

Facial responses of adult humans during the anticipation and consumption of touch and food rewards



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ABSTRACT

Whether cognitive, motivational and hedonic aspects of reward anticipation and consumption can be reliably assessed with explicit and implicit measures, and if different motivational (decision utility) and hedonic (experienced utility) processes get recruited by distinct reward types, remain partly unsolved questions that are relevant for theories of social and non-social decision-making. We investigated these topics using a novel experimental paradigm, including carefully matched social and nonsocial rewards, and by focusing on facial responses. Facial expressions are indeed an often-cited implicit measure of rewards' hedonic impact. For example, food rewards elicit powerful facial responses – characterized by lip smacking, tongue protrusion, and relaxation of the middle face – in human newborns, juvenile monkeys, and adult rats. The same stimuli elicit more nuanced facial reactions in adult humans, which can be best captured with facial electromyography (fEMG). However, little is known about facial expressions preceding reward consumption, reflecting the motivation to obtain and possibly the expected pleasantness of a reward, and whether similar facial expressions are elicited by different types of rewards. To investigate these questions, a novel within-subject experimental paradigm was developed. During the anticipation and consumption of social (affective touch) and nonsocial (food) rewards, explicit (ratings of wanting and liking, physical effort) and implicit (fEMG) measures of wanting and liking were taken in 43 healthy adult participants. Reduced activation of the Corrugator Supercilii (CS) muscle (reflecting less frowning and indicating greater positive response) was found in trials with higher wanting and effort during the anticipation of food rewards, as well as in trials with higher liking and effort during the consumption of food rewards. The CS muscle is thus a sensitive measure of wanting and liking of food rewards both during their anticipation and consumption. Crucially, thanks to careful reward matching, these results cannot be explained by differences in subjective wanting, liking, or effort produced to obtain the two types of rewards. No significant modulation of the Zygomaticus Major (ZM) muscle was found for social or food rewards. Explorative analyses however indicated that the ZM may activate during the delivery of the most wanted touch, but not for the most wanted food. The absence of significant effects of social rewards on the activation of CS and ZM muscles are discussed in relation to the specifics of this innovative task comparing two types of matched rewards in the same participants. The present findings contribute to the understanding of the processes underlying motivational and hedonic aspects of rewards, and may therefore inform models of social and non-social decision-making.

1. Introduction

The subjective value (or utility) we assign to objects, persons, and events determines much of our everyday choices and influences our long-term goals and behavior (Schultz, 2015). Because of that, the

neurobiology of rewards and decision making has become the matter of great scientific interest, and the findings arising from this research field can inform models of decision-making, as well as hold promise for the improvement of current treatments to combat disorders of reward processing such as drug, food, and behavioral dependencies. Over the

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past decades, important advances in the understanding of the psychological and neural mechanisms underlying general reward processing have been made, especially in animals. One dominant theory (Berridge, 1996; Berridge & Robinson, 1998) proposes that reward processing can be subdivided into *wanting* (the motivation to mobilize effort to pursue a reward – best measured before reward consumption) and *liking* (the hedonic response evoked by the consumption of the reward – best measured during and immediately following reward delivery), which rely on partially separate neural and chemical systems (respectively dopamine and opioids). Research in human participants has generally confirmed this view, although separation of wanting and liking has remained controversial (Finlayson & Dalton, 2012; Havermans, 2011), possibly due to methodological differences between animal and human research and to the inconsistent operationalization of these concepts (Pool, Sennwald, Delplanque, Brosch, & Sander, 2016). Similarly, cognitive theories of economic decision making (Kahneman, Wakker, & Sarin, 1997; see also Berridge & O'Doherty, 2014) distinguish between *decision utility* (how much the value attached to an outcome determines its choice or pursuit), and *experienced utility* (referring to the subjective hedonic experience generated by an outcome).

A striking and often-cited hedonic response to reward consists in facial expressions. For example, food rewards (sweet taste) elicit powerful facial responses characterized by lip smacking, tongue protrusion, and middle-face relaxation, in human newborns, juvenile monkeys, and adult rats (Berridge, 2000). In adult humans, however, facial reactions to rewards are more nuanced, often resulting in the relaxation rather than activation of facial muscles (Zeinstra, Koelen, Colindres, Kok, & de Graaf, 2009). Previous research on infants and adults has found that during and after the consumption of food and odor rewards muscles related to negative emotions, including the main frowning muscle Corrugator Supercilii (CS), spontaneously relax, while muscles related to positive emotions, like the main smiling muscle Zygomaticus Major (ZM), occasionally activate (Gilbert, Fridlund, & Sabini, 1987; Horio, 2003; Hu et al., 1999; Zeinstra et al., 2009). This inverse relation of ZM activation and CS deactivation is also typical for spontaneous facial mimicry responses, e.g., when observing emotional facial expressions of happiness (Korb et al., 2015; Korb, Malsert, Strathearn, Vuilleumier, & Niedenthal, 2016; Korb, With, Niedenthal, Kaiser, & Grandjean, 2014). Thus, in response to pleasant taste human adults show only subtle changes in facial expression, which can be best investigated with facial electromyography (EMG) – a technique allowing to capture even small, invisible changes in muscle activation. However, very few studies have used facial EMG to explore implicit hedonic reactions to reward consumption (Pool et al., 2016), and to date no comparison of facial reactions to different types of rewards within the same participants has been performed. Furthermore, previous research focused on reactions during and immediately following reward consumption – little is known about facial expressions of reward anticipation. The phase of reward anticipation reflects, together with the motivational component, also expected pleasantness, i.e. the evaluation, based on memory of past encounters, of how pleasant a specific reward will be¹. Notably, expected pleasantness relates to but is distinct from liking (Pool et al., 2016). Therefore, it is interesting to investigate whether and how hedonic facial expressions differ between the phases of reward anticipation and consumption.

Although many things can be rewarding, the majority of studies in animals and humans have focused on food rewards (Pool et al., 2016) and, especially in the human brain imaging literature, on monetary rewards (Pessiglione et al., 2007; but see Grabenhorst, D'Souza, Parris, Rolls, & Passingham, 2010). Recently, increased scientific interest has

emerged for the class of so-called 'social' rewards.

Many factors speak to the importance of social rewards. Rodents and nonhuman primates are willing to overcome physical and/or mental effort to directly interact with or obtain visual access to conspecifics. Social rewards can be even more rewarding than food rewards. For example, chimpanzees prefer to play (a pleasurable and rewarding experience) with an experimenter than to receive their favorite food, and frequently choose social play over food even when hungry (Mason, Saxon, & Sharpe, 1963). Similarly, thirsty male macaques go as far as to sacrifice a juice reward in order to view images of female perinea (a sexual social reward) and of the faces of dominant monkeys (Deaner, Khera, & Platt, 2005). For all mammals, social play (e.g. running, chasing, climbing, and play fighting) is not only highly pleasurable and stress-reducing, but is also likely to be critical for the healthy development of physical, cognitive, and social capacities (Trezza, Baarendse, & Vanderschuren, 2010). In line with this, deficient or anomalous social play during childhood constitutes a core symptom of autism, and possibly other neuropsychiatric disorders (Jordan, 2003). The importance of social rewards is also exemplified by the negative consequences of social isolation. In adult individuals, including humans, true or perceived social isolation can have deleterious consequences for physical and psychological health, and ultimately result in higher rates of morbidity and mortality in older adults (Cacioppo, Cacioppo, Capitanio, & Cole, 2015; Cacioppo, Hawkley, Norman, & Berntson, 2011). Therefore, social rewards are not just pleasure inducing, but may be regarded, similar to food, as necessary for the survival of the individual and the species. In fact, the British government may have been amongst the first administrations to recognize the importance of social rewards, as evidenced by its recent creation of a ministry for loneliness (Yeginsu, 2018). In extant human research, several types of stimuli have been used as social rewards (Bhanji & Delgado, 2014; Izuma, 2015). These include being evaluated positively by others (Cox et al., 2015; Izuma, Saito, & Sadato, 2008), seeing smiling (Lin, Adolphs, & Rangel, 2012; Rademacher et al., 2010; Spreckelmeyer et al., 2009) and/or sexually attractive faces (Bray & O'Doherty, 2007; Chelnokova et al., 2014), engaging in prosocial behavior, and making donations (Harbaugh, Mayr, & Burghart, 2007; Rilling et al., 2002). Unfortunately, the lack of a clear definition of social rewards, and the large variability in what has been termed a social reward in previous research, currently make it difficult to understand the cognitive and physiological basis of social reward processing, and to compare them to the processing of nonsocial rewards.

A particularly interesting type of social reward is represented by affective (or social) touch, because of its importance for both animals (Burkett et al., 2016) and humans (Gazzola et al., 2012; Nummenmaa et al., 2016; Sailer et al., 2016). Pleasant touch sensations have been proposed to be carried to the brain by specific mechanoreceptors present in non-glabrous (hairy) skin, the so-called C-tactile (CT) afferents. The lack of myelin in CT fibers may be part of the reason why slow (1–10 cm/s) and light caresses are perceived as pleasant (Löken, Wessberg, Morrison, McGlone, & Olsson, 2009; McGlone, Wessberg, & Olsson, 2014). It has been postulated, that CT fibers are specifically tuned to slow, gentle caresses at normal skin temperature (Ackerley, Saar, McGlone, & Backlund Wasling, 2014), and have the role of “providing a peripheral mechanism for signaling pleasant skin-to-skin contact in humans, thereby promoting interpersonal touch and affiliative behavior” (McGlone et al., 2014, p. 743). In line with this, CT-fibers-optimal touch was shown to reduce distress caused by social exclusion (von Mohr, Kirsch, & Fotopoulou, 2017).

Affective touch also elicits facial expressions of reward, which can be captured with EMG. It was found that receiving CT-fibers-optimal pleasant caresses to the forearm results in increased activation of the ZM, a muscle involved in smiling and expressions of pleasure (Pawling, Cannon, McGlone, & Walker, 2017), and in significant relaxation of the CS, the main muscle involved in frowning and negative emotions (Mayo, Lindé, Olsson, Heilig, & Morrison, 2018; Ree, Mayo, Leknes,

¹ In the present study, wanting and expected pleasantness, which are two different constructs, are difficult to disentangle in the anticipation phase. Therefore, throughout the manuscript, facial responses to *reward anticipation* may reflect both.

& Sailer, 2019). These recently published studies point to the usefulness of EMG to track facial responses (related to both smiling and frowning) during the *consumption* of social rewards in adult human participants. It remains unknown, however, if similar facial reactions occur during the *anticipation* of social rewards (i.e. before the reward is delivered). Moreover, facial responses in adult human participants have, to the best of our knowledge, never been compared between social and nonsocial rewards.

The relevance of comparing facial reactions to social and nonsocial rewards is illustrated by the current debate in the field, whether processing of and reactions to different types of rewards emanate from identical or different neural substrates. For the most part, this debate is centered on the distinction between social and nonsocial rewards. According to the ‘common currency hypothesis’, the reward value of all stimuli – e.g., relating to food, money, or social acceptance – is evaluated by the same core neural network (Bhanji & Delgado, 2014; Grabenhorst et al., 2010; Izuma et al., 2008; Peters & Büchel, 2010; Ruff & Fehr, 2014; Sescousse, Caldú, Segura, & Dreher, 2013; Smith et al., 2010). Others have instead proposed that representations coding for different rewards occur in distinct neural structures, albeit on a common scale (Grabenhorst & Rolls, 2011). It has also been specifically put forward that social rewards constitute a separate class of stimuli, and that the neural circuitry dedicated to their processing differs from that for nonsocial rewards (e.g., Rademacher et al., 2010), and can be specifically impaired, for example in people with autism spectrum disorders (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Cox et al., 2015; Gray, Haffey, Mihaylova, & Chakrabarti, 2018; Kennedy & Adolphs, 2012; Kohls et al., 2013; Ruta et al., 2017). In line with this, a growing literature suggests the existence of ‘social-specific cognition’, and the importance of the ‘social brain’, i.e. a network of brain structures which specifically (but not exclusively) performs social cognitive processing and generates social behavior (Frith, 2007; Van Overwalle, 2009), and which is largely shared between humans, nonhuman primates, and rodents (Tremblay, Sharika, & Platt, 2017).

A clear answer to the question if different rewards are processed in the same or different brain areas likely requires the use of brain imaging or other more direct measures of brain activity. However, peripheral physiology can provide insightful clues about cognitive processing, and therefore the question whether different types of rewards elicit distinguishable facial expressions seems of relevance. With this goal in mind, we created and tested a novel paradigm, paying special attention to relevant aspects of stimuli and experimental design.

To compare facial expressions to social and nonsocial rewards, we aimed at reducing and controlling potentially confounding factors. First, reactions to social and nonsocial rewards were compared in the same participants, which is noteworthy because systematic comparisons of the efficacy of social and nonsocial rewards remain rare, both in human and nonhuman subjects (Anderson, 1998; Ruff & Fehr, 2014). Second, stimuli corresponding to social and nonsocial rewards were matched, based on pilot testing, in terms of their subjective hedonic value. The matching of rewards in terms of liking was confirmed, and the matching in terms of wanting was assessed, through ratings and physical effort in each trial. This matching assures that eventual differences in facial EMG are not due to differences in wanting or liking across reward categories. Third, rewards considered to be primary, i.e. for which a biological preparedness can be expected, were used for both social and nonsocial conditions. This necessity is given by the fact that secondary (learned) rewards likely utilize already existing neural systems, i.e. those developed for the processing of primary rewards. Indeed, although a clear distinction of primary and secondary rewards is lacking, most nonsexual social rewards used so far, especially in human subjects, are likely to owe their rewarding properties to learning and top-down processes. These secondary social rewards are typically compared to monetary (i.e. secondary nonsocial) rewards (Chevallier et al., 2016; Izuma et al., 2008; Lin et al., 2012; Rademacher et al., 2010; Smith et al., 2010). Direct comparisons with primary nonsocial

rewards, such as food, are lacking. Fourth, we investigated social rewards that were non-sexual. Social and sexual rewards are often confounded in the literature (Chelnokova et al., 2014; Sescousse et al., 2013). However, although sexual rewards are typically social, the reverse is not necessarily true, and these stimuli may thus constitute separate classes of reward. Fifth, participants obtained real rewards during every trial of the experiment, as opposed to cues for rewards that are only obtained at the very end, as is often done in other research. This design was chosen to measure strong hedonic responses, reflecting true reward consumption, in addition to incentive salience associated with reward-predicting cues (Buchel, Miedl, & Sprenger, 2018).

In summary, the majority of experimental findings to date, which have compared social and nonsocial rewards, have used secondary, that is more abstract social stimuli (e.g. positive written feedback), have not attempted to distinguish social from sexual rewards (e.g. attractive female faces), and typically compared social to monetary instead of to primary nonsocial rewards. Moreover, measures of reward anticipation (including wanting and expected pleasantness before reward delivery), and reward consumption (reflecting liking during and immediately following reward delivery), were rarely measured together in the same participants. Few studies have measured facial responses to rewards in adult humans, and those who did have focused on the phase of reward consumption, and have not compared responses to different types of rewards. There is therefore the need for an experimental paradigm allowing to compare facial reactions to nonsexual social and nonsocial rewards in the same human participants, while ensuring that both types of rewards share some relevant fundamental properties, such as inducing, on a trial-by-trial basis, comparable wanting and liking.

Here, an experiment was conducted with 43 healthy adult human subjects, where for the first time wanting and liking of nonsocial and nonsexual social rewards were both measured explicitly (ratings and effort) and implicitly (facial expressions). Sweet milk with different concentrations of chocolate flavor served as primary food (nonsocial) reward. Gentle caresses to the forearm at different speeds (CT-fibers optimal and non-optimal) – delivered by a hidden same-sex experimenter to guarantee skin-to-skin contact while limiting sexual associations – served as primary touch (social) reward. Importantly, these rewards were chosen based on pilot testing in a different sample of participants, with the intent of making the touch and food conditions comparable in terms of reward magnitude. This allowed to rule out that differences in facial expression are due to differences in reward magnitude. To take into account individual differences and possible changes in reward responding over time, preferences for the three social and three food rewards were measured at the beginning of the session, as well as throughout the task. In each trial of the experiment, wanting of an announced reward was measured through subjective ratings and exerted physical effort (squeezing of a dynamometer with the dominant hand) – the amount of physical effort linearly predicted the probability to receive the announced reward or, alternatively, the least-liked reward. Participants obtained a reward in every trial, and both its anticipation and consumption were measured with ratings and facial EMG of the main smiling (ZM) and frowning (CS) muscles.

In both the touch and the food condition, stimuli with greater reward value were expected to result in higher ratings of wanting and liking and in greater physical effort exerted to obtain them. However, because touch and food rewards had been chosen to be of comparable magnitude, we did not expect differences across conditions in the ratings and the amount of physical effort exerted. Research investigating facial reactions to food stimuli in adult human subjects has generally found that during reward consumption liking is inversely related to participants’ negative facial expressions, and is weakly or not related to participants’ positive facial expressions (Horio, 2003; Hu et al., 1999; Zeinstra et al., 2009). Therefore, greater wanting and liking of food rewards was expected to result in decreased activation of the CS muscle, and no change in the activation of the ZM muscle (typically associated with positive emotions). Previous studies investigating facial reactions

in response to affective touch have found liking of this social reward to result in significantly increased ZM activation and decreased CS activation (Mayo et al., 2018; Pawling et al., 2017; Ree et al., 2019). Therefore, greater wanting and liking of touch was expected to result in increased activation of the ZM muscle and decreased activation of the CS muscle.

In summary, facial reactions measured with EMG were expected to differ for touch (social) and food (nonsocial) rewards, with greater touch rewards resulting in ZM activation and CS deactivation, and greater food rewards resulting in decreased CS activation, but no change in ZM activation. This being the first study comparing facial expression during reward anticipation and consumption, we expected a similar EMG pattern for periods preceding and accompanying reward delivery (respectively corresponding to reward anticipation and consumption).

2. Methods

2.1. Participants

The participants sample included 43 volunteers (20 females) aged 20–41 years ($M = 24.7$; $SD = 4.8$). We aimed for a minimum sample size of 40, based on sample sizes of previous studies reporting EMG modulations by liking of affective touch ($N = 30$ in Mayo et al., 2018; $N = 29$ in Pawling et al., 2017), and expecting possible data loss in some participants. Once this number was reached, data acquisition was stopped shortly afterwards due to time and organizational constraints. All participants reported being right-handed, to smoke less than five cigarettes daily, to have no history of current or former drug abuse, to like milk and chocolate, not to suffer from diabetes, lactose intolerance, lesions or skin disease on the left forearm, and to be free of psychiatric or neurological disorders. Participants' average Body Mass Index (BMI) was 22.23, ($SD = 2.52$, range 18.08–29.36). Their average level of hunger at the beginning of the experiment, as self-rated on a Likert scale ranging from one ('not at all hungry') to seven ('very hungry'), was 2.74 ($SD = 1.52$). On average, they had not eaten for 4.67 h ($SD = 4.29$). To reduce the chances that social touch would be perceived as a sexual reward, the social touch stimulation was always carried out by a same-sex experimenter (see Procedure), and only participants who reported to be heterosexual were included. Average felt 'sociability', which was self-rated on a Likert scale ranging from one ('not at all') to seven ('very much'), was 5 ($SD = 1.30$). The study was approved by the ethics committee of the Medical University of Vienna. Participants signed informed consent and received a monetary compensation of 20 €.

2.2. Questionnaires

Questionnaires were used to investigate if the sample was representative of the general population in terms of social touch appreciation, alexithymia, autism spectrum disorders, and general health and taste attitudes². Before coming to the laboratory, participants completed online the three taste-related subscales ("craving for sweet foods", "using food as a reward", "pleasure") of the Health and Taste Attitudes Questionnaires (HTAS) (Roininen, Lähteenmäki, & Tuorila, 1999), the Social Touch Questionnaire (STQ) (Wilhelm, Kochar, Roth, & Gross, 2001), the 20-item Toronto Alexithymia Scale (TAS-20) (Bagby, Parker, & Taylor, 1994), and the short version of the German Autism Spectrum Quotient (AQ-k) (Freitag et al., 2007). The Positive and Negative Affect Schedule (PANAS) (Watson, Clark, & Tellegen,

1988), was filled out at the beginning of the laboratory session (see [Supplementary material](#) for a description of our sample).

2.3. Stimuli

Three stimuli with identical fat and sugar content (1.5 g fat, 10 g of sugar per 100 g) were used as rewards in the Food condition: milk, chocolate milk, and a 4:1 mix of milk and chocolate milk. Tap water served for rinsing at the end of each trial. The initial stimulus temperature of these liquids was kept constant ($\sim 4^\circ\text{C}$) across participants. Stimulus delivery was accomplished through computer-controlled pumps (PHD Ultra pumps, Harvard Apparatus) attached to plastic tubes (internal \varnothing 1,6 mm; external \varnothing 3,2 mm; Tygon tubing, U.S. Plastic Corp.), which ended jointly on an adjustable arm positioned about two centimeters in front of the participant's mouth. On each trial, two milliliters of liquid were administered during two seconds. Overall, including stimulus pretesting (see Procedure), participants consumed 164 ml of liquids, composed of 82 ml of water, and 82 ml of sweet milk with different concentrations of chocolate aroma (depending on effort, see below).

Touch rewards consisted of gentle caresses over a previously-marked nine-centimeters area of the participant's forearm (measurement started from the wrist towards the elbow). Three different caressing frequencies, chosen based on the literature and pilot testing, were applied during nine seconds by a same-sex experimenter: six cm/s, 21 cm/s and 27 cm/s. To facilitate stroking, the stimulating experimenter received extensive training and in each trial heard the stimulation rhythms through headphones. Because direct skin-to-skin contact constitutes a potent stimulus (Kress, Minati, Ferraro, & Critchley, 2011; Strauss et al., 2019), caresses were delivered by the experimenter using his/her index and middle fingers, instead of a brush.

Between three to five seconds after the end of reward delivery, a 50 ms-long white noise was played at 90–110 dB through headphones (ER1; Etymotic Research, Inc.), to induce a postauricular reflex (PAR) (Benning, Patrick, & Lang, 2004). Due to technical problems with a secondary PC sound card, delivery of this sound probe was imprecise, and no proper PAR could be recorded.

2.4. EMG

After cleansing of the corresponding face areas with alcohol, water, and an abrasive paste, Ag/AgCl electrodes were attached bipolarly according to guidelines on the left corrugator supercilii (CS) and the zygomaticus major (ZM) muscles (Fridlund & Cacioppo, 1986), as well as on the infrahyoid muscles in the left laryngeal region (to monitor deglutition), and on the pinna and postauricular muscle of the left ear (to record the PAR). Results are here reported for the CS and ZM muscles. A ground electrode was attached to the participants' forehead. EMG data was sampled at 1024 Hz with impedances below 20kOHM using a TMS International Refa8 amplifier and the Portilab2 software (www.tmsi.com).

2.5. Procedure

After signing informed consent and filling out the PANAS questionnaire, participants were seated at a table and comfortably rested their left forearm on a pillow. A curtain blocked their view of the left forearm and the rest of the room. This was particularly relevant for the Touch condition, in which one of two same-sex experimenters applied the touch rewards to the participant's left forearm. Two experimenters were always present during testing, to limit the influence of participants' experimenter preferences, and to allow participants to better concentrate on the (touch) stimuli.

2.5.1. Ranking of stimuli

Participants first completed a short task in which they experienced

² Questionnaire scores were also added as covariates to the main statistical analyses, to investigate if behavioral and EMG measures differed by personality traits. This, however, did not affect the here reported results or their interpretation.

and ranked by liking all touch and food stimuli, presented in semi random order in sets of three stimuli of the same condition. Participants' average liking of milk and chocolate, as rated before the experiment on separate Likert scales ranging from one (not at all) to seven (very much), was 6.32 ($SD = 0.81$) and 6.47 ($SD = 0.78$), respectively. In agreement with the literature, most (70%) participants chose the slowest touch frequency (6 cm/second) as their preferred social reward. The milk with the highest concentration of chocolate was chosen by 61% of participants as the preferred food reward.

2.5.2. Main task

In the main task, participants' most liked stimuli (see Ranking of stimuli) were used as 'High' rewards, the stimuli with medium liking as 'Low' rewards, and the least liked stimuli were used as 'Very Low' rewards. Just before and after the main task the maximum voluntary contraction (MVC) was measured in newtons (N), by asking participants to squeeze the dynamometer (HD-BTA, Vernier Software & Technology, USA) with their right hand as hard as possible during three seconds for three successive trials. The overall maximum value was taken as the individual MVC and used to individually calibrate the dynamometer. Average MVCs before the main task (peak force across all three trials) were 187.34 N ($SD = 29.80$) for female participants and 306.76 N ($SD = 54.73$) for male participants. At the end of the main task, MVCs were slightly lower, likely due to fatigue, with an average of 161.15 N ($SD = 29.75$) for female and 302.39 N ($SD = 62.40$) for male participants.

EMG electrodes were attached, participants received detailed instructions, and completed four practice trials (two per condition). The main task comprised four experimental blocks, each with 16 trials. Each block contained either Touch or Food trials, and the blocks were interleaved (ABAB or BABA) in a counterbalanced order across participants. Each trial included (See Fig. 1) the following main steps³: (1) a picture announcing the highest possible reward (3 sec; only High or Low rewards could be announced), (2) a continuous scale ranging from 'not at all' to 'very much' to rate (without time limit, using the left index and ring fingers on a number-keyboard) wanting of the announced reward (ratings were converted to a 20-point Likert scale), (3) a 4-sec period of physical effort, during which probability of receiving the announced reward was determined by the maximum amount of force exerted by squeezing the dynamometer with the right hand, while receiving visual feedback (sliding average of 1 sec, as percentage of the MVC; for a similar task see Lopez-Persem, Rigoux, Bourgeois-Gironde, Daunizeau, & Pessiglione, 2017), (4) a picture announcing the obtained reward (3 sec), which could be High (in trials where a possible High reward had been announced), Low (in trials where a possible Low reward had been announced), or Very Low (in all trials, if insufficient effort had been exerted; the greater participants' effort, the higher the probability of obtaining the announced reward), (5) a phase of reward delivery (2 sec in the Food, 9 sec in the Touch condition – this difference in timing was necessary to obtain sufficiently long tactile stimulation, while keeping the overall trial duration similar across conditions), (6) in the Food condition instructions to lean back and swallow the obtained reward (3 sec; this period is included in the analyses of the Delivery period), (7) a relaxation phase (3 sec), and (8) a continuous scale to rate the liking of the obtained reward (without time limit, using the left index and ring fingers on a number-keyboard). In the Food condition, participants then received water for mouth rinsing. In both conditions trials ended with a blank screen for 3 to 4 s. After each block participants could take a short break.

All tasks were run on a desktop computer with Windows XP using MATLAB 2014b and the Cogent 2000 and Cogent Graphics toolboxes, and presented on an LCD monitor with a resolution of 2560 × 1600 pixels. Before and at the end of the laboratory experiment, participants

self-reported on a series of questions, which served to verify inclusion criteria, and to obtain information regarding their hunger and sociability. Analysis of self-report data confirmed that participants had average personality characteristics – see [supplementary material](#) for details.

2.6. Analyses

See the link https://osf.io/mb2f4/?view_only=92c1e24b19e44c17aea688a8f1536801 for data and analysis scripts. Data were analyzed with linear mixed effects models (LMMs) using the lmer() function of the lme4 package in R (Bates, Maechler, Bolker, & Walker, 2014; R Core Team, 2019). In comparison to ANOVAs, LMMs reduce Type-I errors and allow for better generalization of findings (Judd, Westfall, & Kenny, 2012). For all analyses, categorical predictors (e.g. Condition) were centered through effect coding (e.g. -1, 1), continuous predictors (i.e. ratings of Wanting, ratings of Liking, and Effort, for the EMG analyses) were mean-centered and scaled for each participant, and by-subject random intercepts and slopes for all within-subjects factors and their interactions were included as random effects⁴. Type-III F-tests were computed with the Satterthwaite degrees of freedom approximation, using the anova() function of the lmerTest package. Summary tables of all models were made with the function tab_model() from the sjPlot package, and are reported in the supplementary material. Figures (except Fig. 1 and S1) were created in R using the packages ggplot2, yarr, ggpirate, and cowplot.

Behavioral data were analyzed in the following manner. Outlier trials were identified separately by subject. They were defined as trials with a rating of wanting, rating of liking, or amount of exerted force, which was greater/smaller than the subject's mean ± 2 times the subject's standard deviation. This led to an average rejection of 5.35 trials out of 64 trials per participant ($SD = 3.05$). The number of excluded trials did not differ between the social and nonsocial conditions (all $t < 1.2$, all $p > 0.2$). Three separate models were run for each behavioral dependent variable (ratings of wanting and liking, and force exerted), with Condition (Social, Nonsocial) and RewardType (High, Low, Very Low) as fixed effects, and with by-subject random intercepts and slopes for Condition, RewardType, and their interactions⁵.

Due to technical failure, EMG was not recorded for one participant, and was missing for half of the trials in the social condition in another participant. EMG data were preprocessed in Matlab R2014b (www.themathworks.com), partly using the EEGLAB toolbox (Delorme & Makeig, 2004). A 20 to 400 Hz bandpass filter was applied, then data were rectified and smoothed with a 40 Hz low-pass filter. A small number of outlier trials (sum over all participants $N = 18$ in the Social condition, $N = 27$ in the Nonsocial condition) were removed based on visual inspection.

Epochs were extracted (see Fig. 1 and S1) for a Pre-Effort-Anticipation period at the beginning of each trial, a Post-Effort-Anticipation period following the effort phase and preceding reward delivery, a Delivery period during which participants received either food or social rewards, and a Relax period immediately following reward delivery. The Pre-Effort-Anticipation lasted three seconds, during which the possible reward was presented. The Post-Effort-Anticipation included, for both the Touch and the Food conditions, the periods of reward announcement (3 sec), and preparation for reward consumption (3

⁴ For example, ratings of Wanting were analyzed with this model: lmer(Wanting ~ Condition * RewardType + (Condition * RewardType | sub)). An example of EMG data analyzed by Wanting: lmer(EMG ~ Condition * Wanting + (Condition * Wanting | sub)).

⁵ We also controlled for possible satiation over the course of the experiment by adding as covariates of no interest trial number or experimental block (re-coded to 1 and 2). This did not change the pattern of results nor their interpretation.

³ See Figure S1 in the Supplementary material for all elements in a trial

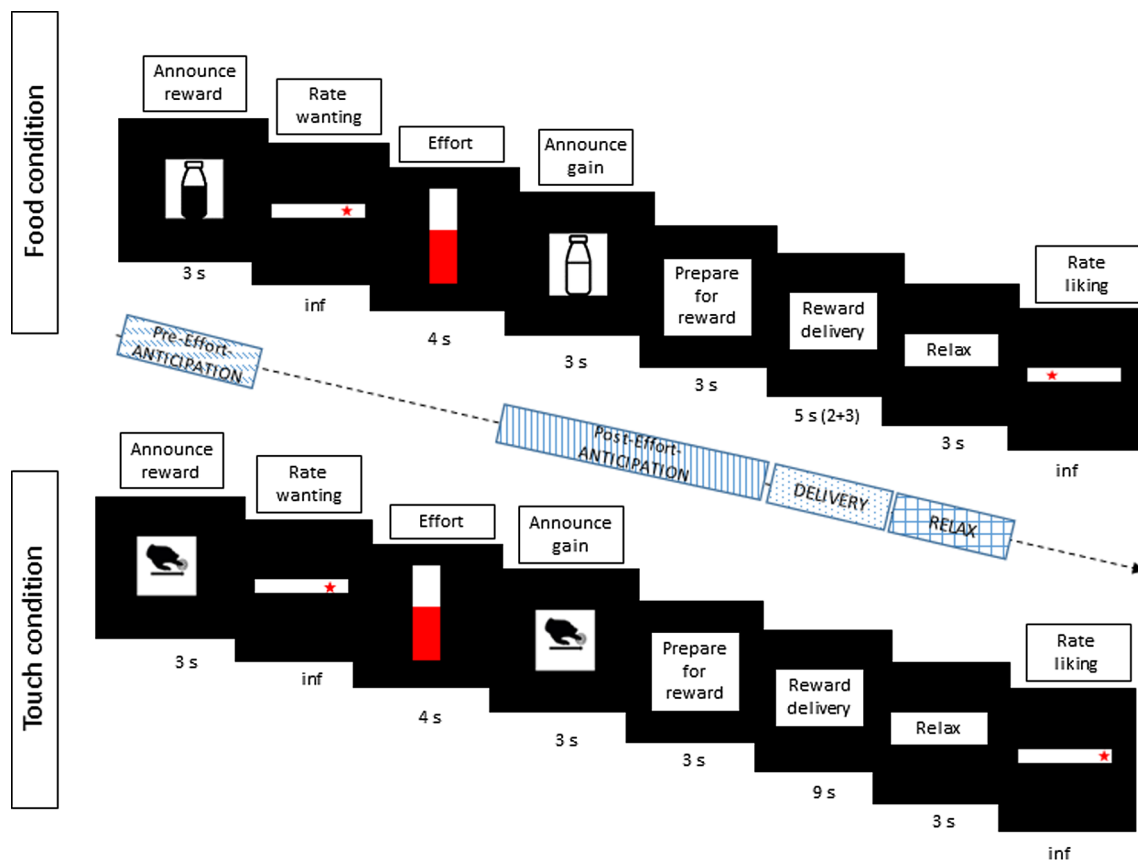


Fig. 1. Main elements of each trial for the social and nonsocial conditions. Before the main task, rewards were ranked by participants' individual liking. In each condition of the main task, only one of the two most liked rewards could be announced at the beginning of each trial. Hand-squeezing effort, indicated in real-time by a rising red bar, determined the probability of obtaining the announced reward. If the announced reward was not obtained (due to insufficient squeezing), the least-liked reward was delivered. EMG analyses were carried out during 4 periods of each trial. To assess reward anticipation, EMG data was analyzed during the Pre-Effort-Anticipation period (3 sec) at the beginning of the trial, when a possible reward was announced, as well as during the Post-Effort-Anticipation period (3 sec announcement + 3 sec preparation), immediately preceding reward delivery. To investigate reward consumption, EMG data was analyzed during reward Delivery (5 sec in the Food, and 9 sec in the Touch condition), and in the immediately following Relax phase (3 sec). "Inf" stands for infinite duration of ratings slides, or until button press by participants. For a complete representation of all trial elements see Fig. S1 in the supplementary material. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sec)⁶. Reward Delivery lasted 5 sec (2 sec of delivery + 3 sec in swallowing) in the Food condition, and 9 sec in the Touch condition. Importantly, a full appreciation of food rewards requires their olfactory components to reach the olfactory receptors in the nasal cavity through swallowing (Seubert, Ohla, Yokomukai, Kellermann, & Lundström, 2015). For explorative analyses, the Delivery window of the Touch condition was further split in two, in order to compare EMG responses to Food and Touch rewards over a time windows of similar duration (5 s). The following relaxation phase always lasted 3 sec. For each trial, values in these four epochs were expressed as percentage of the average amplitude during the fixation cross at the beginning of that trial (2 sec, see Fig. S1).

Because initial reward preferences were not always stable across the entire experiment, the EMG data was analyzed based on trial-by-trial ratings of wanting and liking, as well as the effort exerted⁷. To compare facial reactions during the Pre- and Post-Effort-Anticipation of Touch and Food rewards, separate analyses per muscle were run with the fixed

effects Condition (Touch, Food) and either trial-by-trial ratings of Wanting, or the amount of exerted Effort. Analyses of the Delivery and Relax periods were also computed with ratings of Liking as dependent measure. In all cases, by-subject random intercepts and slopes for all within-subjects factors (Wanting, Effort, or Liking) and their interactions were included as random effects⁸.

For display (see Figs. S2–S7 in the Supplementary Material), EMG data was averaged over time-windows of one second and continuous predictors were made categorical through median-splitting. These graphs also allowed to verify the correct functioning of the electrodes placed over both the CS and the ZM area. For example, activation of the ZM peaked, as expected, during the consumption of food rewards (Fig. S7), due to active ingestion and swallowing of the food samples. For statistical analyses the factor Time was omitted, as it was not a factor of major interest, and its inclusion in both fixed and random effects prevented model convergence.

⁶ Results did not change when restricting analyses to the 3 sec of reward announcement.

⁷ The same general pattern of results, although with fewer significant effects, was obtained when using initial reward categories.

⁸ To control for possible satiation over the course of the experiment the factor experimental block (recoded to 1 and 2) was added as covariate. This did not change the pattern of results nor their interpretation.

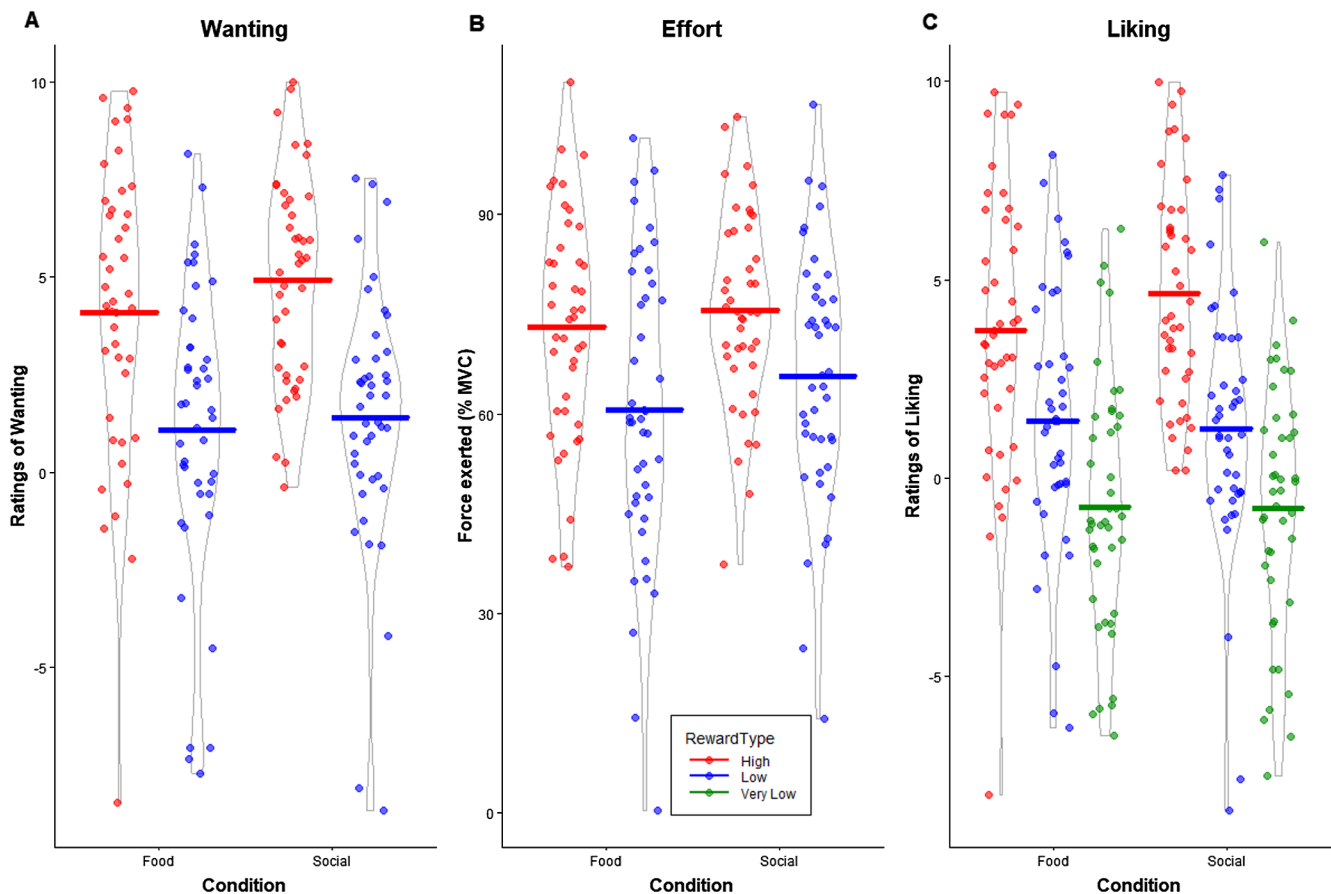


Fig. 2. Violin plots depicting wanting (A), effort (B), and liking (C) for Food and Touch rewards, by initial preferences. Ratings of wanting and liking were recorded on Likert scales ranging from -10 ('not at all') to $+10$ ('very much'). Exerted force is the maximum value (as percentage of the MVC) reached in a 4-sec period. These measures are shown as a function of RewardType, i.e. the individual preferences measured at the beginning of the experiment. Each data point corresponds to the mean for one participant, horizontal lines show means over all participants, outer lines represent the probability densities. Very Low rewards were never announced, and were only received after insufficient effort had been exerted – they therefore only appear for the ratings of liking (C).

3. Results

3.1. Explicit measures: wanting, liking and effort

The mean (SD) number of trials per RewardType were 11.9 (2.6) for 'High', 10.5 (3.4) for 'Low', and 9.6 (5.1) for 'Very Low' in the Touch condition, and 11.5 (3.1) for 'High', 9.8 (3.5) for 'Low', and 10.9 (5.2) for 'Very Low' in the Food condition. Importantly, while these a-priori reward categories were used for analyses of rating and effort behavior, the EMG data was analyzed based on trial-by-trial ratings and effort. The use of trial-by-trial measures of wanting and liking as continuous fixed- and random-effects predictors provides a statistically more powerful approach, and moreover allowed to control for potential subtle between-subject or temporal effects in these key dimensions of reward processing.

The first set of analyses served to verify the matching of rewards across the Touch and Food conditions, allowing us to compare implicit facial reaction to different types of reward. Subjective ratings of

Wanting and Liking, and **Effort** exerted to obtain the announced reward, were analyzed in separate LMMs with Condition (Food, Touch) and RewardType ('High', 'Low' for wanting and effort; 'High', 'Low', 'Very Low' for liking) as fixed effects, and as random effects intercepts for subjects and by-subject random slopes for the effects of Condition, RewardType, and their interaction.

Behavioral analyses on ratings of **Wanting** (Fig. 2A) resulted in a significant main effect of RewardType ($F(1,42.044) = 49.573$, $p < .001$), due to higher ratings of wanting for High reward ($M = 4.60$, $SD = 3.79$) compared to Low reward ($M = 1.22$, $SD = 3.99$). The main effect of Condition and the interaction were not significant (all $F < 2.9$, all $p > .1$).

The same LMM on **Effort** (Fig. 2C) resulted in a significant main effect of Condition ($F(1, 42.081) = 4.5536$, $p = .04$), due to stronger force in the Touch condition ($M = 70.74$, $SD = 21.68$) compared to the Food condition ($M = 66.63$, $SD = 25.40$); and a main effect of RewardType ($F(1,42.189) = 29.5490$, $p < .001$) due to stronger squeezing for High rewards ($M = 74.59$, $SD = 20.21$) compared to Low

EMG of CS during Pre-Effort-Anticipation

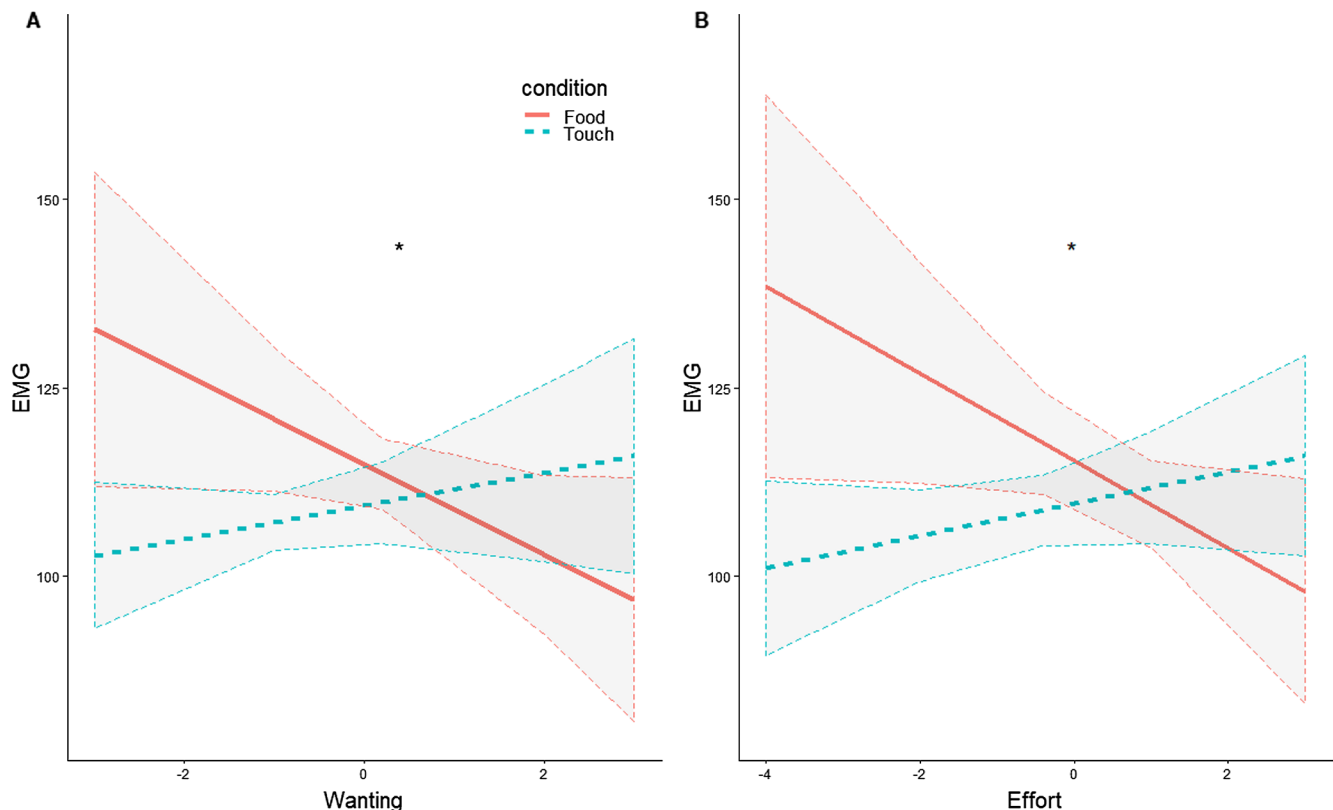


Fig. 3. Fitted values for the CS muscle during Pre-Effort-Anticipation. Activation of the CS was inversely related to both wanting (A) and effort (B) during the presentation of possible future food rewards, but was unrelated to wanting and effort for touch rewards. The Y-axis represents the EMG as percentage of the baseline; the shaded area represents the confidence interval.

rewards ($M = 62.69$, $SD = 25.41$), but no interaction ($F(1, 42.151) = 0.3430$, $p = .56$). Moreover, in line with previous studies using a similar effort task (Lopez-Persem et al., 2017), the average effort ($M = 68.20$, $SD = 24.32$) was not significantly different from 70% of the MVC ($t(42) = -0.86$, $p = .39$).

The same LMM on the Liking ratings (Fig. 2C) resulted only in a main effect of RewardType ($F(2, 42.601) = 36.820$, $p < .001$), with most liking of High rewards ($M = 4.49$, $SD = 3.58$), followed by Low rewards ($M = 1.59$, $SD = 3.76$), and VeryLow rewards at the bottom ($M = -0.62$, $SD = 3.42$). Although the average liking for VeryLow rewards was slightly below zero, this difference was not significant, as tested with one-sample t-tests (for Food and Touch conditions, respectively, $t(42) = -1.52$ and -1.58 , $p = .12$ and $.13$). This confirms the assumption that VeryLow rewards were not perceived as a punishment to be avoided, but rather as a lower (neutral) reward.

In summary, a significant main effect of Condition was found for Effort but not for ratings of Wanting or Liking. None of the analyses of behavioral data resulted in a Condition X RewardType interaction. This confirmed that behavioral results were comparable between the Food and Touch conditions, allowing to investigate physiological differences between otherwise analogous conditions.

3.2. Implicit measures: Facial EMG

Only main or interaction EMG effects involving the factor Condition are reported, as they are central for comparing facial responses across social and nonsocial rewards⁹.

3.2.1. Pre-Effort-Anticipation

For the CS muscle, significant Condition X Wanting ($F(1, 41.993) = 5.6452$, $p = .022$), and Condition X Effort ($F(1, 37.671) = 6.9410$, $p = .012$) interactions were found (Fig. 3). As expected, activation of the CS to food stimuli was inversely related to wanting ($B = -5.98$, $p = .05$) and to effort ($B = -5.78$, $p = .04$). However, activation of the CS to touch was not significantly related to either wanting or effort (both $B < 2.2$, $p > .2$). For the ZM muscle, no significant or trend-like Condition X Wanting or Condition X Effort interaction were found (both $F < 1.6$, $p > .20$).

3.2.2. Post-effort-anticipation

No significant or trend-like Condition X Wanting or Condition X Effort interactions were found for the CS muscle, nor for the ZM muscle (all $F < 2.2$, all $p > .14$). To investigate the possible effects of negative reward prediction error, i.e. in trials in which strong but not maximal ($< 100\%$) effort was followed by a Very Low reward, the predictor RewardObtained (High, Low, Very Low, based on initial reward rankings) was added (separately for the Food and Touch conditions) to the continuous predictor Effort. No simple or interaction effects were found (all $F < 1.6$, all $p > .21$). We conclude that reward prediction errors in this task either did not impact CS activation, or did so in a subtle way that is not captured by our analyses.

3.2.3. Reward delivery

For the CS muscle, significant Condition X Effort ($F(1, 44.577) = 5.1483$, $p = .028$) and Condition X Liking ($F(1, 43.181) = 5.1049$, $p = .029$) interactions were found (Fig. 4B-C). In both cases, the negative slope of the CS was significantly different from zero in the Food condition (both $B < -5.8$, both $p < .05$), but not in

⁹ For a full description of results see tables in Supplementary Material

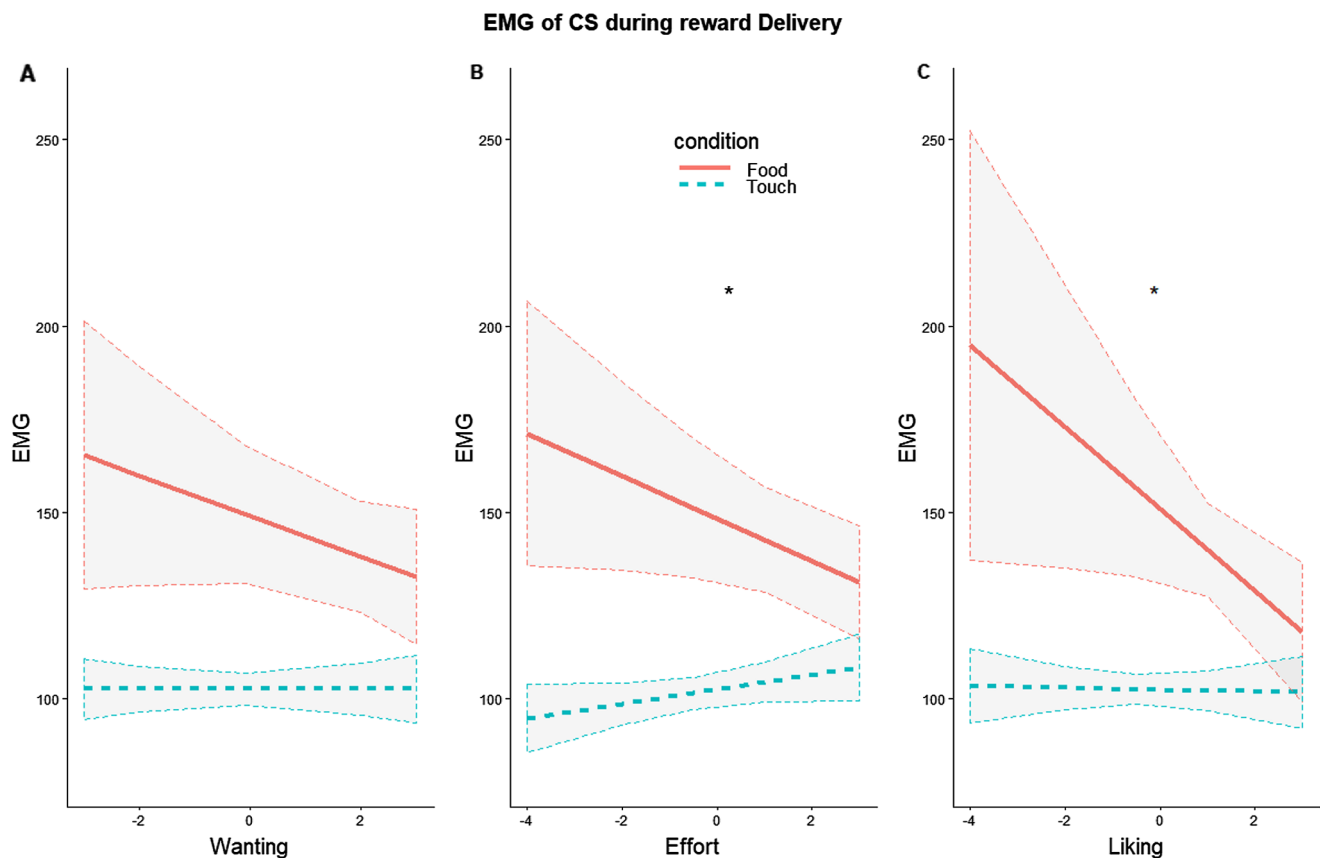


Fig. 4. Fitted values for the CS muscle in the Delivery phase. Significant Condition X Effort (B) and Condition X Liking (C) interactions were found. The CS was inversely related to Effort (B) and Liking (C) of food rewards only. The Y-axis represents EMG as percentage of the baseline; the shaded area represents the confidence interval.

the Touch condition (both $B < 1.8$, both $p > .12$). No main or interaction effects involving Wanting, Effort, or Liking were found for the ZM muscle (all $F < 1.9$, all $p > .18$). In order to explore whether the lack of results for the Touch condition was due to the different duration of the delivery between the two conditions, additional analyses were carried out splitting the Delivery period of the Touch condition into two windows (first:1–5 and second:5–9 s). No significant interaction effects with Condition were found (all $F < 0.9$, all $p > .36$). Further splitting by condition, for the ZM, a significant effect of Wanting was found ($F(1, 40.702) = 7.0146$, $p = .011$) in the second of these time windows, such that greater wanting of Touch rewards was associated with increased ZM activation. ZM activation was however not significantly modulated by Effort or Liking in the Touch condition, nor by Wanting, Effort, or Touch in the Food condition (all $F < 1.8$, all $p > .18$).

3.2.4. Relax phase

For the CS muscle a significant Condition X Liking ($F(1, 41.247) = 9.6422$, $p = .003$) interaction and a marginally significant Condition X Effort ($F(1, 45.809) = 2.8773$, $p = .096$) interaction were found (Fig. 5C). A significant main effect of Effort was also present ($F(1, 43.6665) = 5.6971$, $p = .021$, Fig. 5B). In the Food condition, the slope of CS activation was significant by Liking ($B = -18.46$, $p = .001$), and by Effort ($B = -11.50$, $p = .02$). Slopes for the CS by Liking and Effort were not significantly different from zero in the Touch condition (both $B > -2.6$, $p > .28$). For the ZM muscle, no significant or trend-like main or interaction effects for Wanting, Effort, or Liking were found (all $F < 1.2$, all $p > .29$).

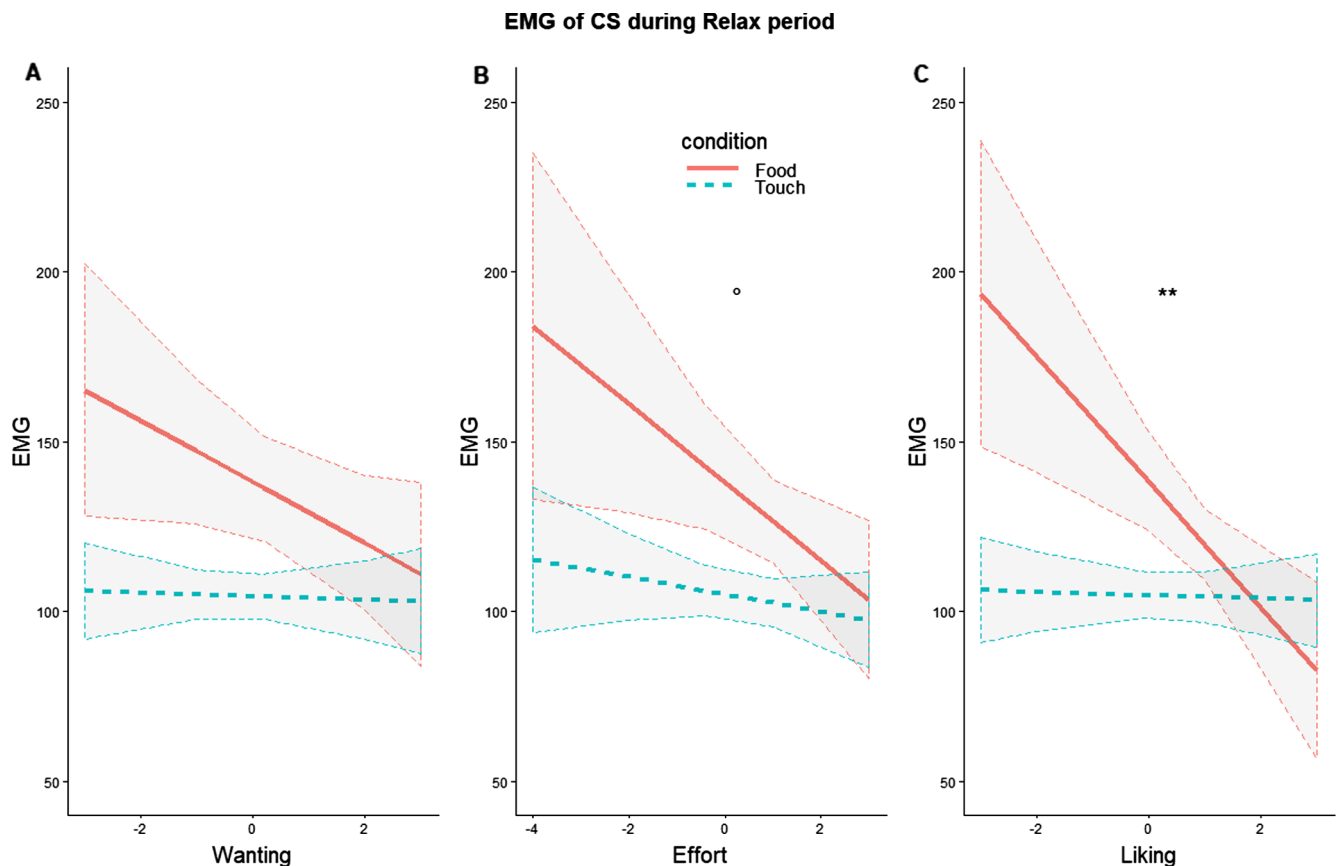


Fig. 5. Fitted values for the CS muscle in the Relax period (following reward Delivery). A marginally significant Condition X Effort interaction (B), and a significant Condition X Liking interaction (C) were found. In both cases, the negative slope of the CS was significantly different from zero in the Food, but not the Touch condition. Liking of a food reward, as well as effort to obtain it, were thus reflected in decreased CS activation. The Y-axis represents EMG as percentage of the baseline; the shaded area represents the confidence interval.

4. Discussion

To assess and compare facial expressions elicited by the anticipation and consumption of social and nonsocial rewards, a new paradigm was developed and tested in 43 healthy human adult participants, while implicit facial reactions were recorded with facial EMG. The reward value of social (touch) and nonsocial (food) rewards was matched based on pilot testing, and this matching was confirmed with comparable ratings of wanting and liking, as well as force exerted to obtain rewards. Implicit facial responses could therefore be compared across reward types, while keeping everything else constant.

The EMG data were analyzed in four time periods of interest: Pre-Effort-Anticipation (announcement of which reward can be obtained, if sufficient effort is exerted), Post-Effort-Anticipation (announcement of the to-be-obtained reward, based on the effort exerted), reward Delivery, and a Relax period immediately following reward delivery. During Pre-Effort-Anticipation, wanting and effort were significantly inversely related to CS activation to food rewards, but not to touch rewards (Fig. 3, and S2). During reward Delivery, effort to obtain, and liking of food, but not of touch rewards, resulted in CS relaxation (Fig. 4 and S6–S7). In the Relax period following delivery, greater food liking, as well as effort to obtain it, resulted in significant CS relaxation (Fig. 5 and S6–S7). In contrast, activation of the ZM was not significantly modulated by any of these factors and for none of the reward types. However, exploratory analyses focusing on the last five seconds of the Delivery period, the results of which should be considered preliminary, revealed that activation of the ZM was increased during the delivery of touch and not food rewards (Figs. S6–S7). In summary, the CS appeared sensitive to anticipation and consumption of food rewards, but not of

touch rewards, while the ZM was not significantly modulated by either reward type, but may be sensitive to wanted touch rewards, as suggested by exploratory analyses.

The lack of ZM activation during the consumption (Delivery and Relax periods) of preferred food rewards is in line with prior research, which has generally failed to find a clear indicator of hedonic pleasure to food in human facial expression, and has instead reported CS activation to be inversely related to reward value of food stimuli (Pool et al., 2016). Possibly, effects of reward magnitude on the ZM may have been masked by movements linked to food intake (e.g. swallowing), which affect the lower face more than the upper face (Figs. S6–7, top panels).

Regarding facial responses to touch rewards, the absence of a modulation of CS activity stands in contrast to the recent findings of increased CS activation to less preferred social touch (Mayo et al., 2018), and of CS relaxation during CT-optimal touch (Ree et al., 2019). However, Pawling et al. (2017) measured both the ZM and CS muscles in response to gentle brush strokes delivered at CT-fibers-optimal speed to the participant's forearm, and failed to find changes in CS activation, but instead reported increased ZM contraction. Thus, three published studies so far have measured responses to the delivery of social touch in the CS and ZM muscles, and reported inconsistent findings with either a modulation of the CS or of the ZM muscle by liking. Here, none of the sampled muscles showed significant differences in activation by wanting of social touch. This may be due to the inclusion of food rewards in the same experiment, or to a different time window compared to Mayo and colleagues, as well as Ree and colleagues.

The importance of social rewards, both during development and adulthood, is well-accepted in the scientific community and in society

at large (Cacioppo et al., 2011; Jordan, 2003; Trezza et al., 2010). It remains unclear, however, if the behavioral, physiological, and neural correlates of the processing of social rewards correspond to those arising in response to nonsocial rewards. So far, few studies have directly compared reactions to social and nonsocial rewards – or have done so without choosing nonsexual primary rewards. Arguably, advancement in the understanding of the processing of social rewards, and of its similarities or disparities with nonsocial rewards, has been slow partly due to the lack of appropriate experimental designs. With the present task, by using rewards that are well-matched across conditions, we were able to detect differences in the implicit measure of facial EMG.

Studies in non-human primates (Morecraft, Louie, Herrick, & Stilwell-Morecraft, 2001; Morecraft, Stilwell-Morecraft, & Rossing, 2004) have shown that regulation of facial expression is likely to be achieved through a distributed multifocal processing system, which includes lateral and medial cortical, as well as subcortical areas. Importantly, this distributed system is differently regulating lower and upper facial muscles, with the upper face being more bilaterally innervated and less under voluntary motor control. As a consequence, a different pattern of facial responses may emerge depending on the stimulus input, suggesting possibly different neural processing systems underlying social and nonsocial rewards. These differences in the innervation of upper and lower-face muscles may be responsible for finding effects of wanting and liking of food rewards in the CS muscle, but not in the ZM muscle. Ultimately, proper testing of the common currency hypothesis, comparing processing of and responding to different types of rewards, will however require brain imaging or other more direct measures of brain activity.

Notably, the here reported EMG differences between social and nonsocial rewards cannot be explained by different subjective reward magnitude or satiety effects on the two types of rewards. Although sensory-specific satiety can occur during the course of an experiment (Havermans, Janssen, Giesen, Roefs, & Jansen, 2009), adaptation to small quantities of high-calories food stimuli, like sweet chocolate milk, is arguably less problematic. Over the course of approximately an hour, participants received in total only 82 ml of sweet (chocolate) milk, with a total intake of calories inferior to 1.5 g of fat and 10 g of sugar. Affective touch, on the other hand, demonstrates stable preferred stroking velocities in humans (Luong, Bendas, Etzi, Olausson, & Croy, 2017), and slow adaptation and satiety effects (Sailer et al., 2016; Tricoli, Ackersley, & Sailer, 2014). Importantly, findings in both conditions remained unchanged when controlling for experimental trial or block.

To conclude, implicit measures of reward processing, that is facial EMG of the CS and ZM muscles, differed in response to social and nonsocial rewards, which were otherwise matched in terms of explicit wanting and liking. Specifically, activity of the CS muscle reflected lower wanting (Pre-Effort-Anticipation) and liking (during and after delivery) of food stimuli, but not of social rewards; the ZM somewhat activated during the consumption of wanted social, but not of food stimuli (but no interaction with the factor condition was found, and these results of exploratory analyses should be interpreted with care). These results point to possibly different physiological responses to social and nonsocial rewards – a hypothesis that should be further tested at the level of the brain. Notably, this study included two major differences between the delivery periods of food and touch rewards. First, the delivery of touch rewards lasted nine seconds, while delivery of food rewards lasted five seconds (including swallowing). This difference in timing was chosen to achieve a sufficiently long tactile stimulation, while keeping the overall trial duration similar across conditions. Second, the delivery period included extensive mouth movements in the Food condition, but not in the Touch condition, a limitation that is hard to avoid. Future research should use the same timing for the delivery of both rewards, and optimize EMG recording during the delivery phase, to allow reliable cross-condition comparison.

Finally, the present real-effort task allows to measure, for the first

time in humans, ratings, behavioral and facial responses during the anticipation and consumption of matched primary social and nonsocial rewards. We hope that the implementation of this task in healthy controls as well as in people presenting anomalies of reward processing (such as autism spectrum disorders), eventually together with concurrent electroencephalographic recording or functional magnetic resonance imaging (Sailer et al., 2016), and possibly in combination with dopaminergic or opiodergic pharmacological challenges and genotyping (Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010; Eisenegger et al., 2013), will allow the research community to advance in the understanding of social and nonsocial reward processing. We believe that the present and future findings comparing behavioral and physiological responses to carefully-matched different types of rewards, have the potential to inform models of social and non-social decision-making.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2019.104044>.

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