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Is comfort food really comforting? Mechanisms underlying stress-induced eating[☆]

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ABSTRACT

Overeating behaviors are nowadays a worldwide issue, and cumulative evidence shows that stress induces excessive pursuit of highly palatable food. However, the role of stress in this phenomenon remains poorly understood. The classic interpretation is that excessive eating is an attempt to reduce the aversive feeling associated with the stress response through the hedonic properties of highly palatable food. In this review, we propose an alternative hypothesis based on theoretical models developed in the framework of reward processing. We review recent literature on animal and human studies suggesting that stress reduces hedonic pleasure during highly palatable food consumption and increases the control that the habitual and Pavlovian systems exert on food-seeking behaviors over the control exerted by the goal-directed system. From this literature, we propose that (a) stress amplifies automatic attentional orienting toward stimuli associated with palatable food (i.e., Pavlovian stimuli), rendering them more likely to be perceived; and (b) once perceived, these stimuli trigger stress-amplified motivational bursts and the control that the habitual system exerts on food-seeking behaviors. We hypothesize that stress-induced eating is driven by habits and Pavlovian motivational bursts, independent of hedonic pleasure or even of the goal of reducing the stress-related aversive state. Thus, if a stressed person encounters an environmental stimulus associated with highly palatable food, this may trigger excessive pursuit of highly palatable food, whether or not the food elicits liking during its consumption.

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1. Introduction

In the last century, many countries have experienced a considerable increase in overeating behaviors (Prentice, 2006). Overeating can have severe consequences, in particular obesity and associated diseases, such as diabetes mellitus type 2, cardiovascular diseases (Ruhm, 2012) and even cognitive deficits and increased risk of dementia (Kerwin et al., 2011). Stress has an important influence on eating behaviors: During stressful periods, a subgroup of people (i.e., 30%) decreases their food intake, whereas most individuals considerably increase their food intake (Epel et al., 2004; Stone & Brownell, 1994; for a review, see Adam & Epel, 2007). Stress-induced overeating is a phenomenon that is particularly robust among people who try to control their

excessive food intake (e.g., restraint eaters). During stressful periods, they often relapse and overeat (Polivy & Herman, 1999).

A stressful event (i.e., a stressor) is defined as (a) an event that is perceived as threatening for the physiological or psychological integrity of the individual, combined with (b) the perception of being unable to successfully cope with such an event (Lazarus & Folkman, 1984). Stressors trigger a complex response in the individual (i.e., stress), which is physiologically characterized by the activation, at the central nervous system level, of dopaminergic and noradrenergic systems (Cabib & Puglisi-Allegra, 2012; Schwabe, Dickinson, & Wolf, 2011), together with the activation of the sympathetic nervous system and the hypothalamic–pituitary–adrenal axis (HPA; Koolhaas et al., 2011). The activation of the HPA leads to the secretion of glucocorticoids (i.e., cortisol in humans) and numerous other hormones, neuropeptides and neurotransmitters (see Herman et al., 2003, for a review). For instance, a powerful stressor that can activate this system in humans consists of situations that are perceived as threatening for the social self because of a form of social evaluation such as public speaking or being judged by other people (Dickerson & Kemeny, 2004).

The kind of food that is overeaten under stressful conditions tends to be highly palatable, which means that it triggers hedonic pleasure and is usually highly caloric (e.g., sucrose or lard; Pecoraro, Reyes, Gomez, Bhargava, & Dallman, 2004; Tomiyama, Dallman, & Epel, 2011; Zellner

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et al., 2006). Experiments modeling stress-induced eating in animals have demonstrated that stressed rodents usually consume less food under stress, unless it is highly palatable, in which case consumption considerably increases (see Bazhan & Zelena, 2013, for a review). Experiments conducted on humans have also shown that participants in stressful conditions eat more highly palatable food than do participants in stress-free conditions (Epel, Lapidus, McEwen, & Brownell, 2001; Tomiyama et al., 2011; Zellner et al., 2006).

The stress-induced increase in consumption of highly palatable food has been widely documented in animals and humans (Adam & Epel, 2007; Dallman, Pecoraro, & la Fleur, 2005; Dallman et al., 2003; Greeno & Wing, 1994; Maniam & Morris, 2012), but the underlying psychological mechanisms of this behavioral change have been poorly explored. The most common explanation in mechanistic terms is the following: Highly palatable food is consumed because its rewarding hedonic properties reduce the discomfort generated by the stressful situation (Adam & Epel, 2007; Dallman et al., 2003, 2005).

Highly palatable food is conceived as one of the most powerful rewards in animals (Berridge, 2009), including humans (Kringelbach, 2004). In this narrative review, we capitalize on a theoretical model developed within a reward processing framework (Berridge & Robinson, 2003; Rangel, Camerer, & Montague, 2008) suggesting that other psychological mechanisms could be involved in stress-induced eating beyond hedonic pleasure. More particularly, we suggest that the theoretical framework proposed by Rangel et al. (2008) is well suited to study the interaction between reward and overeating behavior. This model postulates that reward-seeking behaviors are controlled by three functionally interacting systems: Pavlovian, habitual and goal directed.

The *Pavlovian system* assigns intrinsic affective properties of a rewarding outcome (e.g., highly palatable food) to a neutral stimulus with which it has been systematically associated (e.g., a bell ringing). After the associative learning is completed, the Pavlovian stimulus acquires the ability to evoke behavioral reactions originally triggered by the rewarding outcome (e.g., salivating after hearing the bell ringing).

The *habitual system* controls automatic instrumental actions. An instrumental action (e.g., pressing on a lever) leading to a reward (e.g., highly palatable food) is learned through trial and error. During the course of these repetitions, the action becomes more and more automatized and, eventually, habits are no longer triggered by the representation of a particular reward (e.g., highly palatable food), but rather by environmental stimuli from the context in which the instrumental action has been learned (e.g., seeing the lever, pressing the lever; stimulus–response learning even in the absence of hunger).

In the habitual system, the action is not accomplished with the intention to obtain a reward, whereas in the *goal-directed system*, the representation of the rewarding outcome is critical. The goal-directed system involves learning the association between a specific action (e.g., jogging) and a rewarding outcome (e.g., feeling fit; action–outcome learning). The representation of the outcome and its causal relation with the instrumental action is vital to the goal-directed system, but it is not necessary for the habitual system, which involves direct learning between an environmental stimulus and an instrumental action (stimulus–response learning). Therefore, goal-directed actions demand a higher load of cognitive resources and are slower compared with habits. However, the effort invested in goal-directed actions is flexibly proportional to the value of the rewarding outcome that they are leading to.

In this narrative review, we present recent representative literature investigating how stress influences these three systems in food-seeking behaviors for highly palatable food. First, we illustrate how the stress-induced eating behavior might not exclusively be driven by the goal or the experience of a stress reduction through a pleasant food consumption experience (i.e., the so-called aversive state reduction hypothesis; Robbins & Fray, 1980). Rather, we propose that (a) stress

increases the attention towards and the motivation triggered by the perception of the Pavlovian stimuli, which is then (b) channeled by the habitual system, which predominates over the goal-directed system when an individual is under stress. More precisely, we propose that the Pavlovian system determines the affective intensity of stress-induced eating (i.e., how much effort is mobilized in food-seeking behaviors, how much food is wanted), and the habitual system determines the direction of stress-induced eating (i.e., which kind of food is sought under stressful conditions).

2. Limits of the aversive state reduction hypothesis

The aversive state reduction hypothesis was formulated in the 1980s (see Robbins & Fray, 1980, for a review) and is still the most common explanation of stress-induced eating (Adam & Epel, 2007; Dallman et al., 2003, 2005). According to this hypothesis, stressed people eat highly palatable food because its consumption triggers a hedonic experience that reduces the aversive feeling associated with the stress response. Highly palatable foods are assumed to comfort stressed people, make them feel better and help them cope with the emotional discomfort associated with stress (Dallman et al., 2003). Based on this principle, stress-induced eating is a potentially dysfunctional form of self-medication (Dallman et al., 2005). Consistent with this proposition, Peters, Kubera, Hubold, and Langemann (2011) suggested that eating high-calories foods under stress re-establishes the brain energy's homeostasis, thereby reducing the negative mood associated with the stress response.

Highly palatable food is a powerful primary reward. Its consumption is reported as a pleasurable experience (Kringelbach, 2004) and it triggers a series of neurophysiological reactions that are classically associated with pleasure, such as the activation of the orbitofrontal cortex (Kringelbach, O'Doherty, Rolls, & Andrews, 2003) and the ventral pallidum (Simmons et al., 2014; Smith, Tindell, Aldridge, & Berridge, 2009), as well as the release of opioids and endocannabinoids (Cota, Tschoop, Horvath, & Levine, 2006). According to several investigators (see Adam & Epel, 2007, for a review), the hedonic properties of food play a critical role in stress-induced eating. Notably, in an individual under stress, the quantity of food that is eaten largely oversteps homeostatic needs and the hunger drive (Born et al., 2010). Therefore, it has been proposed that food eaten by individuals under stress is not consumed for its nutritive properties, but rather for its hedonic properties, which attenuate the aversive feeling associated with the stress response.

Although the hedonic properties of highly palatable food can explain many aspects of stress-induced eating, other aspects of stress-induced eating cannot be accounted for exclusively in terms of hedonic pleasure. First, recent evidence suggests that relief does not play a critical role in the increase of food-seeking behaviors observed when organisms are under stress. Peciña, Schulkin, and Berridge (2006) tested the influence of food-associated stimuli (i.e., a sound) on the amount of energy invested in food-seeking behaviors (i.e., press a lever to obtain food). They administered this test under extinction, meaning that during the test, food was not delivered. They demonstrated that stressed rodents are willing to invest more energy to obtain highly palatable food than are non-stressed rodents, even if they never consumed the highly palatable food when under stress during the test. The typical stress-induced food-seeking behavior appeared despite the fact that they could not experience the relieving properties that highly palatable food has in stressful conditions. In this situation, the stress-induced food-seeking behavior cannot be considered in terms of relief, because experiencing stress reduction through the hedonic properties of food was not a necessary element for the behavior.

Second, one of the findings supporting the aversive state reduction hypothesis is that under stressful conditions, the quantity of food consumed oversteps the homeostatic need. However, a consistent corpus of studies conducted on rodents (Berridge & Valenstein, 1991;

Peciña, Cagniard, Berridge, Aldridge, & Zhuang, 2003) has demonstrated that consuming more does not always imply liking more.

Berridge and co-workers demonstrated that it is possible to make an organism consume more of a highly palatable food that it no longer likes (Berridge & Valenstein, 1991; Peciña et al., 2003). They suggest that the consumption of highly palatable food involves not only a hedonic component (i.e., *liking*), but also a motivational component (i.e., *wanting*; see Berridge & Robinson, 2003, for a review). The most innovative aspect of this series of experiments was the use of two distinct measures for the motivational and hedonic components of reward processing. The former was measured through the effort mobilized to obtain food, whereas the latter was measured by a distinct dependent variable consisting of the prototypical orofacial expressions during food consumption. These orofacial expressions are elicited by the consumption of pleasant (e.g., sweet taste) or unpleasant (e.g., bitter taste) food and seem to constitute a reliable index of hedonic experience in several organisms (e.g., rodents, apes, monkey, human babies; Berridge, 2000). Through these measures, Berridge and co-workers suggested that two different dissociable neural networks underlie the hedonic versus the motivational components (Mahler & Berridge, 2012; Peciña et al., 2003; Wyvell & Berridge, 2000). Critically, they demonstrated that the level of dopamine in the mesolimbic region influences the amount of effort mobilized to obtain highly palatable food and the quantity of food consumed, without simultaneously modifying the hedonic pleasure during its consumption. Consumption of highly palatable food can thus exclusively be driven by the motivational component, independent of the hedonic component. More generally, reward consumption does not necessarily reflect the hedonic experience. Studies conducted on humans (Epstein et al., 2004; Fay & Finlayson, 2011) confirmed that non-homeostatic eating does not always correlate with the food's hedonic properties and that people who overeat do not systematically prefer stimuli associated with highly palatable food (Coppin, Nolan-Poupart, Jones-Gotman, & Small, 2014).

Finally, several studies suggest that stress decreases the organism's capability of experiencing hedonic pleasure in general. During stressful periods, people report experiencing less hedonic pleasure in their daily activity than they do during stress-free periods (Berenbaum & Connelly, 1993). In the case of food, stress also influences the hedonic experience that arises from food consumption by attenuating the sweet taste perception (Al'Absi, Nakajima, Hooker, Wittmers, & Cragin, 2012) and by reducing the hedonic experience associated with highly palatable food (Enkel, Spanagel, Vollmayr, & Schneider, 2010). These findings do not necessarily support the aversive state reduction hypothesis, according to which stress should render the hedonic pleasure from consumption of highly palatable food even more intense because of its relieving power from the aversive feeling associated with the stress response. The reduced hedonic capabilities of the stressed organism could thus attenuate, rather than increase, the relieving power of highly palatable food.

Together, these empirical findings suggest that stress-induced eating cannot be accounted for exclusively in terms of stress reduction. They highlight the need to explore how stress could influence other mechanisms involved in reward-seeking behaviors beyond hedonic pleasure.

3. Influence of stress on the Pavlovian system

According to Rangel et al. (2008), phylogenetically, the Pavlovian system is one of the oldest systems controlling reward-seeking behaviors. This system is based on a learned association between an initially neutral stimulus (e.g., a sound) and a rewarding outcome (e.g., highly palatable food). During this associative learning, a value is assigned to the initially neutral stimulus (i.e., becoming the Pavlovian stimulus). After the learning phase, the perception of the Pavlovian stimulus alone evokes the representation of the rewarding outcome

and the behavioral responses associated with it. This simple stimulus–stimulus associative system, which exists even in very simple organisms (i.e., *Caenorhabditis elegans*; Amano & Maruyama, 2011), can have considerable control over complex human behaviors (Allman, DeLeon, Cataldo, Holland, & Johnson, 2010; Hogarth, Dickinson, Wright, Kouvaraki, & Duka, 2007; Nadler, Delgado, & Delamater, 2011). A large corpus of studies conducted on both animals and humans has shown that the Pavlovian system interacts with other motivational (Balleine, Killcross, & Dickinson, 2003; Balleine & Killcross, 2006; Prevost, Liljeholm, Tyszka, & O'Doherty, 2012; Talmi, Seymour, Dayan, & Dolan, 2008) and attentional (Anderson, Laurent, & Yantis, 2011a, 2011b, 2012; Matsumoto & Hikosaka, 2009; Pool, Brosch, Delplanque, & Sander, 2014b) systems. These interactions might critically underlie the effect of stress on highly palatable food-seeking behavior.

3.1. Pavlovian system and motivation

The control of Pavlovian stimuli on motivation is one of the most widely investigated interactions. Motivation can be defined as the direction and energization of an action leading to a desired outcome (i.e., an instrumental action; Elliot, 2006). Classic studies show that the perception of a stimulus (e.g., a sound) that has previously been associated with a rewarding outcome (e.g., sucrose) increases the amount of energy invested in the instrumental action (e.g., pressing a lever to obtain sucrose; for reviews, see Bindra, 1974; Bolles, 1972; Toates, 1998). This phenomenon is known as *Pavlovian-instrumental transfer* and its existence has been largely replicated in animals (e.g., Corbit & Balleine, 2005, 2011; Wassum, Ostlund, Balleine, & Maidment, 2011; Wyvell & Berridge, 2001) and in humans (e.g., Allman et al., 2010; Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008; Pool, Brosch, Delplanque, & Sander, 2014a; Prevost et al., 2012; Talmi et al., 2008; Trick, Hogarth, & Duka, 2011).

The control that Pavlovian stimuli exert on motivation does not exclusively depend on the previous associative learning experience, but also on the physiological state of the organism when perceiving this Pavlovian stimulus (Dickinson & Balleine, 1990; Dickinson & Dawson, 1987; Peciña et al., 2003; Wyvell & Berridge, 2000). This interaction becomes particularly important in the processing of rewards such as highly palatable food because the relevant physiological state (e.g., hunger) has a cycle that rapidly changes over time. In rodents, Pavlovian stimuli increased motivation only if they were associated with highly palatable food while the rodents were in a hungry state, meaning when the stimulus was relevant for the current physiological state of the organism (Dickinson & Balleine, 1990; Dickinson & Dawson, 1987). Another series of studies conducted on rodents demonstrated that the neurophysiological activity state of some deep structures of the brain also influenced the effect of the Pavlovian stimuli on motivation. More particularly, the dopaminergic mesolimbic activity of the organism amplifies the motivational control exerted by Pavlovian stimuli on behavior. Rodents with increased dopaminergic mesolimbic activity mobilize more effort to obtain highly palatable food (e.g., sucrose) after the perception of the Pavlovian stimulus than do rodents in a normal activity state (Wassum et al., 2011; Wyvell & Berridge, 2000, 2001).

Peciña et al. (2006) demonstrated that pharmacologically induced stress has consequences for rodent behavior that are similar to those of increased mesolimbic dopaminergic activity. They manipulated the level of corticotropin-releasing factor, a hormone critically involved in the physiological response to stressors. They showed that rodents who received microinjections of corticotropin-releasing factor invested almost three times more energy into obtaining a sweet reward (i.e., sucrose) after the perception of the Pavlovian stimulus than did rodents that did not receive the injection (see Fig. 1A and B). These effects have been recently replicated in humans (Pool, Brosch et al., 2014a) through behavioral stress induction. In this experiment, a stressful state was induced by asking participants to keep their hand in ice-

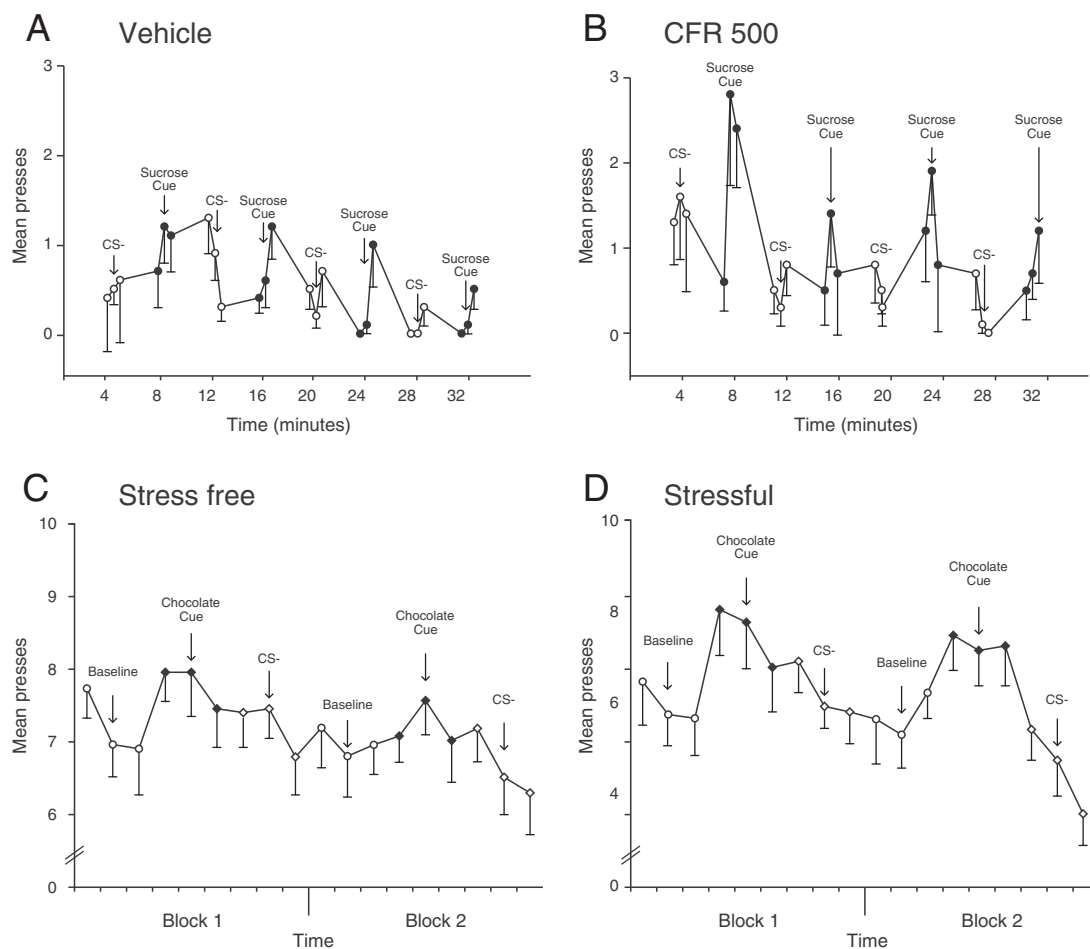


Fig. 1. Comparison of the influence of stress manipulation on the motivational burst triggered by Pavlovian stimuli associated with a sweet reward in rodents (stress manipulation through microinjections of corticotropin-releasing hormone; CFR; panels A and B) and in humans (panels C and D). The negative conditioned stimulus (CS-) is a neutral stimulus that has been associated with the absence of the reward during associative learning. The baseline is a neutral stimulus that has been presented in the intra-trial interval during associative learning. The CS- and the baseline are used to control the influence of the Pavlovian stimulus on motivation so that it is specific to its association with the sweet reward. Reprinted from *Peciña et al. (2006)* and *Pool, Brosch et al. (2014a)*.

cold water while being observed and videotaped. Similar to the behavior of the rodents, stressed participants mobilized more effort to obtain a sweet reward (i.e., a chocolate odor) compared with non-stressed participants after the perception of the Pavlovian stimulus (see Fig. 1C and D). Interestingly, in both rodent and human experiments, stress did not globally increase the motivation for the sweet reward: The motivational increase appeared only after the perception of the Pavlovian stimulus. The relation between stress and food seeking does not appear to be linear; rather, it appears to consist of intense motivational bursts triggered by Pavlovian stimuli. These bursts can be conceived as peaks of motivation to seek a reward that are triggered by the perception of a Pavlovian stimulus, that decay quickly after the Pavlovian stimulus is removed, and that re-appear if the Pavlovian stimulus is re-encountered (Berridge, 2007). This suggests that even under conditions of high stress, highly palatable food is not overconsumed if a Pavlovian stimulus is not perceived.

3.2. Pavlovian system and attention

Pavlovian stimuli are likely to be better perceived than other stimuli present in the environment because the Pavlovian system can also drive attentional processing. Several studies conducted in animals (Matsumoto & Hikosaka, 2009) and humans (Anderson et al., 2011a, 2011b, 2012; Pool, Brosch et al., 2014b; Theeuwes & Belopolsky, 2012) demonstrated that initially neutral stimuli (e.g., a geometrical shape) that have been systematically associated with a rewarding outcome

become perceptually more salient. The increase of perceptual salience by the Pavlovian system is a process that is so automatized that it controls the organism's reactions even when Pavlovian stimuli present in the environment cannot be consciously discriminated (Pool, Delplanque et al., 2014). When several stimuli are competing to access the limited attentional resources of an individual, attention is automatically and involuntarily oriented toward perceptually salient stimuli (i.e., attentional bias). Therefore, Pavlovian stimuli are more likely to access the organism's limited cognitive resources and to be more thoroughly processed.

The control of the Pavlovian system on attention processing, similar to its control on motivation, is dependent on the physiological state of the organism. This aspect becomes particularly important in the attentional processing of rewards such as highly palatable food. Evidence has demonstrated that the attentional bias toward Pavlovian stimuli associated with chocolate is no longer present once an individual has eaten chocolate until satiation (Pool, Brosch et al., 2014b). Similarly, several studies have demonstrated that stimuli that are naturally associated with highly palatable food, for instance, pictures or words of highly palatable food, biased attention only if they were perceived in a physiological state of hunger (Giel et al., 2011; Mogg, Bradley, Hyare, & Lee, 1998; Piech, Pastorino, & Zald, 2010; Talmi et al., 2013; for a similar effect of a physiological state of thirst, see Mazziotti, Sellem, & Koenig, 2014). Newman, O'Connor, and Conner (2008) showed that stress has consequences that are similar to that of a physiological state of hunger. More precisely, they showed that external

eaters (i.e., people who tend to eat in response to external stimuli; Schachter, 1968) have a larger attentional bias for snacks in a stressful condition compared with a stress-free condition. Although this is only indirect evidence, it suggests that, analogous to hunger, stress might amplify the perceptual salience of Pavlovian stimuli associated with highly palatable food. However, further studies are necessary to directly confirm this hypothesis.

Evidence is accumulating to suggest that stress amplifies the control of the Pavlovian system on motivation and attention. If a person in a state of stress encounters a Pavlovian stimulus associated with highly palatable food, this could trigger an intense motivation to obtain the highly palatable food after having their attention oriented toward it, thereby increasing the likelihood of eating.

4. Influence of stress on the habitual and goal-directed systems

As indicated earlier, stress may amplify the motivational bursts triggered by the perception of Pavlovian stimuli associated with highly palatable food before any pleasant experience of stress relief is felt by the organism. One could argue that this increase in motivation is directed toward the anticipatory relief of stress (i.e., the goal) through the pleasure that is expected to be experienced during highly palatable food consumption. However, recent literature does not support such an argument, as it shows that stress reduces the effect of the goal-directed system, favoring the control of the habitual system (e.g., Schwabe & Wolf, 2011b).

The habitual and the goal-directed systems are deeply implicated in reward-seeking behaviors (Rangel et al., 2008). The habitual system controls automatic instrumental actions that are triggered by the environmental stimuli from the context in which they have been learned, whereas the goal-directed system involves the learning of the association between an action and a rewarding outcome. The main difference between these two systems is the representation of the rewarding outcome toward which the instrumental action is directed. Whereas the representation of the outcome and its causal relation with the instrumental action is vital to the goal-directed system, it is not necessary for the habitual system, which involves direct learning between an environmental stimulus and an instrumental action (stimulus–response learning; Dickinson, 1985; Dickinson & Balleine, 1994). These two systems usually operate in tandem: During the first phases of learning, the instrumental action is controlled by the goal-directed system and, as long as the learning proceeds, the control gradually shifts to the habitual system. The more an organism is trained to perform an instrumental action, the more the action becomes efficient and automatized, and the less the goal of the action needs to be effortfully represented (Dickinson, 1985).

Classically, the control of the habitual and goal-directed systems is dissociated by using *outcome devaluation procedures* (Adams, 1982). A typical devaluation procedure is to decrease the value of a particular highly palatable food by feeding the organism with that food until satiation (Balleine, 1992), or by associating that food with a state of illness (Balleine & Dickinson, 1991). The instrumental action is subsequently investigated during a test in which no highly palatable food is delivered (i.e., under extinction) in order to avoid any effect of the now devaluated outcome consumption on the response. When the instrumental action is driven by the representation of the outcome (i.e., the goal-directed system), the effort invested in the instrumental action leading to the devaluated outcome decreases after the devaluation procedure. However, when the instrumental action is driven by the environmental stimuli, independent of the outcome representation (i.e., the habitual system), the instrumental action does not decrease after the devaluation procedure. These effects have been largely demonstrated in both animals (Balleine, 1992; Balleine & Dickinson, 1991; Dickinson & Balleine, 1994) and humans (Tricomi, Balleine, & O'Doherty, 2009; Valentin, Dickinson, & O'Doherty, 2007). Johnson and Kenny (2010) obtained empirical evidence suggesting that

overeating highly palatable food can lead to a strong control of the habitual system that renders food-seeking behavior insensitive to its negative consequences.

This phenomenon seems to be amplified by stress. Dias-Ferreira et al. (2009) demonstrated that chronic stress favors the control of the habitual over the goal-directed system on food-seeking behaviors and reduces rodents' sensitivity to outcome devaluation and extinction. Stressed rodents' instrumental actions were insensitive to the representation of the outcome: They kept performing the instrumental action even if it led to highly palatable food that had been devaluated. In contrast, non-stressed rodents stopped performing the instrumental action associated with the now devaluated food, thereby adapting their behavior to the value of the outcome. Moreover, stressed rats were also insensitive to the causal relation between the action and the outcome; they continued to perform the instrumental action even if it was no longer leading to any kind of outcome (i.e., extinction), whereas non-stressed rodents gradually stopped performing the action (see Fig. 2A).

Schwabe and co-workers replicated these effects in a series of studies conducted on humans (see Schwabe & Wolf, 2011b, for a review). Participants were stressed by being observed and videotaped while keeping their hand in ice-cold water. This stressful state decreased the individuals' sensitivity to outcome devaluation: Stressed participants kept performing the instrumental action that was leading to a previously devaluated highly palatable food (Schwabe, Hoffken, Tegenthoff, & Wolf, 2011; Schwabe & Wolf, 2009; see Fig. 2B). Moreover, similar to the behavior of the rodents, stressed participants also became less sensitive to extinction; they continued to perform the instrumental action associated with the highly palatable food even when it was no longer leading to the food (Schwabe & Wolf, 2011a). Analogous to the case with rodents, stress seems to influence humans' highly palatable food seeking behavior by favoring the habitual system more than the goal-directed system. The hedonic properties of highly palatable food determine how habits are learned and acquired. However, once established, habits do not require the representation of the outcome and its relation with the instrumental action. Therefore, under stressful conditions, the highly palatable food that is usually consumed is automatically sought, whether it is currently liked or not.

Researchers have investigated the influence of stress on the control of habitual and goal-directed systems on highly palatable food-seeking behaviors in highly controlled experimental settings (Dias-Ferreira et al., 2009; Schwabe & Wolf, 2009). However, more recently, Neal, Wood, and Drolet (2013) tested this hypothesis in a series of experiments conducted in the field. They demonstrated that during stressful periods such as exam sessions, the kind of snacks (e.g., yoghurt, candy bars, popcorn, crackers) participants consumed was determined by their preexisting eating habits, regardless of how much the snack was liked or how healthy the snack was perceived to be. For instance, in one of these studies they measured the pre-existing habits through a standardized diary in which participants wrote down the kinds of foods they routinely consumed. The frequency with which these eating habits were performed was measured during a stress free and a stressful period. Results revealed that stress similarly increased the healthy and unhealthy eating habits.

Stress seems to prompt habitual eating behaviors that are performed automatically and – possibly – without a representation of the value of the highly palatable food. If a person in a state of stress can choose between two different kinds of food, the choice would not only be based on the representation of the value of this food, but also on the kind of food that he or she habitually consumes. Therefore, it seems that under stressful conditions, the representation of the hedonic or other positive properties of highly palatable foods does not fully determine which food will be consumed. Note that although the habitual system determines the direction of the food-seeking behavior (i.e., which kind of food is sought under stress), it does not determine the affective intensity of the food-seeking behavior (i.e., the amount of



Fig. 2. Comparison of the influence of stress manipulation on the habitual and goal-directed systems. (A) In the study conducted on rodents, after a training phase, a highly palatable food was devaluated by being eaten until satiation. After devaluation, control rodents diminished the effort invested in the instrumental action leading to the devaluated outcome, whereas stressed rodents did not. (B) A similar effect was found in the study conducted on humans. Reprinted from Schwabe and Wolf (2009) and Dias-Ferreira et al. (2009).

effort mobilized to obtain food, how much food is wanted under stress), which is, rather, controlled by the Pavlovian system.

5. Conclusions and implications

The goal of the present narrative review was to use models developed in the reward processing framework (Berridge & Robinson, 2003; Rangel et al., 2008) to suggest other psychological mechanisms that could underlie stress-induced eating beyond the aversive state reduction hypothesis.

Recent literature reviewed here suggests that stress amplifies the control of the Pavlovian and the habitual systems on highly palatable food-seeking behaviors and reduces the control of the goal-directed system (see Fig. 3d). Stress thereby prompts highly efficient and automatized responses over controlled responses, which require effortful processing (Neal et al., 2013).

More precisely, we reviewed evidence suggesting that stress amplifies the control of Pavlovian stimuli on motivation and attention. Under stressful conditions, Pavlovian stimuli associated with highly palatable food automatically attract attention, increasing their chances of being perceived (Newman et al., 2008) and when they are perceived, they trigger amplified motivational bursts for highly palatable food

(Peciña et al., 2006; Pool, Brosch et al., 2014a). These motivational bursts are likely to be channeled by the habitual system that predominates under stressful conditions over the goal-directed system (Schwabe & Wolf, 2011b). The Pavlovian system might determine the amount of energy invested to obtain highly palatable food, whereas the habitual system might determine the kind of highly palatable food that is sought when an individual is under stress.

Therefore, if a person encounters a stimulus associated with highly palatable food, this could trigger an intense motivation to obtain the food. His or her habits could then determine what kind of highly palatable food will be consumed, regardless of whether the palatable food is currently appreciated or not.

Although we illustrated how the influence of stress on the Pavlovian and the habitual systems can lead to overeating, these mechanisms can potentially be adaptive. The Pavlovian and the habitual systems require low energy levels to function; since the organism under stress is often energy depleted, relying on these effortless systems could help the organism to cope with the situation.

The environmental stimuli that have been associated with highly palatable food play a determining role in these mechanisms, which could underlie stress-induced eating. They trigger both the motivational burst for highly palatable food and food-seeking habits. It is interesting to note that in most countries that have witnessed a large increase of overeating behaviors, people are constantly exposed to stimuli associated with highly palatable food, such as advertising or restaurant logos. From this observation, several scholars (Marreau, Hollands, & Fletcher, 2012; Rangel, 2013) have proposed that the regulation of the food environment could be a promising strategy to reduce overeating behaviors. These kinds of interventions target implicit and automatic processes, which, unlike more high-level cognitive interventions, do not require effort. In the case of stress-induced eating, they could be particularly effective because they specifically target the systems (i.e., habits and motivational bursts triggered by Pavlovian stimuli) that stress seems to amplify. Moreover, if highly palatable food could be accessed only through actions that need to be controlled by the goal-directed system, stress should not increase its consumption since stress decreases control of the goal-directed system.

Although we reviewed several studies showing that the hedonic properties of highly palatable food are not critical in stress-induced eating underlain by the Pavlovian and habitual systems, to model the role of the hedonic properties it is important to consider the time trajectory. After Pavlovian and habitual eating behaviors have been acquired and established their control on eating behaviors do not rely on the hedonic properties of food, however during the associative learning stage in which habits and Pavlovian responses are being

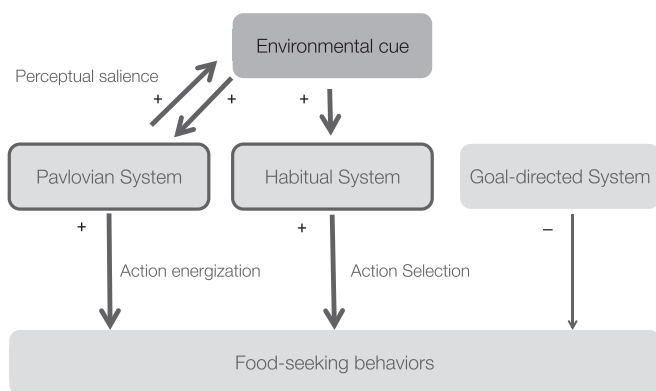


Fig. 3. Illustration of the proposed influence of stress (symbolized with the plus and minus signs) on food-seeking behaviors. Stress increases the control of the Pavlovian and the habitual systems over the control of the goal-directed system. Increased control of the Pavlovian system enhances the perceptual salience of food-associated environmental cues (in dark gray). The perception of these environmental cues (i.e., the box in dark gray) triggers habits (determining the action selection of a particular type of food) and Pavlovian motivation bursts (determining the amount of energy invested in food seeking action).

acquired the hedonic properties of food are fundamental. It has consistently been demonstrated that the association between two stimuli (underlying the Pavlovian system), as well as between a stimulus and a response (underlying the habitual system), are better memorized when a hedonic outcome is involved (Gottfried, Smith, Rugg, & Dolan, 2004; Hull, 1943; Thorndike, 1927; Wittmann et al., 2005). During the learning stage, the hedonic properties of the food render some Pavlovian associations and some habits more predominant than others, making them more likely to be activated under stress. This could explain why stressed animals (Bazhan & Zelena, 2013) and humans (Adam & Epel, 2007) tend to consume highly palatable food instead of healthier food.

It is important to note that the large amount of highly palatable food consumed under stress might particularly promote rapid weight gain, since in stressful conditions, people have slower fat oxidation than in stress-free conditions (Kiecolt-Glaser et al., 2014). Moreover, the fact that stress increases the consumption of highly palatable food instead of healthier food might lead to vicious cycles. Consumption of highly palatable food belonging to the so-called Western diet (high in saturated fat and simple sugars) has consistently been associated with several cognitive impairments (e.g., spatial learning, memory tasks; Kanoski & Davidson, 2011), even in people with a healthy weight, in as few as three days (Francis & Stevenson, 2013). This cognitive impairment could in turn reduce the control of the goal-directed system, leading to higher control by the Pavlovian and habitual systems (see Rangel, 2013 for a review). Moreover, this cognitive impairment could reduce the effectiveness of stress-coping strategies, leading to a larger response to potentially stressful events (e.g., Goretto, Portaccio, Zipoli, Razzolini, & Amato, 2010). Higher stress and higher control by the Pavlovian and habitual systems would then increase the amount of highly palatable food consumed. Note that stress-mediated cortisol release has also been proposed to directly increase eating behaviors (Tataranni et al., 1996).

In conclusion, we suggest that stress-induced eating is driven by more than hedonic pleasure or by the goal of reducing the aversive feeling associated with the stress response through the hedonic properties of highly palatable food. We propose instead that, under stress, people consume a larger amount of highly palatable food as a result of habits and Pavlovian-triggered motivational bursts. The palatable properties of food are important for these two systems during the learning stage, but once acquired, they can become completely independent of the hedonic pleasure experience. Therefore, under stress, people increase the consumption of the food they learned to search for, whether it is currently liked or not.

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