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Basal testosterone moderates responses to anger faces in humans

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Abstract

Prior research [van Honk J, Tuiten A, Verbaten R, van den Hout M, Koppeschaar H, Thijssen J, de Haan E. Correlations among salivary testosterone, mood, and selective attention to threat in humans. Horm Behav 1999;36(1):17–24; van Honk J, Tuiten A, Hermans E, Putman P, Koppeschaar H, Thijssen J, Verbaten R, van Doornen L. A single administration of testosterone induces cardiac accelerative responses to angry faces in healthy young women. Behav Neurosci 2001;115(1):238–42.] showed relationships in humans between testosterone (T) and vigilance to facial expressions of anger, which are considered signals of an impending dominance challenge. In Study 1, we used a differential implicit learning task (DILT) (see [Schultheiss OC, Pang JS, Torges CM, Wirth MM, Treynor W. Perceived facial expressions of emotion as motivational incentives: evidence from a differential implicit learning paradigm. Emotion 2005;5(1):41–54.]) to investigate the degree to which subjects find anger faces reinforcing. In the DILT, separate sequences of actions were paired with presentations of anger faces, neutral faces or a blank screen. After training, performance on the three sequences was measured in the absence of face stimuli. Saliva was collected for T measurement. Higher T predicted better learning on sequences paired with sub-threshold (i.e., presented too fast for conscious awareness) anger faces, suggesting that T is related to reinforcing qualities of these faces. In Study 2, we examined whether morning or afternoon T better predicted attention and vigilance to anger faces. Participants were tested at 9:00 and 15:00. At each session, saliva was collected for T measurement, and participants completed a Stroop task and a dot-probe task [Mogg K, Bradley BP, Hallowell N. Attentional bias to threat: roles of trait anxiety, stressful events, and awareness. Q J Exp Psychol A 1994;47(4):841–64.] with facial expression stimuli. Morning (peak) T was a better predictor of responses to anger faces than afternoon T. Morning T predicted greater Stroop-like interference to sub-threshold anger faces, as well as attentional orienting away from sub-threshold anger faces. These effects were not present for joy faces or for supraliminal anger faces. T may generally decrease aversion to threatening stimuli, and/or may specifically facilitate approach towards signals of dominance challenge.

Keywords: Testosterone; Human; Dominance signals; Emotion; Facial expressions of emotion; Anger; Instrumental learning; Dot-probe; Stroop; Circadian; Subliminal; Reward; Anxiety

1. Introduction

The steroid hormone testosterone (T) is produced by the gonads and the adrenals of both sexes. T is well known to be involved in aggression and dominance in mammals, including humans. In rodents, the winner of a dominance challenge has an increase in T; the loser often shows a decrease, e.g., [1]. Studies in primates often find higher T in dominant individuals [2,3]. In humans, T is sometimes found to relate positively to status in both men and women [4–6]. The association between T and status probably is due to a bi-directional causal relationship [7]; as in other species, manipulations in status lead to changes in T in humans. For example, T rises after winning contests such as tennis matches or chess games; recent medical school graduates had higher T than other medical students [4,8]. In turn, higher T may cause individuals to be less averse to dominance challenges from others: animals with higher T are less likely to submit and more likely to win in future challenges [1,9,10], and in humans, T influences the decision to re-enter competition [11]. These findings are consistent with recent applications of the "challenge hypothesis" [12] to primates. T is hypothesized to rise during contexts associated with mating-related competition in order to motivate competitive and aggressive behavior; in turn, success in such competitions and the associated increase in

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status lead to further increases in T [13,14]. This framework is supported by various lines of evidence in humans [13]. Most relevant to the present research is the finding, in humans, of a reciprocal relationship between T and responses to faces displaying anger [15–17], which will be discussed further below. These findings provide suggestive evidence for relationships between T and approach towards dominance challenge-related cues in this species.

Perceived facial expressions of emotion (FEEs) are important social stimuli that can serve as signals of emotional state and thus future behavior of the displayer [18]. As such, even non-conscious viewing of FEEs can impact the viewer's behavior [19,20]. FEEs of anger are particularly salient, assumedly since they signal imminent verbal or physical attack. Individuals selectively attend to anger faces [21,22]; aversive stimuli condition particularly well to anger faces [23,24]; and anger faces activate brain regions involved in emotional salience and emotional learning, such as the amygdala [25,26].

Van Honk et al. [16] demonstrated that selective attention to anger faces in a face version of a Stroop task depended on basal T levels in men and women. T appears to have a causal effect on response to anger faces: T administration increased heart rate responses to anger faces but not to joy faces [17]. These findings suggest that T levels may impact the salience of anger faces, which are important dominance and/or dominance-related cues for humans. However, the valence, if any, of that salience remains to be determined; i.e., whether anger faces are perceived as signals to approach or to avoid to high T individuals. In general, subjects could preferentially attend to anger faces because they signify threat, and are therefore aversive [27]. However, it is also conceivable that a signal of an impending dominance challenge could be rewarding to individuals that have a history of success in such encounters, or, alternatively, that an anger face signifies the sender's frustration and thus represents a positive outcome of such a challenge for the perceiver. If basal T is a marker of dominance status, it is conceivable that anger faces have approach-related properties for individuals high in T relative to their sex.

In Study 1, we aimed to evaluate whether the incentive value (rewarding/aversive properties) of anger faces differs according to basal T. To best investigate the rewarding or punishing effect of a stimulus, subjects should be trained on an arbitrary behavior that is then associated with the stimulus; subjects' subsequent performance of the behavior will reflect the degree to which they are willing to work for the stimulus [28,29]. We used a differential implicit learning task (DILT) in Study 1 to investigate the degree to which subjects find anger faces reinforcing. In the DILT, separate sequences of actions are paired with presentations of anger faces, neutral faces or a blank screen. After training, performance on the three sequences is measured in the absence of face stimuli. Prior to the DILT, saliva was collected for T measurement.

Importantly, the relationship between T and selective attention to anger faces in van Honk et al. [16] was revealed for a T measurement taken 6 h prior to the Stroop task. The authors refer to the classical, relatively slow, genomic pathway of steroid hormone action to explain this effect. However, steroid hormones can also affect neuronal transmission via fast-acting, membrane-bound receptors, e.g., [30]. Note also that T, like many other steroid hormones, displays a robust diurnal rhythm with a morning peak [31–33]. Since T measurements in van Honk et al. [16] began in the morning and Stroop testing took place in the afternoon, an alternate explanation for the six-hour delay is that peak T is a better predictor of T-related behavior than levels of T as they decrease throughout the day. As a parallel, evidence exists for greater stability in waking (peak) cortisol, and relationships between waking cortisol and behavioral measures that do not appear for cortisol measured later in the day [34].

To test whether peak T better predicts attention to anger faces, in Study 2 we collected saliva and measured attention to anger faces at 9:00 and 15:00 in a within-subjects design. If T only predicts attention to anger faces after a six-hour delay, we would expect T at 9:00 to predict attention at 15:00 but not at 9:00. If peak T is the crucial measure, on the other hand, T at 9:00 should predict attention both at 9:00 and 15:00. In order to measure attention directed at anger faces, we utilized two tasks: a Stroop task similar to that used by van Honk and colleagues [15,16], and a dot-probe task [35], both using face stimuli. We expected that relationships between T and attention directed at anger faces could differ between these two tasks, as they appear to capture distinct mechanisms of attention [22,36]. In addition to anger faces, joy faces were included for comparison in both tasks in Study 2.

Finally, since conscious awareness of faces can change effects on brain activity, hormones, and behavior [15,22,37–39], we used two presentation times for face stimuli in both Studies 1 and 2, one allowing for conscious awareness of the face and one not (as tested repeatedly in our laboratory [40,41]).

2. Study 1: methods

Participants were 41 women and 29 men, mean age 21.5 ± 3.7 years, recruited by advertisement and paid $25 for approximately 2.5 h of participation. The study had received prior approval by the University of Michigan Institutional Review Board, and all participants provided informed consent. Sessions took place between 9:00 and 18:00. These participants are a subset of a larger sample recruited for a study on the incentive values of FEEs; effects of implicit motives on the incentive values of these stimuli have been reported elsewhere [41]. During the session, subjects first provided a saliva sample, which was later analyzed for T. Then, subjects worked on the DILT task on a computer, as described below. The task was administered on a computer, and was programmed using Experimental Run Time System software (ERTS; Berisoft Corp., Frankfurt, Germany).

For the DILT, subjects were required to press a key corresponding to one of four screen locations at which an asterisk could appear. They were instructed to do so as quickly and accurately as possible. During the DILT "learning" phase, asterisks appeared in three distinct repeating sequences of 12 keypresses each. Sequences were differentiated by color of asterisks; thus, sequence color served as a discriminatory stimulus. Subjects were simultaneously engaged in a distractor