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BRIEF REPORT

Stress Increases Cue-Triggered "Wanting" for Sweet Reward in Humans

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Stress can increase reward pursuits: This has traditionally been seen as an attempt to relieve negative affect through the hedonic properties of a reward. However, reward pursuit is not always proportional to the pleasure experienced, because reward processing involves distinct components, including the motivation to obtain a reward (i.e., wanting) and the hedonic pleasure during the reward consumption (i.e., liking). Research conducted on rodents demonstrates that stress might directly amplify the cue-triggered wanting, suggesting that under stress wanting can be independent from liking. Here, we aimed to test whether a similar mechanism exists in humans. We used analog of a Pavlovian-Instrumental Transfer test (PIT) with an olfactory reward to measure the cue triggered wanting for a reward but also the sensory hedonic liking felt during the consumption of the same reward. The analog of a PIT procedure, in which participants learned to associate a neutral image and an instrumental action with a chocolate odor, was combined with either a stress-inducing or stress-free behavioral procedure. Results showed that compared with participants in the stress-free condition, those in the stress condition mobilized more effort in instrumental action when the reward-associated cue was displayed, even though they did not report the reward as being more pleasurable. These findings suggest that, in humans, stress selectively increases cue-triggered wanting, independently of the hedonic properties of the reward. Such a mechanism supports the novel explanation proposed by animal research as to why stress often produces cue-triggered bursts of binge eating, relapses in drug addiction, or gambling.

Keywords: stress, incentive salience, wanting, liking, human Pavlovian-Instrumental Transfer

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Have you ever eaten more high-calorie foods during a stressful period? As documented by a consistent corpus of literature (e.g., O'Connor & Conner, 2011), stress cannot only increase the consumption of high-calorie foods, but it can also increase the use of other kinds of rewards, such as drugs (Sinha, 2001) or sexual stimuli (Chumbley et al., 2014). Although these effects of stress have been proven to have a large impact on public health problems (e.g., addiction relapses or binge eating; Lo Sauro, Ravaldi, Cabras, Faravelli, & Ricca, 2008), the underlying psychological mechanisms remain poorly understood.

It has been proposed that rewards are used to reduce the negative effects of stress, which are compensated by the hedonic pleasure triggered by their consumption (Koob & Le Moal, 2001). According to this proposal, stress increases the pursuit of rewards, as consumption is made even more pleasurable by relieving the negative effects of stress.

The incentive salience theory proposes an alternative mechanism in which the key principle is independent of the hedonic properties of the reward (Berridge & Robinson, 1998). According to this theory, the pursuit of a reward is not always directly proportional to the pleasure experienced, because reward processing involves distinct components, including the motivation to obtain a reward (i.e., wanting) and the hedonic pleasure during the reward consumption (i.e., liking), which are usually correlated but can be dissociated under particular circumstances. Experiments conducted on rodents showed that direct manipulation of mesolimbic dopamine increases effort mobilization after the presentation of a reward-associated cue (i.e., wanting), without simultaneously increasing hedonic pleasure (i.e., liking) during reward consumption (Peciña, Cagniard, Berridge, Aldridge, & Zhuang, 2003;

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Wyvell & Berridge, 2000). This supports the idea that wanting and liking rely on two distinct neuronal networks that can be activated independently of each other (Berridge & Robinson, 1998).

Manipulating the glucocorticoid system in a population of rodents, Peciña, Schulkin, and Berridge (2006) provided evidence suggesting that the stress-induced increase of reward pursuits might be driven by a selective increase of wanting. The glucocorticoid system is known to be involved in the mediation of physiological and behavioral responses to stress (Herman et al., 2003). To investigate its effects on wanting, Peciña and coworkers (2006) used a three-phase paradigm called the Pavlovian-Instrumental Transfer test (PIT; Lovibond, 1983). First, during instrumental conditioning, a behavioral response (e.g., pressing a lever) was associated with the food reward. Second, during Pavlovian conditioning, neutral stimuli (i.e., sounds) were associated with the absence or presence of a food reward (negatively or positively conditioned stimulus: conditional stimulus CS− or CS+). During the transfer test, the Pavlovian stimuli (CS+, CS−) were presented and their influence on instrumental action was measured: The increase in action energization after CS+ presentation was taken to reflect cue-induced wanting. After Pavlovian and instrumental conditioning, but before the transfer test, Peciña and colleagues (2006) manipulated the glucocorticoid system by microinjecting cortisol-releasing factor in the nucleus accumbens. Rodents in which the glucocorticoid system was stimulated showed a larger cue-induced wanting compared with rodents who received a placebo treatment. The transfer test was administered under extinction, thus rodents never experienced any aversive state reduction triggered by the hedonic properties of the reward. The investigators thereby demonstrated that, similar to dopamine manipulation, manipulation of stress-related systems increased wanting, independently of the relieving liking dimension of the reward. Although these findings provide a novel explanation for the stress-induced increase of reward pursuits, to the best of our knowledge, they have never been demonstrated in humans.

This study aimed to investigate whether stress influences wanting in humans by using methods and concept operationalizations comparable with relevant animal research. We used an analog of a PIT adapted to a human population (Talmi, Seymour, Dayan, & Dolan, 2008): During instrumental conditioning, an instrumental action (i.e., pressing a handgrip) was associated with chocolate odor (unconditioned stimulus, US). During an analog of a Pavlovian conditioning task geometric figures were associated with the presence (CS+) or absence (CS− and baseline) of chocolate odor (see Pool, Brosch, Delplanque, & Sander, 2014), and during the transfer test, the effort mobilized on the handgrip was measured during the presentation of the Pavlovian stimuli (CS+, CS−, and baseline). After the instrumental and the analogous Pavlovian conditioning but before the transfer test, participants underwent either a stress-inducing task or a control stress-free task (Schwabe, Haddad, & Schachinger, 2008). Participants in the stress and stress-free conditions then performed the transfer test and evaluated how much they liked smelling the chocolate odor.

Based on the animal literature, our prediction was that the cue-induced wanting would be larger in the stress condition than in the stress-free condition, reflected by a larger increase in the effort mobilized during the presentation of CS+ compared with other CSs. We expected this increase of cue-induced wanting for chocolate odor even in the absence of an increase of hedonic pleasure during chocolate odor presentation.

Method

Participants

Forty-one participants who liked chocolate were recruited at the University of Geneva. They were asked not to eat, practice sport, or drink coffee 4 hr before the experimental session and received 30 Swiss francs for their participation. Five participants were later excluded: 2 for technical problems and 3 for being under psychotropic treatment. The 36 (19 men) remaining participants (24.15 ± 3.05 years old) had no reported olfactory trouble.

Materials

Stimuli. The Pavlovian stimuli consisted of three geometric complex figures typically used in human conditioning paradigms (Gottfried, O'Doherty, & Dolan, 2003; O'Doherty et al., 2004; Valentin, Dickinson, & O'Doherty, 2007) that in a pilot study (n = 26) were rated as similarly neutral on a pleasantness scale (see Pool et al., 2014). They were displayed in the center of the computer screen with a visual angle of 8°. The Pavlovian identities of three images used as CS+, CS−, and baseline were counterbalanced across participants. The US consisted of a chocolate odor (20% dissolved in propylene glycol; Firmenich, SA, Geneva, Switzerland), which was released for 1.5 s by using a computer-controlled olfactometer with an airflow fixed at 1.5 L/min delivering the olfactory stimulation rapidly, without thermal and tactile confounds via a nasal cannula (see Ischer et al., 2014).

Instrumental apparatus. The mobilized effort was measured through an isometric handgrip (TDS121C) connected to the MP150 Biopac Systems (Santa Barbara, CA) with a 1,000 Hz sampling rate. The dynamic value of the signal was read by MATLAB (version 8.0) and used to provide participants with visual online feedback (Psychtoolbox 3.0; for the visual interface implemented in MATLAB) that reflected the force exerted on the handgrip. This visual feedback was illustrated through the "mercury" of a thermometer-like image displayed on the left side of the screen (30° visual angle) that moved up and down according to the mobilized effort (see Figure 1a and 1c). The mercury of the thermometer-like display reached the top if the handgrip was squeezed with at least 50% or 70% (criterion varied every 1 s) of the participants' maximal force.

Procedure

First, participants completed the instrumental and the analogous Pavlovian conditioning. After the instrumental and the analogous Pavlovian conditioning but before the transfer test, 18 participants then performed the stress-inducing task, whereas the other group performed a stress-free task. Subsequently, they took a 10-min break, and then performed the PIT test (adapted from Talmi et al., 2008; see Table 1). Finally, they evaluated the perceived pleasantness of the odors.

Instrumental conditioning. Participants learned to squeeze a handgrip to trigger the release of chocolate odor. There were 24 trials each comprised of a 12-s "task-on" period followed immediately by a "task-off" period of 4–12 s (8 s average).

During the task-on periods, a geometric image and a thermometer were displayed in the center and on the left side of the screen,

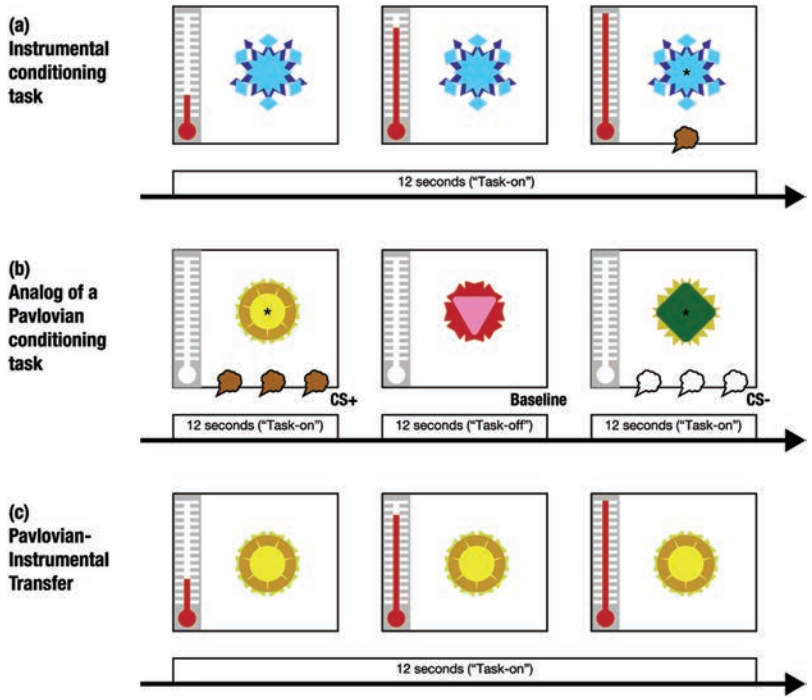

Figure 1. The analog of a human Pavlovian-Instrumental Transfer (PIT) paradigm adapted from Talmi et al. (2008). During instrumental conditioning, (a) participants learned to squeeze a handgrip to trigger the release of a rewarding chocolate odor. During the analogous Pavlovian conditioning, (b) participants were exposed to repeated pairings of the positive conditioned stimulus (CS+) with the rewarding chocolate odor and the negative conditioned stimulus (CS−) with the odorless air. When the CS+ or CS− was displayed, a target appeared in the center of the image and participants had to press a key that triggered odor release. The baseline was displayed without any target, and no odor was released. The PIT test (c) was administered under extinction, the CS+, the CS−, and the baseline were displayed in random order (here a CS+ trial is illustrated), and participants could squeeze the handgrip if they wished to do so. See the online article for the color version of this figure.

respectively. The fluid movement of the thermometer-like display's mercury provided online visual feedback of the effort participants exerted on the handgrip (see Figure 1a). Participants were asked to keep their gaze on the central geometric image and to squeeze the handgrip, thereby bringing the mercury of the thermometer- like display up to the maximum and then down again, without paying attention to the speed of compressing the grips. They were told that during the 12-s presentation of the thermometer-like display, there were three "special 1-s windows" and that if they happened to squeeze the handgrip during one of these time windows, they would trigger the release of chocolate odor. Finally, they were told that they were free to choose when to squeeze on the grip and were encouraged to use their intuition. In reality, only two special 1-s windows were randomly selected in each task-on period to be rewarded with chocolate odor, and if participants happened to squeeze the handgrip with at least 50% or 70% of their maximal force during these time windows, a sniffing signal (a black asterisk; 2° visual angle) was displayed at the center of the geometric image and the chocolate odor was delivered. During the task-off periods, a fixation cross (2° visual angle) was

Table 1
Illustration of the Analog of a Human Pavlovian Instrumental Transfer Test Combined With Stress Induction

Phase 1 Instrumental conditioning	Phase 2 Analogous Pavlovian conditioning	Stress induction	Phase 3 Transfer test in extinction
24 trials R → O1	18 trials CS+ → O1 18 trials CS− → Ø	SECPT or WWT	6 trials CS+ → R? 6 trials CS− → R? 6 trials baseline → R?

Note. The instrumental action (R) consists of pressing a handgrip dynamometer. The conditioned stimuli (CS) consist of geometric images. The CS+ is associated with a chocolate odor (O1), whereas the CS− is associated with the absence of a chocolate odor (Ø). Participants in the stress group performed the socially evaluated cold pressor test (SECPT; Schwabe et al., 2008), thereby inducing stress. Participants in the stress-free group performed a warm water test (WWT; Schwabe et al., 2008). The analog of the human Pavlovian instrumental transfer procedure has been adapted from Talmi et al. (2008) for our research question.

displayed at the center of the screen and participants were asked to keep their gaze on the fixation cross and to relax their hand to recalibrate the baseline force.

Analogous Pavlovian conditioning. The procedure that we previously elaborated (Pool et al., 2014) was applied here. Briefly, three initially neutral images were attributed the Pavlovian roles of "baseline," "CS+," and "CS−." There were 36 trials composed of a 12-s task-on period during which the CS+ or the CS− was displayed on a computer screen, followed by a 12-s task-off period during which a baseline image was displayed.

During the task-on periods, a target appeared every 4 s at the center of the CS image three times per period. Participants had to press the "A" key as fast as possible after they perceived the target that was presented for a maximum of 1 s. Each time the CS+ image was displayed and the participant pressed the key, a chocolate odor was released; when the CS− image was displayed, odorless air was released. Participants were informed that the kind of odor released depended only on the CS image and not on the key-pressing task. They were told that the key-pressing task was a measure of their sustained attention independent of the odor-image contingencies (see also Talmi et al., 2008). To further emphasize this aspect, participants were also informed that the odor would be released after a 1-s interval after target onset if they had not responded until then. However, the odor was released faster when participants pressed on the keyboard than when participants did not press on the keyboard. Because of this instrumental component the conditioning task can be considered a hybrid of Pavlovian and discriminative instrumental learning, rather than a pure Pavlovian learning. During the task-off periods, the baseline image was displayed without any target, and no odor was released (see Figure 1b).

After the analogous Pavlovian conditioning, participants evaluated the pleasantness of the images used as CS+, CS−, and baseline on a visual analog scale (from extremely unpleasant to extremely pleasant) presented at the center of the computer screen with a visual angle of 23°. The order of the images was randomized across participants.

Stress manipulation. After the pleasantness ratings of the images used as CS+, CS−, and baseline, participants belonging to the stress group ($n = 18$; 8 men) performed a socially evaluated cold pressor test (as described by Schwabe et al., 2008). They were asked to immerse their nondominant hand in cold water (0–2 °C) for as long as possible (they could remove the hand at their discretion, but the test was ended by the experimenter after 3 min). They were told that they were being videotaped to analyze their facial expression, and the experimenter observed them the entire time. The stress-free group ($n = 18$; 10 men) was instructed to put their hand in warm water (35–37 °C) for 3 min without being observed (warm water test). Immediately after the cold pressor task, using pencil and paper participants evaluated on a scale how pleasant, stressful, and painful the task was for them, from 0 (*not at all*) to 10 (*extremely*). Ten minutes before and 30 min after the task, samples of saliva were collected through Salivette (Sarstedt AG & co, Nümbrecht, Germany), as a manipulation check.

PIT test. After the stress induction task participants took a 10-min break and then they received the same instructions as in instrumental conditioning. First they completed 12 trials identical to those in instrumental conditioning (two special 1-s windows were rewarded) followed by 12 trials administered under partial extinction (one special 1-s window was rewarded). Immediately afterward, they performed 18 transfer test trials administered under extinction (no time window was rewarded). In the transfer test, one of the Pavlovian stimuli (CS+, CS−, or baseline) replaced the instrumental geometric image during the entire trial (see Figure 1c). The presentation order on the transfer tests was randomized across the three stimuli (CS+, CS−, and baseline). There were two cycles of testing. In each cycle, each cue was presented three times consecutively, so that each Pavlovian stimuli was presented six times for a total of 18 transfer trials.

Odor evaluation. Immediately after the PIT, participants evaluated the pleasantness (from extremely unpleasant to extremely pleasant), the familiarity (from not familiar at all to extremely familiar), the edibility (from not edible to extremely edible), and the intensity (from not perceived to extremely strong) of the chocolate odor and the odorless air on visual analog scales displayed on a computer screen.

Results

Instrumental Conditioning

A repeated-measures analysis of variance (ANOVA) applied to the number of squeezes surpassing 50% of each participant's maximal force (Talmi et al., 2008) over 24 trials revealed a marginal effect of trial, $F(23, 805) = 1.50$, $p = .06$, $\eta^2 = .04$, 95% confidence intervals (CIs) = .00, .05 suggesting that participants learned that squeezing the handgrip triggered the release of the rewarding chocolate odor. Figure 2A shows that participants readily learned to squeeze after five trials; a linear contrast showed that the squeeze frequency increased linearly during these first five trials, $t(35) = 2.99$, $p < .01$, $d = .32$, 95% CIs = .09, .53. This increase was not significant in Trials 6–15 or in Trials 15–24 ($ps > .6$).

To control that participants assigned to stress and stress-free groups did not statistically differ in their Pavlovian learning, we applied a 5 (trials: 1, 2, 3, 4, or 5) × 2 (group: stress or stress-free) mixed repeated-measures ANOVA to the number of squeezes surpassing the criterion of 50% of the participants' maximal force. The analysis revealed a main effect of trial $F(4, 136) = 5.23$, $p < .01$, $\eta^2 = .13$, 95% CIs = .01, .54, without a significant interaction between image and group ($p = .69$); therefore, suggesting that the increase of squeeze frequency over time was similar in participants that would have later been assigned to the stress and the stress-free group. This analysis also revealed a descriptive difference in the average squeeze frequency between the two groups, participants that would have later been assigned to the stress-free group squeezed on average 1.88 more than the participants that would have later been assigned to the stress group. This difference was not significant ($p = .13$), but it was large. Therefore, we decided to control for these pre-existing differences in all the statistical tests assessing the effect of stress by comparing the squeeze frequency between the two groups after the stress induction task.

Analogous of Pavlovian Conditioning

Successful Pavlovian contingency learning was revealed by both the reaction times (RTs) of the key-pressing task and the

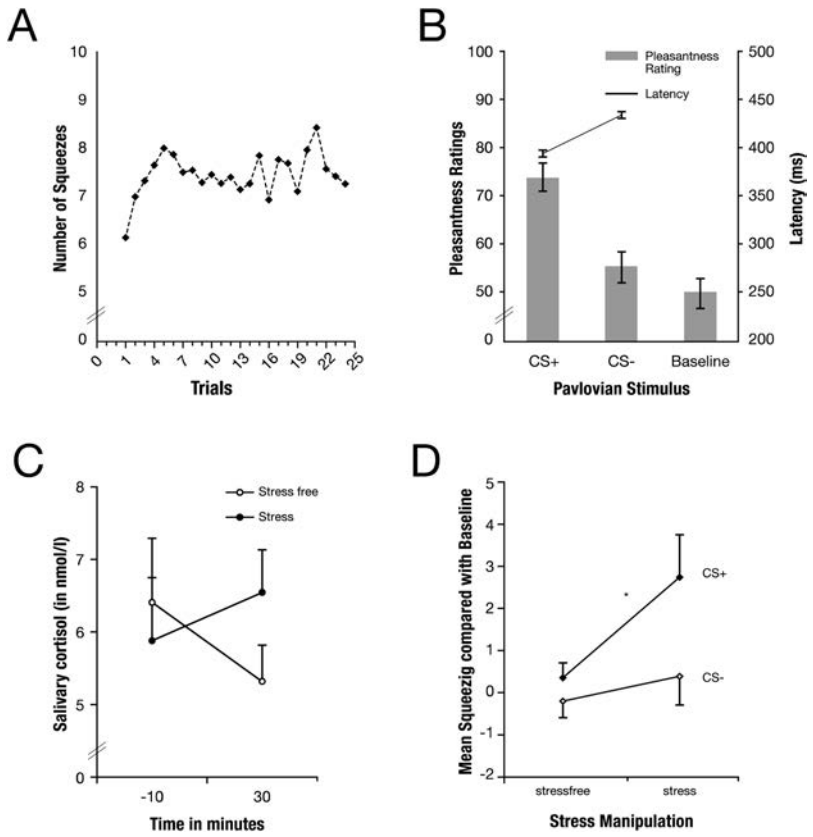

Figure 2. (A) Instrumental conditioning. The number of times participants (n = 36) squeeze the handgrip is displayed as a function of trials over time. (B) The analogous Pavlovian conditioning. The bars (left axis) illustrate the pleasantness rating of the images used as Pavlovian stimuli after conditioning, and the line plot (right axis) illustrates the latency to detect the cue during the presentation of the positive conditioned stimulus (CS+) or the negative conditioned stimulus (CS−). Error bars (±1 *SEM*) are adapted for within-subject design (Cousineau, 2005). (C) Salivary cortisol (nanomoles per liter) 10 min before and 30 min after the stress-inducing and the control task. Error bars represent *SEM*. (D) The PIT in the stress-free and the stress groups (n = 18 in each group). The increase of the number of squeezes compared with the baseline is displayed as a function of the CS+ and the CS−. Error bars represent *SEM*.

likability of the CSs (see Figure 2B). For the key-pressing task, we analyzed RTs on the first target of the on-task period. All responses that were more than 3 *SD*s from the mean (>2% of the trials) or absent (>5.5% of the trials) were removed. A paired t test showed that participants were faster when the CS+ was displayed than when the CS− was displayed, $t(35) = 3.60$, $p < .01$, $d = .37$, 95% CIs = .15, .39.

A repeated-measures ANOVA applied to the likability ratings of the three Pavlovian images (CS+, CS−, or baseline) revealed a significant effect, $F(2, 70) = 10.89$, $p < .01$, $\eta^2 = .23$, 95% CIs = .14, .55; participants liked the CS+ image more than the CS−, $t(35) = 3.47$, $p < .01$, $d = .73$, 95% CIs = .27, 1.17, which did not statistically differ from the baseline in likability ratings ($p = .35$).

To control that participants assigned to the stress and stress-free groups did not statistically differ in their Pavlovian learning, we applied a 2 (image: CS+ or CS−) × 2 (group: stress or stress-free) mixed repeated-measures ANOVA to the RTs. The analysis revealed a main effect of image, $F(1, 34) = 12.66$, $p = .01$, $\eta^2 = .27$, 95% CIs = .05, .48, without interaction between image and group ($p = .67$); therefore, suggesting that the difference between CS+ and CS− was similar in participants that would later be assigned to the stress and the stress-free group. A 3 (image: CS+, CS−, baseline) × 2 (group: stress or stress-free) mixed repeated-measures ANOVA was applied to the likability ratings. The analysis revealed a main effect of image, $F(2, 68) = 10.83$, $p < .01$, $\eta^2 = .24$, 95% CIs = .12, .57, without a significant interaction between the effect of image and group ($p = .44$), thereby suggesting that the effect of image on the likability rating was similar in participants that would later be assigned to the stress and the stress-free groups.

Stress Manipulation

On average, participants who performed the socially evaluated cold pressor test (stress group) kept their hand in the cold water for 80.61 s (*SEM* = 14.75) and they reported a higher level of stress (M = 5.22, *SEM* = 0.67) and pain (M = 6.33, *SEM* = 0.67),

*t*s(34) = 5.95, 9.42, *p*s < .01, *d*s = 2.04; 3.23, 95% CIs = 1.16, 2.77; 2.13, 4.11 compared with the participants who performed the warm water test (stress-free group; *M*s = 0.77, 0.33, *SEM*s = 0.33, 0.16, respectively). Participants in the stress group also reported a lower level of pleasure (*M* = 2.11, *SEM* = 0.46) than participants in the stress-free group (*M* = 6.99, *SEM* = 0.58; *t*(34) = 6.421, *p* < .001 *d* = 2.202, 95% CIs = 1.23, 2.88). Moreover, the prepost variation of cortisol induced by the task was marginally larger in the stress group compared with the stress-free group, *t*(34) = 2.20, *p* = .051 *d* = .75, 95% CIs = .05, 1.40 (see Figure 2C).

PIT test

A 3 (image: CS+, CS−, and baseline) × 6 (extinction trial) × 2 (group: stress or stress-free) mixed repeated-measures ANOVA was applied to the number of squeezes surpassing 50% of the participants' maximal force. Because there was a large difference in the average squeeze frequency during the instrumental conditioning between participants attributed to the stress and the stress-free groups, the average squeeze frequency during the instrumental conditioning was modeled as a covariate in all the between groups tests. The analysis revealed a main effect of image, $F(2, 68) = 6.61$, $p < .01$, $\eta^2 = .16$, 95% CIs = .04, .47, indicating that the squeeze frequency increased during the CS+ compared with the CS−, *t*(35) = 2.79, *p* < .01, *d* = .41, 95% CIs = .11, .72, which did not statistically differ from the baseline (*p* = .83). Moreover, the analysis revealed a main effect of trial number, $F(5, 170) = 2.71$, $p = .02$, $\eta^2 = .07$, 95% CIs = .01, .44, showing that the squeeze frequency globally decreased over time. Most important for our hypothesis, the analysis showed a two-way interaction between image and group, $F(2, 66) = 5.911$, $p < .01$, $\eta^2 = .15$, 95% CIs = .04, .46, revealing that the increase in number of squeezes toward the CS+ (compared with the CS−) was larger in the stress group compared with the stress-free group, *t*(34) = 2.32, *p* = .02, *d* = .77, 95% CIs = .09, 1.44 (see Figure 3A and B and Figure 4A). Furthermore, this analysis did not reveal a main effect of group (*p* > .1), suggesting that the stress and the stress-free groups did not statistically differ in the overall squeeze frequency.

To further investigate whether the effect of stress was specific to the CS+, we computed the relative score for the CS+ and the CS−, by subtracting the squeeze frequency during the presentation of the baseline image from the squeeze frequency during the presentation of the CS (i.e., [CS+− baseline] and [CS−− baseline]). We then conducted two planned contrasts. These contrasts revealed that the relative increase in number of squeezes toward the CS+ was significantly larger in the stress group compared with the stress-free group, *t*(34) = 2.39, *p* = .03, *d* = 1.04, 95% CIs = .11, 1.47, but the relative number of squeezes toward the CS− did not significantly differ between the two groups (*p* > .4; see Figure 2D).

Odor Evaluation

Paired *t* tests revealed that the chocolate odor was evaluated as being more edible, *t*(34) = 9.38, *p* < .01, *d* = 1.27, 95% CIs = .63, 1.43; more intense, *t*(34) = 10.88, *p* < .001, *d* = 2.06, 95% CIs = 1.42, 2.61; more familiar, *t*(34) = 5.28, *p* < .01, *d* = .70, 95% CIs = .38, .99; and more pleasant, *t*(34) = 6.19, *p* < .01, *d* = 1.60, 95% CIs = .63, 1.43, than the odorless air. The perceived pleasantness of the chocolate odor was not significantly different in the stress and the stress-free group, *t*(34) = .19, *p* = .85 (see Figure 4B). Moreover, the two groups did not significantly differ on the perception of the other dimensions of odor (all *p*s > .4), nor in the differential perceived pleasantness of the chocolate odor compared with the odorless air (*p* > .7)

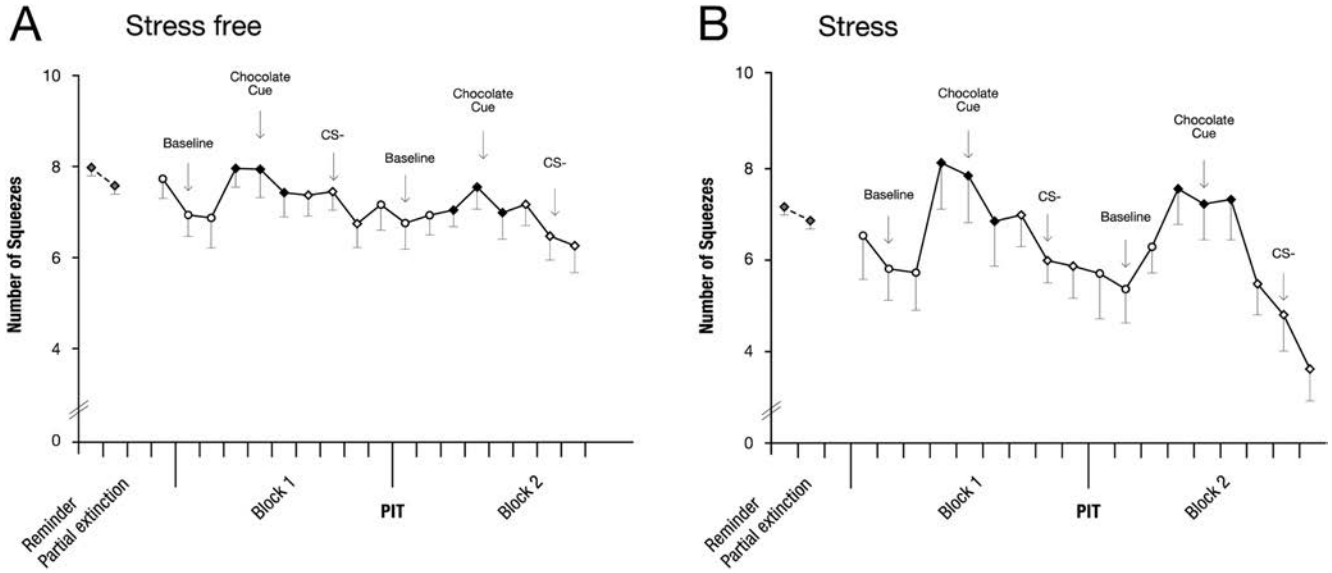

Figure 3. PIT in the stress-free (A) and the stress (B) group. The number of times participants (*n* = 18 in each group) squeezed the handgrip is displayed as a function of the conditioned stimuli (CSs) perceived by the participants during the block administered under extinction. Each CS was presented three times in a row during one block and the presentation order of the CSs in each block was randomized.

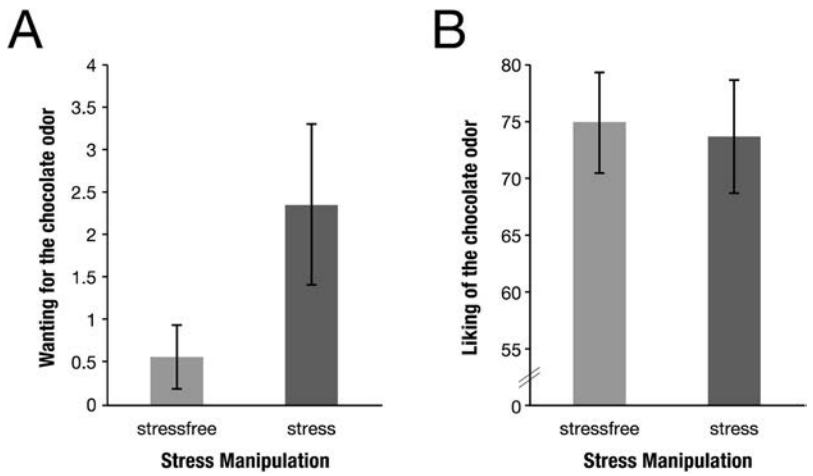

Figure 4. (A) Wanting for chocolate odor (increase in the number of squeezes during presentation of the CS+ compared with the CS−). (B) Liking of chocolate odor (rating on a scale from 0 to 100). Error bars represent *SEM*.

Discussion

This study aimed to investigate whether, as predicted by the incentive salience theory, stress increases wanting in humans. We used paradigms and concept operationalizations that were as similar and comparable as possible to those used in previous research conducted on rodents. We adapted an analog of a human PIT, which originally used a monetary reward (Talmi et al., 2008), by instead using an olfactory reward (i.e., chocolate odor) to assess the effort mobilized to obtain it (i.e., wanting) and the hedonic pleasure during its consumption (i.e., liking); we administered this paradigm in stress and stress-free conditions. Our findings demonstrate, in humans, that the cue-triggered wanting observed in the analog of a PIT was amplified in the stress condition compared with the stress-free condition. Moreover, results showed that global effects in the analog of a PIT with an olfactory reward are similar to those in the analog of a PIT with a monetary reward: The effort mobilized in instrumental action is influenced by the presentation of Pavlovian stimuli. The effort invested in instrumental action was larger during the presentation of the stimulus that was previously associated with chocolate odor, as compared with the presentation of the stimuli that were not.

Note that the analogous Pavlovian conditioning we used involved an instrumental component (i.e., pressing a key to discover whether the image was associated with a chocolate odor or not). Colwill and Rescorla (1988) demonstrated that transfer effect is significantly bigger for discriminative stimuli (i.e., stimuli predicting a privileged time interval during which an instrumental action leads to a reward) compared with Pavlovian stimuli. Nonetheless, in contrast to the discriminative instrumental learning, in our Pavlovian procedure the instrumental action had limited predictive value: the chocolate odor was delivered based on the CS image, even when the instrumental action was not performed.

Comparable with that in rodents (Peciña et al., 2006), this wanting amplification in humans is critically dependent on the interaction between the state of the individual (i.e., stress) and the presence of a reward-associated cue in the environment (see Figure S1 in Supplemental Materials for a visual comparison). Stress did not globally increase effort mobilization, therefore, ruling out possible motor confounds as well as the possibility that the increase of effort induced by stress relied on a general state of arousal. Descriptively, the stress-free group squeezed globally more than the stress group during the PIT; however, this descriptive difference was not statistically significant and it was already present during the instrumental conditioning was administered before the stress manipulation. Therefore, differences in the global squeeze frequency were probably because of a simple sampling effect rather than an effect of stress (see supplementary analysis for more details). Consistent with the animal literature (e.g., Peciña et al., 2006), the stress amplification seemed to be specific to the perception of the reward-associated cue: during the presentation of the reward-associated cue, the stress group mobilized more effort than the stress-free group, but during the presentation of the stimulus that was not associated with the reward the stress-free and the stress group did not seem to behave differently. Moreover, the stress induction procedure was administered after the Pavlovian and instrumental conditioning, thereby excluding possible confounds related to learning processes (see, e.g., Allman, DeLeon, Cataldo, Holland, & Johnson, 2010, for a similar procedure).

Our results also showed that, although participants mobilized more effort to smell the chocolate odor when under stress, they did not report the odor as being more pleasurable. This finding supports the incentive salience theory, which postulates that wanting and liking represent two different components of reward processing that can be activated independently of each other under particular circumstances (Berridge & Robinson, 1998, 2003). It also supports the idea that the increase of reward pursuits induced by stress might not be driven by a top-down attempt to relieve the negative effects of stress through reward consumption (Koob & Le Moal, 2001), but may instead be driven by a direct bottom-up effect of stress on cue-triggered wanting (Peciña et al., 2006). Although the present finding provides evidence showing that stress increases cue-triggered wanting and not self-reported liking, the

mechanism underlying this phenomenon remains to be explored. Recent evidence from animal (Cabib & Puglisi-Allegra, 2012) and human (e.g., Lewis, Porcelli, & Delgado, 2014) literature suggests that stress increases the dopaminergic activity in the ventral striatum. According to the incentive salience theory, the dopaminergic activity in this region is selectively involved in wanting (and not in liking; Berridge & Robinson, 2003); therefore, one could speculate that stress directly and selectively activate the mesolimbic brain network involved in wanting.

In contrast to previous rodent experiments, in our study, we did not manipulate brain activity; instead, we used a more ecological procedure to induce stress behaviorally. This suggests that the selective activation of a reward component can occur not only when the brain is directly manipulated (Havermans, 2011, 2012), but can also occur in more ecological settings such as behavioral manipulation. Note, however, that in our study, differences in the increase of cortisol between the two groups was smaller compared with those in other experiments that used the same procedure of stress induction (Schwabe et al., 2008). This might be because we included female participants, thereby increasing the noise of the cortisol measure, variation being because of menstrual cycle effects on cortisol responses (Kirschbaum, Pirke, & Hellhammer, 1993; see also Figure S2 in Supplemental Materials).

The stress effect on "wanting" was significant but rather moderate. The moderate size of the effect is not surprising given that findings on rodents have similar effect sizes (Peciña et al., 2006) and that in an experimental setting we could only induce a mild stress. Therefore, future studies are necessary to further investigate the effect of more intense everyday life stressors on human wanting and liking.

In conclusion, the present study supports the conceptualization of a hedonic-independent mechanism underlying the increase of reward pursuits induced by stress (Peciña et al., 2006) by showing that, compared with a stress-free situation, in a stressful situation participants are willing to work more to obtain a reward, even though they do not report liking it more. This selective increase of cue-triggered wanting from stress might be crucial for modeling the effects of stress on binge eating, relapses in addiction, and gambling.

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