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Multicomponential affective processes modulating food-seeking behaviors

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Food rewards elicit a variety of affective responses. They emerge from multiple components, including motivational and hedonic processes. Here, we review evidence for these multiple components through an affective science lens. We describe recent advances showing that the motivational and hedonic components are modulated by dopamine and opioids in different ways, involve distinct subregions of the ventral striatum, and are decoupled in addiction. Building on the conceptual links between the food-reward components and appraisal processes in emotion, we propose a multicomponential framework distinguishing between elicitation- and response-based affective-reward processes and suggest that affective relevance could be a key determinant in the elicitation of food-seeking behaviors. We outline how this framework can help identify the psychological and neural processes implicated in affective responses relying on different properties of food rewards and examine the effects of executive control thereon. Altogether, a multicomponential approach to food rewards may contribute a better mechanistic understanding of eating behaviors and affective valuation of food.

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Introduction

Food is one of the most potent rewards in the animal kingdom. It is crucial for the survival of the organism and plays a central role in its everyday life. Food can notably act as a powerful driver of behavior and deeply shapes cognitive processes, such as attention, learning, memory, and decision-making [1–3]. As with many other kinds of rewards, what makes food such an efficient teaching signal is its affective properties. Food rewards typically elicit a variety of anticipatory, preparatory, and consummatory affective responses [4–7]. For instance, the perception of cues associated with food can trigger affective responses to help the organism prepare for the upcoming food (e.g. salivation) and facilitate its obtainment (e.g. increased effort mobilization). In addition, food consumption typically evokes a sensory pleasure or hedonic experience.

A wealth of studies have provided evidence that the affective response elicited by food rewards is not unitary, but rather emerges from multiple components that can be parsed into motivational and hedonic processes. Here, we review recent evidence for the existence of multiple components in food-reward processing through an affective science lens. In particular, we seek to draw parallels between the mechanisms involved in food-reward processing and the notion derived from appraisal theories of emotion [8,9] that emotions are multicomponential and composed of two distinct parts: emotion elicitation and the emotional response. Emotion elicitation consists of appraisal processes that shape the emotional response, which is reflected in changes across multiple components encompassing action tendency, autonomic reaction, expression, and subjective feeling [8,9].

Building on this distinction, we summarize evidence for the multicomponential processing of food rewards at the response-based level and the elicitation-based level. We then illustrate how the psychological construct of affective relevance offers a promising approach that could refine our understanding of food-seeking behaviors. Finally, we explore recent work outlining how a multicomponential conceptualization of food rewards opens new and interesting research avenues for investigating affective valuation of food and the effects of executive control on the affective response to food rewards.

Box 1 Key concepts from the reward processing and appraisal theories of emotion literatures.

Reward processing.

- **Incentive-salience hypothesis: Theoretical framework developed by Berridge and Robinson** [12] according to which reward processing involves multiple components that can be parsed into motivational (incentive salience or 'wanting') and hedonic ('liking') processes. Importantly, the incentive-salience hypothesis advances that, while the reward components are usually correlated, they are underlain by separate neural systems, and are dissociable under certain circumstances, such as addiction or stress [5,12,13].
- **Incentive salience or 'wanting': Motivational process by which an incentive value is attributed to a Pavlovian reward cue. This process is conjointly determined by the associative history between the cue and the reward on one hand, and the reward's relevance to the organism's current homeostatic state on the other hand** [14,15]. It primarily relies on the mesocorticolimbic dopamine system, including brain structures such as the nucleus accumbens [5]. The attribution of incentive salience to Pavlovian cues endows them with motivational properties similar to those of the reward. As a result, this typically triggers the organism to seek and consume the reward signaled by the Pavlovian cue [14,15], which is classically observed as an increased effort mobilization to obtain the reward in response to the cue [41].
- **Hedonic experience or 'liking': Hedonic reactions or pleasure experienced during the consumption of the reward. Liking is generated by small and fragile neural systems called 'hedonic hotspots'** [5,12]. These hotspots are distributed across various brain regions such as the medial shell division of the nucleus accumbens, the ventral pallidum, and the medial orbitofrontal cortex, and are not dependent on dopamine [5].
- **Expected pleasantness: Predictions and expectations about how pleasant or unpleasant the reward is going to be, which are built on episodic memories of past hedonic experiences** [41].

Appraisal theories of emotion

- **Appraisal theories:** Family of emotion theories positing that emotions are elicited and differentiated according to appraisal processes that continuously detect and evaluate the significance of stimulus events or situations in relation to the organism's concerns [8,9]. Appraisal theories conceptualize emotion as a multicomponential, two-step process consisting of an appraisal-based elicitation mechanism that shapes an emotional response [8]. The emotional response is reflected in changes across multiple components of the organism, such as action tendency, autonomic or physiological reaction, expression, and subjective feeling [8,9].
- **Concerns**: Affective representations of physiological and psychological goals, motives, needs, and values that are of major importance to the individual [8]. Concerns are organized in a dynamic hierarchy that flexibly varies as a function of the interaction between individual differences or dispositions and environmental contingencies [45].
- **(Appraisal of) affective relevance**: Rapid and flexible mechanism by which the individual establishes whether a stimulus is relevant to their concerns [42]. Affective relevance reflects the interplay between the present stimulus and the individual's current concerns. It represents a key mechanism involved in emotion elicitation according to appraisal theories, which conceive emotions as being elicited in response to a stimulus or a situation being appraised as affectively relevant to and by the individual [8].

The multicomponential nature of the affective response to food rewards

The notion that reward-seeking behaviors depend on motivational and hedonic processes can be linked to early incentive-motivation models [10,11]. The incentive-salience hypothesis [12] (see Box 1) expands on these classical models by postulating that the motivational (incentive salience or 'wanting') and the hedonic ('liking') components of reward processing are dissociable and rely on distinct neural networks [5,13]. Incentive salience (see Box 1) is conceptualized as a motivational process by which Pavlovian reward cues acquire an incentive value as a function of the reward's relevance to the organism's physiological state (e.g. hunger or stress). Through this process, the cues gain the ability to trigger the organism to seek and consume the associated reward [14,15] and invest a large amount of effort in the reward pursuit. Incentive salience is primarily mediated by the mesocorticolimbic dopamine system, including the nucleus accumbens [5,13] and its core division [16,17], as well as the opioid system [18] and the central amygdala [19]. Liking (see Box 1) refers to the hedonic reactions or the pleasure experienced during reward consumption. It is generated by a collection of small 'hedonic hotspots' distributed across several brain regions such as the medial shell division of the nucleus accumbens, the ventral pallidum, and the medial orbitofrontal cortex [5,13]. Moreover, it is amplified by opioid, orexin, and endocannabinoid stimulation [5,13].

Recently, important advancements have been made in the investigation of the neurobiological substrates of the motivational and hedonic components of food rewards in humans. A study by Korb et al. [6••] reported that dopaminergic and opiodergic modulations via amisulpride (a dopamine antagonist) and naltrexone (an opioid antagonist), respectively, reduced mobilized effort and increased negative facial reactions during the anticipation of food rewards compared with a control group. By contrast, only the opiodergic manipulation induced a reduction in positive facial expressions in response to liked food rewards during their consumption. These results are in line with other human studies suggesting the involvement of the dopamine system in Pavlovian-triggered motivation [20–23] and the implication of the opioid system in motivational and hedonic processes [24–26] (but see [27], for a study suggesting that the opioid system mediates neural connectivity related to motivational, but not hedonic, processes). Furthermore, another recent study [28•] showed that the motivational and hedonic processes involved in the affective response to a reward recruit distinct subregions of the ventral striatum in humans. Using a high-resolution functional magnetic resonance imaging (fMRI) protocol in combination with a Pavlovian-instrumental task and a hedonic reactivity task involving food rewards, this study provides evidence that Pavlovian-triggered motivation relies on the core-like division of the ventral striatum, whereas the sensory pleasure experience relies on the shell-like division and the medial orbitofrontal cortex. These findings shed light on prior work reporting activations of the ventral striatum for both the motivational [29–31] and the hedonic [32] processes.

A key aspect of the distinction between motivational and hedonic components in reward processing relates to their decoupling in addiction [12]. Addiction is typically characterized by compulsive reward-seeking behaviors, where the individual persists in pursuing the substance of use despite the absence of positive consequences or the presence of adverse consequences [33]. Such compulsive behaviors are thought to stem from the hyperreactivity of the Pavlovian-triggered motivation system, which attributes an amplified incentive salience to substance-associated cues and contexts, while liking does not increase — or even decreases — during the substance consumption [12,33]. This imbalance between the motivational and the hedonic processes has been observed in several substance-use disorders such as cocaine use [34], alcohol-use disorder [35], and smoking addiction [36]. Critically, a similar mechanism has been proposed to underlie behavioral addictions [37], as well as some forms of maladaptive eating behaviors [38•]. More specifically, initial evidence has shown that a heightened propensity to attribute incentive salience to food cues is associated with the report of more dysfunctional eating behaviors [39•]. Additionally, it has been suggested that specific neuropsychological disorders, such as depression, Parkinson's disease, and schizophrenia, could be best characterized by avolition (i.e. a lack of motivation) rather than anhedonia (i.e. a lack of experienced pleasure) symptoms, reflecting an imbalance between impaired, hypoactive motivational processes and intact hedonic processes [37]. Such diminished motivational processes in reward processing have also been observed in eating disorders such as anorexia nervosa [40].

The multicomponential elicitation processes of the affective response to food rewards

The mechanisms involved in the elicitation of the motivational and hedonic responses to food rewards are also of particular interest. Although the motivational and hedonic processes both participate in imbuing rewards (and their associated cues) with an affective value, these processes contribute to the affective response to food rewards in different ways. Motivational processes are mainly involved in the moments preceding the food consumption as a response to food-reward cues and in anticipation of the food, thus exerting a powerful impact on food-seeking behaviors. By comparison, hedonic processes are principally implicated in the affective response to the food reward itself during its consumption. As such, their influence on food-seeking behaviors is essentially indirect: it occurs through expected pleasantness (see Box 1), a mechanism distinct from incentive salience consisting of predictions and expectations about the reward pleasantness that are built on episodic memories of past hedonic experiences [41].

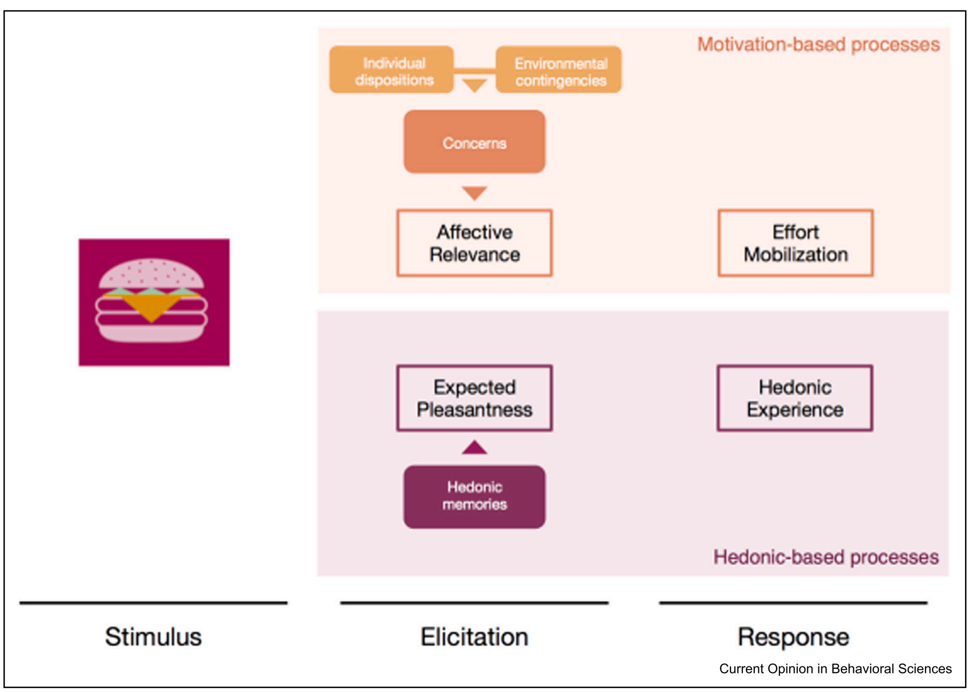
Interestingly, the incentive-salience hypothesis postulates that the motivational response does not rely on expected pleasantness, but rather on a dynamic evaluation of the reward properties in relation to the physiological state of the organism. Appraisal theories [8,9] (see Box 1) provide a framework to expand this elicitation-based mechanism and clearly distinguish it from expected pleasantness. This family of emotion theories suggests that a key mechanism involved in emotion elicitation is appraised affective relevance. Affective-relevance appraisal is a rapid and flexible mechanism whereby the individual detects whether a stimulus encountered in the environment is relevant to their concerns (see Box 1), which consist of affective representations of physiological and psychological goals, needs, and values that are of major importance to the individual [8]. In other words, affective relevance is relational in that it stems from the interaction between the present stimulus and the individual's current concerns. In that sense, affective relevance is closely intertwined with the notion of incentive salience [42], which similarly originates from the interplay between a reward, its associated cues, and the organism's physiological state. Affective relevance and incentive salience are likewise thought to rely on similar neural mechanisms, with the amygdala being a potential shared brain system between appraised affective relevance and reward processing [43]. This suggests that affective relevance could thus represent a key determinant of how individuals learn the affective value of rewards and their associated cues [44•]. This could ultimately have an impact on reward-seeking behaviors and, more specifically, food-seeking behaviors.

A series of experiments has shown that stimuli appraised as affectively relevant are more readily and persistently associated with an aversive outcome than less-relevant stimuli during Pavlovian conditioning [42,45,46]. Critically, such enhanced Pavlovian learning was observed for both negatively (e.g. angry faces, snake pictures) and positively (e.g. baby faces, happy faces, and erotic images) valenced stimuli with high affective relevance [42,46], and was influenced by individual differences in affect and motivation [45,46]. This therefore suggests that affective relevance affects Pavlovian aversive learning, irrespective of valence or pleasantness, and that these effects are modulated by individual differences in current concerns. Initial evidence suggests that affective relevance could likewise modulate appetitive Pavlovian learning and reward-seeking behaviors. A recent study [44•] showed that a cue associated with a sexual outcome (i.e. erotic image) that was affectively relevant to the participants' sexual concerns (manipulated through their sexual orientation) induced enhanced Pavlovian reward learning relative to a cue paired with a less-relevant sexual outcome. The effects of affective relevance moreover impacted instrumental reward learning and instrumental responding to the Pavlovian cues. At the neural level, the anticipation of a rewarding feedback with high affective relevance has been found to increase the stimulus-preceding negativity — an event-related potential component reflecting reward anticipation — compared with a feedback with lower relevance when uncertainty about the feedback was high [47], suggesting that affective relevance modulates reward-anticipation processes.

By extension, appraised affective relevance may contribute to the elicitation of affective responses to food rewards and food-seeking behaviors (see Figure 1). Before the food-reward acquisition, food-associated cues trigger anticipatory and preparatory responses, as well as food-seeking behaviors as a function of their affective relevance. Appraised affective relevance is determined by the reward's relevance to the individual's current concerns. Importantly, these concerns are not limited to physiological needs as is typically posited in the case of incentive salience [15], but can be extended to a wide range of physiological and psychological motives (e.g. homeostatic needs, survival, affiliation, socialization, or momentary goals) [41]. Moreover, concerns are organized in a dynamic hierarchy, with their salience and priority changing rapidly and flexibly as a function of environmental contingencies [45]. They also vary across individuals, thereby incorporating and highlighting the pivotal role of individual differences in this process [44•–46]. After its obtainment, the food reward generates consummatory responses, including hedonic reactions reflecting experienced pleasure during its consumption. The experience of pleasure is typically related to the food value, which does not solely rely on liking but also on the individual's current concerns [43] such as hunger.

It is worth noting that the affective relevance of food can be partly influenced by the appraisal of intrinsic

Figure 1



Multicomponential elicitation- and response-based processes involved in the affective response to food rewards and food-seeking behaviors. A food reward or a food cue can trigger motivational (i.e. effort mobilization or 'wanting') and hedonic (i.e. sensory pleasure experience or 'liking') responses as a function of the distinct elicitation mechanisms of affective relevance and expected pleasantness. Affective relevance is an essentially motivation-based process that stems from the interaction between the food reward or cue and the individual's concerns, such as their goals, needs, or values. These concerns vary according to individual differences and environmental contingencies. By contrast, expected pleasantness consists of predictions and expectations about the food reward's pleasantness that are built on episodic memories of past hedonic experiences.

pleasantness or valence [9]. Affective relevance is often correlated with pleasure in the context of food-reward processing (i.e. food rewards that are appraised as more affectively relevant generally tend to be more pleasurable as well). However, affective relevance is not based on hedonic processes, but on the number of concerns and their importance for which the properties of the food reward and its associated cues are relevant [41]. Additionally, affective relevance acts as a distinct mechanism from expected pleasantness. Affective relevance dynamically varies according to the current concerns of the individual, which directly affects the food reward's appraised relevance without requiring the individual to re-experience its pleasantness [41].

Accordingly, the affective-relevance approach provides a flexible theoretical framework that could inform our understanding of the psychological mechanisms modulating how the affective response to food rewards and food-seeking behaviors are elicited. This framework builds on and integrates the rich reward-processing literature on the distinction between motivational and hedonic processes. It also takes advantage of the conceptual links and similarities between reward processing and the appraisal processes in emotion to expand this approach to humans and foster the translation of research from animals to humans. In this light, the affective-relevance framework aims to complement and extend the neurophysiological perspective put forward by the incentive-salience hypothesis [12] in providing a psychological mechanism whereby the attribution of affective value to food rewards or cues does not solely depend on homeostatic needs, but also on psychological needs and individual dispositions. This approach has the potential to provide psychological explanations for a large spectrum of nonproblematic and problematic eating behaviors in which psychological factors play an important role above and beyond purely homeostatic aspects, such as overeating or binge eating [48].

Implications of a multicomponential approach to food rewards

Considering a reward as multicomponential has important implications for the understanding of how affective value is learned, especially with respect to food rewards. Recently, it has been proposed that the distinction between the motivational and the hedonic components of food rewards could be used to inform how affective value learning operates in the framework of reinforcement learning [49••]. In reinforcement-learning models, the affective outcome that acts as a teaching signal is often considered to be unitary and coded as 1 when it is present and 0 when it is absent. However, the teaching signal might actually vary in time according to the affective component of the reward. Specifically, the instant hedonic impact of the food-reward consumption could provide an immediate teaching signal, but it would only be useful as preliminary information and it would have to later be completed and revised based on slower post-ingestion assessments by gut signals [49]. Such signals might indeed provide more complete and diagnostic information about the long-term value of the food reward. This hypothesis suggests that, in reinforcement learning, the hedonic response to food-reward consumption is used to build a temporary and editable value representation [49••].

Multiple disciplines have proposed that the representation of the reward is multicomponential, with attributes expanding beyond affective features. For instance, Pavlovian learning theories [50] have postulated that the reward representation triggered by Pavlovian cues is a compound of multiple attributes, including motivational and hedonic ones as well as attributes relating to the reward's sensory features or temporal occurrence. Similarly, behavioral economics theories have delineated a wide range of values — or utilities — related to reward processing such as expected utility or remembered utility [49••,51].

Importantly, conceptualizing the reward as a compound of sensory- (i.e. aspects related to the physical detection and identification of the reward) and value-related (i.e. aspects pertaining to the reward-motivating function) properties also had a significant impact on the understanding of the seminal findings on the dopaminergic reward-prediction error [52]. These conceptual and empirical advances have notably shown that the phasic dopaminergic response to prediction errors has a quick activation to the sensory component, which later evolves differently according to the value component of the reward [52].

Recent Pavlovian conditioning studies in humans have likewise started considering the response to an affective outcome as multicomponential [53,54]. These studies measured the responses elicited by Pavlovian cues on multiple, parallel levels such as responses based on the reward's affective value and responses based on a specific sensory property of the reward (e.g. its lateralized location delivery). The results highlighted that these different classes of responses depend on dissociable learning processes and neural bases. These developments paved the way to deepen our understanding of the behavioral and neural mechanisms involved in affective-value learning, as well as in outcome devaluation.

In the context of food rewards, the effects of reward devaluation through sensory-satiation processes are of special interest. Food-seeking behaviors that are insensitive to devaluation processes are considered to be a signature of a variety of problematic behaviors such as binge eating [33]. Accordingly, there has been a strong effort in the literature to implement manipulations inducing behaviors that are insensitive to devaluation, with the intent of providing an experimental model for the study of their underlying mechanisms [55]. Based on the conceptualization of a reward as a compound of multiple attributes, evidence has shown that parallel responses to Pavlovian cues can exhibit different sensitivities to food-reward devaluation [54]. For instance, Pavlovian responses linked to the outcome's affective-value representation are sensitive to devaluation, however, Pavlovian responses related to the representation of some specific sensory aspect of the outcome appear to be resistant to outcome devaluation [54]. At the neural level, outcome-devaluation procedures have been used to investigate how the different representations of food rewards are integrated into the valuation process [56]. The integration of the representations of the food's perceptual identity and affective value has been shown to depend on the orbitofrontal cortex and its connectivity with the ventromedial prefrontal cortex, respectively [56] (see also [57,58], for recent reviews). This is congruent with findings indicating that the orbitofrontal-cortex circuitry is key for the integration of the nutritive properties into the representation of the food value [59]. A recent study in monkeys further elucidated the neural circuitry underlying food-reward devaluation by investigating the links between reward-specific satiety and neuronal signals in the orbitofrontal cortex during multicomponent economic choices [60••]. In this study, food rewards consisted of compounds of multiple values (i.e. 'bundles') such as a reward composed of two different amounts of two different juices. Subjects had to perform a series of choices between two reward bundles, where the two value components were systematically varied through their associated degree of satiety. This allowed to precisely assess how sensory-specific devaluation induced variations in food-reward value and how these variations were integrated into value-coding signals in the orbitofrontal cortex. This experimental paradigm has been recently adapted to a human population to investigate how multiple reward components are integrated into a single-dimensional scalar signal at the behavioral [61] and neural [62•] level. This demonstrated in particular the pivotal role of the orbitofrontal cortex in such an integration process [62•].

Effects of executive control on the multicomponential affective response to food rewards

A multicomponential perspective on food rewards can also provide insights into the investigation of how cognitive processes, and more specifically executive control, interact with the affective response to food rewards. Executive control plays an important regulatory role in eating behaviors [63] and interventions training executive functions, such as inhibition, have been shown to be efficient in reducing the perceived value of food items [64]. However, the relationships between executive functions and the affective response to food rewards are complex and may in fact differ across the multiple affective processes and reward properties involved. For instance, obesity has been linked to impaired executive functions [65] and an increased motivation to obtain food rewards in the absence of a corresponding increase in experienced pleasure during reward consumption [38•]. This suggests that impairments in executive control in obesity would be specifically associated with hyperreactive motivational processes [66], but not with hedonic processes.

The distinction between elicitation- and response-based processes is likewise of relevance in that the impact of executive control on the affective response to food rewards can vary depending on whether elicitation- or response-based reward processes are targeted. This is notably exemplified by the effects of emotion regulation on food craving and subsequent intake. Emotion-regulation strategies focusing on elicitation-based processes such as cognitive reappraisal have been reported to be in general more effective in reducing food craving [67,68] and food intake [68] than strategies focusing on response-based processes such as suppression.

In addition, operationalizing food rewards as multicomponential has implications for understanding the nature of the relation between executive functions and food-seeking behaviors. The influence of executive functions on reward-seeking behaviors has often been described as a hierarchical, top-down, and inhibitory control [69]. Nonetheless, it has been demonstrated that executive functions do not always inhibit cue-triggered behaviors, but can sometimes amplify specific forms of cue-triggered responses relying on the reward identity rather than on the reward value [70•]. Using a Pavlovian-instrumental transfer task, a recent study [70•] reported a positive correlation between working-memory capacity and the selection of an instrumental action associated with the same reward as the Pavlovian cue shown over another instrumental action with a similar reward value but paired with a different reward (i.e. outcome-specific Pavlovian-instrumental transfer). By contrast, no relationship was observed between working memory and the selection of an instrumental action associated with a reward during the presentation of a Pavlovian cue paired with a different reward versus a nonrewarded Pavlovian cue (i.e. outcome-general Pavlovian-instrumental transfer) [70•]. These results suggest that individuals with higher working-memory capacity preferentially integrate information about the identity of the reward and its sensory properties, but do not rely more strongly on the reward value, to guide their reward-seeking behaviors. This illustrates how the interaction between executive control and affective processes relating to different properties of food rewards can have differential effects on food-seeking behaviors.

Conclusions

Conceptualizing food rewards as multicomponential entities offers a clear benefit to reliably appraise their multifaceted nature and the multifarious affective responses they elicit. In particular, combining this multicomponential element with insights from affective science, distinguishing elicitation- and response-based affective processes, might provide a fruitful framework to identify the factors involved in the elicitation of the affective response to food rewards. In that sense, a multicomponential approach to food rewards has the potential to contribute to a better mechanistic understanding of food-seeking behaviors, food-affective valuation processes, their relation with executive functions, and the impairments of these processes in specific eating disorders.

Conflict of interest statement

The authors declare no conflict of interest.

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