Brain and Cognition xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

A core eating network and its modulations underlie diverse eating phenomena

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ARTICLE INFO

Article history:
Received 2 June 2015
Revised 3 January 2016
Accepted 15 April 2016
Available online xxxx

Keywords:
Core eating network
Food cues
Grounded cognition
Neuroimaging

ABSTRACT

We propose that a *core eating network* and its modulations account for much of what is currently known about the neural activity underlying a wide range of eating phenomena in humans (excluding homeostasis and related phenomena). The core eating network is closely adapted from a network that Kaye, Fudge, and Paulus (2009) proposed to explain the neurocircuitry of eating, including a ventral reward pathway and a dorsal control pathway. In a review across multiple literatures that focuses on experiments using functional Magnetic Resonance Imaging (fMRI), we first show that neural responses to food cues, such as food pictures, utilize the same *core eating network* as eating. Consistent with the theoretical perspective of grounded cognition, food cues activate eating simulations that produce reward predictions about a perceived food and potentially motivate its consumption. Reviewing additional literatures, we then illustrate how various factors modulate the core eating network, increasing and/or decreasing activity in subsets of its neural areas. These modulating factors include food significance (palatability, hunger), body mass index (BMI, overweight/obesity), eating disorders (anorexia nervosa, bulimia nervosa, binge eating), and various eating goals (losing weight, hedonic pleasure, healthy living). By viewing all these phenomena as modulating a core eating network, it becomes possible to understand how they are related to one another within this common theoretical framework. Finally, we discuss future directions for better establishing the core eating network, its modulations, and their implications for behavior.

1. Introduction

Multiple research literatures have examined the neural responses to food cues and actual eating in a variety of different eating situations and populations. So far, however, no integrated theoretical account for all these eating-related phenomena exists. The primary aim of this article is to develop a theoretical framework that integrates the major findings across these literatures. As will become clear, this theoretical framework includes a core eating network, together with modulations of this network in different eating situations and populations. Importantly, our account primarily focuses on the higher-level processing of food cues and their relations to eating, not addressing homeostasis and related processes (cf. Hege, Stingl, & Preissl, 2014).

Specifically, our theoretical framework aims to integrate the following phenomena: (1) high-level neural responses during eating, (2) neural responses to food cues in healthy individuals, (3) neural responses to food cues as palatability and hunger vary, (4) neural responses to food cues in overweight/obese individuals, (5) neural responses to food cues in individuals with eating disorders, and (6) neural responses to food cues in populations with different eating-related goals, such as losing weight via dieting, pursuing hedonic pleasure from eating, and eating for a healthy life.

Many previous reviews and meta-analyses have addressed research in the individual areas just described. One review established brain areas associated with actual eating (Kaye, Fudge, & Paulus, 2009). Another review and meta-analysis established the brain areas that process food cues in healthy individuals (van der Laan, de Ridder, Viergever, & Smeets, 2011). Other reviews have investigated the neural bases of eating disorders, including anorexia nervosa, bulimia nervosa, and binge eating (e.g., Kaye, Wagner, Fudge, & Paulus, 2010; Kaye, Wierenga, Bailer, Simmons, & Bischoff-Grethe, 2013; Kaye et al., 2009; O'Hara, Campbell, & Schmidt, 2015; Pietrini et al., 2011; Stefano et al., 2013; van

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http://dx.doi.org/10.1016/j.bandc.2016.04.004
0278-2626/

Please cite this article in press as: Chen, J., et al. A core eating network and its modulations underlie diverse eating phenomena. *Brain and Cognition* (2016), http://dx.doi.org/10.1016/j.bandc.2016.04.004

Kuyck et al., 2009; Zhu et al., 2012). A related review established neural differences to food cues between individuals with eating disorders, obese individuals, and healthy individuals (García-García, Narberhaus, et al., 2013). Another review focused on altered neural responses to both the anticipation and consumption of food in obesity (Stice, Spoor, Ng, & Zald, 2009). Finally, a meta-analysis focused on aberrant neural responses to food cues in obesity, showing both increased and reduced activations in various brain areas (Brooks, Cedernaes, & Schiöth, 2013). Again, however, no work has attempted to integrate the findings from these reviews and their related literatures into a comprehensive account.

Besides attempting to fill this gap, our theoretical framework establishes how the processing of food cues is related to actual eating. Establishing the neural systems that underlie actual eating is clearly important. Establishing the neural systems that underlie the processing of food cues is no less important, given the powerful roles that they play in motivating eating, especially unhealthy eating (Marteau, Hollands, & Fletcher, 2012). The perspective of grounded cognition offers a natural account of how food cues and actual eating are related: When encountering a food cue, a simulation of eating the cued food becomes active, with the simulation predicting the food's taste and reward value (e.g., Barsalou, 2008, 2010; Papies, 2013; Papies & Barsalou, 2015). To the extent that a simulation represents a food as tasty and rewarding, it potentially motivates the food's consumption. From this theoretical perspective, neural systems that underlie eating a food become active on encountering cues for it. As we will see, the empirical literatures that address eating and food cue processing strongly support this proposal.

1.1. Methodological considerations

The literatures that we review primarily address neural activity established from linear contrasts during functional Magnetic Resonance Imaging (fMRI), establishing brain areas for important food processing in contrast with nonfood stimuli as controls. Tables A.1–A.4 in Appendix A present examples of the specific contrasts used. As will be seen, the controls used in a given contrast vary widely across phenomena. When considering food significance, for example, high-calorie foods are often contrasted with low-calorie foods, but when considering the effects of body mass index (BMI), obese individuals are contrasted with normal weight individuals, or BMI is viewed as a continuous variable.

For the purpose of this review, we assume (like most current researchers) that the brain areas active for a particular type of eating situation or population constitute a network, even though, technically speaking, network connectivity remains to be demonstrated formally. As described later, establishing these networks using functional connectivity, causal modeling, and related methods remains an important goal for future research.

At certain points in our review, findings from behavioral, event-related potential (ERP), and eye tracking paradigms are included to better understand a particular eating network and the behavior it produces. More detailed reviews of relevant findings from these paradigms are beyond the scope of this article, given that we focus primarily on the neural networks that underlie food cue processing as established in fMRI research. Nevertheless, it is important to bear in mind that other literatures are relevant for evaluating the issues we address as well.

1.2. Relations to other appetitive behaviors

Although we focus on brain areas associated with eating, some of these areas are also important in other appetitive behaviors. Some meta-analyses, for example, show that the amygdala, orbitofrontal cortex (OFC), and ventral striatum become active not only when processing food cues, but also when processing smoking cues (Tang, Fellows, Small, & Dagher, 2012) and other drug cues (García-García et al., 2014; Volkow, Wang, Fowler, Tomasi, & Baler, 2012; Volkow, Wang, Tomasi, & Baler, 2013). Nevertheless, the core eating network, as a whole, is unique for food, because it includes food-specific regions, such as regions responsible for gustatory processing and body image. Simon et al. (2015), for example, demonstrated that neural responses to food cues differ from those to monetary cues. Thus, the networks for eating and other appetitive phenomena differ, while sharing important overlapping regions.

1.3. Overview

In the next section, we first address the network that underlies normal eating, proposed originally by Kaye et al. (2009). We then address an important variant of this network related to processing food cues. Consistent with the perspective of grounded cognition, the food cue network produces eating simulations in response to food cues that inform and motivate decisions to consume or not consume a cued food. Once we establish the networks for eating and processing food cues, we then define the core eating network as the network variant that processes visual food cues (for reasons presented later). We then describe how various factors modulate the activity of the core eating network, increasing and/or decreasing the activity of its neural areas. First, we address how two forms of food significance—palatability and hunger—modulate neural activity in the core eating network. Second, we address modulations that result as BMI increases in overweight and obese individuals. Third, we address modulations associated with the eating disorders of anorexia nervosa (AN), bulimia nervosa (BN), and binge eating disorder (BED). Fourth, we address modulations associated with the eating goals of weight loss, hedonic pleasure, and healthy living. For each modulation of the core eating network, we do not exhaustively review all relevant articles in the fMRI literature, but instead cover a selection that represents examples of relevant research. To provide a more complete overview, we include tables in Appendix A that list larger sets of relevant articles in each area.

Finally, we adopt the following strategy in evaluating our theoretical claims. First, we start with the assumption that the core eating network adapted from Kaye et al. (2009) underlies all of the eating phenomena we address. Second, as we review a particular literature on an eating situation or a specific population, we assess whether the relevant brain areas fall within the core eating network or not (in the large majority of cases they do). Third, in a bottom-up empirical manner, we use each literature addressed to develop an account of how the relevant eating situation or population modulates this network. What brain areas inside (or outside) the core eating network are affected by the eating situation or population, and how? Whereas we adopt the core eating network in an a priori manner, we develop modulations of it in an empirical manner based on each literature reviewed. Of general interest is whether existing areas of the core eating network can accommodate these modulations, or whether additional brain areas are necessary for explaining them. As we will see, the core eating network generally accommodates these modulations with a few relatively minor exceptions. As we will also see, however, modulation of a specific brain area doesn't always occur across experiments, and in a few cases is modulated in opposite directions (i.e., both higher activation and lower activation than normal across experiments). It follows that further research is necessary to establish the core eating network and its modulations more definitively, together with conditions that cause modulations to vary.