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Individual Concerns Modulate Reward-Related Learning and Behaviors Involving Sexual Outcomes

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Abstract

Pavlovian and instrumental conditioning are fundamental processes helping organisms learn about stimuli that predict rewards in the environment and actions that lead to their obtainment. These two forms of learning and their interplay notably exert a strong impact on reward-seeking behaviors. Here, we examined in humans whether Pavlovian and instrumental learning along with their effects on cue-driven behaviors involving sexual rewards are modulated by the reward relevance to the individual's sexual orientation. In two experiments, we manipulated the concern-relevance of sexual outcomes in a Pavlovian-instrumental transfer paradigm by recruiting heterosexual and homosexual men and selecting sexual stimuli for each sexual orientation. Results showed enhanced instrumental and Pavlovian learning in response to the most relevant sexual outcome to participants' sexual orientation as well as increased reward-seeking behaviors in response to its associated cue compared to the less relevant sexual outcome and its associated cue, respectively, thereby reflecting that inter-individual differences in sexual concerns modulated these effects. These findings suggest that motivational influence on reward-related learning and behaviors involving sexual stimuli relies on inter-individual differences in concerns and contribute to fostering further insight into the mechanisms underlying human reward-seeking behaviors.

Keywords: reward-seeking behaviors, sexual outcomes, individual differences, learning, affective relevance

Individual Concerns Modulate Reward-Related Learning and Behaviors Involving Sexual Outcomes

Rewards are an essential part of the environment; they enhance species' chances at surviving and reproducing by guiding their eating, drinking, and mating behaviors (Schultz 2015). Learning about stimuli that predict rewards and behaviors that lead to their obtainment thus holds a pivotal adaptive value to organisms. Across a wide range of species in the animal kingdom, these varieties of learning are notably achieved through Pavlovian and instrumental conditioning (e.g., Bouton, 2007; Fanselow & Wassum 2016). While Pavlovian conditioning allows organisms to learn predictive relationships between stimuli and rewarding outcomes, thereby helping them prepare for the upcoming reward before its actual occurrence (Domjan, 2005; Pavlov, 1927; Rescorla, 1988), instrumental conditioning enables them to learn specific actions that contingently produce rewarding outcomes (Bouton, 2007).

Albeit independent, Pavlovian and instrumental learning processes interact in a number of ways, their interplay having a powerful influence on reward-seeking behaviors (Corbit & Balleine, 2016; O'Doherty et al., 2017; Rangel et al., 2008). In particular, the perception of a Pavlovian cue that predicts the occurrence of a reward can invigorate an instrumental action associated with that reward, even though the cue and the action have never been formally associated (e.g., Dickinson & Balleine, 2002; Estes, 1948; Rescorla & Solomon, 1967). This phenomenon is known as Pavlovian-instrumental transfer (PIT) and can generally take two forms: outcome-specific and general (Cartoni et al., 2016; Corbit & Balleine, 2005; Holmes et al., 2010). In outcome-specific PIT, the Pavlovian cue exerts a selective influence on the instrumental action associated with the same reward, whereas in general PIT, the cue determines the vigor of instrumental responding irrespective of the specific outcome involved (e.g., Garofalo et al., 2019; Nadler et al., 2011; Prévost et al., 2012). PIT has been suggested to underlie a large spectrum of common behaviors such as

food seeking or decision-making (Cartoni et al., 2016; Holmes et al., 2010; Talmi et al., 2008). It has also been suggested to play a central role in addiction-related disorders (Belin et al., 2009; Everitt & Robbins, 2005; Garbusow et al., 2016), although evidence for this claim remains equivocal in humans (see, e.g., Hogarth & Chase, 2011; Hogarth & Field, 2020; van Timmeren et al., 2020).

A strong line of research in animals and humans has highlighted that a key factor modulating Pavlovian and instrumental learning along with their influence on reward-seeking behaviors consists of the reward's relevance for the organism's motivational state (e.g., Bindra, 1974; Dickinson & Balleine, 1990, 1994; Zhang et al., 2009; see also Pool, Sennwald et al., 2016). More specifically, manipulation of the organism's homeostatic or physiological needs (e.g., hunger, thirst, salt appetite, stress) has been shown to exert a strong and immediate influence on reward-seeking behaviors triggered by the perception of a reward-associated stimulus (e.g., Balleine, 1994; Dickinson & Balleine, 1990; Pool et al., 2015; Robinson & Berridge, 2013). For instance, Dickinson and Balleine (1990) showed that rats trained to press a lever to receive a sucrose solution or saline upon the perception of a cue, selectively increased their pressing performance to obtain the sucrose solution under extinction only when it was relevant to their physiological state (i.e., when they were hungry). Such shifts in physiological states have been most consistently shown to impact the general motivational influence of Pavlovian cues on instrumental responding (i.e., general PIT) both in animals (e.g., Corbit et al., 2007) and humans (e.g., Hebart & Gläscher, 2015; Watson et al., 2014; but see Colagiuri & Lovibond, 2015; De Tommaso et al., 2018, for conflicting results). By contrast, evidence for the influence of the reward motivational relevance on outcome-specific PIT is more mixed. Some studies have reported that outcome-specific PIT effects are sensitive to devaluation procedures (e.g., satiation) diminishing the motivational value of the outcome (e.g., Eder & Dignath, 2016; Seabrooke et al., 2017,

2019), whereas others suggest these effects are insensitive to such procedures (e.g., Corbit et al., 2007; Holland, 2004; Hogarth & Chase, 2011; van Steenbergen et al., 2017; Watson et al., 2014; see Mahlberg et al., 2019, for a review in humans).

Based on incentive motivation models (e.g., Bindra, 1974; Bolles, 1972; Toates, 1998) and the incentive salience hypothesis (Berridge & Robinson, 1998, 2016), the findings that the organism's physiological state can modulate Pavlovian cues' influence on (nonselective) instrumental responding have been interpreted as reflecting that homeostatic motivation states act to enhance the incentive value of relevant rewards and their associated cues. Such heightened incentive value in turn contributes to facilitating learning and potentiating the general motivational influence of reward-associated cues on reward-seeking behaviors (Dickinson & Balleine, 2002). Incentive value enhancement occurs through an increase in incentive salience and typically—but not necessarily (see, e.g., Robinson & Berridge, 2013; Wassum et al., 2011)—liking (see Berridge, 2018; Toates, 1998). In particular, the organism's physiological state has been postulated to directly determine the incentive salience of a reward-predicting cue in concert with the associative history between the cue and the reward (Dayan & Berridge, 2014; Zhang et al., 2009).

Although animal and human research has mainly investigated the interactions between the organism's motivational states and homeostatic rewards, several human studies have indicated that the outcome motivational relevance can also influence cue-driven behaviors involving non-homeostatic rewards, such as monetary or social rewards (e.g., Garbusow et al., 2016; Huys et al., 2011; Lehner et al., 2017; Sebold et al., 2016). Notably, Lehner et al. (2017) showed that general PIT effects were elicited by cues associated with a food, a monetary, or a social reward that were matched in subjective value independently of the reward type, and that the strength of these effects was positively related to individual variations in ratings of the reward value. This therefore suggests that the effects of the reward

relevance on cue-elicited reward-seeking behaviors are not specific to homeostatic motivational states but extend to a larger variety of motives.

Consistent with this notion, it has been recently proposed that the concept of incentive salience could be expanded, at least in humans, to the psychological construct of affective relevance (Pool, Sennwald et al., 2016; Sennwald et al., 2017) deriving from appraisal theories of emotion (Sander et al., 2005, 2018; Scherer & Moors, 2019). Affective relevance appraisal is a rapid, adaptive process that establishes whether a stimulus encountered in the environment is relevant to the organism's concerns (Pool, Brosch et al., 2016; Sander et al., 2005, 2018; Stussi et al., 2019, 2021; Stussi, Pourtois et al., 2018). Concerns refer to affective representations of physiological and psychological needs, goals, and values that are of major importance to the organism (see Frijda, 1986; Pool, Brosch et al., 2016; Sander et al., 2018; Stussi, Pourtois et al., 2018). Of particular importance, these concerns are pertinent for a given individual at a certain moment in time (Scherer, 2013), the process of affective relevance and its influence on learning and behaviors being thereby largely affected by individual differences (Sander et al., 2005; Stussi et al., 2019, 2021). Accordingly, whereas affective relevance and incentive salience are closely related in that they both stem from the synergetic interplay between the stimulus event and the organism's motivational state, affective relevance is not limited to physiological needs, but encompasses multiple categories of concerns, including momentary goals or more complex aspects tied to self-concepts for instance (Pool, Sennwald et al., 2016).

Within this framework, we here sought to test further the hypothesis that inter-individual differences in concerns beyond purely homeostatic needs modulate Pavlovian and instrumental learning along with their influence on reward-seeking behaviors by using sexual stimuli as rewarding outcomes. Sexual stimuli exert strong effects on human behavior (e.g., Gola et al., 2016; Pool, Brosch et al. 2016; Sennwald et al., 2016, 2020), rendering them a

powerful tool to investigate human reward processing. More importantly, although sexual reward processing relies on some shared neurobiological and psychological mechanisms with food reward processing (Toates, 2014), they differ in some aspects, with sexual rewards being generally relevant to more complex concerns than primarily physiological ones (e.g., Georgiadis & Kringelbach, 2012). Food and drink are types of rewards organisms will seek to try to correct homeostatic imbalances (Schultz, 2015) and are biologically imperative behaviors (Toates, 2014). If an organism is extremely hungry or thirsty, any food or drink ingested (on condition that they contain the necessary nutrients) will suffice no matter how abhorrent it is to the organism in order to maintain chemical and energy levels within their body (Toates, 2014). By contrast, while sex is a primary reward in the sense that it is important for the species' reproduction and survival (Olsen, 2011), deprivation of sex will not result in the death of the organism and certain conditions will still need to be met for it to engage in sexual behaviors (Toates, 2014). Indeed, sexuality is critically dependent on inter-individual differences (Chivers et al., 2007; Toates, 2009), which means that the same stimulus will not elicit sexual desire and sexual arousal in everyone. An individual's sexual identity, including their sexual orientation, will strongly influence their sexual behavior and sexuality in general (Chivers et al., 2007; Talley & Stevens, 2017).

In two experiments, we examined to what extent the sexual outcome's relevance for the sexual orientation of the participants modulates Pavlovian and instrumental learning and cue-elicited reward-seeking behaviors. To this end, heterosexual (Experiments 1 and 2) and homosexual (Experiment 2) human male participants were recruited, and sexual outcomes were selected for each sexual orientation. Participants first indicated their liking of erotic images of women and men, as well as of neutral scrambled images. Subsequently, they underwent a single-response PIT procedure typically used on animals (Holmes et al., 2010), which has also been adapted to humans (e.g., Pool et al., 2015; Talmi et al., 2008). This

procedure has been suggested to specifically trigger general as opposed to outcome-specific PIT effects (Cartoni et al., 2016). In an instrumental learning phase, participants initially learned to associate sexual outcomes—their most liked image of a naked woman and of a naked man—with an instrumental action (i.e., squeezing a handgrip). In the following phase, they learned to associate geometric shapes (i.e., conditioned stimuli, CSs) with said image of the woman (CS_{w+}), of the man (CS_{m+}), and of the scrambled image (CS_{s+}) rated as the most neutral, during a Pavlovian learning task. Learning of the contingencies between the CSs and the outcomes was assessed through reaction times in a keypress task and liking ratings of the CSs (see, e.g., Gottfried et al., 2003; Pool et al., 2015; Talmi et al., 2008). In the final transfer test phase, the CSs were presented without being followed by their previously associated outcome (i.e., under extinction), while the number of squeezes exerted in the presence of each CS was measured and served as an indicator of cue-elicited reward-seeking behaviors.

We predicted that participants would show enhanced instrumental and Pavlovian learning, as well as heightened reward-seeking behaviors, in response to the sexual outcomes and their associated cues that are more relevant to their sexual concerns as a function of inter-individual differences in sexual orientation. Specifically, our hypothesis was that heterosexual men would exhibit (a) a higher squeezing frequency to reveal the image of the woman than that of the man in the instrumental learning phase, and (b) faster reaction times in the Pavlovian learning phase and (c) a larger increase in squeezing frequency in the transfer test phase during the presentation of the cue associated with the woman compared to the cue associated with the man, whereas homosexual men would show the opposite pattern.

Method

Participants

Two independent groups of healthy male participants were recruited from the general population in Geneva. All participants provided informed consent prior to the start of the experiment. The study was conducted in accordance with the Declaration of Helsinki and approved by the Regional Research Ethics Committee in Geneva (protocol number: 14-246). We complied with all relevant ethical regulations throughout the study.

Experiment 1 exclusively sampled heterosexual participants, whereas Experiment 2 sampled both heterosexual and homosexual participants. Across both experiments, participants' sexual orientation was established using their summed Kinsey ratings (Kinsey et al., 1948) on four different aspects of sexual orientation: sexual attraction, sexual behavior, sexual fantasies, and sexual identity. These ratings were measured on a 7-point scale going from 0 (*exclusively heterosexual*) to 6 (*exclusively homosexual*), with an additional option allowing participants to not disclose this information (*I would rather not say*). A participant was considered heterosexual if his summed score was equal to or less than 5, and homosexual if his summed score was equal to or more than 19.

In Experiment 1, 38 men between the ages of 18 and 37 participated. Data from three participants were omitted from the analyses as their summed Kinsey ratings exceeded five. The final sample included 35 heterosexual men (M sexual orientation sum = 0.34, SD = 1.08; M age = 26.34, SD = 4.97). The sample size was determined based on a power analysis performed with G*Power 3 (Faul et al., 2007). This analysis showed that at least 34 participants were required to detect a moderate effect (d = 0.50; see Pool et al., 2015; Talmi et al., 2008) with a power of 80% using a two-tailed paired t test. For counterbalancing purposes in the associations between the CSs and the outcomes, we aimed for a final sample of 35 participants with analyzable data. Data collection ended once that number was reached.

In Experiment 2, 45 men aged between 18 and 42 years old were recruited. Data from three participants were excluded from the analyses due to their summed Kinsey scores being

situated between 6 and 18. Two additional participants were excluded for failing to comply with the instructions (they squeezed the handgrip less than once per trial on average during instrumental learning). The final sample consisted of 20 heterosexual men (M sexual orientation sum = 0.65, SD = 1.14; M age = 24.83, SD = 5.85) and 20 homosexual men (M sexual orientation sum = 23.05, SD = 1.50; M age = 23.94, SD = 3.80). This sample size was established by means of a power analysis using the effect size observed for the finding pertaining to the PIT index from Experiment 1. The analysis revealed that at least 20 participants per group with analyzable data were necessary to detect a moderate effect (d = 0.67) with a power of 80% using a two-tailed paired t test. We stopped collecting data once that number was reached.

Materials

Stimuli

The outcomes consisted of three images (an erotic image of a woman, of a man, and a scrambled image) chosen by each participant from a set of 60 images (256×384 pixels). This set of images was composed of 24 images of partially or completely nude women, 24 images of partially or completely nude men (see supplemental materials), and 12 scrambled images created by applying a Photoshop filter on top of 12 images of the women. Four geometric figures typically used in human conditioning paradigms (Gottfried et al., 2003; Stussi, Deplanque et al., 2018; Valentin et al., 2007) and rated as similarly neutral (see Pool et al., 2014) were utilized as Pavlovian stimuli, whereas an additional geometric figure was used during instrumental learning (see Figure 1). They were displayed at the center of a computer screen for the PIT task. The associations between each geometric figure and Pavlovian identity (i.e., CS_w^+ , CS_m^+ , CS_s^+ , and baseline) were counterbalanced across participants. Given that the baseline stimulus mainly served as an inter-trial interval that was devoid of

any predictive value during Pavlovian learning and was hence not comparable to the other Pavlovian stimuli, it was omitted from the analyses.

Instrumental apparatus

Participants' instrumental responses were measured using an isometric handgrip (TDS121C) connected to a BIOPAC MP150 system (Santa Barbara, CA). MATLAB (version 7.9; The MathWorks, Inc., Natick, MA) read and recorded the dynamic value of the signal with a 27-Hz sampling rate, and provided participants with a visual feedback of the force they exerted on the handgrip using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The visual feedback was illustrated through an animation resembling a thermometer on the left side of the screen, the "mercury" moving up and down as force was exerted on the handgrip. The mercury of the handgrip would reach the top if the handgrip was squeezed with at least 50% or 70% (criterion varied every second) of the participant's maximal force (Pool et al., 2015; Talmi et al., 2008). Squeezes surpassing a threshold of 50% of the participant's maximal force were considered as responses (Pool et al., 2015; Talmi et al., 2008), and were detected and counted using a custom MATLAB script.

Procedure

Participants first filled out several questionnaires, consisting of the Sexual Desire Inventory 2 (Spector et al., 1996), the Sexual Arousalability Inventory (Hoon & Chambless, 1998), the State-Trait Anxiety Inventory in its trait version (Spielberger et al., 1983), and the Beck Depression Inventory – II (Beck et al., 1996; see supplemental materials). They then rated their liking of the 60 images, and underwent instrumental and Pavlovian learning, followed by the PIT test (see Figure 1). All tasks after the image ratings task were adapted from Pool et al. (2015) and Talmi et al. (2008).

Figure 1*Illustration of the Pavlovian-instrumental transfer paradigm*

Note. (A) In the instrumental learning task, participants learned to associate the squeezing of a handgrip with the apparition of the sexual outcomes. During each trial, they received online feedback of their mobilized effort through a thermometer-like illustration (on the left side of the screen). (B) In the Pavlovian learning task, participants learned to associate geometric figures with an erotic image of a woman (CS_w+), a man (CS_m+), and a neutral scrambled image (CS_s+). (C) In the transfer test, participants performed an instrumental action during which they squeeze the handgrip while they simultaneously saw the geometric figures used as conditioned stimuli. The transfer test was performed under extinction; thus, no rewarding outcome was displayed during this phase. The erotic images shown were retrieved from Flickr.com and taken by Jim Morrison and Enrique Lin (CC BY-NC 2.0 license), and are displayed for illustrative purposes as more explicit and arousing images were used in the experiments.

Outcome liking

Participants were asked to rate on a visual analog scale (VAS) from 0 (*not at all*) to 100 (*extremely*) how much they liked looking at the images presented. The images were presented one at a time in the center of the screen with the VAS displayed underneath it.

Based on their ratings, three images were selected for the subsequent tasks: their most liked image of a woman, their most liked image of a man, and the most neutral scrambled image rated as closely to 50 as possible.

Instrumental learning

In the instrumental learning task, participants learned to squeeze the handgrip to trigger the apparition of the woman and man images. Before the beginning of the task, participants were asked to squeeze the handgrip with their maximal force as a calibration procedure. The task consisted of 30 12-s “task-on” periods in which they were asked to squeeze the handgrip multiple times, while receiving online feedback of their force exerted through a thermometer-like illustration displayed on the left side of the computer screen (see Figure 1A). The “task-on” periods were followed by 4-to-8-s “task-off” periods, during which participants had to look at a fixation cross. Throughout the “task-on” periods, a geometric figure was displayed in the center of the screen, with a gray rectangle presented above it for half of the trials and below it for the other half. Participants were told the images were hidden by the gray rectangle and that they could trigger their apparition if they happened to squeeze the handgrip when two special 1-s windows occurred. They had to squeeze with 50% or 70% of their maximal force—this criterion randomly changing every second—during these windows to trigger the apparition of the image, which visually translated to the mercury hitting the top of the thermometer. The geometric figure did not predict anything nor did participants receive any predictive cues as to when the windows occurred or which image would be presented throughout the trial. Through each trial, the two 1-s rewarded windows were randomly selected. If the participants managed to squeeze the handgrip during one of the special windows, the image would then appear for 1 s. They had the possibility to trigger the image appearance twice at maximum for each trial, which allowed for assessing differences in squeezing frequency as a function of the outcome type.

The instrumental response was equally reinforced for the image of the woman and of the man through a probabilistic schedule. Participants used their dominant hand for this task.

Pavlovian learning

In this task, participants learned to associate three different complex geometric figures with the previously selected images of the woman (CS_w+), the man (CS_m+), and the scrambled images (CS_s+ ; see Figure 1B). The task was composed of 36 12-s “task-on” periods, in which the CS_w+ , CS_m+ , or CS_s+ were presented, followed by a 4-s “task-off” period, during which a baseline stimulus was presented. These 12-s “task-on” periods consisted of three 4-s trials where one CS was presented alongside a gray patch. Participants were asked to quickly press a key with their non-dominant index finger upon the perception of a gray patch on the screen. Pressing the key removed the gray patch from the screen, revealing the outcome associated with that CS. Participants were explicitly told that there was no link between their performance on this task and the display of the images. In fact, the outcome image appeared 1 s after the trial onset even if participants did not press the key during this interval, the delivery of the outcome thus not being contingent on the keypress. Participants were informed about this aspect and it was emphasized that the keypress was solely necessary to gauge sustained attention to the task (Talmi et al., 2008). However, the outcome image was displayed faster when participants pressed on the keyboard than when they did not. Because of this instrumental component, the Pavlovian learning task can be considered as a hybrid of Pavlovian and discriminative instrumental learning rather than pure Pavlovian learning (Pool et al., 2015; Talmi et al., 2008). The images appeared above the geometric figure for half of the trials and below for the other half. The time participants took to press on the key for each CS during the first trial of each “task-on” period was used as an index of Pavlovian learning. Trials for which participants did not press the key ($M = 10.93\%$, $SD = 13.22$ in Experiment 1; $M = 5.81\%$, $SD = 8.04$ in Experiment 2) or responded faster

than 150 ms ($M = 0.95\%$, $SD = 1.13$; $M = 0.81\%$, $SD = 1.15$ in Experiment 2) were omitted from analyses. One participant was excluded from the reaction times analyses in Experiment 1 because he did not press the key at all in the CS_{m+} trials. The association between the CSs and the outcomes was pseudorandomized across participants.

Subsequent to the Pavlovian learning task, participants were asked to rate how pleasant they found each CS presented in the middle of the screen one at a time, using a VAS going from 0 (*not at all*) to 100 (*extremely*) underneath the geometric figure. The presentation order of the images was randomized across participants.

Pavlovian-instrumental transfer test

In the test phase, participants were given the same instructions as the ones they received for the instrumental learning phase. The first 16 trials consisted of eight trials identical to the instrumental learning trials and eight partial extinction trials, in which only one special rewarded window occurred. Immediately thereafter, the transfer test followed and participants underwent 24 trials under extinction (see Figure 1C). Unbeknownst to participants, they were no longer rewarded during the transfer trials. During each trial, one of the Pavlovian stimuli (CS_{w+} , CS_{m+} , CS_{s+} , or baseline) replaced the geometric image used in the instrumental learning phase. Each Pavlovian stimulus was presented three times consecutively in two different cycles for a total of 24 trials. The number of squeezes exerted on the handgrip during the presentation of the different CSs was used as an indicator of cue-triggered reward-seeking behaviors. The order of the trials was randomized across CSs and participants.

Statistical analyses

Statistical analyses were performed with RStudio (version 1.1.442; RStudio Team, 2016) using the afex (Singmann et al., 2019) and BayesFactor (Morey & Rouder, 2018) packages. Data from the PIT task were analyzed with analyses of variance (ANOVAs) and two-tailed

planned contrasts. Adjustments of degrees of freedom using Greenhouse-Geisser correction were applied when the sphericity assumption was not met. When the planned contrasts were nonorthogonal, we applied a Holm-Bonferroni sequential procedure (Holm, 1979) to correct for multiple comparisons by adjusting the alpha level for these contrasts. We additionally computed the Bayes factor (BF_{10}) quantifying the likelihood of the data under the alternative hypothesis relative to the likelihood of the data under the null hypothesis using Bayesian ANOVAs (e.g., Rouder et al., 2012) and Bayesian two-tailed paired t tests (e.g., Rouder et al. 2009). For the Bayesian ANOVAs, Bayes factors were calculated using a default Cauchy prior distribution with a width of 0.5 (Rouder et al., 2012). The Bayes factors reported for main effects compared the model with the main effect in question versus the null model, while Bayes factors reported for interaction effects compared the model including the interaction term with the model including all the other effects but the interaction term. For the Bayesian t tests, Bayes factors were computed using a noninformative Cauchy prior distribution with a width of 0.5 in Experiment 1, whereas, in Experiment 2, they were calculated based on an informative normal prior distribution using the median and standard deviation of the standardized effect size (Cohen's δ) posterior distribution observed in Experiment 1 (see Tables S2-S5 in the supplemental materials; Gronau et al., 2020; Verhagen & Wagenmakers, 2014). Partial eta squared (η_p^2) or Hedges' g_{av} and their 90% or 95% confidence interval (CI) are reported as estimates of effect sizes (see Lakens, 2013) for the ANOVAs and the planned contrasts, respectively.

Results

Experiment 1

Outcome liking

To verify that there were differences in the likability of the images selected as outcomes as rated by heterosexual male participants, a one-way repeated-measures ANOVA was applied to the outcome liking ratings with the outcome type (woman vs. man vs. scrambled) as a within-participant factor. This analysis revealed a statistically significant main effect, $F(1.54, 52.20) = 152.31, p < .001, \eta_p^2 = .818, 90\% \text{ CI } [.733, .858], \text{BF}_{10} = 2.4 \times 10^{30}$, indicating the outcomes were not equally liked.

Planned comparisons confirmed that for heterosexual participants the most liked image of the woman ($M = 96.55, SD = 8.79$) was more liked than the most liked image of the man ($M = 26.89, SD = 22.60$), $t(34) = 17.22, p < .001, g_{av} = 3.973, 95\% \text{ CI } [2.990, 5.124], \text{BF}_{10} = 1.5 \times 10^{15}$, and the neutral scrambled image ($M = 29.36, SD = 21.03$), $t(34) = 18.29, p < .001, g_{av} = 4.076, 95\% \text{ CI } [3.080, 5.245], \text{BF}_{10} = 9.3 \times 10^{15}$. No statistically significant difference was observed between the image of the man and the scrambled image, $t(34) = 0.44, p = .663, g_{av} = 0.111, 95\% \text{ CI } [-0.394, 0.619], \text{BF}_{10} = 0.27$. These results reflect that participants liked the selected images of the woman more than the selected images for the other categories.

Instrumental learning

Learning of the associations between the various outcomes and the instrumental action during the instrumental learning phase was analyzed with a repeated-measures ANOVA on the number of squeezes for each outcome type (woman vs. man) over the 15 instrumental trials. A main effect of outcome type was found, $F(1, 34) = 17.95, p < .001, \eta_p^2 = .345, 90\% \text{ CI } [.134, .505], \text{BF}_{10} = 3.0 \times 10^{21}$, such that participants squeezed the handgrip more to reveal the image of the woman ($M = 10.36, SD = 3.99$) than the man ($M = 8.34, SD = 4.69$; Fig. 2A). No main effect of trials or interaction between the outcome types and the trials were found (all $ps > .16$, all $\text{BF}_{10} < 0.01$).

Pavlovian learning

To determine whether participants successfully learned the contingencies between the CSs and the outcomes during the Pavlovian learning task, reaction times (RTs) in the presence of the CSs (CS_w+ vs. CS_m+ vs. CS_s+) and their liking ratings were entered into two separate one-way repeated-measures ANOVAs. Both ANOVAs revealed a statistically significant main effect, $F(1.46, 48.05) = 5.98, p = .010, \eta_p^2 = .153, 90\% \text{ CI } [.023, .295], \text{BF}_{10} = 9.02$ and $F(2, 68) = 41.54, p < .001, \eta_p^2 = .550, 90\% \text{ CI } [.404, .636], \text{BF}_{10} = 2.3 \times 10^{12}$, respectively.

Planned contrasts showed that participants were faster to press the key in the CS_w+ trials than the CS_m+ trials, $t(33) = 2.67, p = .012, g_{av} = 0.515, 95\% \text{ CI } [0.116, 0.931], \text{BF}_{10} = 4.27$, and the CS_s+ trials, $t(33) = 3.59, p = .001, g_{av} = 0.454, 95\% \text{ CI } [0.184, 0.739], \text{BF}_{10} = 31.08$ (see Figure 3A). RTs in the CS_m+ and the CS_s+ trials did not statistically differ, $t(33) = 0.83, p = .415, g_{av} = 0.128, 95\% \text{ CI } [-0.182, 0.442], \text{BF}_{10} = 0.33$. The CS_w+ was also rated as more pleasant than both the CS_m+, $t(34) = 8.33, p < .001, g_{av} = 2.151, 95\% \text{ CI } [1.458, 2.926], \text{BF}_{10} = 9.1 \times 10^6$, and the CS_s+, $t(34) = 6.26, p < .001, g_{av} = 1.405, 95\% \text{ CI } [0.866, 1.994], \text{BF}_{10} = 3.5 \times 10^5$ (see Figure 3D). Moreover, the CS_m+ was deemed less pleasant than the CS_s+, $t(34) = 3.27, p = .002, g_{av} = 0.737, 95\% \text{ CI } [0.264, 1.234], \text{BF}_{10} = 15.39$ (see Figure 3D).

Pavlovian-instrumental transfer test

The number of squeezes exerted on the handgrip in the presence of the various CSs during the PIT test was analyzed with a 3 (CS type: CS_w+ vs. CS_m+ vs. CS_s+) $\times$ 6 (extinction trials) repeated-measures ANOVA. The results yielded a main effect of CS type, $F(1.30, 44.19) = 5.83, p = .013, \eta_p^2 = .146, 90\% \text{ CI } [.018, .295], \text{BF}_{10} = 9.2 \times 10^7$, reflecting the existence of differences in the number of squeezes across the CSs. A main effect of extinction trials additionally emerged, $F(3.52, 119.76) = 9.53, p < .001, \eta_p^2 = .219, 90\% \text{ CI }$

[.102, .303], $BF_{10} = 34.98$, indicating a decrease in squeezing frequency over time. No interaction effect between the CS types and extinction trials was observed, $F(5.66, 192.39) = 1.72$, $p = .123$, $\eta_p^2 = .048$, 90% CI [.000, .079], $BF_{10} = 0.01$.

Critically, planned contrasts showed that participants squeezed the handgrip more in the presence of the CS_{w+} ($M = 12.56$, $SD = 8.52$) than both in the presence of the CS_{m+} ($M = 8.86$, $SD = 7.89$), $t(34) = 2.55$, $p = .016$, $g_{av} = 0.441$, 95% CI [0.085, 0.811], $BF_{10} = 3.37$, and the CS_{s+} ($M = 9.82$, $SD = 6.96$), $t(34) = 2.53$, $p = .016$, $g_{av} = 0.345$, 95% CI [0.065, 0.635], $BF_{10} = 3.30$, whereas the latter two did not statistically differ, $t(34) = 1.34$, $p = .190$, $g_{av} = 0.126$, 95% CI [-0.063, 0.319], $BF_{10} = 0.53$ (see Figure 4A).

To further investigate whether enhanced PIT effects were specific to relevant sexual outcomes, we calculated a PIT index using relative scores by subtracting the number of squeezes in the presence of the CS_{s+} from the number of squeezes in the presence of the CS_{w+} ($CS_{w+} - CS_{s+}$) and the CS_{m+} ($CS_{m+} - CS_{s+}$; see Pool et al., 2015). As expected, the PIT index was greater for the CS_{w+} than for the CS_{m+} , $t(34) = 2.55$, $p = .016$, $g_{av} = 0.667$, 95% CI [0.128, 1.226], $BF_{10} = 3.37$ (see Figure 4D).

Experiment 2

Outcome liking

A mixed-design ANOVA with participants' sexual orientation (heterosexual vs. homosexual) as a between-participant factor and outcome type (woman vs. man vs. scrambled) as a within-participant factor was conducted on the outcome liking ratings. This analysis revealed a main effect of sexual orientation, $F(1, 38) = 11.17$, $p = .002$, $\eta_p^2 = .227$, 90% CI [.057, .392], $BF_{10} = 0.87$, though the Bayes factor suggests that the data were not more likely to be observed under a model including this main effect than the null model. A main effect of outcome type was likewise found, $F(2, 76) = 57.76$, $p < .001$, $\eta_p^2 = .603$, 90% CI [.477, .677], $BF_{10} = 2.4 \times 10^5$. These main effects were however qualified by their

interaction, $F(2, 78) = 110.58, p < .001, \eta_p^2 = .744, 90\% \text{ CI } [.654, .793], \text{BF}_{10} = 1.5 \times 10^{24}$, suggesting that the outcome liking ratings were contingent on the participants' sexual orientation.

For the heterosexual men, the most liked image of the woman ($M = 92.79, SD = 10.25$) was more liked than the most liked image of the man ($M = 28.78, SD = 25.39$), $t(38) = 11.65, p < .001, g_{av} = 3.174, 95\% \text{ CI } [2.098, 4.492], \text{BF}_{10} = 1.6 \times 10^8$, and the neutral scrambled image ($M = 27.73, SD = 21.27$), $t(38) = 12.95, p < .001, g_{av} = 3.741, 95\% \text{ CI } [2.545, 5.231], \text{BF}_{10} = 1.2 \times 10^{10}$, whereas there was no statistical difference between the image of the man and the scrambled image, $t(38) = 0.20, p = .843, g_{av} = 0.043, 95\% \text{ CI } [-0.516, 0.605], \text{BF}_{10} = 0.78$. Inversely, homosexual participants liked the most liked image of the man ($M = 97.21, SD = 4.59$) more than that of the woman ($M = 50.38, SD = 22.23$), $t(38) = 8.52, p < .001, g_{av} = 2.801, 95\% \text{ CI } [1.790, 4.021], \text{BF}_{10} = 2.9 \times 10^6$, and the scrambled image ($M = 39.08, SD = 15.07$), $t(38) = 11.00, p < .001, g_{av} = 5.011, 95\% \text{ CI } [3.466, 6.957], \text{BF}_{10} = 3.1 \times 10^{11}$. Additionally, homosexual participants rated the image of the woman as more pleasant than the scrambled image, $t(38) = 2.25, p = .030, g_{av} = 0.571, 95\% \text{ CI } [-0.0001, 1.176], \text{BF}_{10} = 1.08$, but evidence for this difference was very weak. Overall, these results confirm that the most liked image in each group of participants was dependent on their sexual orientation.

Instrumental learning

A mixed-design ANOVA with participants' sexual orientation (heterosexual vs. homosexual) as a between-participant factor and outcome type (woman vs. man) and instrumental trials (15 trials) as within-participant factors was applied to the number of squeezes during the instrumental learning phase. The analysis yielded a statistically significant interaction between participants' sexual orientation and outcome type, $F(1, 38) =$

Figure 2*Results for the instrumental learning task*

Note. Number of squeezes exerted on the handgrip as a function of the type of outcome over the 15 instrumental trials for (A) the heterosexual participants in Experiment 1 ($n = 35$), (B) the heterosexual participants in Experiment 2 ($n = 20$), and (C) the homosexual participants in Experiment 2 ($n = 20$). Error bars represent ± 1 standard error of the mean adjusted for within-participant designs.

17.94, $p < .001$, $\eta_p^2 = .321$, 90% CI [.124, .477], $BF_{10} = 2.7 \times 10^{24}$, suggesting that the squeezing frequency to obtain the outcomes was dependent on the participants' sexual orientation. No other effect reached statistical significance (all $ps > .25$, all $BF_{s10} < 0.41$).

Planned comparisons showed that heterosexual participants squeezed the handgrip more to reveal the image of the woman ($M = 8.43$, $SD = 4.74$) than the man ($M = 6.52$, $SD = 4.52$), $t(38) = 3.11$, $p = .004$, $g_{av} = 0.398$, 95% CI [0.110, 0.709], $BF_{10} = 35.29$ (see Figure 2B), whereas homosexual participants squeezed the handgrip more to reveal the image of the man ($M = 7.78$, $SD = 4.32$) than that of the woman ($M = 6.00$, $SD = 3.45$), $t(38) = 2.88$, $p = .006$, $g_{av} = 0.442$, 95% CI [0.119, 0.791], $BF_{10} = 33.03$ (Fig. 2C).

Pavlovian learning

The RTs in the keypress task in the presence of each Pavlovian stimulus (CS_w+ vs. CS_m+ vs. CS_s+) and the liking ratings thereof were analyzed with separate mixed-design ANOVAs with participants' sexual orientation as an additional between-participant factor.

These analyses revealed a statistically significant interaction between the participants' sexual orientation and the Pavlovian stimuli, $F(1.59, 60.25) = 12.90, p < .001, \eta_p^2 = .253$, 90% CI [.100, .382], $BF_{10} = 1490.59$ and $F(2, 76) = 24.42, p < .001, \eta_p^2 = .391$, 90% CI [.240, .495], $BF_{10} = 4.8 \times 10^8$, respectively. No other effect was observed (all $ps > .07$, all $BF_{s10} < 0.47$ for the RTs; all $ps > .05$, all $BF_{s10} < 0.60$ for the liking ratings).

Planned contrasts indicated that heterosexual participants were quicker to press the key in the CS_{w+} trials than the CS_{m+} trials, $t(38) = 2.79, p = .008, g_{av} = 0.584$, 95% CI [0.072, 1.131], $BF_{10} = 9.62$, and the CS_{s+} trials, $t(38) = 3.43, p = .001, g_{av} = 0.647$, 95% CI [0.170, 1.164], $BF_{10} = 28.66$ (see Figure 3B). These participants also evaluated the CS_{w+} as more pleasant than the CS_{m+} , $t(38) = 5.90, p < .001, g_{av} = 1.865$, 95% CI [0.983, 2.873], $BF_{10} = 4750.82$, and the CS_{s+} , $t(38) = 4.89, p < .001, g_{av} = 1.720$, 95% CI [0.856, 2.699], $BF_{10} = 1815.16$ (see Figure 3E). No statistical differences were found in RTs or likability between the CS_{m+} and the CS_{s+} , $t(38) = 0.06, p = .950, g_{av} = 0.008$, 95% CI [-0.280, 0.296], $BF_{10} = 0.75$ and $t(38) = 0.92, p = .362, g_{av} = 0.270$, 95% CI [-0.373, 0.928], $BF_{10} = 0.67$, respectively.

Homosexual participants presented the opposite pattern: They were quicker to press the key in the presence of the CS_{m+} than the CS_{w+} , $t(38) = 3.13, p = .003, g_{av} = 0.595$, 95% CI [0.241, 0.987], $BF_{10} = 73.25$, and the CS_{s+} , $t(38) = 4.10, p < .001, g_{av} = 0.499$, 95% CI [0.247, 0.784], $BF_{10} = 524.44$ (see Figure 3C). They also rated the CS_{m+} as more pleasant than the CS_{w+} , $t(38) = 3.88, p < .001, g_{av} = 1.411$, 95% CI [0.660, 2.254], $BF_{10} = 504.34$, and the CS_{s+} , $t(38) = 2.35, p = .024, g_{av} = 0.786$, 95% CI [0.135, 1.483], $BF_{10} = 6.23$ (see Figure 3F). No statistically significant differences in RTs or liking ratings emerged between the CS_{w+} and the CS_{s+} , $t(38) = 0.66, p = .512, g_{av} = 0.097$, 95% CI [-0.142, 0.342], $BF_{10} = 1.12$ and $t(38) = 1.50, p = .143, g_{av} = 0.501$, 95% CI [-0.180, 1.210], $BF_{10} = 2.11$, respectively.

Figure 3*Results for the Pavlovian learning task*

Note. (A-C) Reaction times in the keypress task in response to the conditioned stimuli for (A) the heterosexual participants in Experiment 1 ($n = 34$), (B) the heterosexual participants in Experiment 2 ($n = 20$), and the homosexual participants in Experiment 2 ($n = 20$). (D-F) Liking ratings of the Pavlovian stimuli for (D) the heterosexual participants in Experiment 1 ($n = 35$), (E) the heterosexual participants in Experiment 2 ($n = 20$), and (F) the homosexual participants in Experiment 2 ($n = 20$). In each panel, the upper plot shows the individual participants' data (dots and distributions) and means $\pm$ 1 standard error adjusted for within-participant designs (error bars). The lower plot shows the distributions of difference scores between paired conditions, the mean difference scores (dots) and 95% confidence intervals (vertical lines).

Pavlovian-instrumental transfer

The squeezing frequency in response to the CSs during the PIT test was applied to a mixed-design ANOVA with participants' sexual orientation (heterosexual vs. homosexual) as a between-participant factor, and CS type (CS_w+ vs. CS_m+ vs. CS_s+) and extinction trials (6 trials) as within-participant factors. The results yielded a main effect of trials, $F(2.76, 104.99) = 3.14, p = .032, \eta_p^2 = .076, 90\% \text{ CI } [.004, .149], \text{BF}_{10} = 1.94$, reflecting a modest decrease of squeezing frequency over time. More importantly, there was an interaction between participants' sexual orientation and CS type, $F(2, 76) = 11.35, p < .001, \eta_p^2 = .230, 90\% \text{ CI } [.093, .343], \text{BF}_{10} = 1.0 \times 10^{10}$, which highlights that the number of times participants squeezed the handgrip in the presence of a certain CS was dependent on their sexual orientation. No other statistically significant effect was observed (all $ps > .19$, all $\text{BF}_{10} < 0.54$).

Heterosexual participants squeezed the handgrip more in the presence of the CS_w+ ($M = 9.84, SD = 6.17$) than in the presence of the CS_m+ ($M = 5.76, SD = 5.11$), $t(38) = 3.76, p = .001, g_{av} = 0.692, 95\% \text{ CI } [0.301, 1.127], \text{BF}_{10} = 88.81$, and the CS_s+ ($M = 7.03, SD = 4.13$), $t(38) = 3.11, p = .004, g_{av} = 0.515, 95\% \text{ CI } [0.148, 0.913], \text{BF}_{10} = 23.91$ (Fig. 4B), thereby replicating findings from Experiment 1. The squeezing frequency for the CS_m+ and the CS_s+ did not statistically differ, $t(38) = 1.18, p = .244, g_{av} = 0.262, 95\% \text{ CI } [-0.131, 0.670], \text{BF}_{10} = 1.86$.

Of importance, homosexual participants' behavior showed the opposite pattern. They squeezed more in the presence of the CS_m+ ($M = 10.68, SD = 7.18$) than in the presence of the CS_w+ ($M = 7.88, SD = 6.17$), $t(38) = 2.58, p = .014, g_{av} = 0.402, 95\% \text{ CI } [0.047, 0.780], \text{BF}_{10} = 9.21$, and the CS_s+ ($M = 8.14, SD = 5.63$), $t(38) = 2.38, p = .023, g_{av} = 0.378, 95\% \text{ CI } [0.006, 0.773], \text{BF}_{10} = 6.11$ (see Figure 4C), which did not statistically differ from one another, $t(38) = 0.29, p = .777, g_{av} = 0.042, 95\% \text{ CI } [-0.253, 0.340], \text{BF}_{10} = 0.77$.

Similar to Experiment 1, a PIT index using relative scores was additionally computed for Experiment 2. The PIT index for both sexual orientations (heterosexual vs. homosexual) and CS types (CS_w⁺ vs. CS_m⁺) was entered in a mixed-design ANOVA. This analysis revealed an interaction between sexual orientation and CS type, $F(1, 38) = 20.12, p < .001, \eta_p^2 = .346, 90\% \text{ CI } [.146, .499], \text{BF}_{10} = 1.3 \times 10^{127}$. No statistically significant main effect of sexual orientation, $F(1, 38) = 0.10, p = .756, \eta_p^2 = .003, 90\% \text{ CI } [.000, .076], \text{BF}_{10} = 0.37$, nor CS type, $F(1, 38) = 0.70, p = .408, \eta_p^2 = .018, 90\% \text{ CI } [.000, .133], \text{BF}_{10} = 230.98$, were found, although Bayesian analyses indicated that the data were substantially more likely to be observed under a model including a main effect of CS type than the null model. These results hence reflect that the PIT index for a given cue was dependent on the sexual orientation of the participants.

Specifically, heterosexual participants had a greater PIT index for the cue associated with the woman than the cue associated with the man, $t(38) = 3.76, p = .001, g_{av} = 0.949, 95\% \text{ CI } [0.413, 1.546], \text{BF}_{10} = 88.81$ (see Figure 4E). By contrast, homosexual participants had a greater PIT index for the cue associated with the man relative to the cue associated with the woman, $t(38) = 2.58, p = .014, g_{av} = 0.570, 95\% \text{ CI } [0.067, 1.107], \text{BF}_{10} = 9.21$ (see Figure 4F).

Discussion

In the present work, we examined whether individual differences in the reward's appraised relevance to the organism's concerns modulate reward learning and reward-seeking behaviors in humans. Using a similar methodology to animal studies investigating motivational states related to homeostasis such as hunger and thirst (e.g., Balleine, 1994; Robinson & Berridge, 2013), we tested whether the outcome's relevance for the individual's sexual concerns influence instrumental and Pavlovian learning, as well as their impact on

Figure 4*Results for the transfer test*

Note. (A-C) Number of squeezes exerted on the handgrip in the presence of the Pavlovian stimuli over the six extinction trials for (A) the heterosexual participants in Experiment 1 ($n = 35$), (B) the heterosexual participants in Experiment 2 ($n = 20$), and (C) the homosexual participants in Experiment 2 ($n = 20$). (D-F) Pavlovian-instrumental transfer (PIT) index (number of squeezes exerted in the presence of the conditioned stimulus associated with the image of the woman or the man *minus* the conditioned stimulus associated with the scrambled image) for (D) the heterosexual participants in Experiment 1 ($n = 35$), (E) the heterosexual participants in Experiment 2 ($n = 20$), and the homosexual participants in Experiment 2 ($n = 20$). In panels A-C, errors bars represent ± 1 standard error adjusted for within-participant designs. In panels D-F, the left plot shows individual participants' data (dots and distributions) and means ± 1 standard error adjusted for within-participant designs (error bars). The right plot shows the distribution of difference scores between the two conditions, the mean difference score (dot) and 95% confidence interval (vertical line).

cue-driven behaviors involving sexual stimuli. Altogether, our results indicate that the sexual outcome most relevant to participants' sexual orientation and its associated cue induced enhanced instrumental learning, Pavlovian learning, and reward-seeking behaviors during the

transfer phase, thereby suggesting that these effects were modulated by the outcome's appraised affective relevance for the concerns of the individual.

In Experiment 1, heterosexual men performed the instrumental action more often to reveal the erotic image of the woman than that of the man during instrumental learning and were quicker to respond to the cue associated with the image of the woman than to the cue associated with the image of the man during the Pavlovian learning task. In addition, they exhibited increased instrumental responding in response to the cue associated with the image of the woman than to the cue associated with the image of the man during the PIT test. Experiment 2 replicated these findings and, critically for our hypothesis, expanded them by showing that homosexual men showed the opposite pattern of results than heterosexual men. These results indicate that sexual stimuli led to differential instrumental and Pavlovian learning, and had different effects on cue-triggered reward-seeking behaviors depending on the participants' sexual orientation.

Our findings mirror, at a conceptual level, recent empirical evidence in the Pavlovian aversive learning literature showing that stimuli that are relevant to the individual's concerns enhance Pavlovian conditioning compared to less relevant stimuli (Stussi et al., 2019, 2021; Stussi, Pourtois et al., 2018), and suggest that a similar mechanism may likewise be at play in the appetitive domain. Of importance, the current results moreover contribute to demonstrating that the effects of affective relevance are not confined to stimulus-outcome learning processes, but also play a critical role in modulating reward-seeking behaviors. Taken together, this therefore provides evidence that reward-related learning and behaviors are not determined exclusively by a stimulus' intrinsic properties, but rather rely on the interplay between the stimulus at stake and the individual's concerns (see Pool, Sennwald et al., 2016).

The present study aligns with existing work in the reward processing literature (e.g., Balleine, 1994; Corbit & Balleine, 2005; Corbit et al., 2007; Dickinson & Balleine, 1990, 1994; Pool et al., 2019; Robinson & Berridge, 2013) in highlighting that the motivational value of the reward and its associated cues can flexibly shape Pavlovian and instrumental processes, and how they impact reward-seeking behaviors. More specifically, our results are consistent with prior empirical findings in animals and humans showing that the influence of Pavlovian cues on nonselective instrumental responding is sensitive to the motivational relevance of the outcome signaled by the cue (e.g., Corbit et al., 2007; Hebart & Gläscher, 2015; van Timmeren et al., 2020; Watson et al., 2014), and that such general PIT effects also occur for rewards that do not hinge on homeostatic or physiological needs, such as monetary gains or social approval (Garbusow et al., 2016; Huys et al., 2011; Lehner et al., 2017; Sebold et al., 2016). Importantly, our study further adds to this body of research by showing that similar effects can be observed with sexual stimuli and that these effects are dependent on the individual's sexual concerns, such as sexual orientation. These findings thereby suggest that individual differences in concerns may play a crucial role in modulating reward learning and reward-seeking behaviors.

In that sense, our results appear consistent with the proposal that affective relevance could be a key mechanism influencing reward learning and reward-seeking behaviors in humans (Pool, Sennwald et al., 2016). According to this view, Pavlovian and instrumental learning as well as their influence on cue-triggered reward-seeking behaviors are modulated by the relevance of the outcome to the organism's current concerns. These concerns can relate to a wide range of explicit and implicit motives (e.g., homeostatic needs, survival, reproduction, affiliation, socialization, moral values, or momentary goals), and are organized in a dynamic hierarchy that varies depending on the situation and the individual (Pool, Brosch et al., 2016; Pool, Sennwald et al., 2016; Sander et al., 2005, 2018), thus assigning a

pivotal role to individual differences (Stussi et al., 2019, 2021). Alternatively, our results could be interpreted as reflecting that individuals learn preferentially about, and work harder to obtain, rewards that they like more or find more rewarding (see, e.g., Hursh & Silberberg, 2008). Of note, these two explanations are however neither incompatible, nor mutually exclusive. In fact, reward value depends not only on pleasure or liking, but also on the organism's needs and goals (e.g., Dayan & Berridge, 2014; Sander & Nummenmaa, 2021; Zhang et al., 2009). Albeit dissociable under certain circumstances such as addictions or stress, the affective relevance of a reward and its liking are often correlated in the case of reward processing (Pool, Sennwald et al., 2016): Rewards that are appraised as more affectively relevant generally tend to be likewise more liked. In this context, affective relevance emerges as a flexible mechanism that can account for how individuals differentially learn about rewards and their associated cues, and how these cues can dynamically elicit reward-seeking behaviors as a function of the outcome's motivational value, as well as the influence of individual differences on these processes (see Garofalo & di Pellegrino, 2015; Wuensch et al., 2021).

It is nonetheless important to note several limitations of our study. First, because we only recruited male participants, we cannot be sure that our results can generalize to women. The choice to include only men was motivated by the fact that men have been reported to be more sensitive to the gender of the individuals depicted in sexual stimuli than women (Chivers et al., 2007; Rupp & Wallen, 2008), thus facilitating the manipulation of sexual outcomes' relevance through participants' sexual orientation. Further research is hence needed to assess whether reward learning and cue-guided reward-seeking behaviors involving sexual outcomes are modulated by the outcome relevance for the individual's sexual concerns in women too. Given that typical visual sexual stimuli are generally primarily tailored for men—who are correspondingly thought to be more interested in such

stimuli than women (e.g., Hamann et al., 2004; Strahler et al., 2019)—such endeavor should notably employ appropriate experimental sexual stimuli with their content being specifically tailored to be of interest for women (see Rupp & Wallen, 2008).

Second, the fact that the sexual outcomes led to differential instrumental and Pavlovian learning as a function of their relevance to participants' sexual orientation raises the possibility that the enhanced instrumental responding observed to the cue associated with the most relevant sexual outcome relative to the cue associated with the less relevant outcome during the test phase could reflect a difference in strength of the learned relationships between the cues or the instrumental action and the outcomes rather than in the strength of Pavlovian-instrumental transfer per se. Relatedly, the inclusion of an instrumental component (i.e., keypress) during the Pavlovian learning task might have induced some form of instrumental-instrumental transfer (the keypress action transferring to the handgrip squeeze), facilitating instrumental responding during transfer. These considerations underscore that additional studies are necessary to pinpoint the precise nature of the effects exerted by the outcome motivational relevance on cue-driven behaviors for sexual stimuli and whether these effects are specifically driven by pure Pavlovian-instrumental transfer.

In addition, the effect size for the PIT index in homosexual participants (Hedges' g_{av} = 0.570) in Experiment 2 was somewhat lower than the effect size estimate used in the a priori power analysis (Cohen's d = 0.67) for this experiment. Although we observed statistically significant differences in PIT index for both heterosexual and homosexual participants, this suggests that Experiment 2 might have been underpowered to a certain degree to detect an effect in terms of PIT index for homosexual participants and that a larger sample size should be selected in studies aiming to replicate this effect.

Finally, although single-response PIT paradigms as the one used here have been suggested to usually elicit only general transfer (Cartoni et al., 2016), the design we

implemented did not allow for distinguishing the specific contributions of outcome-specific and general motivational effects. Accordingly, an interesting avenue for future experiments would be to implement a paradigm that could disentangle these effects. In such a paradigm, the female and male sexual outcomes could for instance be associated with distinct instrumental actions. This would allow for assessing whether the cue associated with the most relevant sexual outcome selectively increases instrumental responding for the action associated with that same outcome (i.e., outcome-specific effects) or more generally increases instrumental responding for all actions available irrespective of the outcomes involved (i.e., general effects; see Sennwald et al., 2020).

In conclusion, the present study expands on existing evidence suggesting that reward-related learning and behaviors depend upon the relevance of the outcome and its associated cues for the organism's motivation. Our results lend support to the view that motivational effects on Pavlovian and instrumental reward learning processes and their general influence on cue-guided behaviors can extend to motives such as sexual concerns, and are critically dependent on inter-individual differences. As such, our findings are in line with the hypothesis that affective relevance could be a key mechanism modulating reward learning and reward-seeking behaviors in humans (Pool, Sennwald et al., 2016). By considering the interplay between reward-associated stimuli and the individual's current concerns beyond mere physiological states, this framework could contribute to providing new insights into the understanding of both problematic and non-problematic reward-seeking behaviors and the role of individual differences therein.

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Supplemental Materials

Individual Concerns Modulate Reward-Related Learning and Behaviors Involving Sexual Outcomes

by Y. Stussi*, V. Sennwald*, E. R. Pool, S. Delplanque, T. Brosch,
F. Bianchi-Demicheli, and D. Sander

Supplemental Method and Results

Questionnaires

Prior to the outcomes' selection and the Pavlovian-instrumental transfer (PIT) task, participants filled out two questionnaires on their perception of the intensity of their sexuality in everyday life: the Sexual Desire Inventory 2 (SDI-2; Spector et al., 1996) and the Sexual Arousability Inventory (SAI; Hoon & Chambless, 1998). Considering anxiety and depression can have an effect on sexuality (Laurent & Simons, 2009), they also filled out the State-Trait Anxiety Inventory in its trait version (STAI-T; Spielberger et al., 1983) and the Beck Depression Inventory – II (BDI-II; Beck et al., 1996). The questionnaires were administered to verify whether participants differed from each other on those aspects.

The SDI-2 is a 14-item scale that aims to measure dyadic and solitary sexual desire. It consists of 4 items on the frequency of desire, which are scored on an 8-point Likert scale ranging from 0 (*not at all*) to 7 (*more than once a day*), while the remaining items on the intensity of their desire are scored on a 9-point Likert scale ranging from 0 (*no desire*) to 8 (*strong desire*). The total score for the dyadic sexual desire ranges from 0 to 62, whereas it ranges from 0 to 23 for the solitary sexual desire. The SAI aims to measure how participants perceive their sexual arousability to different experiences. This inventory consists of 28 items, which are scored on a 7-point Likert scale ranging from -1 (*adversely affects arousal; unthinkable, repulsive, disturbing*) to 5 (*always induces sexual arousal; extremely arousing*).

The total score can range from -28 to 140. The STAI-T is a commonly used measure of trait anxiety. It comprises 20 items rated on a 4-point scale going from 1 (*almost never* or *almost always* for reverse-coded items) to 4 (*almost always* or *almost never* for reverse-coded items). The total score can range from 20 to 80, and higher scores reflect greater anxiety. The BDI-II is a 21-item inventory classically used for assessing depression symptoms severity. Each item is scored on a scale going from 0 to 3, with higher scores indicating heightened symptom severity. The total score can range from 0 to 63, with score below 14 being considered as reflecting minimal depression, scores between 14 and 19 as mild depression, between 20 and 28 as moderate depression, and scores above 28 as severe depression.

The questionnaires' mean scores for heterosexual participants in Experiments 1 and 2, and for homosexual participants in Experiment 2 are reported in Table S1. A one-way ANOVA showed a statistically significant difference across these three groups for the STAI-T, $F(2, 71) = 5.14, p = .008, \eta_p^2 = .126, 90\% \text{ CI } [.020, .235], \text{BF}_{10} = 5.91$. Follow-up analyses using Tukey's HSD indicated that the heterosexual men from Experiment 1 had less anxiety than the homosexual men from Experiment 2 ($p = .006, g_s = 0.980, 95\% \text{ CI } [0.284, 1.438]$), though heterosexual men's scores from both experiments did not statistically differ ($p = .260, g_s = 0.479, 95\% \text{ CI } [-0.140, 0.977]$), nor did the heterosexual and the homosexual men's scores from Experiment 2 ($p = .336, g_s = 0.362, 95\% \text{ CI } [-0.258, 0.992]$). No statistically significant differences were observed between the three groups on any of the other questionnaires (all $p_s > .13$, all $\text{BF}_{s10} < 0.61$).

Table S1

Questionnaire mean scores (and SD) for each group of participants in both experiments

	Experiment 1	Experiment 2	
	Heterosexual men	Heterosexual men	Homosexual men
SDI-2, dyadic desire	46.37 (9.19)	42.95 (10.17)	42.95 (10.06)
SDI-2, solitary desire	11.38 (6.74)	12.40 (6.24)	14.21 (4.28)
SAI	101.32 (18.01)	96.20 (16.37)	99.50 (15.37)
STAI-T	32.74 (6.34)	36.95 (11.66)	41.20 (11.34)
BDI-II	4.35 (4.26)	6.75 (6.99)	6.95 (4.78)

Note. SDI-2 = Sexual Desire Inventory-2, SAI = Sexual Arousalability Inventory, STAI-T = State-Trait Anxiety Inventory-trait version, BDI-II = Beck Depression Inventory-II.

Erotic image database

A pilot study was run to select and validate the final 48 erotic images used as sexual stimuli in the present study. In order to increase the possibility of finding an erotic image that would be rewarding for each participant based on their sexual preferences, 160 images of partially or fully naked women and men with varying degrees of explicitness (40 images per racial group—Black, Asian, Mestizo, and White) were initially taken from the Internet and Prévost et al. (2010). The aim of the validation study was to select the images that were the most arousing for heterosexual and homosexual men. Heterosexual participants were recruited through Amazon Mechanical Turk (www.mturk.com) and homosexual participants were recruited through acquaintances. Heterosexual (number of participants per image category: Black, $n = 21$; Asian, $n = 21$; Mestizo, $n = 20$; White, $n = 21$) and homosexual (number of participants per image category: Black, $n = 24$; Asian, $n = 16$; Mestizo, $n = 21$; White, $n = 26$) men were asked to rate how sexually arousing they found the images to be on a 10-point Likert scale from 0 (*not at all arousing*) to 10 (*extremely arousing*). Based on

these ratings, the set of images was reduced to the six most sexually arousing images per racial group for each sexual orientation. In total, 24 images were chosen for the heterosexual men (M arousal = 8.23, SD = 0.43) and 24 images were chosen for the homosexual men (M arousal = 7.30, SD = 0.38).

Descriptive statistics for the standardized effect size posterior distributions in Bayesian t tests

The median and standard deviation of the standardized effect size (Cohen's δ) posterior distributions, along with the corresponding 95% credible interval, observed for the Bayesian t tests in Experiments 1 and 2 are reported in Tables S2-S5. The median and standard deviation of the standardized effect size posterior distribution for each comparison in Experiment 1 were used to determine the informative normal prior distributions for the Bayesian t tests performed in Experiment 2 (see Gronau et al., 2020; Verhagen & Wagenmakers, 2014).

Table S2

Median standardized effect size (and SD) of the posterior distributions and 95% credible intervals (CI) for the outcome liking ratings in Experiment 1 and Experiment 2

	Experiment 1		Experiment 2			
	Heterosexual men		Heterosexual men		Homosexual men	
	Md (SD)	95% CI	Md (SD)	95% CI	Md (SD)	95% CI
Woman vs. Man	2.82 (0.39)	[2.06, 3.62]	2.67 (0.30)	[2.08, 3.27]	-2.44 (0.29)	[-3.00, -1.88]
Woman vs. Scrambled	3.00 (0.41)	[2.22, 3.83]	3.06 (0.33)	[2.42, 3.71]	0.10 (0.13)	[-0.15, 0.35]
Man vs. Scrambled	-0.06 (0.16)	[-0.37, 0.24]	-0.03 (0.13)	[-0.28, 0.23]	3.27 (0.34)	[2.60, 3.95]

Note. Woman = image of the woman, Man = image of the man, Scrambled = scrambled image.

Table S3

Median standardized effect size (and SD) of the posterior distributions and 95% credible intervals (CI) for the instrumental learning task in Experiment 1 and Experiment 2

	Experiment 1		Experiment 2			
	Heterosexual men		Heterosexual men		Homosexual men	
	<i>Md</i> (<i>SD</i>)	95% CI	<i>Md</i> (<i>SD</i>)	95% CI	<i>Md</i> (<i>SD</i>)	95% CI
Woman vs. Man	0.65 (0.19)	[0.28, 1.03]	0.66 (0.15)	[0.37, 0.96]	-0.65 (0.15)	[-0.95, -0.36]

Note. Woman = image of the woman, Man = image of the man.

Table S4

Median standardized effect size (and SD) of the posterior distributions and 95% confidence intervals (CI) for the analogous Pavlovian learning task in Experiment 1 and Experiment 2

	Experiment 1		Experiment 2			
	Heterosexual men		Heterosexual men		Homosexual men	
	<i>Md</i> (<i>SD</i>)	95% CI	<i>Md</i> (<i>SD</i>)	95% CI	<i>Md</i> (<i>SD</i>)	95% CI
Reaction times						
CS _w + vs. CS _m +	-0.40 (0.18)	[-0.75, -0.06]	-0.45 (0.14)	[-0.73, -0.17]	0.55 (0.15)	[0.26, 0.84]
CS _w + vs. CS _s +	-0.55 (0.19)	[-0.92, -0.19]	-0.59 (0.15)	[-0.88, -0.30]	0.14 (0.13)	[-0.11, 0.40]
CS _m + vs. CS _s +	0.12 (0.16)	[-0.18, 0.44]	0.08 (0.13)	[-0.17, 0.34]	-0.72 (0.16)	[-1.03, -0.41]
Liking ratings						
CS _w + vs. CS _m +	1.34 (0.24)	[0.87, 1.83]	1.28 (0.19)	[0.92, 1.65]	-1.20 (0.18)	[-1.55, -0.84]
CS _w + vs. CS _s +	0.99 (0.21)	[0.58, 1.42]	1.03 (0.17)	[0.69, 1.38]	-0.43 (0.14)	[-0.71, -0.16]
CS _m + vs. CS _s +	-0.49 (0.18)	[-0.85, -0.15]	-0.38 (0.14)	[-0.65, -0.10]	0.81 (0.16)	[0.49, 1.13]

Note. CS_w+ = conditioned stimulus associated with the image of the woman, CS_m+ = conditioned stimulus associated with the image of the man, CS_s+ = conditioned stimulus associated with the scrambled image.

Table S5

Median standardized effect size (and SD) of the posterior distributions and 95% credible intervals (CI) for the Pavlovian-instrumental transfer (PIT) test in Experiment 1 and Experiment 2

	Experiment 1		Experiment 2			
	Heterosexual men		Heterosexual men		Homosexual men	
	<i>Md</i> (<i>SD</i>)	95% CI	<i>Md</i> (<i>SD</i>)	95% CI	<i>Md</i> (<i>SD</i>)	95% CI
Number of squeezes						
CS _w + vs. CS _m +	0.38 (0.17)	[0.05, 0.73]	0.54 (0.14)	[0.26, 0.82]	-0.43 (0.14)	[-0.71, -0.16]
CS _w + vs. CS _s +	0.38 (0.17)	[0.05, 0.72]	0.48 (0.14)	[0.21, 0.75]	-0.15 (0.13)	[-0.40, 0.11]
CS _m + vs. CS _s +	-0.19 (0.16)	[-0.51, 0.11]	-0.23 (0.13)	[-0.49, 0.03]	0.41 (0.14)	[0.14, 0.69]
PIT index						
CS _w + vs. CS _m +	0.38 (0.17)	[0.05, 0.72]	0.54 (0.14)	[0.26, 0.82]	-0.43 (0.14)	[-0.71, -0.16]

Note. CS_w+ = conditioned stimulus associated with the image of the woman, CS_m+ = conditioned stimulus associated with the image of the man, CS_s+ = conditioned stimulus associated with the scrambled image.

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