1	Testosterone administration in women increases the size of their peripersonal space
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17	Abstract
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19	Peripersonal space (PPS) is the space immediately surrounding the body, conceptualised as a
20	sensory-motor interface between body and environment. PPS size differs between individuals
21	and contexts, with intrapersonal traits and states, as well as social factors having a determining
22	role on the size of PPS. Testosterone plays an important role in regulating social-motivational
23	behaviour and is known to enhance dominance motivation in an implicit and unconscious
24	manner. We investigated whether the dominance-enhancing effects of testosterone reflect as
25	changes in the representation of PPS in a within-subjects testosterone administration study in
26	women (N=19). Participants performed a visuo-tactile integration task in a mixed-reality setup.

27 Results indicated that the administration of testosterone caused a significant enlargement of 28 participants' PPS, suggesting that testosterone caused participants to implicitly appropriate a 29 larger space as their own. These findings suggest that the dominance-enhancing effects of 30 testosterone reflect at the level of sensory-motor processing in PPS.

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- 32 Keywords: Visuo-tactile, hormones, bodily self-consciousness, multisensory integration,
- 33 social dominance
- 34

#### 35 Introduction

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37 A growing body of research has demonstrated the important role of testosterone in regulating 38 social behavior, particularly in relation to dominance, that is, behavior in the service of gaining 39 or maintaining social status (Carré & Archer, 2018; Eisenegger, Haushofer, & Fehr, 2011; 40 Terburg & van Honk, 2013). Indeed, in both sexes throughout the mammalian species, 41 testosterone has been linked to power and high status on a range of dominance indices, both 42 pro- and anti-social in nature (Eisenegger et al., 2011; Mazur & Booth, 1998; Stanton & 43 Schultheiss, 2009; van der Westhuizen & Solms, 2015). For instance, testosterone has been 44 shown to reduce anxiety and physiological stress responses – particularly in anxiety-prone 45 individuals (Hermans et al., 2007; Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006; 46 van Honk, Peper, & Schutter, 2005), to reduce submissive avoidance behavior (Enter, 47 Spinhoven, & Roelofs, 2014; Enter, Terburg, Harrewijn, Spinhoven, & Roelofs, 2016; Terburg 48 et al., 2016) and to promote social approach and fair bargaining (Eisenegger et al., 2010). At 49 the same time, testosterone increases aggression toward threatening stimuli (van Honk & 50 Tuiten, 2001; van Honk et al., 1999; Wirth & Schultheiss, 2007) and is well known for its 51 ability to reduce certain indices of empathy, such as moral reasoning (Montoya et al., 2013), 52 facial expression mimicry (Hermans, Putman, & van Honk, 2006) while promoting 53 egocentricity (Wright et al., 2012). A number of these effects are thought to arise via interaction 54 with the dopaminergic system (Bell & Sisk, 2013) and aromatisation to estradiol (Eisenegger 55 et al., 2011) or in concert with cortisol (Casto & Edwards, 2016). Importantly, several studies 56 show that testosterone influences behavior in an automatic and implicit way (Terburg, Aarts, 57 & van Honk, 2012; Terburg & van Honk, 2013; van Honk et al., 2005). This points to the utility 58 of experimental frameworks that study social processes from the perspective of bodily self-59 consciousness (Serino, 2019). While peripheral effects of testosterone on the body are well 60 established and known to support a variety of processes that enhance physical performance, 61 including stamina, strength, bone mass, male virility and reduced inflammation (Bianchi, 2019; 62 Sinervo, Miles, Frankino, Klukowski, & DeNardo, 2000; Sinnesael, Boonen, Claessens, Gielen, & Vanderschueren, 2011; Wang et al., 2000), research has only recently started to 63 64 explore the sensory-motor processes that may be affected by testosterone in mediating its effects in social dominance behavior. 65

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A recent study that adopted this approach (van der Westhuizen, Moore, Solms, & van Honk,
2017) found that the administration of a single dose of testosterone to healthy women increased

69 their implicit feeling of control over goal-directed actions – namely, an increase in their sense 70 of agency as measured by the intentional binding task. This finding was taken to suggest that 71 feelings of control and power may manifest firstly in the body, as control over the body's 72 actions. In the present study we aimed to further explore this association between testosterone 73 and bodily representations by indexing whether the former facilitates social dominance in part 74 by modulating not only the perception of one's body (or control over it; van der Westhuizen et 75 al., 2017) but also the encoding of space immediately surrounding the body; the peripersonal 76 space (PPS; di Pellegrino & Làdavas, 2015; Graziano & Cooke, 2006; Serino, 2019).

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78 A set of neurons in the intra-parietal sulcus (Duhamel, Colby, & Goldberg, 1998) and ventral 79 pre-motor (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a, 1981b) regions respond both 80 to the somatosensory stimulation on the body, and to visual or auditory stimuli near but not far 81 from the body; that is, they encode the PPS. This spatial representation remaps plastically as a 82 function of the individual's potential of acting in space (Noel et al., 2020; Patané et al., 2019). 83 PPS has been shown to extend after the use of a tool (Canzoneri et al., 2013; Guterstam, 84 Szczotka, Zeberg, & Ehrsson, 2018; Iriki, Tanaka, & Iwamura, 1996; Serino, Bassolino, Farne, 85 & Ladavas, 2007), to contract after immobilization (Bassolino, Finisguerra, Canzoneri, Serino, 86 & Pozzo, 2015) and to blur after sensory deprivation (Noel, Park, et al., 2018). PPS remaps in 87 the direction of approaching movements (Brozzoli, Cardinali, Pavani, & Farnè, 2010; Noel et 88 al., 2015) and as a function of the velocity of approaching stimuli, i.e., it extends towards faster 89 stimuli so as to anticipate potential contacts (Fogassi et al., 1996; Noel, Blanke, Magosso, & 90 Serino, 2018). If electrically stimulated, regions hosting PPS neurons engender defensive 91 behaviors such as ducking (Graziano & Cooke, 2006). Thus, PPS representation is thought to 92 mediate body-environment interactions. More recently, PPS magnitude has been shown to be 93 modulated by social context, such as the valence of an interaction with a conspecific (Teneggi, 94 Canzoneri, di Pellegrino, & Serino, 2013) or the perceived moral quality of the conspecific 95 (Pellencin, Paladino, Herbelin, & Serino, 2018). Further, neurophysiological (Ishida, Nakajima, Inase, & Murata, 2010) and psychophysical (Maister, Cardini, Zamariola, Serino, 96 97 & Tsakiris, 2015; Teramoto, 2018) studies have shown that PPS does not only index the space 98 of the self (Noel, Pfeiffer, Blanke, & Serino, 2015; Salomon et al., 2017), but also that of others 99 (Makin, Holmes, & Ehrsson, 2008). Thus, by measuring PPS during testosterone 100 administration we can build upon prior work examining body perception after testosterone 101 administration (van der Westhuizen et al., 2017) to include the space near one's body, as well 102 as the space near bodies of others. This ability to study space around the self and others answers

- 103 questions as to whether an increased dominance motivation, associated with testosterone, is
- 104 reflected implicitly in the encoding of one's own body, the body of others, or both.
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106 Testosterone is strongly involved in the regulation of social approach and the defence of social 107 status (Terburg & van Honk, 2013), while PPS mapping functions to regulate approaching and 108 defensive behaviors. Furthermore, previous research found that testosterone modulated 109 interpersonal distance, causing a significant reduction in the amount of personal distance that 110 healthy male participants preferred from aggressive individuals (Wagels, Radke, Goerlich, 111 Habel, & Votinov, 2017). Following these lines of evidence, we hypothesised that raised testosterone would expand participants' PPS boundary when they faced a neutral stranger -112 113 conferring a larger 'self-space'. In keeping with the egocentric effects of testosterone (van 114 Honk et al., 2011; Wright et al., 2012), we hypothesised that changes in PPS would be specific 115 only to the self and that there would be no changes in the encoding of PPS around a neutral 116 stranger. Moreover, given that testosterone administration has been shown to reduce 117 physiological stress responses more effectively in individuals prone to anxiety (Hermans et al., 118 2007), we hypothesised that the effects of testosterone administration would be most 119 pronounced in anxious participants. To test these hypotheses, we assessed whether testosterone 120 influences the encoding of PPS around the self and others, by mapping PPS as a function of 121 different testosterone levels. This was achieved by means of testosterone and placebo 122 administration in a double-blind within-subjects design. We also included personality measures 123 to run further exploratory analyses on the role of individual differences in mediating the effects 124 of testosterone on PPS given the increasing interest in the relationship between trait anxiety 125 and interpersonal space (de Haan et al., 2015; Lachini et al., 2015; Spaccasassi & Maravita, 126 2020).

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### 128 Methods

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Participants. 19 right-handed females from the University of Cape Town between the ages of 18 and 25 participated in the study. Based on self-report, participation occurred during the preovulatory stage, that is, during the first 10 days following last menstruation - the most stable period in a woman's cycle. Male participants were excluded as the reliability of the testosterone administration protocol has only been established in females (Tuiten et al., 2000), and necessary and safe doses and the times course of effects in males is not yet known. This sample size is on par with the vast majority of PPS studies (e.g., 20 in Noel, Samad, et al., 2018; 18 137 and 19 in Stone, Kandula, Keizer, and Dijkerman, 2018; Stone et al., 2019; 19 in Hobeika, Taffou, Carpentier, Warusfel, and Viaud-Delmon, 2020), while additionally requiring 138 139 participants to all be female, within a particular stage of menstrual cycle, and to partake in 140 multiple experimental sessions always at the same time of the day (see below). Further, women 141 on hormonal medication were excluded to prevent potential confounding interactions. 142 Participants had no history of neurological or psychiatric disease and no visual impairments. 143 One participant's data was discarded due to excessive outliers in her data set (51.3% of her 144 responses were outliers, defined as having studentised residuals with an absolute value greater 145 than 3), suggesting that she did not understand the task. All participants were financially 146 reimbursed for their time (R350 – approximately \$25) and gave informed written consent to 147 take part in the study, which was approved by the University of Cape Town (UCT) Psychology 148 Department and the UCT Health Sciences Human Research Ethics Committee.

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# 150 Materials and Apparatus

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152 **PPS measurement task.** The PPS task was administered using an augmented reality (AR) head 153 mounted display (HMD, an Oculus Rift, DK1) and RealiSM software (Reality Substitution 154 Machine, http://lnco.epfl.ch/realism) an in-house purpose-made software developed at the 155 Laboratory of Cognitive Neuroscience at the Ecole Polytechnique Federale de Lausanne 156 (EPFL). This software superimposed a programmed virtual approaching visual stimulus, 157 travelling from far to near, on the participant's external world (perceived via cameras attached to the VR HMD) – creating a 'mixed-reality' setup (Serino et al., 2018). The approaching visual 158 159 stimulus was a tridimensional virtual tennis ball, 6.5cm in diameter, looming toward the face 160 of the participant. The ball travelled in virtual space from far to near, approaching the 161 participant's face at a velocity of 0.75 m/s. Participants were fitted with in-house custom made 162 (EPFL) vibrotactile devices, attached to their cheek using skin-sensitive plasters and activated 163 for 35 ms.

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165 **Physiological Materials** – **Testosterone and placebo solution.** A single dose of 0.5mg of 166 testosterone, with a hydroxypropyl-β-cyclodextrin liquid carrier, was administered 167 sublingually. Following administration at this dosage, testosterone level is known to peak 168 between 3 and 4.5hrs after being ingested (Tuiten et al., 2000) and the effects of this method 169 of testosterone administration have been demonstrated on the physiological, psychological, social and economical level many times (Boksem et al., 2013; Bos, Terburg, & van Honk,
2010; Bos, van Honk, Ramsey, Stein, & Hermans, 2013; Hermans et al., 2006; Hermans et al.,
2006; Schutter & Honk, 2004; van Honk & Schutter, 2007; van Honk & Tuiten, 2001). Vials

- 173 were filled and coded by an external researcher to maintain double- blind-administration.
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175 **Ouestionnaires.** We used the STAI-Trait inventory (STAI, Spielberg, et al., 1970) to measure 176 participants' trait anxiety given the increasing interest in the relationship between anxiety and 177 interpersonal space (de Haan et al., 2015; Lachini et al., 2015; Spaccasassi & Maravita, 2020) 178 and the general hypothesis that the PPS represents a kind of 'safety margin' around the self (see 179 Introduction and Sambo & Iannetti, 2013). The STAI-Trait consists of 20 questions scored on 180 a 4-point likert scale. It has excellent psychometric properties and has been widely utilised in 181 studies on bodily consciousness (For example, Spaccasassi & Maravita, 2020; Dunn et al., 182 2015). We also used the Brief Affective Neuroscience Personality Scales (BANPS) to measure 183 additional personality variables. The BANPS consists of 33 questions scored on a 5-point likert 184 scale. It has been validated in several studies (Barrett, Robins & Janata, 2013; Geir et al., 2014) 185 and is based on six of the primary-process subcortical brain emotion systems – namely, 186 SEEKING, RAGE, FEAR, CARE, PANIC/GRIEF and PLAY – which are known to confer 187 motivational drives imperative to survival and social hierarchy (Davis & Panksepp, 2018). 188 ANPS traits are believed to be foundational for personality development and show good 189 correspondence with the Big Five traits (Barrett, Robins, & Janata, 2013; Davis & Panksepp, 190 2011).

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192 Confederates. Our experiment involved the measurement of the PPS boundary in the face of 193 a single stranger unknown to the participants – both to study how PPS around the self changes 194 in a social context with testosterone administration, but also to examine if the representation of 195 PPS around the other changes. Thus, confederates were hired to perform this role. We matched 196 participants and a confederate on ethnicity and gender, to prevent potential confounding effects 197 of a confederate from a different ethnic or gender group. For example, male confederates have 198 been found to elicit a larger defensive PPS boundary than female confederates, especially in 199 female participants (Iachini et al., 2016). In addition, participants were matched with a 200 confederate who fell in a height range of 149 – 169cm (10cm below or above the average South 201 African female height) to ensure that height did not impact on perception of the confederate. 202 Moreover, to prevent a familiarity effect on the second day of testing (which itself could

influence the PPS boundary), a different confederate was used on each day of testing. To induce
a degree of uniformity, confederates dressed in the same way. Finally, confederates were
instructed to stand at a designated point approximately 1.6 meters in front of the participant
and face her while maintaining a neutral expression. Confederates did not interact in any way
with participants.

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### 209 **Procedure**

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Prior to their research visit, participants completed the STAI-Trait and BANPS questionnaires 211 212 electronically. Each participant was allocated to four session slots - two per day 213 (testosterone/placebo administration session and experimental session four hours later), on two 214 separate days, two days apart. Participants were seen at the same time of day for each 215 administration and experimental session, respectively, as testosterone fluctuations are known 216 to occur according to the time of day (Wirth & Schultheiss, 2007). Only one participant was 217 seen at the lab at a time for all four sessions. Participants were randomly assigned (using a 218 randomization engine – GraphPad) to either receive placebo or testosterone on the first day of 219 testing, and the alternative substance on the second day of testing.

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During the administration session, the testosterone or placebo solution was administered blind.
Participants held the solution under their tongue for one minute, timed by the administrator,
before swallowing it.

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225 During the experimental session four hours later, participants were seated comfortably at a desk 226 and outfitted with the vibro-tactile devise and the AR HMD. To measure PPS, we used a well-227 established visuo-tactile interaction task (Serino, Canzoneri, Marzolla, di Pellegrino, & 228 Magosso, 2015; Serino, Noel, et al., 2015). Participants were informed that they will feel a 229 vibration on their cheek and see a virtual ball and that a person unknown to them will enter the 230 room and stand in front of them before the task begins. They were also told that the virtual ball 231 and confederate are task irrelevant, and instead asked to respond as quickly as possible to the 232 tactile vibration by pressing a key on the keyboard. The travelling virtual ball was 233 superimposed on the participants' real surroundings, captured by cameras on the HMD and 234 presented during the task. Participants were also instructed to look in the direction of the 235 confederate for the duration of the task, but not to interact with her. At this point, the

confederate entered the room and stood in front of the participant, at a designated point in far
space approximately 1.6 meters in front of the participant (see Figure 1). The experimental
task was run and there was a pause half-way through the task where the participant was given
the option of a short break if they felt they needed it.

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241 The logic of the PPS measure is as follows: PPS neurons respond both to touch and the visual 242 stimuli presented in the near space (Duhamel et al., 1998; Graziano & Cooke, 2006). Thus, 243 when visual stimuli are far, there should be no multisensory interaction. But when visual 244 stimuli are presented near, within the receptive fields of visuo-tactile neurons, visuo-tactile 245 multisensory interactions should speed reaction times to touch (e.g., Canzoneri et al., 2013; 246 Serino et al., 2015). Thus, we present tactile stimulation while visual stimulus is at different 247 distances, and we aim to determine the furthest distance from the body at which a visual 248 stimulus significantly speeds up tactile processing. That is, the distance at which visuo-tactile 249 RTs are significantly faster than RTs to unimodal tactile stimulation is a proxy for the PPS 250 boundary (Serino, Noel, et al., 2015; Serino et al., 2018).

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252 Each trial in the task was 2660ms long and on each trial, tactile stimulation (vibration) was 253 administered at one of five different temporal delays from the onset of the trial and the onset 254 of the visual stimuli looming toward participants (after 2165, 1732, 1299, 866, and 433 ms). 255 Thus, tactile stimuli were presented when the virtual ball was at 5 different distance points 256 from the participant (D1 - D5 - ranging from 37.12cm to 167.03cm from the participant, in257 32.5cm intervals, see Figure 1). Specifically, when the tactile stimulation was administered 258 after 2165 ms from the start of the trial, the virtual ball was at the closest distance to the 259 participant (D1). Conversely, when the tactile stimulation was administered 433ms post trial 260 onset, the virtual ball was at its furthest distance from the participant (D5).

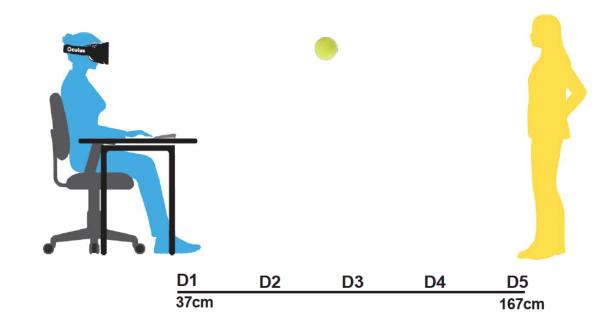
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262 We included three types of trials presented in a randomised order - tactile-only trials, visuo-263 tactile trials, and catch trials. 60.60% of the trials were experimental bimodal visuo-tactile 264 trials, in which the tactile stimulus was delivered in combination with the approaching visual 265 stimulus (as described above). 30.30% of trials were unimodal tactile-only trials, in which the tactile stimulus was delivered in the absence of the visual stimulus. These trials are considered 266 267 baseline trials and are used to show the bimodal facilitation effect on RTs to tactile stimuli (see Analysis). Tactile-only trials are important in that they can be used to control for individual 268 269 differences in RTs to tactile stimuli (see Analysis). In both the unimodal and bimodal trials,

270 the tactile stimulus was delivered at one of the five distance points (D1-D5) in a randomised 271 order, to prevent entrainment or expectancy effects. Lastly, 9.10% of trials were catch trials in 272 which the approaching visual stimulus was presented and no tactile stimulus was delivered. 273 Catch trials necessitate withholding a response and thus ensure that participants are attentive 274 to the task. Further, they mitigate the entrainment of an automatic motor response and an 275 expectancy effect - that tactile stimuli is more likely to occur the longer it has been since trial 276 onset (Hobeika et al., 2020; Kandula, Van der Stoep, Hofman, & Dijkerman, 2017). In total 277 the task consisted of 165 trials: 20 visuo-tactile trials per distance (100 total) + 10 tactile-only 278 trials per distance (50 total) + 15 catch trials. A fixation cross was presented at the beginning 279 of the task and during the break and was offset once a key was pressed to begin trials. The 280 duration of the task was approximately 11 minutes.

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The administration and experimental sessions were repeated two days later, and were identical with the exception of the substance administered and the confederate present, who was swapped on the second day of testing to prevent a familiarity effect.



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Fig. 1 The experimental setup. A mixed-reality setup was used, whereby participants (blue figure) were seated at a desk and dressed with the VR HMD and a vibrotactile device on their cheek. Cameras attached to the VR HMD allowed participants to perceive their external world while also perceiving a virtual tennis ball approaching their face travelling from far to near space. Participants completed the PPS task by pressing a key on a keyboard as quickly as possible when they felt a vibration on their cheek. The task was completed while facing a confederate standing in far space (yellow figure)

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## 294 Analyses

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296 Peripersonal Space. RTs to visuo-tactile (VT) and tactile-alone (T) stimulation were recorded 297 as the temporal duration between vibrotactile stimulus onset and button press. For each subject 298 individually, we binned RTs as a function of the distance between the visual stimuli and the 299 observer (D1 through D5), and as a function of sensory stimulation (VT vs. T) and testosterone 300 condition (testosterone vs. placebo). Then, mean tactile RTs for each sensory stimulation and 301 testosterone condition were subtracted from the analogous VT condition in order to compute 302 "baseline-corrected" RTs (see Pfeiffer, Noel, Serino, and Blanke, 2018; Noel, Park, et al., 2018 303 for a similar approach). This correction is employed to offset temporal expectancy effects 304 (Kandula et al., 2017) and determine whether any putative modulation in RTs as a function of 305 distance is truly a multisensory PPS effect (i.e., visuo-tactile RT < tactile RT). That is, after 306 correction for unisensory RTs, values under zero correspond to multisensory facilitation.

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308 After correcting multisensory RTs in the pre-processing step described above, we first 309 ascertained whether a PPS effect was observed in our mixed-reality setup. To do so, we 310 computed grand average RTs to VT stimulation as a function of distance (but regardless of 311 testosterone condition), and submitted these to a one-sample ANOVA. Planned one-sample t-312 tests to zero were then performed in order to establish at which distances a PPS effect was 313 observed. As detailed below, this analysis suggested a shortening of RTs when visual stimuli 314 were presented both near the participants (i.e., self, D1) and the confederate (i.e., other, D5. 315 See Teramoto, 2018, for a similar effect). Thus, in a last step, we aimed at estimating the size 316 and gradient of PPS representation both around the self and the confederate.

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Estimation of the size and gradient of PPS was accomplished via function fitting, which permitted for fine-grain estimates (vs. solely indicating at which discrete distance did VT  $\neq$  T) and served as a data-reduction technique. Visuo-tactile RTs were fit to a sigmoidal function (Eq. 1),

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$$y(x) = \frac{y_{min} + y_{max} \times e^{(x - x_c)/b}}{1 + e^{(x - x_c)/b}}$$
(Eq.1)

(a a )/b

325

326

327 where x represents the distance between visual and tactile stimuli and y(x) is the RT to tactile stimulation at a given visual distance, x.  $y_{min}$  and  $y_{max}$  are saturation points of the sigmoidal, 328 and are fixed to the slowest and fastest average RT in the VT trials. The quantities x<sub>c</sub> and b 329 330 respectively represent the central point and a parameter dictating the slope of the sigmoidal at x<sub>c</sub>, and are free to vary in order to maximize goodness of fit. The central point of this function 331 332 is taken as a proxy for the size of PPS, the location of the PPS boundary, while the slope of the 333 function (inversely proportional to b) represents the gradient with which the near (peri-334 personal) and far (extra-personal) space are divided (Noel, Blanke, et al., 2018; Noel, Park, et 335 al., 2018; Pfeiffer et al., 2018). To limit impact of the confederate on self-PPS estimates, 336 distances D1 through D4 were utilized in the self condition. Similarly, distances D2 through 337 D5 were utilized in the confederate-PPS estimates, and these were inverted (from D5 to D2) 338 before fitting, such that distances were relative to the self (D1 through D4) or the other (D5 339 through D2). In this manner central point estimates for self and other were on the same scale 340 (i.e., low values for the central point indicate a small PPS, while large values indicate a large 341 PPS).

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343 Personality Questionnaires. Questionnaire scores for the STAI-Trait and each of the 6
344 BANPS personality categories were correlated with the change in PPS size as a function of
345 testosterone administration.

- 346
- 347348 Results

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Peripersonal Space. Overall, participants were very accurate at the visuo-tactile interaction task, with 0.95% omissions (i.e., lack of response to a visuo-tactile or tactile-alone trial), and 0.4% false alarms (i.e., response during a visual-only catch trial). In turn, the analysis is centered around reaction times (see Serino et al., 2015, 2017, for a similar approach).

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An initial 2 (testosterone vs. placebo) x 2 (tactile vs. visuo-tactile) x 5 (distances) repeatedmeasures ANOVA on reaction times demonstrated a significant effect of distance (F(4, 68) = 8.68, p < 0.001,  $\eta_p^2 = 0.33$ ), and a three way interaction between variables (F(4, 68) = 18.09, p < 0.001,  $\eta_p^2 = 0.51$ ). To better understand the nature of this complex interaction and to succinctly describe the profile of multisensory vs. unisensory reaction times as a function of distance, we then computed 'baseline corrected' reaction times on a subject-by-subject basis. That is, we computed the difference between unisensory tactile and multisensory visuo-tactile 363 reaction times for matched distances (e.g., VT at distance 3 - T at distance 3). This comparison between tactile and visuo-tactile reaction times at a given distance corrects for potential 364 365 changes in the baseline reaction time to touch as a function of space or time (Holmes et al., 2020). In corroboration to the above-mentioned repeated-measures ANOVA, a one-way 366 ANOVA on baseline-corrected visuo-tactile reaction times as a function of distance revealed a 367 significant effect of distance (F(4, 68) = 15.27, p < 0.001,  $\eta^2_p$  = 0.47), confirming that we 368 369 successfully mapped a PPS effect within our mixed-reality setup. One-sample t-tests to zero 370 (i.e., tactile-alone reaction times) suggested that multisensory reaction times at D1 (t(17) =371 4.36, p < 0.001) and D5 (t(17) = 2.76, p = 0.013) were significantly faster (raw: mean  $\pm$  sem; 372 D1: 338.8ms  $\pm$  15.4ms; D5: 340.1ms  $\pm$  16.1ms) than reaction times to tactile stimulation alone 373 (raw: D1:  $372.7\text{ms} \pm 16.5\text{ms}$ ; D5:  $350.5\text{ms} \pm 15.4\text{ms}$ ). Thus, seemingly a PPS representation 374 was successfully delineated near the self (D1) and near the other (D5). Interestingly, a direct 375 comparison between baseline-corrected multisensory reaction times at D1 -33.9ms  $\pm$  9.5ms, 376 negative values indicating a multisensory facilitation) and D5 (-10.4ms  $\pm$  6.3ms) suggested a stronger PPS effect near the self than near another individual (t(17) = 2.57, p = 0.020). Reaction 377 378 times at distances D2 - D4 were not different from baseline (all p-values >0.05; D2 through 379 D4:  $8.4\text{ms} \pm 8.8\text{ms}$ ;  $9.5\text{ms} \pm 10.5\text{ms}$ ;  $9.4\text{ms} \pm 10.3\text{ms}$ ).

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Having established that a multisensory PPS representation was successfully indexed (i.e., a multisensory facilitation effect that was space-dependent), we subsequently fit individual subject data and extract estimates of the location (central point) and gradient (slope) of PPS representation around the self and other, and as a function of testosterone or placebo administration (see *Methods* for detail). Goodness-of-fit was variable (see Serino et al., 2018), with 4 participants showing poor fits (average  $R^2 < 0.2$ , cut-off set a priori), and thus their data was discarded for the rest of analyses. The average  $R^2$  of the remaining participants was 0.55.

389 Regarding the central point, as illustrated in Figure 2, a 2 (testosterone vs. placebo) x 2 (self vs. other) repeated-measures ANOVA revealed a significant main effect of testosterone 390 administration (placebo: 2.21 ± 0.17; testosterone: 2.67 ± 0.13; F(1,13) = 8.9, p = 0.010,  $\eta^2_p =$ 391 392 0.40), a significant main effect of self vs. other (self:  $2.11 \pm 0.08$ ; other:  $2.76 \pm 0.16$ ; F(1, 13) = 19.3, p < 0.001,  $\eta^2_p$  = 0.59), and most importantly a significant interaction between these 393 variables (F(1, 13) = 6.29, p = 0.026,  $\eta_p^2 = 0.32$ ). The interaction was driven by the fact that 394 395 the central point was farther in space for the self condition after administration of testosterone 396 (placebo:  $1.80 \pm 0.16$ ; testosterone:  $2.42 \pm 0.35$ ; t(13) = 6.07, p < 0.001, Figure 2), indicating an extended PPS around one's own body. On the other hand, there was no central point difference for the other conditions, indicating that the space around the other remained unaltered by testosterone administration (placebo:  $2.57 \pm 0.51$ ; testosterone:  $2.60 \pm 0.49$ ; t(13) 400 = 0.162, p = 0.87, **Figure 2**).

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In terms of the gradient of PPS, a 2 (testosterone vs. placebo) x 2 (self vs. other) repeatedmeasures ANOVA demonstrated a main effect of self vs. other (F(1, 13) = 46.22, p < 0.001,  $\eta^2_p = 0.78$ ; self: 0.43 ± 0.11; other: 2.07 ± 0.26), yet no main effect of testosterone administration (placebo: 1.00 ± 0.29; testosterone: 1.51 ± 0.26; F(1, 13) = 3.41, p = 0.08), nor an interaction between these variables (F(1, 13) = 0.030, p = 0.86). The main effect was driven by a steeper gradient around the self (b-parameter value: 0.43 ± 0.42) than around the other  $(2.0 \pm 0.98, Figure 2)$ .

409

Lastly, to further support the enlargement of PPS around the self during testosterone 410 411 administration we estimated the central point of the sigmoidal-like pattern of RTs via the 412 Spearman-Karber Method (Bausenhart, Di Luca, & Ulrich, 2018; Miller & Ulrich, 2001). This 413 approach allows for estimating psychometric parameters (e.g., central point) without 414 performing a model fit, and thus we did not have to discard any participant. Corroborating the above finding, this analysis suggested a larger PPS around the self during testosterone 415 administration than placebo (testosterone =  $2.52\pm0.58$ ms; placebo =  $2.26\pm0.52$ ms; p = 0.029. 416 417 All other results also remain unaltered).

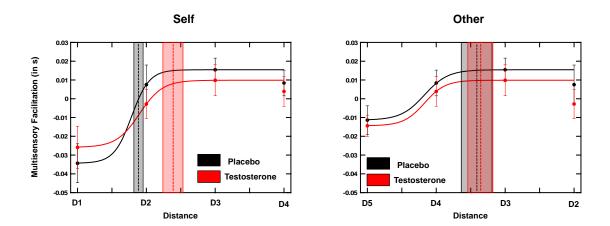




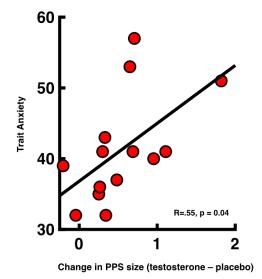
Fig. 2 Effect of testosterone on PPS representation of the self and other. Left Panel; Multisensory facilitation in
seconds (visuo-tactile reaction times corrected for tactile reaction times; negative values indicating multisensory
facilitation) as a function of distance (near to far; 1-4) from the self, and administration of either placebo (black)
or testosterone (red). Dots are mean reaction time and error bars represent +/- 1 standard error of the mean (SEM).

423 Dashed vertical lines represent the average central point (size) of PPS for the given condition, and shaded area 424 around the dashed lines is SEMs. Note sigmoidal functions are fit for the average reaction time, while the vertical 425 dashed lines are average central points of individually fitted sigmoidals. **Right Panel**; Multisensory facilitation 426 as a function of distance from the other (confederate), and administration of either placebo or testosterone. 427 Conventions follow as for the left panel

429 Interplay Between Personality Traits and Change in Peripersonal Space Due to 430 **Testosterone.** Since testosterone administration seemingly enlarged the PPS representation 431 around the self, we queried whether this remapping was related to personality variables (see 432 Noel, Park, et al., 2018 for a similar approach). In order to limit the possibility for Type I errors 433 (i.e., false positives), correlational analyses are restricted to the change in PPS size (i.e., central 434 point) due to administration of testosterone (i.e., testosterone - placebo). No correlational 435 analysis is conducted on the slope of PPS – as this variable did not change due to testosterone - and no correlational analysis is conducted on central point values during placebo or 436 437 testosterone (only on the difference of these). In line with our prediction and as illustrated in 438 **Figure 3**, this analysis suggested that participants with higher trait anxiety were particularly prone to enlargements of PPS due to administration of testosterone (Pearson correlation; r =439 440 0.55, p = 0.04). None of the BANPS personality trait scales significantly correlated with the 441 change in peripersonal space due to testosterone administration, which is not altogether 442 surprising given that the BANPS in its current form does not account for a 'social dominance' trait (but see van der Westhuizen & Solms, 2015). 443

444

428



445

Fig. 3 Correlation between trait anxiety and change in self-PPS due to testosterone. Trait anxiety (STAI-T) scores
 (y-axis) as a function of change in PPS size (testosterone – placebo). Each dot represents a participant

448

### 449 **Discussion**

450

451 In the present study, we asked whether testosterone facilitates social dominance in part by 452 changing or co-varying with peripersonal space mapping. We used a visuo-tactile interaction 453 task to identify the distance at which an approaching visual stimulus speeded up tactile 454 processing as a proxy for the boundary of PPS. We measured participants' PPS both around 455 their own body and around a confederate unknown to the participant. We measured PPS around 456 the self and other under different levels of testosterone, by means of testosterone and placebo 457 administration. Our results indicated that when testosterone is increased, the PPS around the 458 self expands, while that around the other remains a constant size.

459

460 Our finding that testosterone administration caused participants to unconsciously appropriate 461 a larger space as their own suggests that implicit changes in body representation may 462 accompany and even support the well-established effect of testosterone on social dominance (for a review see Eisenegger et al., 2011; Terburg & van Honk, 2013). For instance, previous 463 work found that testosterone administration increased participants' perception of their sensory-464 465 motor agency (van der Westhuizen et al., 2017). Furthermore, in the Rubber Hand Illusion, where reductions in limb temperature have been related to a decreased sense of body ownership 466 467 (Moseley et al., 2008), testosterone has been shown to prevent this cooling effect (van der Westhuizen, Page, Solms, & van Honk, 2019). Our current findings extend this evidence by 468 469 showing that testosterone also changes the encoding of the space immediately surrounding the 470 body, causing an enlargement in participants' PPS. Given that testosterone is known to increase 471 social dominance motivation, the extension of one's own PPS in the presence of another 472 individual in the testosterone condition may be interpreted as an *implicit index* of such dominance motivation. This is in keeping with previous research which found that raising 473 474 testosterone modulated interpersonal distance, causing a significant reduction in the amount of 475 personal distance that healthy male participants preferred from aggressive individuals (Wagels 476 et al., 2017). This finding suggests that the enhanced social aggression associated with 477 testosterone may produce changes in the apportioning of own space. Moreover, a recent study 478 showed that after being primed to feel high power through recollection of a memory in which 479 participants felt powerful, participants' vertical PPS boundary expanded (Vergallito et al., 480 2019). The authors concluded that high power may cause an expansion of PPS in all directions, 481 and that this should be investigated on the horizontal axis – which is indeed supported by the 482 present study.

15

483

484 Our results replicated previous studies showing that PPS can be measured around others (Ishida 485 et al., 2010; Maister et al., 2015; Serino, 2019; Teramoto, 2018). We found that the PPS effect 486 is stronger around the self (represented by a sharper boundary gradient) than around the other. 487 This finding adds to recent evidence suggesting that PPS is the space of the bodily self (Noel 488 et al., 2015; Noel et al., 2019; Noel, Blanke, & Serino, 2018; Serino, 2019). However, a 489 limitation in this regard, is that in the VR task used, the virtual ball always travelled *toward* 490 participants and did not recede in the direction of the confederate. Had the ball approached and 491 receded, the PPS effect around the other may have been stronger, given that neurons encoding 492 for PPS are known to respond preferentially to looming stimuli (Fogassi et al., 1996), and may 493 have been represented by a sharper boundary gradient. Future studies will be required to 494 systematically address these issues.

495

496 We found a correlation between the increase in PPS size due to testosterone administration and 497 trait anxiety, indicating that participants higher in trait anxiety were most prone to PPS 498 enlargement after testosterone administration. This is noteworthy, given that both anxiety 499 (Iachini, Ruggiero, Ruotolo, di Cola, & Senese, 2015; Sambo & Iannetti, 2013; Taffou & 500 Viaud-Delmon, 2014), and also paradoxically, testosterone, which is known to reduce anxiety (Hermans et al., 2006; van Honk et al., 2005), increase PPS. At this point we can only speculate, 501 502 but it is possible that the enlargement of PPS corresponds to a social coping strategy that 503 anxious individuals employ implicitly to manage feelings of social discomfort and which 504 people with high testosterone utilise instead more proactively as a basic form of empowerment. 505 In this way, as in previous studies (Hermans et al., 2007), the dominance enhancing effects of 506 testosterone may be most pronounced in anxious participants. Future studies that are able to 507 evaluate the emotional and behavioural repercussions of expanded PPS in social settings are 508 needed to disentangle the functional differences in PPS among high and low anxiety groups.

509

## 510 Conclusion

The present study makes a novel contribution to our understanding of the means by which testosterone enhances social dominance. Our results indicated that raising participants' testosterone caused the PPS around their bodies to expand, while PPS around the confederate remained unaltered. These results suggest that the known relationship between testosterone and the motivation for social dominance may reflect in implicit changes in individuals' sensorymotor processing, and not changes in the perceived sensorimotor affordances of others. 519

### 520 **Declarations**

- 521
- 522 **Funding.** CJM received support from the University of Cape Town and the Ernst & Ethel
- 523 Erickson Trust.
- 524 Conflicts of Interest/Competing interests. On behalf of all authors, the corresponding author
   525 states that there is no conflict of interest.
- 526 Ethics approval. This research involved human participants. The study was approved by the
- 527 local ethics committees the University of Cape Town (UCT) Psychology Department and
- 528 the UCT Health Sciences Human Research Ethics Committee. The study was performed in
- 529 accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.
- 530 **Consent to participate.** All participants gave informed written consent to take part in the
- 531 study.
- 532 **Availability of data and material.** Not applicable.
- 533 **Code availability.** Not applicable.
- 534
- 535 **References**
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