The effect of anxiety on gait: a threat-of-scream study

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Abstract

It is known that fear responses to clearly identified threats can inhibit motion, slowing down gait and inducing postural freezing. Nonetheless, it is less clear how anxiety, which emerges during threat anticipation, affects gait parameters. In the present work, we used a threat-of-scream paradigm to study the effects of anxiety on gait. Twenty-five participants (15 female, aged 23.4 ± 1.8) were instructed to walk on a 5-meter walking track, while motion was recorded in 3D, via a VICON system. Four alternating blocks, two “threat” and two “safe” blocks of 10 trials each, were signaled by colored stripes on a screen in front of the walking path. Participants were informed that they could hear a human scream in their headphones at any time during threat blocks, which were in fact always delivered during walking. On the contrary, no screams were delivered in the safe blocks. Results indicated that participants reported higher subjective anxiety during threat vs. safe blocks. Furthermore, increases in self-reported anxiety from safe to threat showed significant moderate correlations with increased stride speed and length, decreased stride time and decreased stance phase duration. Increases in anxiety were also moderately correlated with increased arm/leg swing amplitude, an effect that was fully mediated by increased stride speed. Overall, these results indicate that anxiety invigorates motion in healthy subjects, by increasing speed. These results are discussed in terms of the recent advancements in the understanding of defensive behavior, its neural correlates and on clinical implications relative to pathological anxiety.

1. Introduction

The capacity to produce adaptive behavioral responses in threatening situations is of paramount importance for adaptation (LeDoux & Daw, 2018). Humans and other animals show privileged processing of threat information, leading to prioritized action control, through rapid activation of both cortical and subcortical motor regions (Mennella & Grèzes, 2023). Nonetheless, the precise determinants of behavior under threat are a matter of debate. The predatory imminence model suggests that the perceived spatial and temporal distance to the threat organizes defensive behaviors, but also cognitions and subjective emotional experiences (Fanselow, 1994; Fanselow et al., 2019; Fanselow & Lester, 1988; Mobbs et al., 2009, 2020). This model is consistent with a view of threat-related emotions and affects, such as panic, fear and anxiety, as multidimensional and coordinated policies to face environmental challenges (for other perspectives, see e.g. LeDoux & Hofmann, 2018; for a discussion about the different perspectives, see Engelen & Mennella, 2023). Fear is typically generated in response to a clearly identified threat and becomes panic when the same threat is imminent or attacking. Anxiety, on the other hand, emerges when the threat is not present, but is anticipated with apprehension based on general priors about the environment and/or previous encounters. Notably, fear and anxiety may exhibit partially dissociable neural correlates (Davis, 2006; Fanselow, 1994; Klumpers et al., 2017), as well as distinct effects on postural and gait control.

Converging evidence in humans indicates that exposure to a clearly identified and proximal threat, such as a threatening individual, can induce freezing, a passive defensive state characterized by reduced body sway and cardiac deceleration (Bastos et al., 2016; Noordewier et al., 2020; Roelofs et al., 2010). Similarly, imagined, recalled or simulated fear states influence gait mainly by reducing speed (Barliya et al., 2013; Fawver et al., 2014; Hicheur et al., 2013). This is accompanied by a shorter swing phase, shorter strides, despite a faster cadence (Halovic & Kroos, 2018), reduced joint angle amplitudes and widespread postural tension (Halovic & Kroos, 2018; Hicheur et al., 2013; Roether et al., 2009; for a review, see Deligianni et al., 2019). It is noteworthy that when opportunities for avoidance or escape are available, humans can transition from a passive (freezing) to an active defensive strategy, as evidenced by faster reaction times, more extensive and rapid postural responses, as well as increased step length and velocity (Fawver et al., 2022). In the case of fear, the switch from passive (freezing) to active defensive strategies - both innate (flight) and learned (avoidance/escape) - is strictly dependent on threat proximity and the presence of action opportunities (Mennella & Grèzes, 2023). However, the case of anxiety is more ambiguous and less investigated.

During anxiety the threat is nor clearly identified in space or time, which generates apprehension and threat anticipation (Mobbs et al., 2020). In this context, it is unclear whether active or passive defensive behaviors, respectively leading to action invigoration or inhibition, ought to be privileged. Previous studies on posture control showed that, unlike fear, experimentally induced anxiety in healthy individuals invigorates motion. Anxiety during demanding cognitive tasks (e.g., mental arithmetic, Stroop) has been associated with larger and faster body sway (e.g., Hainaut et al., 2011; Maki & McIlroy, 1996). Similar results were obtained when inducing anxiety via the anticipation of randomly presented aversive sounds (Ishida et al., 2010), or of unpredictable postural perturbations (Holmberg et al., 2009; Johnson et al., 2019; Shaw et al., 2012).

To the best of our knowledge, fewer studies have investigated the effect of experimentally induced anticipation anxiety on gait parameters. A substantial corpus of literature exists on the effects of anxiety related to the risk of falling. For example, research in young samples on the effects of anxiety induced by walking on high paths on gait has shown that the threat of falling induces a postural stiffening strategy, as well as cautious slow walking with reduced stride length and increased double-support phases (for reviews, see Hall et al., 2023; Huppert et al., 2020). This is accompanied by changes in joint kinematics, such as a reduction in anteroposterior velocity and mediolateral shift of the center of mass (CoM), and reduced range of angular displacement (Brown et al., 2002). These results are of pivotal importance, for instance to better characterize anxiety related to the possibility of falling in older individuals and patients with motor impairment. Nonetheless, anxiety generated by anticipating a fall is unique, as it directly depends on the execution of a movement in conditions of precarious equilibrium, which may not generalize to other and more common forms of anxiety (Hall et al., 2023). In addition to the aforementioned literature, one study investigated the influence of anxiety induced via 7.5% carbon dioxide (CO2) inhalation on gait, reporting slower gait speed in the anxiety vs. safe condition (Attwood et al., 2021). While these findings suggest that anxiety may influence gait, they should be interpreted with caution, given the inability to distinguish the effects of CO2-induced anxiety from those of hypercapnia on motion control (Attwood et al., 2021). It is noteworthy that the correlation between changes in anxiety levels between conditions and changes in speed was not reported.

To overcome the methodological limitations of previous studies, here we induced anxiety employing a recently developed experimental paradigm called "threat-of-scream" (Beaurenaut et al., 2020), an acoustic version of the well-known threat-of-shock paradigm (Robinson et al., 2013). This anxiety-inducing procedure consists in alternating blocks in which participants are at risk of hearing unpredictable aversive distress screams (threat blocks) with blocks during which no aversive stimulation can occur (safe blocks). The unpredictable delivery of aversive distress screams has been shown to effectively induce sustained aversive states in participants (Silva et al., 2023). This is evidenced by increased subjective reports of anxiety and elevated skin conductance level during threat blocks compared to safe, and by the significant positive correlation between these two measures (Beaurenaut et al., 2020). Furthermore, participants' subjective anxiety and physiological arousal are positively correlated with preoccupation about the potential delivery of aversive stimuli and are sensitive to social buffering (i.e., reduced negative state in the presence of conspecifics; Beaurenaut et al., 2021). Several studies highlighted that anxiety induced by threat-of-scream can influence both cognitive and motor processes. Cognitively, it induces prioritized processing of social threatening expressions (Beaurenaut et al., 2023), compromises recognition memory for complex multi-dimensional information (Zlomuzica et al., 2022), and reduces working memory accuracy (Patel et al., 2017), reproducing findings typically observed in trait-anxious individuals. Furthermore, it can influence the action representation of others, depending on contextual salience (Beaurenaut et al., 2021). Altogether, the threat-of-scream procedure appears to be an appropriate noninvasive tool to investigate how anxiety of an unpredictable and unidentified threat influences gait. In particular, the specificity of the employed paradigm rendered impossible for participants to predict the temporal occurrence, as well as the spatial localization, of the threat, preventing the occurrence of instrumental defensive strategies, such as instrumental avoidance.

We hypothesized that changes in gait parameters would emerge between threat and safe blocks, as a function of the intensity of the induced anxiety state. More precisely, these changes were expected to correlate with the difference of subjective anxiety scores between the type of blocks and the safe blocks reported by each participant. As there is theoretical support for both inhibition and invigoration of movement in anxiety states, our hypothesis was bidirectional. Specifically, we wanted to test whether anxiety induces a cautious slow walking mode, mainly measured by reduced stride speed and associated changes in related spatiotemporal parameters (i.e., increased stride time and reduced stride length and swing phase duration), as in the case of fear (Deligianni et al., 2019) and height exposure (Huppert et al., 2020) or, conversely, a fast walking mode. To further explore walking characteristics under anxiety, we applied dimensional reduction to the kinematic data via Principal Component Analysis (PCA), to decompose whole-body motion into a few meaningful components (“gait primitives”; Michalak et al., 2009; Troje, 2002), while accounting for most of the variance.

2. Methods

2.1. Participants

In Beaurenaut et al. (2020), the main effect of condition (threat vs. safe) on subjective anxiety had an effect size of η^2_p = .38 (Study 1) and η^2_p = .60 (Study 2). Based on the smallest effect estimate, a minimum sample of n = 25 was required to replicate the effect with an a priori significance level α = .05 and a desired power of 1 - β = .95 (GPower 3. 1; Faul et al., 2007). We therefore recruited 28 volunteers, of whom three were discarded from analyses, one because VICON's audio messages of start/and trial were not switched off during recording and two because of total absence of data for one or more markers. The final sample (n = 25; females = 15) was aged 23.4 ± 1.8 (mean ± sd; min/max$_{age}$ = 18/27). Participants were selected via a set of questionnaires accessible via a Qualtrics link. Online prescreening assessed inclusion criteria, namely the absence of a history of neurological disorders (e.g. epilepsy, head trauma), bulimic, addictive or anorexic behaviors, medical follow-up for anxiety or depressive disorders, as well as the absence of current drug treatment. In addition, participants had to have normal color vision and be able to walk for at least 30 minutes. They also agreed to abstain from alcohol and other drugs for 24 hours prior to the experiment, as well as to only wear tight clothes or underwear during the experiment to facilitate sensor positioning the day of the experiment. Finally, following previous recommendations (Beaurenaut et al., 2020) and to exclude the presence of high trait anxiety and post-traumatic stress disorder (PTSD) symptoms, participants had to score lower than 40 at the French translation of the State-Trait Anxiety Inventory, form Y (STAI-Y; Spielberger et al., 1983) and below 40 at the French adaptation of the Post-Traumatic stress Disorder Checklist Scale (Paul et al., 2013; Weathers et al., 1993). Only participants who met the criteria had access to the rest of the procedure. They were asked to contact the experimenter to book a slot and a second link was sent to them to complete several questionnaires, described in the procedure. All included participants gave their written consent. This project has received a favorable opinion from INSERM's ethics assessment committee (IRB00003888 - Avis 18-544-ter - 25.10.2021) and was conducted in accordance with the ethical standards set out in the Declaration of Helsinki.

2.2. Materials

2.2.1. Motion recording

Motion characteristics were recorded with a VICON motion capture system via Vicon Nexus 2.12 software, using six Vero 2.2 cameras positioned on either side of a 5-meter walking track (volume of capture: length and width = 6m, height = 2m). Thirty-nine sensors, 19 mm-diameter spheres covered with light-reflecting tape, were placed on the subjects, following the standard Plug-in-Gait model, and data were recorded with a 100Hz time resolution. Postural oscillations were recorded with a 1000Hz time resolution using a force plate (AMTI Biomechanic Platform, Model OR6-5; 120 × 60 cm), synchronized with the VICON hardware and positioned at the start of the track. This measure was originally collected as a sanity check measure to replicate the well-known effect of postural freezing, characterized by a reduction in body sway, while standing still in situations perceived as threatening (Bastos et al., 2016; Noordewier et al., 2020; Roelofs et al., 2010). However, subsequent investigations revealed that the recorded forces were inaccurate due to a hardware miscalibration, rendering the data unusable. The walking track was traced on wooden pallets of the same height as the force plate. Instructions for the experiment were displayed on a screen at the end of the walking track, programmed using PsychoPy2 software (Peirce et al., 2019).

2.2.2. Stimuli

Six human screams (3 women) served as sound stimuli and were fear screams selected from Professor Armony's experiment on the perception of emotional sounds (Fecteau et al., 2007). Bluetooth headphones (BOSE) were used to broadcast the cries into the participants' ears and noise reduction helped isolating participants. Screams were emitted at controlled intensity, measured using a sonometer so as not to exceed 70 dB, to avoid any physical disturbance/pain (see Beaurenaut et al., 2020).

2.3. Procedure

Upon arrival, participants were given a note explaining the task in general terms and reminding them that markers would be attached to their bodies to measure variations in gait parameters. After written consent to participate, weight, height and anthropometric data were entered into the Nexus software, to facilitate software’s adaptation of the Plug-In-Gait model to the participant's body. The sensors were placed on the participant's skin or on tight clothes, leaving at least the legs and arms bare.

Secondly, the subject was calibrated in the center of the walking track in a standing position, with feet hip-width apart, torso slightly arched, shoulders at 90° and elbows bent. After capturing the markers in a static position and checking that all the sensors were visible, sensors were labelled, and the “Auto Initialize” pipeline, which calibrated the model based on the given labels, was launched. The participant was then asked to stand on the force plate in a natural, comfortable position. The outline of their feet was marked with chalk on the force plate, so that the subject could return to the same position at the start of each trial. Instructions and explanations of the task were given on a screen positioned at the end of the track and facing the subject. The experiment began with a familiarization phase involving three trials per type of block, to ensure that the participant fully understood the task. Once it was clear that the participant understood the instructions, the experiment began.

At the start of each trial (see Fig. 1), participants stood on the force plate wearing headphones. Participants fixated a central cross on a screen on the wall at the end of the walk path. Once ready, they had to say it aloud and the trial then began with a 5-second countdown on screen, after which the participants had to walk as they wish until the end of the track, marked by two strips of tape, and finally turn and go back to the initial position. The walking period was announced by the word "walk" on the screen and 3D-motion parameters were recorded for 5 seconds after start, which allowed all participants to reach the strips at the end of the track. After the 5 seconds, a message appeared on screen to remind participants to go back to their initial position. Once participants returned to the starting point by repositioning their feet in the marks on the floor, a new trial began.

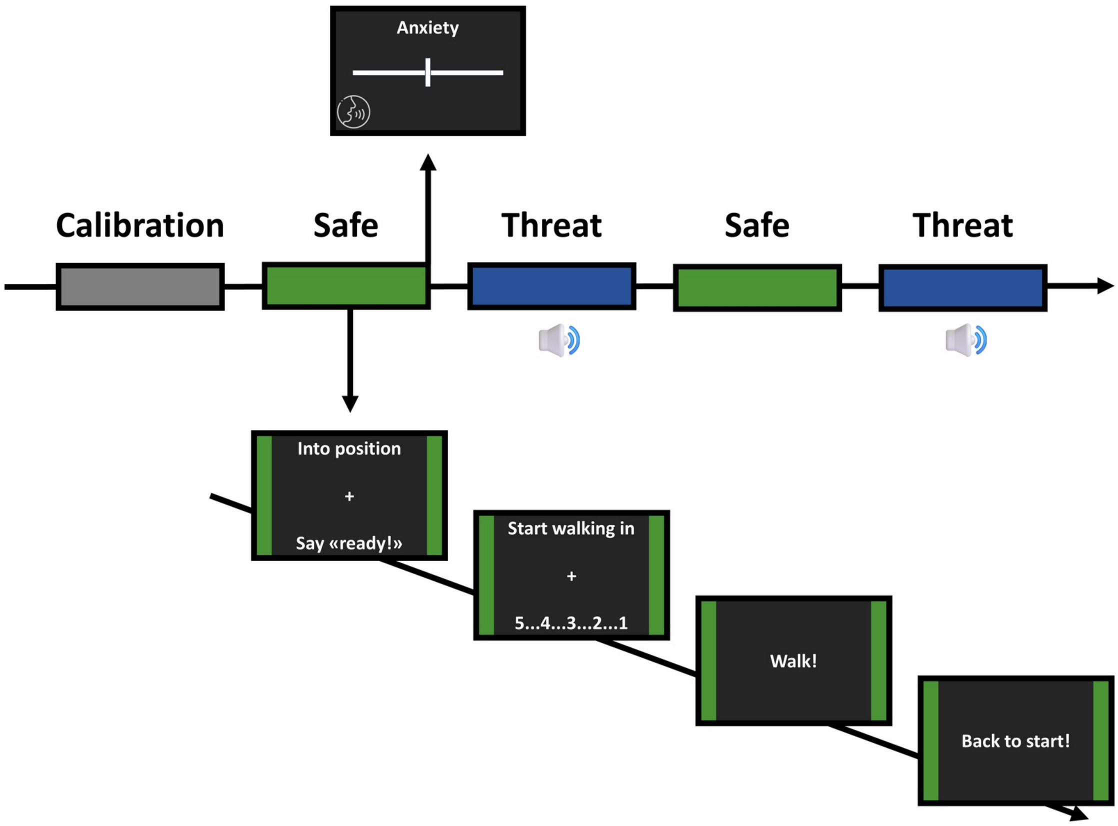

Fig. 1 Experimental design. Temporal organization of the blocks (Top). Participants performed the task in the threat or safe condition, with the condition of the first block counterbalanced between participants. Blue-colored bands on the screen indicated

Trials were included in four alternating blocks, two “threat” and two “safe” blocks of 10 trials each. As in Beaurenaut and colleagues (2020), participants were informed that they could hear a scream in their headphones at any time during the "threat" blocks. On the contrary, they were informed that they would not hear any screams in the "safe" block. The type of block was announced at the start of each block and was signaled throughout the trials by means of colored strips on either side of the screen (blue stripes indicated threat and green stripes safe). Possible order effects were controlled by counterbalancing whether the first block was threat or safe between participants. During the experimental phase, each participant heard both a female and a male scream, pseudo-randomly selected from the original six. Specifically, for each threat block, one scream was delivered on random trials one or three seconds after the "walk" signal. The order of the two times of scream delivery (1 or 3 s) was counterbalanced across subjects. A different scream was presented to illustrate threat blocks in the training phase. At the end of the block, a rating scale was displayed asking participants to self-assess their level of subjective anxiety during the block, from 1 "relaxed" to 10 "stressed". At the end of the experiment, an analog scale was presented to measure self-assessed screams' anticipation during the threat blocks, ranging from 1 (i.e., never thought about them) to 10 (i.e., thought about them all the time). Participants on average reported an anticipation score of 5.44 (min/max = 2/10), indicating that the procedure was successful in inducing scream anticipation.

2.4. Experimental design and statistical analyses

Our research design is a within-subjects factorial design, with Condition (threat, safe) as the two-modality within-subjects independent variable of interest. All analyses were run on R (R Core Team, 2021) via Rstudio (RStudio Team, 2020) and Matlab (MATLAB, 2021). Scripts and data are publicly available on OSF (see Data, Material and/or Code availability declaration).

2.4.1. Self-reported anxiety

It has been previously reported that subjective anxiety induced by threat-of-scream can reduce over time throughout the task (Beaurenaut et al., 2020), therefore we checked for the stability of the anxiety throughout the first and second part of the task (i.e., the first and second threat/safe blocks). We run a repeated-measure ANOVA on the self-reported anxiety scores, with Condition and Task Half (first, second) as predictors. As one subject's session terminated ahead of time, we could not recuperate the rating for the last block ("safe"). Thus, we assigned a score of 1 to it, consistently with the score assigned by the subject to the to the training's safe block as well as to the first safe block. As anxiety did not reduce over time (see Results), the Task Half variable was not included in the following analyses.

2.4.2. Motion data treatment and analysis

2.4.2.1. Data extraction and treatment

3D-motion data were extracted to Matlab, using the Nexus-Matlab Integration. For each trial the “Reconstruct and Label” as well as the “Auto Intelligent Gap Fill” pipelines were run to identify and label markers and to fill gaps in trajectories. Trajectories for the 39 markers on the x, y and z axes were extracted for each of the forty ten-seconds trial and stored in a matrix for each participant. Three trials for three different subjects were excluded, two because of participant false start after the “walk” signal, and one because the participant stop as a marker detached and fall. Then, for each good trial, the first four heel strikes (three for two subjects due to marker data loss toward the end of the walk path) after the first step of the starting leg were extracted to identify the three first strides. More specifically, a gait cycle (stride) was defined as going from one heel strike, i.e. the minimum in the z-coordinates of the HEE marker of the starting leg, to the next (see Fig. 2A). For each participant, a linear regression was fitted to the coordinates on the z-axis in correspondence to each heel strike, to identify possible deviations from the horizontal axis in the calibration. Based on the obtained angle, trajectories were adjusted via a matrix rotation on the x-axis to correct for possible slight z-axis misalignment. The same procedure was run on the x-coordinates of the “C7” marker of the Plug-in-Gait model, to correct x-axis calibration, via matrix rotation on the z-axis. Finally, “threat” trials in which a scream was presented were excluded from the analyses, not to contaminate the gait results with the response to the scream. For one subject, due to software termination ahead of time, we could not determine the trials where a scream was delivered, so we eliminated two random “threat” trials. As a sanity check, comparable results were obtained when the analyses were repeated without the above-mentioned participant.

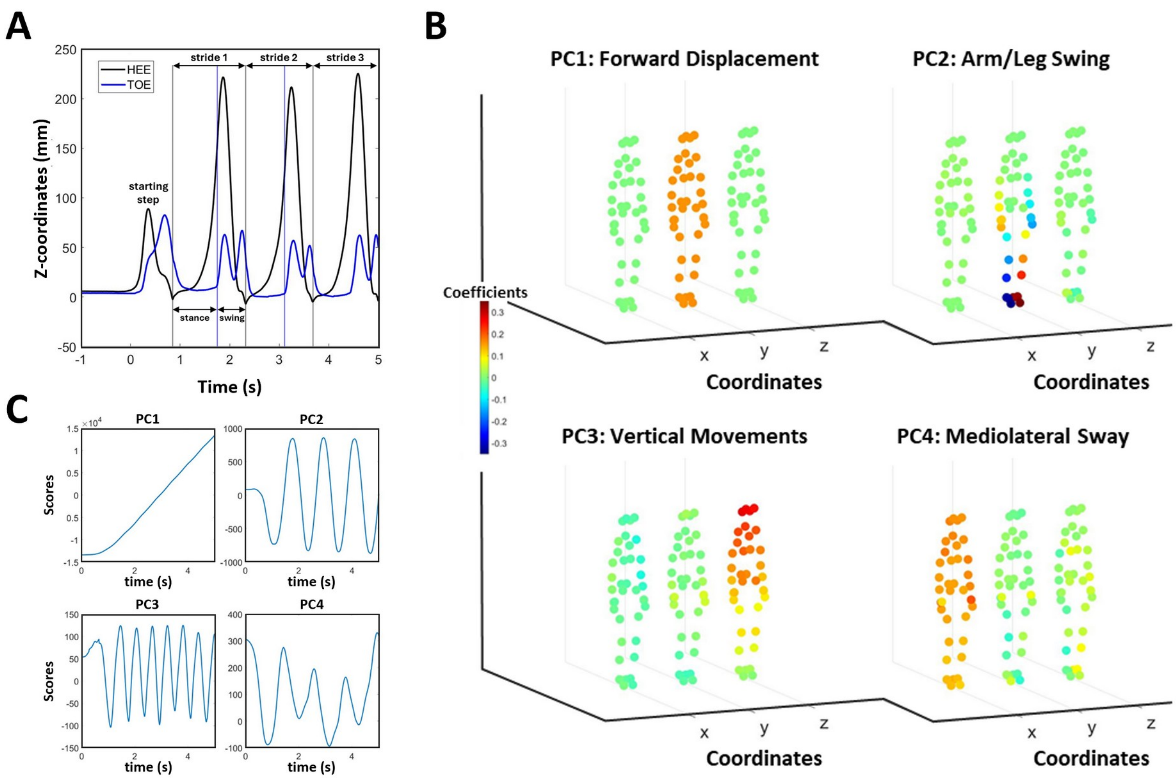

Fig. 2 Motion data treatment. A – Spatiotemporal gait parameters for one trial of a representative participant (HEE and TOE being respectively the heel and toe markers of the Plug-In-Gait model). **B –** PCA coefficients for each component, forward displacement (PC1), arm/leg swing (PC2), upper body vertical movements (PC3) and mediolateral sway (PC4), in each spatial dimension. **C -** Example of component scores in time for one trial of a representative participant

2.4.2.2. Gait cycle

We extracted stride length, duration and speed, as well as the percentage of the stance phase for each of the three launched strides per trial and averaged them. The stance phase was defined as going from the previous heel strike to the next toe-off, identified as the raising point of the TOE marker of the Plug-in-Gait model (see Fig. 2A). We then calculated subject averages and run paired nonparametric comparisons (Wilcoxon test) to account for the effect of Condition on each variable.

2.4.2.3. Analysis of “gait primitives” via PCA

Aside from traditional gait parameters, we ran further analyses to take advantage of the full complexity of the 3D motion VICON data. Gait is cyclic and implies the coherent and interdependent movement of all body parts. For this reason, the complexity of the 3D trajectories of the body markers is redundant and can be reduced using principal component analysis (PCA).

Importantly, each component captures meaningful and stable aspects of gait ("gait primitives") across subjects and trials (Michalak et al., 2009; Troje, 2002). This method allowed to reduce the complexity of the motion data to low-dimensional representations that can be easily interpreted in terms of their biomechanical meaning. The Fourier decomposition on oscillatory PC scores also provides efficient and linear decompositions of the periodic motion data. We chose this method for our exploratory analyses, beyond our main hypothesis on stride speed, because it allows covering a maximum of variance with a minimum of components, providing a holistic characterization of body kinematics when contrasting anxious vs. non-anxious states, as it has been done in the past for example to distinguish depressed vs. non-depressed states (e.g., Michalak et al., 2009). We therefore concatenated trajectory data from the 39 markers position in the three dimensions (x,y,z; 117 lines), by the 5 seconds following the "walk" signal for each trial and subject in a common matrix. On this matrix we run the "PCA" function in Matlab using the nonlinear Alternating least squares (ALS) algorithm, which deals with missing values. We extracted the first four components in terms of variance explained, because it has been previously shown that this is sufficient to capture almost all of the variance in the motion data during walking (Troje, 2002). The selected components captured, respectively, the forward displacement (PC1; variance explained 99.47%), arm/leg swing (PC2; variance explained 0.39%), upper body vertical movements (PC3; variance explained 0.08%) and mediolateral sway (PC4 ; variance explained 0.06%. See Fig. 2 and click here for an animation of the components).

To analyze the first component, we compared the scores obtained in trials from each Condition, using a cluster-based permutation approach (Oostenveld et al., 2011). First, we computed paired t-tests between scores at each time point. Second, clusters were defined as at least ten contiguous points (100ms) where the t-test p-value was < .05. The data within each condition were permuted 50000 times with data from the other condition for half of participants, randomly selected. For each permutation, clusters of data were identified with the same criteria and a 'null' distribution was generated with the sum of the t-values (t_{mass}) within each detected cluster. Finally, the t-masses for each observed cluster were compared to this null distribution to obtain non-parametric cluster-corrected p-values (p_{corr}) as the proportion of the absolute value of the null distribution that exceeded the absolute value of the observed t-mass. Clusters with a $p_{corr}<.05$ were considered significant.

To analyze the second, third and fourth components, we applied Fast Fourier Transformation (FFT) to determine the peak frequency, as well as its amplitude and phase, of the oscillations in time. Before applying FFT, we inversed the phase of the trials where the starting leg was the left one for the second and fourth component, for which the phase depended on the starting leg. Components' peak frequency, amplitude and phase were compared between Conditions via nonparametric paired Wilcoxon test.

2.4.2.4. Correlations

To take into account inter-individual variability in anxiety induction, we run correlation between changes in anxiety between safe and threat blocks and changes in gait parameters and PCs. Therefore, difference scores were calculated between threat and safe conditions for the subjective anxiety and correlated with difference scores for all the motion measures, using Spearman's nonparametric correlation coefficients.

3. Results

3.1. Self-reported anxiety

The repeated-measures ANOVA yielded a main effect of Condition, $F_{(1, 96)} = 38.34$, $p < 0.001$, $\eta^2_p = 0.29$, but no main effect of Task Half, $F_{(1, 96)} = 0.72$, $p = 0.397$, $\eta^2_p = 0.01$, nor Condition by Task Half interaction, $F_{(1, 96)} = 0.13$, $p = 0.716$, $\eta^2_p = 0.00$. As the ANOVA normality assumption was not met, we tested the effect of Condition (i.e., the difference in anxiety scores for Threat and Safe trials throughout the task) using a nonparametric Wilcoxon test against zero. The effect of Condition was significant and large ($CI_{95} = [0.75-1.5]$, $p < .001$, $r= 0.86$. For descriptives, see Table 1), indicating greater anxiety scores in threat vs. safe blocks.

Table 1. Subjective anxiety ratings

Task half	**first**		**second**	
Condition	**safe**	**threat**	**safe**	**threat**
Mean (SD)	1.36 (0.57)	2.32 (1.14)	1.16 (0.37)	2.24 (0.97)
Median (IQR)	1.00 (1.00, 2.00)	2.00 (2.00, 3.00)	1.00 (1.00, 1.00)	2.00 (1.00, 3.00)
Range	1.00, 3.00	1.00, 5.00	1.00, 2.00	1.00, 4.00

SD = standard deviation; IQR = interquartile range

3.2. Motion data

3.2.1. Gait cycle

Results from Wilcoxon paired tests showed that stride time significantly decreased in Threat vs. Safe blocks ($p = 0.024$, $r = 0.45$) and the percentage of the stance phase duration showed a tendency toward decrease ($p = 0.075$, $r = 0.36$). No effect of Condition has been observed on stride length and speed (*ps* > 0.12. For descriptives see Table 2).

Table 2. Gait parameters as a function of Condition (safe vs. threat)

Condition	safe	threat	p[1]	r
Stride length (m)			0.3	0.2
Mean (SD)	1.274 (0.094)	1.283 (0.095)		
Median (IQR)	1.268 (1.223, 1.317)	1.265 (1.244, 1.315)		
Range	1.119, 1.520	1.121, 1.557		
Stride time (s)			0.024	0.45
Mean (SD)	1.13 (0.09)	1.11 (0.09)		
Median (IQR)	1.14 (1.06, 1.16)	1.09 (1.06, 1.17)		
Range	0.99, 1.41	0.96, 1.44		
Stride speed (m/s)			0.12	0.32
Mean (SD)	1.139 (0.107)	1.168 (0.12)		
Median (IQR)	1.141 (1.071, 1.228)	1.155 (1.069, 1.254)		
Range	0.962, 1.320	0.935, 1.447		
Stance phase duration (%)			0.075	0.36
Mean (SD)	57.64 (1.81)	57.18 (2.03)		
Median (IQR)	57.64 (56.73, 59.33)	57.35 (56.23, 58.66)		
Range	52.42, 60.05	51.46, 60.64		

SD = standard deviation; IQR = interquartile range; p = p-value ; r = effect size

[1] Wilcoxon signed rank exact test

3.2.2. PCA: Gait primitives

3.2.2.1. PC1: Forward displacement

A significant cluster emerged from 2.15 to 3.83 s after trial start (t_{mass} = 747.07, p = 0.036), indicating faster forward displacement for threat vs. safe trials (see Fig. 3).

3.2.2.2. PC2 to PC4: Arm/leg swing, vertical movement and mediolateral sway

As reported in Table 3, threat trials were significantly associated with higher peak frequency for vertical movement (PC3: p = 0.042, r = 0.41) while this association was marginal for arm/leg swing (PC2: p = 0.075, r =

0.36) and mediolateral sway (PC4: $p = 0.067$, $r = 0.37$). Additionally, threat trials were also associated with lower phase for arm/leg swing (PC2: $p = 0.001$, $r = 0.61$) and show a trend for vertical movements (PC3: $p = 0.063$, $r = 0.37$). No effect of condition was found on oscillation amplitude (all *ps* > 0.17).

Table 3. PCA components and oscillation parameters as a function of Condition (threat vs. safe)

	PC2				PC3				PC4			
	Arm/leg swing				Vertical movement				Mediolateral sway			
Condition	**safe**	**threat**	**p[1]**	**r**	**safe**	**threat**	**p[1]**	**r**	**safe**	**threat**	**p[1]**	**r**
Peak frequency (Hz)			0.075	0.36			0.042	0.41			0.067	0.37
Mean (SD)	0.90 (0.06)	0.92 (0.07)			1.79 (0.13)	1.82 (0.14)			0.92 (0.07)	0.93 (0.07)		
Median (IQR)	0.89 (0.86, 0.94)	0.92 (0.86, 0.94)			1.78 (1.72, 1.87)	1.83 (1.72, 1.90)			0.90 (0.88, 0.97)	0.94 (0.88, 0.97)		
Range	0.73, 1.02	0.73, 1.04			1.43, 2.07	1.41, 2.11			0.75, 1.03	0.75, 1.05		
Amplitude (mm)			0.12	0.31			0.4	0.17			0.2	0.24
Mean (SD)	423 (37)	427 (41)			38 (9)	38 (9)			59 (9)	60 (8)		
Median (IQR)	423 (406, 441)	426 (405, 453)			37 (31, 45)	37 (32, 44)			61 (55, 66)	59 (56, 65)		
Range	348, 481	335, 489			21, 55	22, 61			42, 73	43, 73		
Phase (rad)			0.001	0.61			0.063	0.37			0.4	0.19
Mean (SD)	-1.25 (0.78)	-0.94 (0.97)			-0.36 (0.60)	-0.12 (0.64)			-0.45 (0.65)	-0.37 (0.74)		
Median (IQR)	-1.35 (-1.80, -0.95)	-1.21 (-1.64, -0.34)			-0.33 (-0.78, -0.10)	-0.14 (-0.65, 0.32)			-0.31 (-0.82, -0.06)	-0.32 (-1.00, 0.07)		
Range	-2.31, 1.24	-2.09, 2.16			-1.26, 1.11	-1.19, 1.30			-2.04, 0.69	-1.56, 1.38		

SD = standard deviation; IQR = interquartile range, p = p-value, r = effect size

[1] Wilcoxon signed rank exact test

3.2.3. Correlations

3.2.3.1. Subjective anxiety and gait parameters

Changes in subjective anxiety strongly correlated with increased stride length (R = 0.4, p = 0.05) and reduced stride time (p = 0.006, R = -0.54), therefore with increased speed (R= 0.48, p = 0.016), as well as decreased stance phase duration (R = -0.37, p = 0.067; See Fig. 3).

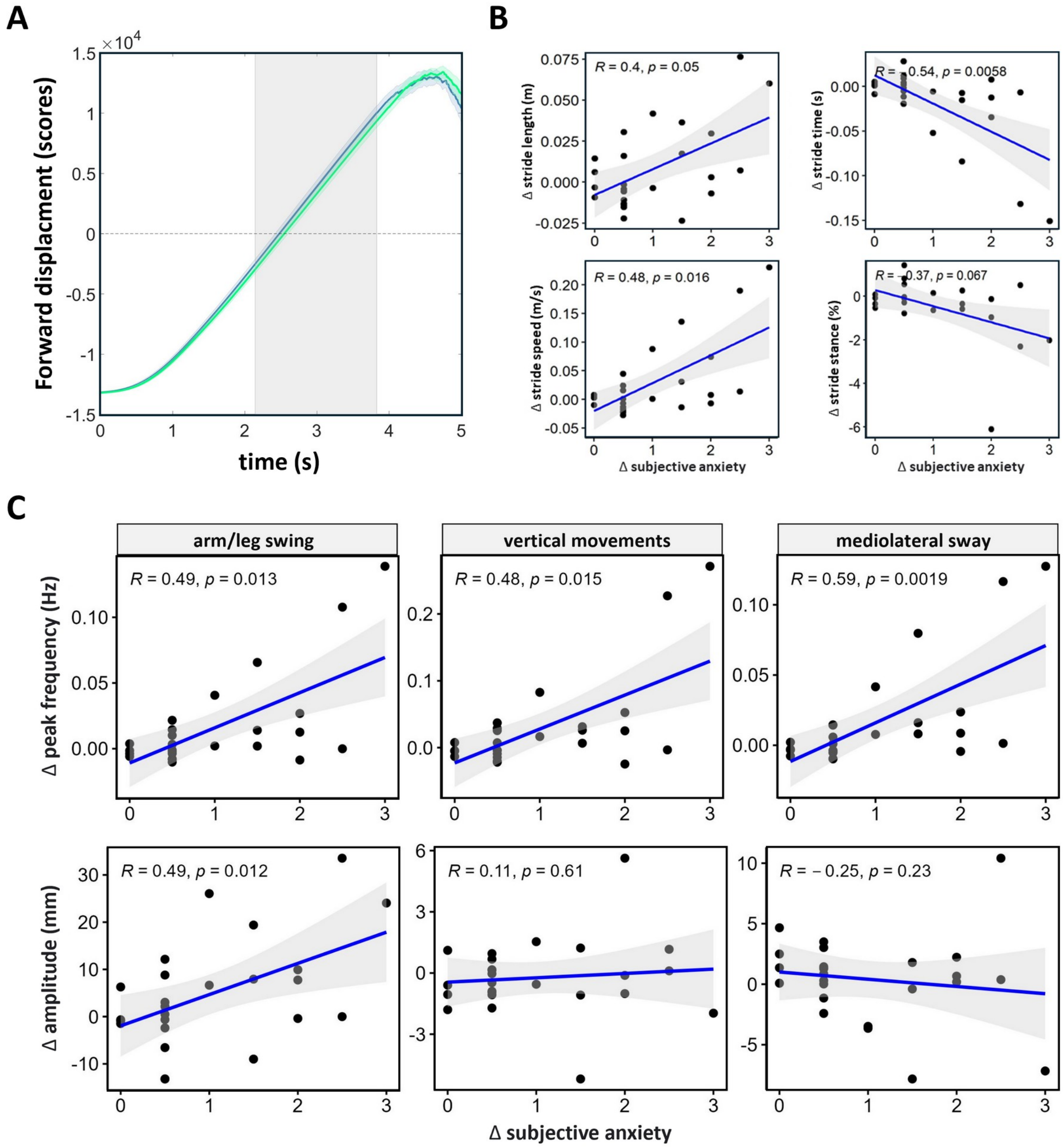

Fig. 3 **Gait results. A** - Forward Displacement in threat (blue) and safe (green) trials. Significant clusters revealing a difference between the two conditions are highlighted in grey. **B -** Correlation between changes in reported anxiety levels and gait parameters in threat versus safe trials. **C -** Correlation between changes in reported anxiety levels and changes in arm/leg swing (Left), vertical movements (Middle) and mediolateral sway (Right) principal component parameters (Top: peak frequency, Bottom: amplitude)

3.2.3.2. Subjective anxiety and PCs (2 to 4)

Changes in subjective anxiety strongly correlated with increased peak frequency for all components (all Rs > 0.47, all *ps* < 0.015) and with increased amplitude of the arm/leg swing (R = 0.49, p = 0.012, see Fig. 3). Changes in subjective anxiety did not correlate significantly with phase for any component (arm/leg swing: R = .17, vertical movements: R = .31, mediolateral sway, R = .24; all *ps* > .13).

3.2.4. Mediation analysis

Finally, we set out to clarify whether the significant correlations between the changes in subjective anxiety and the other spatiotemporal parameters (stride length and time), as well as the amplitude of the arm/leg swing, was mediated by the increased stride speed. Mediation analyses were performed using the "mediation" R package (Tingley et al., 2014) to extract the indirect (average causal mediation effects - ACME) and direct (average direct effects - ADE) effects. The significance of the direct and indirect paths was assessed by nonparametric bootstrapping (method percentile, two-sided, 10000 simulations). In our regression models the change in stride speed was the mediator variable, and the change in subjective anxiety was the independent variable. The dependent variable, in three different models, was the change from safe to threat in stride length, stride time, and arm/leg swing (PC2) amplitude, respectively.

Table 4. Mediation analyses. How stride speed mediates the significant effects of anxiety on gait parameters.

Dependent variable	Stride speed effect (b)	ACME	ADE	Total effect (c)	Prop. Mediated
Stride length (m)	0.35	0.018	-0.00	0.016	1.16
CI (95%)	[0.29, 0.42]	[0.00, 0.03]	[-0.01, 0.00]	[0.00, 0.03]	[0.79, 2.11]
p-value	<0.001	0.002	0.394	0.018	0.017
Stride time (s)	-0.63	0.02	-0.001	0.02	1.08
CI (95%)	[-0.68, -0.58]	[0.00, 0.03]	[-0.007,0.00]	[0.00, 0.03]	[0.78, 1.85]

Table 4. Mediation analyses. How stride speed mediates the significant effects of anxiety on gait parameters.

Dependent variable	Stride speed effect (b)	ACME	ADE	Total effect (c)	Prop. Mediated
p-value	<0.001	0.001	0.564	0.013	0.013
Arm/leg swing amplitude (mm)	137.06	6.68	-0.07	6.61	1.01
CI (95%)	[90.7,183.4]	[1.51, 12.49]	[-4.15, 4.35]	[1.34, 11.24]	[0.40, 2.05]
p-value	<0.001	0.002	0.956	0.011	0.013

ACME = average causal mediation effects; ADE = average direct effects; CI (95%) = Confidence interval at 95%

First, change in stride speed was significantly and positively associated with changes in all considered dependent variables (see Table 4 for statistics). Second, all the mediation analyses revealed a significant total effect, accompanied by a significant indirect effect, while the direct effect was always non-significant. Overall, these results indicated that the effect of anxiety on stride length, stride time and arm/leg swing amplitude was fully mediated by increases in gait speed.

4. Discussion

It is undebated that threatening situations demand priority over motor control, to select the most appropriate behavioral policy (Mennella & Grèzes, 2023). However, such policies, as well as the accompanied subjective feelings, might change as a function of the perceived spatial and/or temporal proximity of threat (Fanselow & Lester, 1988; Mobbs et al., 2020). While fear responses after encountering a well-identified (but not imminent) threat generally lead to passive defensive responses, such as postural freezing or reduced gait speed, the effect on gait of anxiety for undetected and unpredictable threats is less clear. The present study set out to investigate for the first time the effects of anxiety generated by the anticipation of an auditory social threat on gait. Our results clearly indicated that anxiety of unpredictable and unlocalized threats is associated with motion invigoration during gait.

Indeed, the main result of the present study is that changes in anxiety from safe to threat blocks correlated with increased gait speed. This was evident both by results from standard analyses on stride speed extracted from heel and toe trajectories and from the PCA analysis. We showed greater forward displacement (PC1) in threat vs. safe conditions, from around 2 seconds after the gait starting signal, as well as a correlation of anxiety changes with changes in the peak frequency of the cyclic components (i.e., arm/leg swing (PC2), upper body vertical movements (PC3) and mediolateral sway (PC4)). From a biomechanical point of view, the rest of our findings aligned with the existing literature on the effects of speed on gait parameters. Notably, an increase in gait speed is typically accompanied by both an increase in stride length and a decrease in stride time, as well as by a reduction in the stance relative to the swing phase (e.g., Ciprandi et al., 2017; Wu et al., 2019; for a review, see Fukuchi et al., 2019). Here we showed that changes in anxiety from safe to threat blocks correlated with changes in the three parameters, in line with the abovementioned results (although the reduction in stance phase duration was marginally significant). Finally, our mediation analyses revealed that the effects of changes in anxiety on gait length and time were fully mediated by changes in stride speed.

Furthermore, during gait at customary velocity, the swing of the upper limbs has similar direction to the movement of the contralateral lower limb and opposite to the ipsilateral lower limb (e.g., Donker et al., 2001), which is well-captured by the coefficients of our second component (see Fig. 2). It has been shown that increased speed enhances the amplitude of the arm swing, presumably because the greater excursion of the lower limbs and pelvis during faster walking needs to be counterbalanced by the more prominent arm swing, to maintain balance (Murray et al., 1967; but see also e.g., Plate et al., 2015; Kubo et al., 2004). Our results align with these findings, showing that increases in anxiety induce more ample arm and leg swings on the anteroposterior axis. Our mediation analyses clarified that the effects of anxiety on arm/leg swing are fully mediated by the anxiety-related increase in stride speed. Of note, the present results do not allow testing whether anxiety has effects on gait parameters beyond the increase in stride speed. This can be accounted for in future studies, for instance by comparing threat blocks with non-threatening conditions imposing comparable speed (e.g., Hicheur et al., 2013).

Our hypothesis concerning the effect of anxiety on gait was bidirectional, as the previous literature supported both motor inhibition (i.e., speed reduction/freezing) and invigoration (i.e., speed increase/flight). Accordingly, from a neural point of view, it is well known that rhythmic locomotor patterns are generated by networks in the spinal cord and that planning of locomotion takes place in supraspinal structures, such as the basal ganglia and premotor cortices (Takakusaki, 2013, 2017). Nonetheless, immediate control of locomotion, including the capacity to regulate locomotion initiation and speed, reside in the brainstem (Leiras et al., 2022). In this regard, animal studies identified the mesencephalic locomotor region (MLR), which includes both the cuneiform nucleus (CnF) and the pedunculopontine nucleus (PPN; Dautan et al., 2021). Recent studies in mice, using optogenetic activation, have shown that activation of excitatory glutamatergic neurons in both CnF and in caudal PPN is related to locomotion speed (for a review, see Leiras et al., 2022). In more details, slow exploratory locomotion seems to be supported by caudal PPN glutamatergic neurons, while higher-speed locomotion, typical of flight or escape responses, needs the activation of CnF glutamatergic excitatory neurons (Caggiano et al., 2018). Notably, the CnF has extended bidirectional connections with the adjacent periaqueductal gray (PAG) and with the superior colliculus, both associated with innate defensive behaviors, as well as with the hypothalamus (Bindi et al., 2023; Caggiano et al., 2018). Intriguingly, the CnF receives projections from both the central nucleus of the amygdala (AMY) and the bed nucleus of the stria terminalis (BNST; Bindi et al., 2023), which have been respectively implicated in defensive responding upon acute danger or during uncertain threat anticipation (Davis, 2006; Fanselow, 1994; Klumpers et al., 2017). This evidence emphasizes the role of gait analysis in the investigation of the effects of threat on behavior. Here, the present results suggest that anxiety of an unpredictable and unlocalizable threat while walking promotes innate active defensive responses (i.e., flight), presumably thanks to the connections between the CnF and the PAG, and through inputs from the AMY and/or the BNST. This interpretation remains speculative at present and ought to be tested in future studies, together with the precise conditions that determine the prevalence of passive vs. active defensive responses during gait.

The abovementioned interpretation of the present results is consistent with the notion that when an individual's actions have little or no effect on the future positive or negative outcome, like in the present experimental context, innate or automatic behavioral strategies prevail, at the detriment of more instrumental, goal-directed, ones (Dorfman & Gershman, 2019). Nonetheless, one could argue on the contrary that the observed increase in stride speed during threat blocks is part of an instrumental defensive strategy (i.e., avoidance). Indeed, even though the scream could be delivered in theory at any moment during the block (i.e., there was no safe zone during the block), the trial succession was somehow self-paced. Theoretically, a great increase in back-and-forth gait speed could result in shorter trial duration, thus shorter threat vs. safe blocks overall, a potentially efficient strategy to reduce exposure to threat. Nonetheless, our exploratory analysis disconfirmed this intuition, as the threat blocks did not last significantly less than the safe ones (in seconds, $\text{Median(IQR)}_{\text{threat}}$ = 242.6(37.9); $\text{Median(IQR)}_{\text{safe}}$ = 247.0(26.6), p_{Wilc} = .715) and the correlation between changes in anxiety from safe to threat and changes in duration was also non-significant (Spearman's ρ = -.28, p = .177). This can be explained by the fact that, between each trial, participants had no temporal constraint to place their feet on the initial starting point, find a comfortable position, say that they were ready and wait for the experimenter to launch the next trial. Overall, this likely increased variability in block duration and explain why the increase in gait speed under threat anticipation did not result in a significant reduction in block duration, providing no evident instrumental advantage. Future studies ought to control for block duration in order to prevent instrumental strategies, or, on the other hand, actively manipulate it, for instance via explicit instructions to participants, in order to test for the implementation of instrumental defensive strategies.

Interestingly, the present findings regarding the effect of anxiety on gait are the opposite of what has been observed using other anxiety-inducing paradigms that have investigated height-induced postural threat, often by having participants walk on virtual (e.g., Raffegeau et al., 2024) or real (e.g., Ellmers et al., 2020) elevated platforms. Collectively, these studies reported that anxiety related to the risk of falling induced cautious slow walking, with reduced stride length and increased double-support phase (Tersteeg et al., 2012). A recent study confirmed these findings and further showed that these changes were more pronounced with high trait anxiety (Norouzian et al., 2024). These consistent findings clearly show that, when anxiety directly affects movement execution under conditions of precarious equilibrium, it induces a cautious walking strategy to avoid falling. Interestingly, the present study supports the idea that when threat anticipation is unrelated to motor execution, motor invigoration is observed, suggesting that the effects of the threat of falling may not generalize to other and more common forms of anxiety (Hall et al., 2023). While the present findings need to be replicated in future studies, they support the idea that the balance between motor invigoration and inhibition is highly dependent on the existing environmental constraints and opportunities for action.

The present study comes with some limitations. First, the magnitude of the anxiety induction in the present study was quite low on average. Nevertheless, previous studies in the literature using the threat-of-scream procedure have often found similar levels of anxiety modulation (i.e. an increase of 1 to 2 points on a scale of 10 between threat and safe). Importantly, such increases in subjective anxiety have been reported to correlate with increases in sympathetic activity (i.e., skin conductance level; Beaurenaut et al., 2020, 2021) and to be accompanied by increases in threat reactions (i.e., startle reflex amplitude; Patel et al., 2017). Although we were unable to obtain such complementary measures of anxiety during walking, here we add to the literature that changes in subjective anxiety correlate with changes in gait parameters, strengthening the interpretation that our results are driven by anxiety. Nevertheless, the present results should be interpreted in light of the low level of anxiety induced, and future studies should generalize them to more anxiogenic contexts.

Second, our walking track was relatively short (5 meters). As the transition from gait initiation to steady state gait at habitual velocity is typically achieved after one (Breniere & Do, 1986) to three steps (e.g., Kang et al., 2018; Muir et al., 2014), our setting and analyses did not allow a strong dissociation between gait initiation and steady state gait. Some elements support the idea that the present results are not limited to gait initiation. First, the effect of condition on forward displacement (PC1) started 2.15 seconds after the start signal, once the participants had presumably initiated their gait. Consistently, a supplementary analysis showed that the correlation between changes in anxiety and stride speed remained significant when considering only the last measured stride ($r = .4$, $p = .049$). Nonetheless, and beyond the previous considerations, the length of the walking track has an impact on gait, and thus the present results should be replicated using real-life and/or longer walking distance, to assess their generalizability.

Third, our sample size calculation was initially based on a power analysis on the effect of the Threat-of-Scream procedure on subjective anxiety ratings (Beaurenaut et al., 2020), but not on the expected changes in gait parameters. It is noteworthy that our main result, the correlation between changes in subjective anxiety and gait speed had a moderate to strong effect size (.48), and the post hoc power calculation indicated a power of .75, close to the .8 standard. Nevertheless, our analyses may be underpowered to detect more subtle effects or to account for interindividual variability in affective or personality traits on the results. It is well known, for instance, that affective traits, such as depression, correlate with specific posture and gait changes, namely reduced gait speed, reduced stride length, increased double limb support and reduced vertical up-and-down movements (Adolph et al., 2021; Belvederi Murri et al., 2020; Michalak et al., 2009). On the contrary, the effects of pathological anxiety on gait are much less investigated (Belvederi Murri et al., 2020). The present findings relating anxiety to invigorated locomotion might give insight on psychomotor agitation during anxiety episodes, which often include erratic and purposeless motion. This potential dissociation between gait characteristics related to depression and anxiety might be of interest to better discriminate between these often-comorbid conditions, through objective assessment of gait. Second, motor control has neural determinants, as well as accompanying physiological changes, which have not been investigated in the present study. These measures could be important to discriminate between the defensive mode during anxiety and fear in response to threat, as suggested by previous studies (e.g., Klumpers et al., 2017).

In conclusion, we showed here for the first time that anxiety of an acoustic social threat induces motor invigoration during walking, in the form of increased gait speed. These results could be a starting point for future fundamental research on the dissociation of fear and anxiety defensive modes in humans, as well as for clinical understanding of pathological anxiety.

5. Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Authorship contribution statement

Conceptualization: RM, MB; Methodology: RM, CF, SVM, MB; Validation: RM, MB; Formal Analysis: RM; Investigation: RM, SB; Data Curation: RM; Writing – Original Draft: RM; Writing – Review & Editing: RM, SB, CF, SVM, MB; Visualization: RM, MB; Supervision: RM; Project Administration: RM.

Ethics approval and consent

This project has received a favorable opinion from INSERM's ethics assessment committee (IRB00003888 - Avis 18-544-ter - 25.10.2021) and was conducted in accordance with the ethical standards set out in the Declaration of Helsinki.

Data, Material and/or Code availability

All data and code are publicly available at this OSF link: https://osf.io/ru2vw/.

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