Stress
The International Journal on the Biology of Stress

ISSN: 1025-3890 (Print) 1607-8888 (Online) Journal homepage: informahealthcare.com/journals/ists20

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To cite this article: Changiz Mohiyeddini & Stuart Semple (2013) Displacement behaviour regulates the experience of stress in men, Stress, 16:2, 163-171, DOI: 10.3109/10253890.2012.707709

To link to this article: https://doi.org/10.3109/10253890.2012.707709

Published online: 01 Oct 2012.

Stress, March 2013; 16(2): 163–171

ISSN 1025-3890 print/ISSN 1607-8888 online
DOI: 10.3109/10253890.2012.707709

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Displacement behaviour regulates the experience of stress in men

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(*Received 8 May 2012; revised 26 June 2012; accepted 26 June 2012*)

Abstract
Behavioural coping strategies represent a key means by which people regulate their stress levels. Attention has recently focused on the potential role in coping of 'displacement behaviour' – activities such as scratching, lip biting and face touching. Increased levels of displacement behaviour are associated with feelings of anxiety and stress; however, the extent to which displacement behaviour, as a short-term behavioural response to emotionally challenging stimuli, influences the subsequent experience of stress remains poorly understood. The aim of this study was to investigate the potential role of displacement behaviour in coping with stress. In a study population of 42 healthy adult men (mean age = 28.09 years, SD = 7.98), we quantified displacement behaviour during a Trier Social Stress Test (TSST), and used self-report questionnaires to assess trait and state anxiety before the TSST, and the experience of stress afterwards. We predicted displacement behaviour would diminish the negative impact of the stressful situation, and hence be associated with lower post-TSST stress levels. Furthermore, we predicted displacement behaviour would mediate the link between state and trait anxiety on the one hand and the experience of stress on the other. Results showed the rate of displacement behaviour was positively correlated with state anxiety but unrelated to trait anxiety, and negatively correlated with the self-reported experience of stress, in agreement with the idea that displacement behaviour has a crucial impact on regulation of stress. Moreover, serial mediation analyses using a bias-corrected bootstrapping approach indicated displacement behaviour mediated the relationship between state anxiety and the experience of stress, and that state anxiety and displacement behaviour – in combination, respectively – mediated the link between trait anxiety and experience of stress. These results shed important new light on the function of displacement behaviour, and highlight promising new avenues for research into emotional expression and stress regulation.

Keywords: *Behaviour, displacement, mediation analysis, state anxiety, stress, trait anxiety*

Introduction

Stress is an omnipresent phenomenon in human life that refers to 'any event in which environmental demands, internal demands, or both, tax or exceed the adaptive resources of an individual, social system, or tissue system' (Monat and Lazarus 1991, p. 3). The negative impacts of prolonged stress on human physical and psychological well-being are significant and broad ranging (Diener 1984; Diener et al. 1999; Miller et al. 2002; Lantz et al. 2005; Bekkouche et al. 2011; Braveman et al. 2011; Contrada 2011). Understanding the way in which stress can be regulated therefore represents a fundamental goal for scientists and practitioners working in a wide range of fields including biology, psychology, psychiatry and medicine (Fleshner et al. 2011; Tamashiro et al. 2011; Opacka-Juffry and Mohiyeddini 2012). Behavioural coping strategies represent a key means by which people can regulate their stress levels (Snyder 2001). Studies of coping behaviour have typically focused on affiliative (Taylor et al. 2000) or aggressive (Marcus-Newhall et al. 2000) responses to stressful situations. Recently, however, attention has started to focus on the potential role in coping of 'displacement behaviour' – a group of activities such as scratching, lip biting and face touching, which have no apparent relevance to the situation in which they occur (Maestripieri et al. 1992; Troisi 2002; Pico-Alfonso et al. 2007; Higham et al. 2009).

A number of studies of both human and non-human primates have provided evidence that displacement

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behaviour is related to negative affective states, and thus provides a good external indication of such states (Troisi 2002). Ekman and Friesen (1972), for example, found that rates of self-contact actions correlated positively with ratings of anxiety among healthy adults exposed to a social stressor (attempting to deceive another person). Working with a group of schizophrenic patients, Troisi et al. (1998) found a positive correlation between frequency of displacement behaviour and the anxiety/depression score on the Brief Psychiatric Rating Scale. Schino et al. (1996) found that among captive long-tailed macaques (*Macaca fascicularis*), rates of displacement behaviour increased after administration of anxiety inducing drugs, and decreased when anxiety-relieving drugs were given.

Studies of humans and other mammalian species have provided evidence that the expression of displacement behaviour, far from being solely an external manifestation of emotional state, may represent an adaptive behavioural coping strategy to regulate the physiological stress response (Troisi 2002). Pico-Alfonso et al. (2007), for example, found that women who showed higher rates of displacement behaviour during a stressful interview showed a lower heart rate during the post-stressor recovery period. Working with a strepsirhine primate, the small-eared bushbaby (*Otolemur garnettii*), Watson et al. (1999) found that individuals that exhibited higher rates of displacement behaviour (scent marking) when exposed to a novel environment subsequently showed lower cortisol responses to physical restraint. In mice (*Mus musculus*) and rats (*Rattus norvegicus*), there is evidence that the displacement behaviour of chewing significantly attenuates a range of physiological stress responses (Hennessy and Foy 1987; Berridge et al. 1999; Hori et al. 2004).

Displacement behaviour may therefore play an important role in the regulation of stress levels in humans. At present, however, there are several key gaps in our knowledge. Firstly, while the occurrence of displacement behaviour has been linked to anxiety, the exact nature of the relationship between such behaviour and both trait and state anxiety remains unclear [trait anxiety refers to individual tendency to experience state anxiety, which is the temporary uncomfortable experience that occurs when a person feels threatened by a situation (Spielberger et al. 1983)]. Secondly, while a number of studies have quantified changes in displacement behaviour related to the occurrence of social stressors, to our knowledge none have quantified emotional state before and after such stressors. Thirdly, studies in humans that provide evidence that displacement behaviour represents a behavioural coping strategy have typically relied on physiological indicators of stress rather than self-report, and thus how displacement behaviour may affect the subjective experience of stress remains poorly understood. Finally, previous research has focused only on the direct link between displacement behaviour and stress, and no study has investigated whether displacement behaviour as a coping mechanism may mediate or moderate the link between trait and state anxiety and the experience of stress.

Mediation analysis addresses the question 'how' or 'why' an independent predictor variable can predict an outcome variable (Frazier et al. 2004). Hence, mediation analysis explores the mechanism through which the independent variable is able to influence the dependent variable. In addition, in a serial mediation analysis (Hayes 2009) more than one mediator can be considered simultaneously, allowing mediators to be linked together in a serial causal sequence with the first mediator affecting the second, the second the third, and so forth. Accordingly, introducing state anxiety and displacement behaviour as mediator variables may provide an explanation for the possible link between trait anxiety and experience of stress. In contrast, the moderation function of third variables investigates whether the impact of the predictor (trait anxiety or state anxiety) on the outcome variable (experience of stress) depends on the levels of moderator variables. Put simply, the moderator analysis addresses the question 'for whom' a third variable predicts an outcome variable, and establishes the domains of maximal effectiveness of a predictor in explaining the variance of the dependent variable. Accordingly, establishing displacement behaviour as a moderator addresses whether the impact of state anxiety on experience of stress depends on the level of displacement behaviour (Baron and Kenny 1986).

To address these issues, we investigated the link between displacement behaviour, trait anxiety, state anxiety and the experience of stress in a healthy population of male adults exposed to social stress. We hypothesised firstly that:

H1a: Displacement behaviour will be positively correlated with state anxiety, reflecting that displacement behaviour is a response to short-term elevations in anxiety levels.

H1b: Displacement behaviour will be negatively correlated with experience of stress, reflecting the coping function of displacement behaviour.

We then examined a serial mediation model (Figure 1) in which we hypothesised that:

H2a: The link between trait anxiety and displacement behaviour will be partially mediated by state anxiety (indirect effect of trait anxiety on displacement behaviour; path a_1a_3 in Figure 1).

Next, examining the same model and considering the potential for displacement behaviour to mediate the experience of stress, we also hypothesised that:

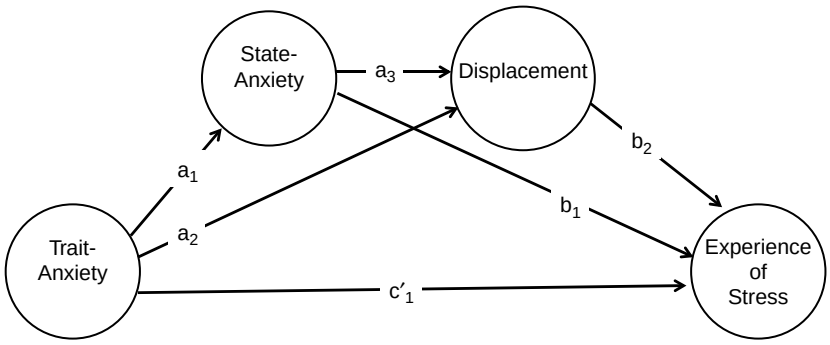

Figure 1. Theoretical serial mediation model with state anxiety and displacement behaviour as mediators between trait anxiety and experience of stress. This figure indicates the hypothesised (H) path by which the link between trait anxiety and displacement behaviour could be partially mediated by state anxiety (path a_1a_3 – **H2a**), hypothesised paths by which the link between trait anxiety and the experience of stress could be partially mediated by displacement behaviour (path a_2b_2 – **H2b**) or state anxiety (path a_1b_1 – **H2c**), or serially mediated by these two variables in combination (path $a_1a_3b_2$ – **H2d**) and the hypothesised path by which the link between state anxiety and experience of stress could be partially mediated by displacement behaviour (a_3b_2 – **H2e**). Path c'1 depicts the mediated regression link between trait anxiety and the experience of stress.

H2b: The link between trait anxiety and experience of stress will be partially mediated by displacement behaviour (indirect effect of trait anxiety on experience of stress; path a_2b_2).

H2c: The link between trait anxiety and experience of stress will be partially mediated by state anxiety (indirect effect of trait anxiety on experience of stress; path a_1b_1).

H2d: The link between trait anxiety and experience of stress will be partially mediated by state anxiety and displacement behaviour (multiple mediation; path $a_1a_3b_2$).

H2e: The link between state anxiety and experience of stress will be partially mediated by displacement behaviour (indirect effect of state anxiety on experience of stress; path a_3b_2).

Finally, we carried out a moderator analysis to investigate whether displacement behaviour alters the strength of the relationship between trait anxiety and experience of stress, as well as between state anxiety and experience of stress. Here, we hypothesised that:

H3: The impact of state anxiety and trait anxiety on experience of stress will be weaker for individuals who have displayed higher levels of displacement behaviour.

Methods

The project was approved by the Roehampton University Ethics Board and was carried out in accordance with the Declaration of Helsinki principles.

Participants

The study was carried out on 47 normal healthy adult male volunteers who were recruited through advertisements. The optimal sample size of $n = 47$ to detect an effect size of $\eta 2 = 0.4$ (representing a small–medium effect size) with a power 0.90 or greater and $\alpha = 0.05$ was calculated *a priori* with the statistical software G-Power (Faul et al. 2007). Participants were informed that their behaviour would be videotaped during a simulated job interview in order to represent a professional setting and signed informed consent and received £20 as an incentive. Using a self-report questionnaire, the following criteria were applied, to exclude individuals with factors that might have an impact on displacement behaviour under stress: medical conditions (e.g. heart disease, diabetes mellitus and hypertension), any current or previous clinical psychosomatic or psychiatric diseases, any allergies, atopic diathesis, rheumatic diseases, recreational drug use, medication or poor sleep pattern. The volunteers were instructed to relax and answer the questionnaires (see below) prior to the stress exposure.

Five participants were excluded due to incomplete questionnaire data, or technical issues during the recording. The remaining 42 participants (89% of the initial sample) were on average 28.09 years old (SD = 7.98; range = 18–56); 83.3% of participants were native English speakers, 66.7% of participants described themselves as employed or self-employed, 19.0% were students and 14.3% were unemployed. Age was not correlated with any of our measures (Pearson correlations: for all analyses, $n = 42$, $r < 0.25$, $p > 0.08$), and there were no differences in any of these measures between native and non-native speakers (ANOVA: for all analyses $F_{1,40} < 0.05$, $p > 0.48$), or between the groups of different occupational status (ANOVA: for all analyses $F_{2,39} < 1.46$, $p > 0.24$); these three variables were therefore not considered any further.

Stress paradigm

As a psychosocial stress test, we used the Trier Social Stress Test (TSST), which has repeatedly been found to induce profound levels of stress (Kirschbaum et al. 1993). The TSST involves giving a simulated job interview (5 min) followed by a mental arithmetic task (5 min) in front of two people (one man and one woman), with both tasks being done while standing. Twenty minutes after arrival at the laboratory and baseline measurement of psychological variables, subjects were introduced to the TSST (2 min). They were then returned to a different room, where they had 5 min to prepare their free speech. Afterwards, subjects were taken back into the TSST room, where they were exposed to the TSST. The TSST situation was videotaped with a camera adjusted so that the subject's face and torso were in full view.

Assessment of state and trait anxiety

Both state and trait anxiety subscales (each 20 items) of Spielberger's State-Trait Anxiety Inventory (STAI; Spielberger et al. 1983) were used. The STAI is a commonly used instrument that differentiates between the temporary condition of state anxiety and anxiety as a disposition (trait). State anxiety items include 'I am tense; I am worried' and 'I feel calm; I feel secure.' Trait anxiety items include 'I worry too much over something that really doesn't matter' and 'I am content; I am a steady person.' The state subscale had a four-point response format ranging from 1 (not at all) to 4 (very much so). The trait subscale had a four-point response format ranging from 1 (almost never) to 4 (almost always). Cronbach's α was 0.93 for the trait subscale and 0.92 for the state subscale.

Quantification of displacement behaviour

Displacement behaviour during the TSST was measured using a revised version of the Ethological Coding System for Interviews (ECSI). ECSI is an ethogram developed for measuring nonverbal behaviour during interviews (Troisi 1999). The use of the ECSI requires videotaping to allow quantification of nonverbal behaviour. Subsequently, trained observers, who are unaware of the subject's verbal reports, observe the videotape and score the subject's behaviour according to the patterns listed in the ECSI. The current version of the ECSI includes 37 different behaviour patterns. This study focuses only on the displacement scale (Table I). Videos were rated independently by two extensively trained observers. The recording method was one to zero sampling, a type of time sampling (Martin and Bateson 1986). The recording session was divided into successive 15-s sample intervals, which were identified by a beeper. On the instant of each sample point, the observer recorded whether or not the behaviour pattern had occurred during the preceding sample interval. In a first step, video data of three randomly selected participants were rated, and interobserver reliability calculated ($\kappa = 0.81$). After the calibration phase and adjustment of the rating protocol, the observers rated the remaining video data ($\kappa = 0.89$).

Table I. Ethogram of the displacement behaviours recorded in this study.

Behaviour	Definition (after Troisi 1999).
Groom	The fingers are passed through the hair in a combing movement.
Hand-face	Hand(s) in contact with the face.
Hand-mouth	Hand(s) in contact with the mouth.
Scratch	The fingernails are used to scratch part of the body, frequently the head.
Yawn	The mouth opens widely, roundly and fairly slowly closing more swiftly. Mouth movement is accompanied by a deep breath and often closing of the eyes and lowering of the brows.
Fumble	Twisting and fiddling finger movements with wedding ring, handkerchief and other hand.
Twist mouth	The lips are closed, pushed forward and twisted to one side.
Lick lips	The tongue is passed over the lips.
Bite lips	One lip usually the lower is drawn into the mouth and held between the teeth.

Assessment of experience of stress

Experience of stressfulness of the stress paradigm was obtained by completion after the TSST of visual analogue scales (VASs) ranging from 0 to 10 with 0 indicating no stress experienced at all. The VAS requires that the respondents specify their level of agreement to a statement by indicating a position along a continuous line between two end-points. Empirical evidence indicates VAS items are more reliable and show higher content validity than discrete scales such as the Likert scale, and thus a wider range of statistical methods can be applied to these measurements (Reips and Funke 2008). After cessation of the TSST, participants were required to rate whether the stress situation was relaxing/stressful, clear/confusing, controllable/uncontrollable, energising/exhausting, interesting/boring, pleasant/unpleasant, comfortable/embarrassing, challenging/fearful and calming/frightening. The average intercorrelations of VAS items was 0.51 ($p < 0.001$) and Cronbach's α was 0.90.

Statistical analyses

All calculations were carried out using SPSS v.20 (SPSS, Inc., Chicago, IL, USA). Data are presented as mean ± SD. In case of missing data, cases were excluded listwise. Data were tested for a normal

distribution using the Kolmogorov–Smirnov test before statistical procedures were applied. All variables were normally distributed. Results were considered statistically significant at the $p < 0.05$ level.

Bivariate correlations. The associations between trait anxiety, state anxiety, displacement behaviour and experience of stress values were explored using Pearson's correlations (two tailed).

Mediation analysis. According to Kenny et al. (1998) multiple mediators should be tested simultaneously rather than separately, in order to establish whether the mediation is independent of the effect of the other mediators. A multiple mediators analysis requires that the different mediators (state anxiety and displacement behaviour in this study) are conceptually distinct and not too highly correlated. In this study, it could be assumed that state anxiety and displacement behaviour are conceptually distinct and they are only moderately correlated ($r = 0.33$, $p < 0.05$). Following Preacher and Hayes (2004), a mediation procedure based on nonparametric resampling, known as bias-corrected bootstrapping (Shrout and Bolger 2002), was conducted. Preacher and Hayes (2008) indicate that investigating multiple mediation involves two parts: (1) examining the total indirect effect and (2) examining the specific indirect effect associated with each mediator variable. Bias-corrected bootstrapping can be used to examine both specific and total indirect effects in the context of multiple mediation (Frazier et al. 2004; MacKinnon et al. 2004). Bootstrapping allows one to gather many alternative versions of a single statistic ordinarily only calculated from one sample. In regard to mediation, bootstrap data resampling procedures establish confidence intervals (CIs) for testing the statistical significance of an indirect effect (Shrout and Bolger 2002). This method allows the distribution of a mediation effect to be examined empirically by randomly sampling observations with replacement from the data-set to create a pseudo (bootstrap) sample of N persons and estimating the mediation path for each bootstrap sample a total of K times (recommended to be 10,000; Mallinckrodt et al. 2006). Examination of the distribution of the estimated indirect effects from K bootstrap samples determines whether the indirect effect of the predictor variable on the outcome variable is significant. If the 95% CI does not contain zero, one can conclude that the indirect effect is significantly different from zero at $p < 0.05$ (two tailed). The analysis was based on 10,000 bootstrap iterations and the CI was set to 95%, as recommended by Mallinckrodt et al. (2006).

Moderation analysis. To explore interaction effects between the psychological measures in this study, multiple regression analyses were carried out. Although there were no signs of multicolinearity (the variance inflation factor values were clearly below 2.5 and tolerance statistics were all well above 0.2), all variables were standardised in order to equate different metrics used in measuring variables (Dunlap and Kemery 1987). The interaction terms were created as product terms (trait anxiety × displacement behaviour, state anxiety × displacement behaviour, trait anxiety × state anxiety and trait anxiety × state anxiety × displacement behaviour). Computing a hierarchical multiple regression, trait anxiety, state anxiety and displacement behaviour were entered first in the equation, followed by the interaction terms trait anxiety × displacement behaviour, state anxiety × displacement behaviour, trait anxiety × state anxiety and finally trait anxiety × state anxiety × displacement behaviour. A moderator effect is indicated by a significant effect of product term while the impact of trait anxiety, state anxiety and the moderator variable are controlled.

Results

Trait anxiety scores at the start of the study were 2.14 ± 0.64 (mean ± SD), and state anxiety scores just prior to the TSST were 2.12 ± 0.59. During the 10-min TSST, subjects showed displacement behaviours in 22.2 ± 9.05 of the forty 15-s time blocks; scratch was the most frequent displacement behaviour (5.29 ± 2.86), followed by hand-mouth (3.14 ± 2.08), groom (2.93 ± 1.31), fumble (2.93 ± 1.60), hand-face (2.87 ± 1.70), bite lips (1.73 ± 1.37), lick lips (1.68 ± 0.96), twist mouth (1.57 ± 0.88) and yawn (0.05 ± 0.22). After the TSST, subjects scored their experience of stress on the VAS as 4.70 ± 1.01.

Bivariate correlations

Table II displays the results of the bivariate correlation analyses. Displacement behaviour was positively correlated with state anxiety ($r_{42} = 0.326$, $p = 0.03$), in support of **H1a** (see Introduction), but not correlated with trait anxiety ($r_{42} = 0.002$, $p = 0.99$);

Table II. Results of the bivariate correlation analyses.

	Trait anxiety (score)	State anxiety (score)	Displacement behaviour (rate)
State anxiety (score)	$r = 0.352$*		
Displacement (rate)	$r = -0.002$	$r = 0.326$*	
Experience of stress (score)	$r = 0.344$*	$r = 0.389$*	$r = -0.360$*

$n = 42$ in all cases; *indicates $p < 0.05$.

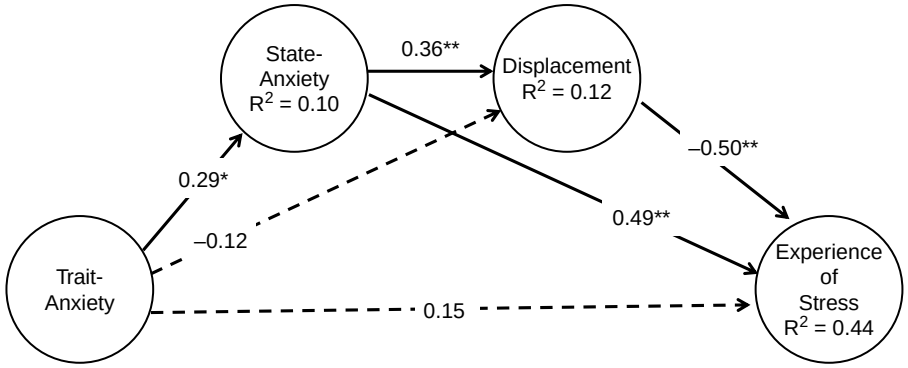

Figure 2. State anxiety and displacement behaviour as mediators between trait anxiety and experience of stress. Solid lines represent significant direct effects in serial mediation analysis using a bias-corrected bootstrapping in conjunction with multiple regression analysis; dashed lines indicate non-significant effects. Numbers on the lines show standardised regression weights and R^2 values reflect the percentage of explained variance ($n = 42$ in all cases; *indicates $p < 0.05$, **indicates $p < 0.01$).

these results indicate that elevations in levels of state anxiety, but not individual differences in trait anxiety *per se*, are associated with increases in the rate of displacement behaviour. Displacement behaviour was negatively correlated with experience of stress ($r_{42} = -0.360$, $p = 0.02$), in support of **H1b**, and in line with the idea that displacement behaviour ameliorates the experience of stress.

Mediation analysis

Figure 2 depicts the results of the mediation analysis. **H2a** was supported: state anxiety mediated between trait anxiety and displacement behaviour. The mediation link a_1a_3 is 0.10 (SE = 0.08), which is the product of $a_1 = 0.29$ and $a_3 = 0.36$, and is substantial with a 95% bootstrap confidence of 0.01–0.34. Individuals with higher levels of trait anxiety responded with higher levels of state anxiety in interview (a threatening situation for self-esteem), and this was associated with higher levels of displacement behaviour.

By contrast, the indirect effect of trait anxiety on experience of stress mediated by displacement behaviour was not significant (in contrast to **H2b**): the a_2b_2 path was estimated to be 0.06 (SE = 0.08) and lay between -0.67 and 0.25 with 95% confidence. The bootstrap confidence contains zero, which emphasises that it is very unlikely for a true mediation link a_2b_2 to be significant in the general population.

Although the direct effect of trait anxiety on experience of stress (path $c'1$ in Figure 2) was not statistically significant ($\beta = 0.15$; ns.), there are two specific indirect effects that were, as evidenced by bootstrap CIs that do not contain zero. The first carries the effect of the trait anxiety on experience of stress through state anxiety only, bypassing displacement behaviour (in support of **H2c**). This indirect effect is the product of $a_1 = 0.29$ and $b_1 = 0.49$, or 0.14, with a 95% bootstrap confidence of 0.01–0.35. Individuals with higher levels of trait anxiety responded with higher levels of state anxiety in interview, and this was associated with higher levels of experienced stress, independent of displacement behaviour. The next indirect effect flows from trait anxiety to experience of stress and passes through both state anxiety and displacement behaviour (in support of **H2d**). It is estimated as the product of a_1, a_3 and b_2, or -0.05, with a 95% bootstrap confidence of -0.19 to -0.01.

H2e suggests that state anxiety predicts experience of stress both directly and indirectly through displacement behaviour. The direct effect of state anxiety on experience of stress was 0.56 and highly substantial ($p < 0.001$, SE = 0.13). The mediation effect was estimated to be -0.17 (SE = 0.10) and lay between -0.43 and -0.20 with 95% confidence. That is, displacement behaviour was a significant mediator of the relationship between high levels of state anxiety and lower levels of experience of stress.

Moderation analysis

The results reveal that none of the interactions explored were significant, and thus **H3** is not supported; this indicates that displacement behaviour does not alter the strength of the relationship between either trait anxiety or state anxiety and experience of stress.

Discussion

In this study, we combined a TSST with ethological analysis and self-report questionnaires, in order to investigate the potential role of displacement behaviour in coping with stress. Working with a healthy population of adult men, we investigated whether displacement behaviour, as a short-term behavioural response to emotionally challenging stimuli, would diminish the negative impact of the situation and hence reduce the levels of stress experienced. Our results supported this idea: the rate of displacement

behaviour was positively correlated with state anxiety but unrelated to trait anxiety, and was negatively correlated with the self-reported experience of stress. Moreover, serial mediation analyses indicated that displacement behaviour mediated the relationship between state anxiety and the experience of stress, and that state anxiety and displacement behaviour – in combination, respectively – mediated the link between trait anxiety and experience of stress (the latter two variables were not directly correlated). Our results provide new insights into the role of displacement behaviour in regulating the levels of stress that people experience following emotionally challenging situations.

The finding that displacement behaviour was positively related to state levels of anxiety adds to evidence from humans and other species (Troisi 2002) linking temporal variation in expression of this behaviour to short-term changes in emotional state. Consistent with this are our findings of no direct impact of trait anxiety on displacement behaviour, nor any evidence of mediation by displacement behaviour of a direct effect of trait anxiety on the experience of stress; these results indicate that as a coping mechanism, displacement behaviour needs to be triggered by elevated levels of state anxiety. However, the results of serial mediation analysis indicate that for the fullest understanding of how emotionally challenging situations may impact on the experience of stress, both trait and state anxiety should be considered: our data indicate that the experience of higher state anxiety results from the habitual tendency towards anxiety (trait anxiety), and translates itself into higher levels of displacement behaviour, which in turn reduces the experience of stress.

The evidence found in this study that displacement behaviour may alleviate the subjective experience of stress raises questions about the mechanism(s) underlying this process. At a proximate behavioural level, displacement behaviour may allow an individual temporarily to 'cut-off' attention from a threatening stimulus, and this short-term diversion of attention could reduce the negative arousal associated with the stimulus (Chance 1962; Sgoifo et al. 2003). At a physiological level, evidence from studies of rodents indicates that engagement in displacement behaviour attenuates the glucocorticoid stress response (Hennessy and Foy 1987), reduces stress-related activation of the prefrontal cortex dopamine system (Berridge et al. 1999) and suppresses stressor-induced expression of corticotropin-releasing factor (Hori et al. 2004). In humans, Pico-Alfonso et al. (2007) found evidence that engagement in displacement behaviour during a stressful interview reduced heart rate and increased parasympathetic tone after this event. Further work in humans, integrating behavioural assessment with a comprehensive range of cognitive and physiological measures of diverse stress responses, is needed to elucidate further the mechanism(s) by which increases in displacement behaviour may lead to a reduced experience of stress.

Our findings prompt investigation of the potential communicative value of displacement behaviour. It has long been speculated that such behaviour may reveal information about an individual's emotional state (Ingram 1960). This information may be available to potential receivers as a result of 'leakage' (Ekman and Friesen 1969) rather than as a result of intentional communication, i.e. displacement behaviours may represent 'cues' rather than 'signals' (Ruxton and Schaefer 2011). Our results suggest that displacement behaviour may also reveal information about an individual's ability to regulate their emotion; as emotional regulation profiles correlate with a broad range of personality traits (Gross 1999), displacement behaviour may thus represent a rich source of information to bystanders. Whether, and how, others perceive or use the information revealed by temporal variation in displacement behaviour remains poorly understood, and further studies in this area will provide new insights into the importance of displacement behaviour in the realm of interpersonal communication. One situation in which the 'reading' of displacement behaviour has already been proposed to be important, however, is that of job interviews. Fidgeting in such contexts is strongly warned against (Florman 2005), but our results indicate that such suppression of displacement behaviour may have negative impacts on an individual's ability to manage the stress they experience during the interview itself.

A number of studies in humans have explored displacement behaviour as a response to stressful situations, and/or as a correlate of subsequent stress levels (Sgoifo et al. 2003; Pico-Alfonso et al. 2007; Wemm et al. 2010; Bardi et al. 2011). Our study advances research in this area by explicitly exploring displacement behaviour as a potential mediator or moderator of the link between anxiety and stress. Our approach can be readily adapted to explore the role of displacement behaviour in coping with other types of stress than the social stress explored here. In addition, the method we adopted can potentially be used to investigate the role of displacement behaviour in dealing with other emotional states, such as anger, sadness and terror, which if poorly regulated can lead to debilitating psychopathologies (Werner and Gross 2010). Studies of this kind will shed important new light on the functional significance of displacement behaviour, and may also indicate promising new avenues for understanding of emotional expression and stress regulation.

Acknowledgements

Stephanie Bauer, Valiollah Golkaramny and the members of the Centre for Research in Evolutionary and Environmental Anthropology provided invaluable feedback on an earlier version of this manuscript.

Declaration of interest: The authors thank the University of Roehampton for financial support. The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

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