 4.12, *p* = 0.0003, 95% CI [0.14, 0.42]; Reward vs. Neutral: *t*(29) = 0.31, *p* = 0.76, 95% CI [− 0.16, 0.22]) or Study 2B (Neutral: *t*(29) = 3.41, *p* = 0.002, 95% CI [0.11, 0.46]; Threat: *t*(29) = 4.43, *p* = 0.0001, 95% CI [0.20, 0.54]; Neutral vs. Threat: *t*(29) = 0.80, *p* = 0.43, 95% CI [− 0.30, 0.13]). Thus, participants generally learned to navigate more efficiently.

In contrast, and replicating Study 1, participants did not show shorter Detour path lengths with experience, for either Study 2A (Reward: *t*(29) = 1.47, *p* = 0.15, 95% CI [− 0.94, 0.15]; Neutral: *t*(29) = 0.47, *p* = 0.64, 95% CI [− 0.40, 0.25]; Reward vs. Neutral: *t*(29) = 1.12, *p* = 0.27, 95% CI [− 0.90, 0.27]) or Study 2B (Neutral: *t*(29) = 0.034, *p* = 0.97, 95% CI [− 0.35, 0.34]; Threat: *t*(29) = 0.24, *p* = 0.81, 95% CI [− 0.71, 0.56]; Neutral vs. Threat: *t*(29) = 0.006, *p* = 0.995, 95% CI [− 0.65, 0.65]). This was, however, expected because a given object was only obstructed once and there were relatively few Detours, making it unlikely that participants would plan for them or show robust improvements in route updating on the fly.

Navigation performance

Non-detour navigation

We first examined performance for Non-Detour objects (Fig. 3B, C). We hypothesized that imperative states induced by threat account for the observed navigation differences in Study 1. We therefore expected a similar navigational impairment when threat was compared to a neutral condition in which rewards were absent. Confirming this, participants took longer paths overall to find objects in the Threat vs. Neutral condition (Threat: *M* = 38.5, SD = 9.8. 95% CI [34.88, 42.20]; Neutral: *M* = 27.8, SD = 15.2, 95% CI [22.14, 33.52]; *t*(29) = 3.14, *p* = 0.004, 95% CI [3.73, 17.69]; Cohen's dz = 0.57, 95% CI [0.18, 0.97]; sensitivity power analysis: Cohen's dz = 0.53). These results confirm and extend our results from Study 1, suggesting that threat affects the ability to retrieve or dynamically operate on a cognitive map.

Similarly to Study 1, we conducted an exploratory analysis to determine if navigation differences for Non-Detour objects in the Threat vs. Neutral conditions differed based on which condition was navigated first vs. second. Participants who navigated the Threat condition first (vs. second) showed greater navigational impairment in the Threat vs. Neutral condition, evidenced by greater differences in the Threat vs. Neutral difference scores (*t*(19.94) = 4.05, *p* = 0.00063, 95% CI [10.83, 33.85]). Part of this effect may be due to longer path lengths in the Neutral condition when that condition was navigated first vs. second (*t*(16.46) = 2.49, *p* = 0.024, 95% CI [1.93, 23.59]). Performance on the Threat condition was also worse when Threat occurred first vs. second (*t*(27.98) = 3.03, *p* = 0.0053, 95% CI [− 16.06, -3.09]). Thus, participants who navigated a given condition first were generally worse at that condition than participants who navigated it second, consistent with practice effects. However, participants showed a threat-related impairment in navigation overall, as noted above.

We next compared the Reward and Neutral conditions. If rewards further promote an interrogative state, then the resulting enhanced attentional and memory processes should improve navigational efficiency in the Reward vs. Neutral conditions. However, we failed to find any difference in path length between those conditions for Non-Detour objects (Reward: *M* = 29.9, SD = 10.3, 95% CI [26.05, 33.46]; Neutral: *M* = 27.8, SD = 7.2, 95% CI [25.15, 30.50]; *t*(29) = 1.08, *p* = 0.29, 95% CI [− 1.84, 6.01]; Cohen's dz = 0.20, 95% CI [− 0.17, 0.57]; sensitivity power analysis: Cohen's dz = 0.53).

As above, we conducted an analysis to determine if the order in which each condition was navigated influenced differences between them. We found that the difference between the Reward and Neutral conditions was reversed based on condition order (*t*(22.89) = 3.05, *p* = 0.0056, 95% CI [3.33, 17.34]). This effect arose because of numerically (but not significantly) longer path lengths in the Reward condition for participants who navigated the Reward condition first vs. second (*t*(26.44) = 1.59, *p* = 0.12, 95% CI [− 1.71, 13.39]) and marginally longer path lengths in the Neutral condition for participants who navigated the Neutral condition first vs. second (*t*(26.02) = 1.78, *p* = 0.086, 95% CI [− 9.68, 0.69]). Overall, within participants, performance was poorer for whatever condition was navigated first, suggesting that practice with the task may have made participants more efficient navigators, even on a different map. These effects averaged out at the group level, so that (as noted above), there was no difference between the Reward and Neutral conditions overall.

Detour navigation

We next assessed the efficiency of detour paths to objects blocked by an obstruction as a method to probe the flexible use of relational memories (Fig. 4B, C). Based on our results in Study 1, we predicted that the threat-induced imperative motivational state would result in reduced navigation efficiency when compared to the Neutral condition. Extending Study 1, paths were longer in the Threat vs. Neutral Condition (Threat: *M* = 14.4, SD = 2.9, 95% CI

[13.3, 15.46]; Neutral: $M = 12.0$, SD = 1.8, 95% CI [11.29, 12.62]; $t(29) = 3.78$, $p = 0.001$, 95% CI [1.11, 3.72]; Cohen's dz = 0.69, 95% CI [0.29, 1.10]; sensitivity power analysis: Cohen's dz = 0.53).

As for Non-Detour objects, we explored whether differences in path length between the Threat and Neutral conditions varied based on which condition was navigated first vs. second. Participants who navigated the Threat condition first (vs. second) showed a larger difference in path length for Detour objects for the Threat vs. Neutral condition ($t(27.71) = 3.00$, $p = 0.0057$, 95% CI [1.07, 5.71]). This difference was driven by worse Detour navigation in the Neutral condition when that condition was navigated first vs. second ($t(18.06) = 3.60$, $p = 0.002$, 95% CI [0.82, 3.13]). There were no differences in Detour navigation in the Threat condition when that condition was navigated first vs. second ($t(26.16) = 1.35$, $p = 0.19$, 95% CI [− 3.55, 0.73]).

We next ran an Analysis of Covariance using the same procedures and variables as Study 1 to determine if the impairment for Detour objects (in the Threat vs Neutral condition) survived controlling for performance on Non-Detour objects. We replicated the results from Study 1, indicating impairment over and above that observed for Non-Detour objects (main effect of condition: F(1, 27) = 17.64, $p < 0.001$, $\eta_p^2 = 0.395$, Cohen's $F = 0.808$; sensitivity power analysis: $\eta_p^2 = 0.22$, Cohen's $F = 0.532$).

There was no main effect of condition order, i.e., Threat first or Neutral first (F(1, 27) = 0.22, $p = 0.64$, $\eta_p^2 = 0.0093$) but there was a significant condition order by condition interaction (F(1, 27) = 4.59, $p = 0.04$, $\eta_p^2 = 0.145$). This interaction arose because of a greater impairment in Detour navigation (controlling for navigation for Non-Detour objects) when the Threat condition was navigated first vs. second. Finally, there was a marginal effect of path length for Non-Detour objects (F(1, 27) = 4.13, $p = 0.052$, $\eta_p^2 = 0.13$).

Thus, as for Study 1, the main effect of condition in this critical analysis suggests a specific impairment in flexible navigation in response to unpredictable obstacles — an impairment that is unlikely to be explained by predator avoidance or more general cognitive processes impaired during navigation for Non-Detour objects.

We then compared the Reward and Neutral conditions. Consistent with our finding with respect to Non-Detour objects, reward did not improve navigational efficiency for Detour objects (Reward: $M = 12.2$, SD = 2.0, 95% CI [11.46, 12.92]; Neutral: $M = 12.2$, SD = 1.8, 95% CI [11.47, 12.83]; ($t(29) = 0.09$, $p = 0.93$, 95% CI [− 0.89, 0.97]; Cohen's dz = 0.02, 95% CI [− 0.35, 0.38]). Similarly to above, we explored whether any differences arose in Detour path length between the Reward and Neutral conditions based on which condition was navigated first vs. second; however, Reward vs. Neutral condition differences for Detour objects did not vary based on condition order ($t(17.02) = 1.22$, $p = 0.24$, 95% CI [− 0.81, 3.01]). Together, these results suggest that the Reward condition did not promote an interrogative state different in nature from the Neutral condition.

Discussion

We extended the results from Study 1, demonstrating impairment in navigational efficiency in the Threat condition compared to the Neutral condition. Navigational paths were longer for the Threat vs. Neutral condition for both Non-Detour and Detour objects. Impairments persisted for Detour objects even when controlling for path length on Non-Detour objects; this analysis controls for effects of predator avoidance or divided attention that may be present during Non-Detour navigation. That the impairment remains with this important control suggests that threat specifically disrupts the ability to guide flexible, efficient navigation in response to obstacles encountered in real time. Study 2 also showed that the Threat vs Reward difference in navigation observed in Study 1 was unlikely to be due to improvements incentivized by rewards, because no differences were observed between the Reward and Neutral conditions for any navigation measure we collected.

Study 3

Overview

Studies 1 and 2 contrasted a Threat condition containing an interactive agent with Reward and Neutral conditions in which the participant navigated alone. This asymmetry leaves open the possibility that some navigational or memory differences could be a result of distraction due to the presence of an agent, or avoidance of the agent so as to not be interrupted during navigation. Although our control analysis (i.e., controlling for performance on Non-Detour objects) mitigates this concern for the analysis of Detour objects, avoidance or divided attention may have affected performance for Non-Detour objects. Study 3 sought to address this asymmetry and to replicate and extend the findings of Studies 1 and 2. To that end, we included, in our contrast condition for Study 3, a harmless, wandering hiker whose movements were identical to the predator in the Threat condition. If distraction is responsible for navigational differences, we should obtain similar navigational results for both conditions, because now they both contain agents that are active in the environment and move in identical ways.

Methods

Participants

40 (26 female; mean age = 23) participants were recruited and paid $20 for completion of the tasks. Eight (8) participants were unable to complete the task due to motion sickness or discomfort during the navigation portion of the studies. These participants are excluded from data presentation, resulting in net participation of 32 individuals.

Procedure

Stimuli, software, and procedures were identical to Study 1 with the following exceptions. The Reward condition was modified to include the addition of a harmless hiker who roamed around the environment and, upon encountering the participant, provided a greeting. The hiker's behavior was mapped from the predator character (i.e., the hiker and the predator moved through the maze in the same way). Thus, the only differences between them were their appearance and whether or not shock was administered. This condition controlled for the presence of an actively navigating agent, which may have changed behavior of participants in the Threat condition. In particular, 'capture' by the hiker or the predator led to an interruption of navigation (i.e., the participant could not move) while the character engaged in a 3-s animation. If participants are motivated to succeed at their primary goal—collecting items as fast as possible—they should try to evade both the hiker and predator to avoid lost time.

The Threat condition was identical to that used in Study 1 and Study 2. The post-navigation memory tests were also administered, as in Study 2 (Supplementary Information).

As before, the assignment of maps to conditions (Threat or Reward-Agent), and which condition was navigated first, were counterbalanced across participants.

Shock intensity for the Threat condition was again calibrated for each participant. Average shock intensity was 6.2 (on a scale from 10 to 0 where zero (0) was the strongest available shock), with a standard deviation of 2.8.

Results

Manipulation checks

We compared participants' mean anxiety ratings between the Threat and Reward-Agent conditions to determine whether our threat manipulation was successful. As expected, participants reported significantly more anxiety in the Threat condition vs the Reward-Agent condition (Reward-Agent: $M = 1.44$, SD = 1.43; Threat: $M = 3.47$, SD = 1.63; $t(31) = 7.25$, $p < 0.001$, 95% CI [1.46, 2.61]; Cohen's dz = 1.28, 95% CI [0.82, 1.77]).

We also examined how often participants were captured by the predator in the Threat condition, leading to electric shock. Participants were captured (and shocked) an average of 15.5 times (SD = 7.1).

Finally, as for prior studies, we examined whether navigation improved over the course of the task by testing whether path lengths to goal objects became progressively shorter. Indeed, participants showed this learning effect for Non-Detour objects in both the Reward-Agent ($t(31) = 6.48$, $p < 0.00001$, 95% CI [0.31, 0.59]) and Threat ($t(31) = 3.19$, $p = 0.003$, 95% CI [0.10, 0.44]) conditions, and these effects did not differ ($t(31) = 1.47$, $p = 0.15$, 95% CI [− 0.43, 0.07]).

Replicating our prior studies and, as expected, this learning effect did not extend to Detour objects, for which path lengths did not become progressively shorter (Reward-Agent: $t(31) = 1.63$, $p = 0.11$, 95% CI [− 0.56, 0.062]; Threat: $t(31) = 1.22$, $p = 0.23$, 95% CI [− 2.16, 0.55]; Reward-Agent vs. Threat: $t(31) = 0.84$, $p = 0.41$, 95% CI [− 0.81, 1.93]). Thus, participants generally learned to navigate more efficiently for Non-Detour objects but did not show detectable improvement over the relatively few unique Detours.

Navigation performance

Non-detour navigation

We found that navigational differences persisted even after the inclusion of an agent in the non-threat condition (Fig. 3D). Navigation in the Threat condition ($M = 35.5$, SD = 10.3, 95% CI [31.77, 39.22]) was associated with longer paths to goal items in comparison with the Reward-Agent condition ($M = 28.3$, SD = 9.2, 95% CI [25.01, 31.67]; $t(31) = 4.46$, $p = 0.0009$, 95% CI [3.88, 10.42]; Cohen's dz = 0.79, 95% CI [0.39, 1.20]; sensitivity power analysis: Cohen's dz = 0.51). These results reinforce our findings from Studies 1 and 2, providing additional evidence that Threat, as opposed to distraction or avoidance, is largely responsible for the reduced navigational efficiency observed across all three (3) studies.

Similarly to Studies 1 and 2, we conducted an exploratory analysis to determine if navigation differences for Non-Detour objects in the Threat vs. Reward-Agent condition differed based on which condition was navigated first vs. second. Participants who navigated the Threat condition first (vs. second) showed greater navigational impairment in the Threat vs. Reward-Agent condition ($t(27.10) = 2.98$, $p = 0.006$, 95% CI [2.66, 14.40]). This difference was driven by worse performance in the Threat condition when Threat occurred first vs. second ($t(29.998) = 2.69$, $p = 0.011$, 95% CI [2.17, 15.79]). There was no difference in performance in the Reward-Agent condition when it was navigated first vs. second (t(26.06) = 0.14, p = 0.89, 95% CI [− 7.27, 6.37]). Thus, as in Study 1, these results are not consistent with general practice effects; instead, performance in the Threat condition was disproportionately worse (vs. the Reward-Agent condition) when Threat was navigated first vs. second. This concords with Study 1 in suggesting that practice navigating in a safe context, even if in a different map, can reduce threat-related impairments in Non-Detour navigation.

Detour navigation

We next examined performance for Detour objects, in which the path to some goal objects was obstructed, forcing the participant to select a detour route (Fig. 4D). If distraction or avoidance due to the presence of an agent was responsible for navigational differences in Studies 1 and 2, then these differences should disappear when both conditions feature a dynamic, interactive agent. However, replicating our prior results, we observed that navigation efficiency (assessed with path length) was impaired in the Threat condition (M = 15.4, SD = 8.0, 95% CI [12.55, 18.30]) relative to the Reward-Agent condition (M = 12.04, SD = 1.31, 95% CI [11.56, 12.51]; t(31) = 2.40, p = 0.02, 95% CI [0.50, 6.27], Cohen's dz = 0.42, 95% CI [0.06, 0.80]; sensitivity power analysis: Cohen's dz = 0.51).

As before, we also explored whether navigation differences for Detour objects in the Threat vs. Reward-Agent conditions differed based on which condition was navigated first. There was a marginal effect, such that those who navigated the Threat condition first (vs. second) showed a trend for a larger impairment in the Threat condition vs. Reward-Agent condition (t(17.46) = 2.04, p = 0.056, 95% CI [− 0.17, 11.17]). However, this marginal effect arose because of general practice effects that coincided with the main effect of condition: Detour performance in the Threat condition was marginally worse when that condition occurred first vs. second (t(16.76) = 1.80, p = 0.089, 95% CI [− 10.65, 0.84])), and Detour performance in the Reward-Agent condition was numerically worse when that condition occurred first vs. second (t(29.89) = 1.29, p = 0.21, 95% CI [− 0.34, 1.53]). Thus, participants who navigated the Threat condition first (vs. second) tended to do worse in the Threat condition and better in the Reward-Agent condition, consistent with general practice effects, although neither of these direct comparisons reached statistical significance.

The threat-related impairment in Detour navigation endured after controlling for performance on Non-Detour objects, evidenced by an Analysis of Covariance using the same parameters as Studies 1 and 2 (main effect of condition [Threat vs. Reward-Agent]: F(1, 29) = 6.25, p = 0.018, $\eta_p^2 = 0.18$, Cohen's F = 0.464; sensitivity power analysis: $\eta_p^2 = 0.209$, Cohen's F = 0.51). There was no main effect of condition order, i.e., Threat first or Reward-Agent first (F(1, 29) = 2.60, p = 0.12, $\eta_p^2 = 0.08$) nor a condition order by condition interaction (F(1, 29) = 2.22, p = 0.15, $\eta_p^2 = 0.03$). The main effect of path length for Non-Detour objects was also not significant (F(1, 29) = 2.53, p = 0.12, $\eta_p^2 = 0.08$). Thus, as for Studies 1 and 2, the main effect of condition in this critical control analysis suggests a specific threat-related impairment in flexible navigation to unpredictable obstacles. These results add further support to our interpretation that a dynamic threat disrupts the ability to bring forth and/or flexibly operate on representations required for optimal navigation performance.

Discussion

Study 3 replicated navigation results obtained in both Study 1 and Study 2 when comparing the Threat condition to the non-threat (here, Reward-Agent) condition. Participants took less efficient paths for both Non-Detour and Detour objects during threat, and the latter effect held when controlling for the former. This control analysis suggests that threat specifically impairs flexible navigation in response to unexpected obstacles, over and above more general cognitive impairments that may occur under threat. Study 3 also extended prior results by providing evidence that the navigational differences observed could not be explained by the mere presence of an agent. Thus, social distraction is unlikely to account for the impairments observed in our first two (2) studies.

General discussion

Summary

We induced imperative motivational states (Murty & Adcock, 2017) with a dynamic, threatening agent who roamed the environment as individuals navigated, delivering electric shock when participants were 'captured'. We found that threat, compared to the absence of threat, impaired navigation, as evidenced by longer path lengths to goal objects. This navigational impairment was observed both on trials that required a detour and those that did not, and the impairment on the former held after controlling for performance on the latter. This critical analysis demonstrates that threat specifically impairs flexible navigation when unexpected obstacles are encountered online: that impairment remained for Detour objects even when controlling for performance on Non-Detour objects suggests that performance deficits are unlikely to be purely explained by distraction or predator avoidance that may be present for Non-Detour objects. Indeed, navigation performance for Non-Detour objects was not a reliable predictor of performance for Detour objects, further suggesting that threat may drive a specific impairment when individuals are required to flexibly navigate in response to unexpected obstacles. Furthermore, impairment in the Threat condition could not be attributed to the mere presence of an actively navigating agent in the environment, because performance continued to be impaired when a non-threatening agent was added to the non-threat condition. Additionally, an exploratory analysis failed to show any differences in time spent in different parts of the map in Threat vs. non-threat conditions: i.e., individuals did not tend to stick to one quadrant of the map more in the Threat vs. non-threat conditions (Supplementary Fig. 4). This suggests that poorer navigation in the Threat condition cannot be attributed to a preference for one part of the map over others. Our current results therefore collectively show that threat impairs the ability to bring forth and / or flexibly operate on a cognitive map. Future studies can systematically manipulate variables like environmental connectivity (Brunec et al., 2023) to determine if threat causes individuals to prefer parts of an environment that are less well-connected to other parts, and whether this may contribute to differences in spatial learning and memory.

It is possible, nevertheless, that divided attention continued to play a role in threat-related navigation impairments for Detour objects. This may have occurred if the nature of attentional distraction by the predator differs for Non-Detour objects and Detour objects: an unexpected obstacle may potentially alter the way individuals can exert top-down control over distraction. Future studies could compare a threatening agent with an appetitive agent that individuals are motivated to track, to determine how effects of attentional monitoring under reward conditions differ from those under threat conditions. In our studies, individuals may not have been motivated to track the hiker in Study 3, because finding him did not confer rewards.

One key finding was that threat-related impairments in Non-Detour navigation were larger when the Threat condition was navigated first vs. second. In Study 1 and 3, this was driven by worse performance in the Threat condition when it was navigated first vs. second, with no difference in the non-threat (Reward or Reward-Agent) conditions when they were navigated first vs. second. In Study 2, participants who navigated the Threat condition first (vs. second) performed worse in the Threat condition and better in the Neutral condition; both of these contributed to a greater threat-related impairment when threat occurred first. Such a pattern cannot be explained by general practice effects (in contrast to Study 2, in which more general effects of learning were observed alongside a main effect of condition). For Detour navigation, condition order differences were less consistent: only Study 2 showed a reliable effect, and it was driven by performance in the Neutral rather than Threat condition. Across all 3 Studies, our critical analysis—examining Detour navigation when controlling for path length for Non-Detour objects—continued to show a main effect of condition (Threat vs. non-threat) even after controlling for condition order. Together, these results suggest that—at least in some circumstances—navigating a safe environment first may reduce threat-related navigation impairments for Non-Detour objects, even if this navigation occurs in a different environment (albeit with similar structure, e.g., size, wall heights, etc.). However, such ‘protective’ effects for navigation under threat—obtained from navigating in a safe environment first—are not reliable when navigation occurs in response to unexpected obstacles (for Detour objects). This finding—together with our finding of threat-related impairments in Detour navigation, even when controlling for Non-Detour navigation performance—suggests that threat may particularly affect the ability to navigate flexibly and efficiently in the face of unexpected obstacles—an impairment not easily rescued by navigation practice in safe contexts.

Below, we relate our work to prior studies, consider the implications of our research for real-world behavior, and discuss limitations and future directions.

Relation to prior work

Relation to studies of motivational states and memory

Our research is complemented by recent work investigating the neural correlates of navigation performance under threat. This work has shown disruption in human hippocampal and prefrontal activity, resulting in increased reliance on familiar, learned strategies and reduced probability of engaging in flexible simulation (Brown et al., 2020). A related investigation demonstrated that the threat of random shock led to more errors on a hippocampally mediated radial maze task that required flexible, allocentric representations, and greater reliance on less efficient navigation strategies (Goodman et al., 2020). However, threat did not affect performance in a version of the task where stimulus–response associations were sufficient for performance. In both of these latter studies, threat was operationalized as the random delivery of electric shock, and navigation was assessed after learning had occurred in the absence of threat.

Another relevant study induced an avoidance motivational state, in which participants received a shock for navigating to an incorrect destination in a modified Morris water maze task (Murty et al., 2011). Poorer performance and learning rates were observed in this threat condition, compared to a condition that used reward incentives to trigger an approach motivation.

The consistency between our results and those of Brown et al. (2020), Goodman et al. (2020), and Murty et al. (2011) suggest that dynamic (as opposed to static) threats are not necessary to show impairments in navigation under threat.

Nevertheless, our work extends these prior studies by showing that the observed impairments replicate in situations with more ecologically valid threats—threats that are visible, wax and wane, and can be responded to in real-time.

The use of an active, observable threat in the environment, which directly causes electric shock—as opposed to risk of probabilistic electric shock—may be an important difference between our study and that of (Brown et al., 2020). Agentic threat may tax cognitive resources more than anticipation of an unpredictable electric shock. The presence of an actively navigating threat requires tracking and a degree of attention in order to avoid being captured. Further, our design forced alternative routes to goal objects online, because those goal objects were obstructed just as they were reached. In contrast, the Brown et al. study gave participants a period in which they could plan an efficient, novel shortcut to reach a goal location. Our study therefore tested how quickly and efficiently individuals could find an alternate route when their path was unexpectedly blocked. The results, which consistently showed poorer use of shorter detour routes in the Threat condition, even after controlling for overall worse navigation in that condition (for Non-Detour objects), suggested that participants struggled to bring forth or use complex relational representations when faced with such a decision under threat.

We emphasized the threatening nature of the predator and electric shock because other studies have used similar manipulations to evoke fear and defensive behaviors; in particular, the dynamic nature of waxing and waning visible threats activates defensive systems as a function of threat imminence (e.g.Faul et al., 2020; Mobbs et al., 2007; Qi et al., 2018). Nevertheless, our threat manipulation likely affected arousal, stress, and/or fear responses. Our results suggest open questions for future work, such as whether each of these states in isolation could produce our observed effects. A relevant line of work, for example, comes from research that has used emotional images to investigate how valence and arousal influence memory for central vs. peripheral details (Mather & Sutherland, 2011); such work could be extended to examine such memories during navigation. Furthermore, future studies could test whether results similar to ours are observed in response to fear or anxiety evoked by social or emotional stress (e.g., fear of embarrassment rather than fear of physical harm).

Indeed, stress, as opposed to arousal, has also been shown to impact hippocampal-dependent memory systems through sympathetic nervous system activation, which initiates a cascade of processes that upregulate threat systems. Stress systems impact hippocampal memory systems at retrieval, reducing capacity and accuracy for recollection of event details (Gagnon et al., 2019); also see Shields et al. (2017). This effect is associated with downregulation of hippocampal activity, and appears even when other cortical systems are online. Stress at retrieval also funnels response tendencies towards more rigid behavior and inhibits executive systems responsible for flexible, adaptive cognition (Gagnon & Wagner, 2016)). Our results complement and extend this work by examining how information is encoded and used online when a dynamic threat is present in the environment throughout an entire learning session.

Limitations and future directions

The current work utilized a dynamic agent that could detect and capture participants, much like predators or opponents in recreational video games. In such games, players often explore environments and have to evade visible threats that can impact their ability to achieve goals. Much like these video game scenarios, participants in our studies may have had a secondary goal in the Threat condition (a goal to avoid the predator). Such a secondary goal was not present in the non-threat conditions in two (2) of our studies. Because of this, attention may have been divided in the Threat condition more than the other conditions, as individuals try to multitask between avoiding the predator and reaching the goal items. Critically, however, threat impaired navigation for Detour objects above and beyond the impairment for Non-Detour objects. If the threat-related impairment was entirely due to predator avoidance (or the divided attention associated with it), the impairment for Detour objects should have disappeared (not remained) when controlling for performance on Non-Detour objects, for which divided attention or predator avoidance may have been at play. Thus, this evidence suggests that threat affects flexible navigation when detours are required, and this impairment is unlikely to be explained by divided attention or predator avoidance that may have been present for Non-Detour objects. Furthermore, we believe the hiker in Study 3 offers a good control for social distraction. The hiker moved through the environment in the same way as the predator, and upon encountering the participant, interrupted their navigation with a 3-s animation — exactly as the predator did, except without accompanying electric shock. If participants' goal is to maximize points received by collecting goal objects as fast as possible, they should avoid the hiker so that they can prevent the interruption of navigation. Thus, both the predator and hiker conditions should have induced a secondary goal to evade the navigating character for optimal performance on the main task.

There are nevertheless at least two possible mechanisms by which threat produced impairment of Detour navigation: (1) individuals may be engaging in route planning after an obstacle is encountered, but this online planning is disrupted by anxiety or stress due to the threatening context; or (2) participants fail to engage in route planning after an obstacle and are instead intent on quickly moving away from the obstacle to avoid being trapped by the predator. The current studies cannot adjudicate between these possibilities, because taking an inefficient route could be due to either a failure of planning or belief that a particular route may be safer. We speculate that Detour navigation impairments are due to difficulty in using spatial knowledge to plan efficient, flexible routes in real time; but future work should directly test this hypothesis by examining how quickly individuals plan new routes after encountering unexpected obstacles under threat vs. safety.

Another potential limitation of the current work arises from the non-navigational spatial memory tasks (Supplementary Information). These tests were meant to enable us to determine if threat affected the online use of information but not its encoding or accessibility after the threat was removed. These tests were also a way for us to probe what aspects of the environment were encoded, e.g., object-in-place information, incidental perceptual details. Unfortunately, performance was either poor or inconsistent across Studies, limiting our ability to reach strong conclusions. These results are discussed in detail in Supplementary Information, along with recommendations on how future work can improve upon the memory tasks we used.

Future work may benefit from development of, and research on, new concepts such as motivational flexibility (the ability to shift motivational states in response to environmental demands) and motivational adaptiveness (the appropriateness of motivational state shifts vis a vis environmental demands). Such concepts may yield insights in a host of areas, from educational learning and decision making, to disaster and emergency response, to performance at work. For example, low motivational flexibility reflected by persistence of imperative states may be linked with anxiety and be detrimental for mental health. Conversely, low motivational flexibility characterized by an inability to enter an imperative state may impair appropriate response to threats. High motivational adaptiveness should be evident in individuals that can perform and excel in a host of different contexts that require shifting between motivational states. Coupling these concepts with experimental frameworks like those described herein promise to yield new insights into the relationship between motivational profiles and cognitive and behavioral outcomes. Nevertheless, it is important to be cognizant of differences between threats that can be operationalized and manipulated in cognitive psychology laboratories, and the myriad socioeconomic threats and stressors that affect individuals in the real world.

Application of our findings to real-world domains, such as emergency escape behaviors, will require additional work to include both threat and non-threat conditions in the same physical space, and interventions or training to improve the ability to perform under threat. Many natural and human-caused disaster situations in the real world involve extreme experience of imperative motivational states. In most instances of imminent threat, people are required to navigate through spaces that were encoded in the absence of threats, such as familiar schools or office spaces. Experimental navigation conditions that vary whether a dynamic, active threat is present or absent on the same map layout may provide further insight into how people respond to such situations. Designs that first require and confirm learning in a non-threatening environment, and then introduce an active threat would mimic common emergency situations. These results would expand on our findings, in which the entire learning session occurred under threat.

Conclusions

Across three studies, we found that an active, dynamic threat significantly impaired efficient and flexible navigation. Critically, participants showed threat-related impairments in flexible navigation when unexpected obstacles were encountered online, and this impairment held even after controlling for performance on non-detour navigation—a good control for more general impairments, such as those due to divided attention or predator avoidance. Threat therefore disrupts the ability to retrieve and / or use relational information online in the service of flexible behavioral goals. These results add to the extensive literature on how motivational states affect learning, memory, and behavioral flexibility. They have important implications for how real-world navigational efficiency may be affected in stressful situations with threatening agents.

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Declarations

Conflict of interest None.

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