Neurobiological Perspectives

9 Appetite, Consumption, and Choice in the Human Brain

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According to the Tibetan Buddhist *bhavacakra* (wheel of life), people who have lived less-than-exemplary lives are reborn in lower realms. Those unfortunate enough to be sent to the realm of *pretas* (hungry ghosts) awaken as ravenous beings whose tiny mouths and necks block sustenance from entering their large but empty stomachs. The hungry ghosts thus continually suffer from insatiable appetites (Gyatso 1992). This seemingly exotic fate of the hungry ghosts symbolizes a more common earthly state of affairs: when appetite cannot be sated with consumption, as in the case of addiction, the rhythm of life is permanently disrupted. Without the eventual calming effects of consumption, excessive appetites may drive organisms to ruin. The plight of the hungry ghosts implies that appetite and consumption are different but must eventually connect.

From the perspective of neuroscience, this mythical dilemma raises a number of questions. Can different phases of reward processing be distinguished neurally? How do they interact? Can their coordinated function contribute to optimal choice and well-being? In this chapter, we attempt to define appetite and consumption psychologically, and then to describe human neuroimaging research indicating that these phases of reward processing can be visualized in the human brain. We then survey emerging research suggesting that neural study of these processes may help scientists to better predict choice and understand processes that promote decision making.

Definitions

More than 100 years ago, the ethologist Wallace Craig defined appetitive and consummatory behavior as follows (Craig 1918): "An appetite . . . is a

state of agitation which continues so long as a certain stimulus . . . is absent. When the appeted stimulus is at length received it stimulates a consummatory reaction, after which the appetitive behavior ceases and is succeeded by a state of relative rest." Craig's prescient definition has a number of implications. First, the cycle of appetite and consumption has distinct behavioral components that occur sequentially. Second, although both appetite and consumption evoke arousal, appetite involves higher arousal than consumption. Third, consumption forms a negative feedback loop that can eventually reduce appetite. Fourth, although the terms *appetitive behavior* and *consummatory behavior* may have originally referred to eating episodes, they can also extend to a broader range of activities (see the chapter by Plassmann and Wager, the chapter by Preston, Kringelbach, and Knutson, the chapter by Preston and Vickers, the chapter by Kringelbach, and the chapter by Robinson, Robinson, and Berridge).

As with most scientifically useful definitions, Craig also clarified what appetitive and consummatory behavior are not. He argued that appetitive and consummatory behaviors were driven by positive motivation, but not by negative motivation (associated with avoidance behavior). He also specified that appetitive and consummatory behaviors were not reflexive (as might be assumed by later behaviorists), nor were they strictly yoked to goals (as might be assumed by later cognitive theorists). In this chapter, we use Craig's ethological definition as a starting point. We further assume that, although appetitive behavior clearly involves motor processes and consummatory behavior clearly promotes sensory stimulation, the motivational elements of these phases cannot be *reduced* to either primary motor or primary sensory processes.

Beyond outlining the core elements of reward processing, these definitions imply that if one could measure appetitive processes one might use them to predict future consummatory behavior (e.g., eating or drinking). Further, if this predictive framework extends beyond primary (or directly sensed and unlearned) rewards to secondary (or more abstract and learned) rewards, predictions of consumption might extend to a broad range of human activities (e.g., investing and shopping), and into the future. Further, the relative appetitive response to different potential rewards might allow investigators to predict which is eventually chosen and consumed. An underlying theme involves the notion that appetitive processes eventually lead to choice and consumption, and that these sequential processes

are critical components of value-based decision making. (For a discussion of anticipatory effects on consumption, see also the chapter by Plassmann and Wager.)

Over the past century, animal research has suggested that evolutionarily conserved neural circuits deep below the cortex can unconditionally elicit positive and negative emotional states that coordinate approach toward opportunities and avoidance of threats (MacLean 1990; Panksepp 1998). Until recently, scientists lacked techniques with adequate resolution to determine whether people also recruit these circuits during appetitive and consummatory phases of reward processing and during processing of primary and secondary rewards. New technology with sufficient spatial and temporal resolution to resolve distinct stages of reward processing, however, has begun to yield coherent answers to these questions.

Localizing Appetite and Consumption

Consistent with early ethological distinctions between appetite and consumption, investigations of animals have implicated different neural circuits and chemistries in different phases of reward processing. (See also the chapter by Kringelbach and the chapter by Robinson, Robinson, and Berridge.) For instance, research on feeding in rats suggests that manipulating dopamine activity in the nucleus accumbens (NAcc), lateral hypothalamus, and midbrain ventral tegmental area (VTA) can induce appetitive behavior (indexed by eventual quantity of food consumed). On the other hand, manipulations of opioid activity in "hotspots" (including the NAcc, ventral pallidum, and brain-stem parabrachial nuclei) instead evoke consummatory behavior (indexed by lip smacking during consumption (Berridge and Kringelbach 2008).

Technological advances at the close of the twentieth century enabled animal researchers to temporally distinguish appetitive from consummatory phases of reward processing. For instance, using electrophysiological recordings of ventral tegmental neurons in monkeys, researchers established that dopamine firing increases in response to cues that signal upcoming delivery of juice rewards (Schultz et al. 1997). Further, using *in vivo* cyclic voltammetry in rats, researchers demonstrated that NAcc dopamine release also occurs when rats anticipate the impending delivery of food and drug rewards (Roitman et al. 2004; Stuber et al. 2004). Though this animal

research implicated specific neural circuits in the appetitive phase of primary reward processing, it could not establish whether these findings would generalize to humans, or whether they would extend to more abstract secondary rewards.

At about the time of these animal discoveries, human neuroimaging methods with better resolution emerged. Historically, although electroencephalography had afforded excellent temporal resolution on the order of milliseconds, it could not spatially localize activity, particularly in subcortical circuits. In contrast, positron emission tomography had allowed investigators to visualize changes in subcortical metabolic and chemical activity, but suffered from limited temporal resolution, on the order of minutes or longer. The development of functional magnetic resonance imaging (fMRI) in the early 1990s offered an optimal tradeoff, allowing visualization of activity in smaller subcortical circuits on a second-to-second time scale. This led to the development of novel experimental designs and analyses that could deconstruct different stages of reward processing into appetitive and consummatory phases. Below, therefore, we focus primarily on fMRI studies of reward processing and choice.

Initial human fMRI experiments attempted to "localize" sensory and motor circuits by systematically varying relevant aspects of stimuli (e.g., the size of a flickering circle or the rate of finger tapping) and identifying correlated neural activity. Subsequent studies of reward processing adopted a similar localization strategy by presenting primary and secondary rewards to humans undergoing fMRI. Primary rewards included a variety of pleasant stimuli, including tastes (Berns et al. 2001; O'Doherty et al. 2002), smells (Anderson and Sobel 2003; Gottfried et al. 2002), touch (Rolls et al. 2003), sights (Aharon et al. 2001; Arnow et al. 2002), and sounds (Menon and Levitin 2005). Secondary rewards included monetary gain (Delgado et al. 2000; Elliott et al. 2000; Knutson et al. 2000; O'Doherty et al. 2001) and pleasant social interactions (Rilling et al. 2002). Building from and extending animal research, these early experiments demonstrated reward-correlated activity in regions innervated by mesolimbic dopamine projections—including subcortical regions in the ventral striatum (such as the NAcc, ventral putamen, and ventral caudate), as well as in the medial orbital frontal cortex (MOFC) and medial prefrontal cortex (MPFC). Together, these findings implied that activity in overlapping mesolimbic projection areas responds to both primary and secondary rewards—a

conclusion supported by later reviews of the literature (e.g., Haber and Knutson 2010; see also the chapter by Kringelbach, the chapter by Plassmann and Wager, the chapter by Robinson, Robinson, and Berridge, and the chapter by Preston and Vickers).

With enhanced temporal resolution, investigators began to explore not only how the human brain *responded* to rewards (which might occur during the consummatory phase) but also how it *anticipated* rewards (which might occur during the appetitive phase). Answering these questions required temporally precise designs and analyses that could split single trials into anticipation and outcome phases—innovations that also promoted studies of reward learning which are not reviewed here owing to their dynamic nature (O'Doherty 2004). These experiments utilized both primary rewards (e.g., juice) and secondary rewards (e.g., money), and typically presented cues that elicited anticipation of uncertain reward followed by either reward outcomes or nonreward outcomes (sometimes after requiring a response). Initial findings suggested that ventral striatal activity (including activity in the NAcc) increased during anticipation of both monetary and juice rewards (Knutson et al. 2001a; O'Doherty et al. 2002), and further that medial prefrontal cortical (MPFC) activity increased in response to reward outcomes (Knutson et al. 2001b; Knutson et al. 2003; Ramnani and Miall 2003). Other studies, however, did not find such clearly distinct patterns of activity in response to reward anticipation and outcomes (e.g., Breiter et al. 2001).

Recent reviews of the literature unanimously implicate mesolimbic circuitry (including MPFC, the NAcc, and VTA) in reward processing. Not all concur, however, on whether different parts of this circuit respond preferentially to different phases of reward processing. Specifically, some meta-analyses support the notion that NAcc activity primarily increases during reward anticipation, and that MPFC activity increases in response to reward outcomes (Knutson and Greer 2008; Diekhof et al. 2012), but others do not (Liu et al. 2011; Bartra et al. 2013; see also the chapter by Plassmann and Wager). Powerful and efficient methods for inferring the likelihood of functional descriptions from an observed activation (rather than the inverse) have recently been developed (Yarkoni et al. 2011). By controlling for the base rate of activity in different regions, this quantitative "reverse inferential" meta-analytic technique can yield information about the specificity of functional inferences from local activity. Thus, to

reevaluate the conclusions of recent reviews, we conducted a reverse inferential meta-analysis of the terms "reward" (203 studies), "anticipation" (74 studies), and "outcome" (114 studies) using the Neurosynth database (Yarkoni et al. 2011; date April 15, 2013; $p < 0.05$; false discovery rate corrected for whole brain; Z ranging from 2 to 9). This meta-analysis confirmed that increased activity in the MPFC, in the NAcc, and in the VTA was clearly associated with the appearance of the word "reward" in a study description. Activity in different subsets of these regions, however, was associated with the words "anticipation" and "outcome." Whereas increased activity in the NAcc and VTA was associated with the word "anticipation," increased activity in the MPFC and NAcc was associated with the word "outcome" (see figure 9.1). Interestingly, forward inference analyses of brain activity given these same terms revealed less selective associations (Bartra et al. 2013).

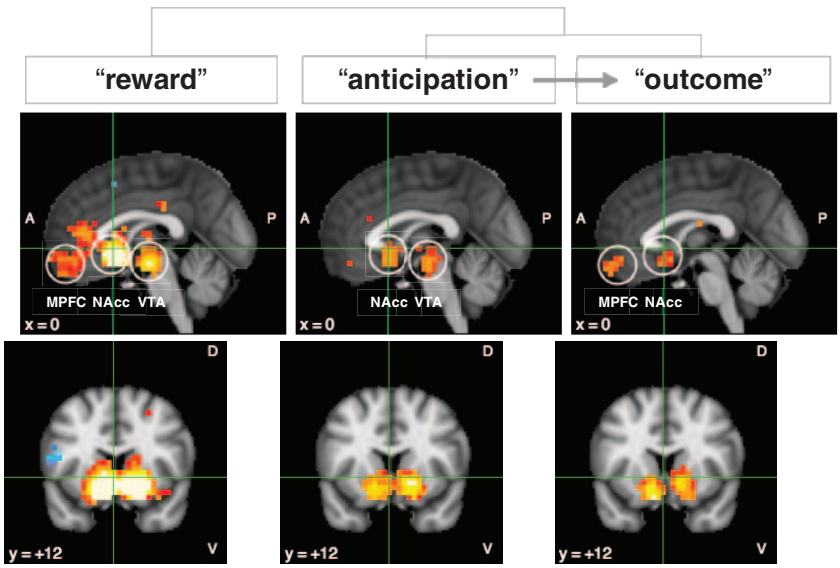

Figure 9.1
Neurosynth reverse-inferential meta-analysis of the probability of incentive processing terms appearing in a report based on localized brain activity (i.e., whole brain tests; FDR corrected at $p < .05$; Z ranging from 2 to 9. "Reward" is associated with MPFC, NAcc, and VTA activity (203 studies). "Anticipation" is associated with NAcc and VTA activity (74 studies). "Outcome" is associated with MPFC and NAcc activity (114 studies).

These reverse inferential findings suggest that increased NAcc activity is associated with both reward anticipation and outcomes, and that increased MPFC activity is preferentially associated with reward outcomes. Even the apparent association of NAcc activity with both reward anticipation and outcomes could be questioned, though, since brain activation contrasts describe the difference between two conditions (reward versus nonreward in this case) but cannot describe the relation of activity to a common standard (e.g., average activity over time). In fact, when NAcc activity time courses are plotted, NAcc activity during reward anticipation increases, whereas NAcc activity during nonreward anticipation stays close to baseline, generating a positive contrast value. On the other hand, NAcc activity in response to reward outcomes typically stays close to baseline, whereas NAcc activity in response to nonreward outcomes dips below baseline, *also* generating a positive contrast value (Knutson et al. 2003). Thus, NAcc activity may differ during reward anticipation and outcomes, even though statistical contrast maps appear similar (Knutson and Wimmer 2007). These differences in activity take on significance when investigators seek to use that activity (rather than contrasts) to predict choice.

The reverse inferential findings also more specifically associate MPFC activity with responses to reward outcomes, which might imply that MPFC is more involved in consummatory processing. Reward outcomes, however, usually involve integration of different values before the act of consumption. For instance, reward outcomes often involve shifts from uncertainty to certainty, even before a reward is physically obtained. Thus, MPFC activity might increase before consumption as a function of value integration. Indeed, localization studies suggest that while manipulating the magnitude of anticipated monetary reward activates the NAcc, manipulating its probability additionally activates the MPFC, even before revelation of outcomes (Knutson et al. 2005). This "value integration" account of MPFC activity has gained popularity in the literature on neuroimaging of choice. (See, e.g., Blair et al. 2006.)

In summary, a substantial literature now implicates NAcc (and VTA) activity in reward anticipation and MPFC (and possibly NAcc) activity in responding to reward outcomes—both primary and secondary. These findings may help investigators to localize reward-related activity in the human brain, and also to predict subsequent choice and consumption. By reversing the typical logic of neuroimaging studies, instead of searching for

neural correlates of input into the brain (e.g., an "input" model), one could use brain activity to predict subsequent behavior (e.g., an "output" model). In fact, researchers have pursued exactly this predictive strategy in a growing number of studies, which we survey below.

Predicting Choice and Consumption

Shifting from input studies to output studies raises several new questions, including whether previous appetitive or consummatory neural activity best predicts future choice and consumption and whether relative neural responses to different options might allow investigators to predict which option will ultimately be chosen and consumed. Since evolutionarily conserved mesolimbic circuits process both primary and secondary rewards, their activity might provide a neural "common currency" for evaluating diverse rewards (Montague and Berns 2002; Levy and Glimcher 2012). Specifically, if this activity not only correlates with reactions to the current state of affairs but also implies future action, investigators might then use it to predict consumption and choice. (See also the chapter by Plassmann and Wager.) In the simplest case these predictions might involve the choice of whether or not to approach and consume a single reward, but more complex scenarios might involve predicting the choice of one among many rewards.

Following on the successes of reward localization studies, researchers began to examine neural correlates of consumer preferences. Early fMRI studies of preferences for consumer products found increased MPFC and sometimes increased NAcc activity in response to presentation of images of preferred cars (Erk et al. 2002) and drinks (Paulus and Frank 2003; Deppe et al. 2005), as well as to delivery of preferred drinks (McClure et al. 2004). Though these findings did not involve choice, they suggested similar processing of primary and secondary rewards—not just metaphorically, but also concretely in the form of overlapping brain circuits. (For a similar argument, see the introductory chapter and the chapter by Preston and Vickers.) Thus, as in consumer research, choice may index the intent to consume products.

Subsequent neuroimaging studies have examined consumer choice either by presenting several choice options simultaneously—e.g., a product or multiple products along with an asking price; see, e.g., Plassmann et al.

2007—or by presenting information sequentially—e.g., a product followed by an asking price followed by a choice prompt; see, e.g., Knutson et al. 2007. Each type of design has strengths and limitations. On the one hand, while simultaneous tasks are designed to elicit immediate and integrated evaluations, it is difficult to determine whether correlated neural activity occurs in response to all options or only in response to some subset of those options (e.g., the most valued option, the entire set of options, or a reaction to choice). On the other hand, although sequential tasks are designed to elicit isolated responses to each newly presented piece of information before choice, those responses may or may not eventually influence the final choice.

Consistent with reward localization findings, preferred products typically elicit increased MPFC activity and sometimes NAcc activity in simultaneous designs (Levy and Glimcher 2012). (See also the chapter by Plassmann and Wager.) For this reason, researchers often report having found that mesolimbic activity correlated with product valuation "at the time of" but not before choice. The present ethological framework, however, implies that earlier activity, whether appetitive or consummatory, may drive eventual choice. Since sequential designs can distinguish antecedent neural activity from choice, we will review the collected findings of sequentially designed studies that have used neural activity to predict choice in greater detail below.

Sooner predictions

Encouraged by the demonstration that brain activity could be used to predict financial choices (Kuhnen and Knutson 2005), researchers sought to also predict consumer choice. To elicit typical purchasing behavior in the scanner, Knutson et al. (2007) gave subjects a cash endowment and asked them to consider buying eighty consumer products while undergoing fMRI scanning. During each trial of this "Save Holdings Or Purchase" (SHOP) Task, subjects saw a product (e.g., a box of chocolates), then a discounted price associated with that product (e.g., 25 percent of the retail price), and then a choice prompt. At the prompt, subjects indicated whether or not they wanted to purchase each item at its designated price. After leaving the scanner, subjects rated how much they wanted each product and what they would be willing to pay for it. Finally, two trials were selected at random to count "for real" and evaluated—that is, if subjects had

previously indicated they would buy the product, they were sent the product and they kept the remainder of their endowment; otherwise, they retained their entire endowment).

Traditional "input" analyses showed that NAcc activity correlated with wanting during product presentation, and that MPFC activity correlated with perceived worth (what economists call "consumer surplus") during price presentation. New "output" analyses that used volume of interest neural activity from these regions to predict choice indicated that positive NAcc responses to the product and positive MPFC responses and negative anterior insula responses to the price predicted choice on a trial-to-trial basis (i.e., 60 percent versus 50 percent chance, cross-validated across subjects, $p < .001$). (For a discussion of the role of the insula in choice in this task, see the chapter by Rick.) When combined with (correlated) self-report variables, neural predictions remained significant, though adding only slight additional power over self-report. These findings demonstrated that neural activity alone could predict consumer choice, but raised further questions. For instance, could activity in these circuits predict choices that occurred later—after scanning, without purchase intent, and even without attention to the options?

Subsequent research explored potential limits of the neural predictions of consumer choice. One study showed that ventral striatal activity and MFPC activity in response to passively presented images of faces, houses, and paintings could still predict preferences for those images, even when preferences were assessed after scanning (Lebreton et al. 2009). A second study showed that ventral striatal activity and MPFC activity in response to passively presented products predicted product valuation and choice, which were both elicited after scanning (Levy et al. 2011). A third study showed that ventral striatal activity and MPFC (and insular) activity predicted intention to buy products (i.e., cars) elicited after scanning regardless of whether subjects viewed the products while rating how much they liked them or while being distracted by an attentionally demanding symbol identification task (Tusche et al. 2010). These findings indicate that neural responses to an item can predict valuation and choice minutes later—even in the absence of any explicit intention to evaluate the item, and even when explicit attention is directed elsewhere. These automatic neural evaluations, as foreseen by Zajonc (1980), nonetheless allow prediction of later choice.

In most of these studies, both NAcc activity and MPFC activity predicted eventual choice. The ability of NAcc activity to predict future choice is consistent with an appetitive interpretation. The ability of MPFC activity to predict future choice, however, is more consistent with a "value integration" interpretation than with a strict consummatory interpretation, since consumption in these experiments presumably occurred at some point in the future after choice. Further, in some of these experiments (e.g., those reported in Knutson et al. 2007) MPFC activity began to predict choice only after a second attribute (e.g., price) was added to the initial presentation of a product. Since these experiments elicited choices at the end of each experimental session, though, they could not address whether neural activity could predict choices in the more distant future.

Later predictions

Since reviews suggest that rewarding images of pleasing food or attractive people can activate mesolimbic circuits, this activity might then predict individual differences in choice and consumption, both in the near future and in the distant future. In one experiment, individual differences in subjects' MPFC responses to monetary rewards and their responses to faces predicted their willingness to pay to see the same faces at the end of a scanning session (Smith et al. 2010). In a second experiment, though, individual differences in subjects' NAcc responses to appetizing food predicted weight gain, and NAcc responses to erotic pictures predicted sexual activity more than six months after scanning (Demos et al. 2012). The latter findings suggested that activity in mesolimbic circuits can predict individual differences in choice, and presumably in consumption, long after the conclusion of an experiment. But could the brain activity of a few subjects further scale to the aggregate level and predict the choices of many?

Aggregate predictions

If the neural responses of a few could predict the preferences of many, this could increase the relevance of neuroimaging for marketing and policy applications (Ariely and Berns 2010). In line with findings that mesolimbic activity predicts individuals' willingness to pay for consumer goods, a subsequent study indicated that increased NAcc activity during exposure to unfamiliar songs predicted individuals' willingness to pay to download

those songs after scanning (Salimpoor et al. 2013). In an ambitious investigation of whether individual neural reactions to novel songs could further predict aggregate demand, Berns and Moore (2011) had adolescent subjects listen to and rate how much they liked novel songs as they were scanned with fMRI. More than three years later, the researchers obtained aggregate song download statistics from Nielsen's SoundScan database. Remarkably, group NAcc activity in response to each song predicted (log-transformed) downloads several years later. Though MPFC activity also predicted downloads, this association could be fully accounted for by including NAcc activity in the model. Interestingly, subjects' group liking ratings of each song did not predict download rates. These findings suggest not only that NAcc activity in response to novel stimuli can predict choice and consumption, but also that predictions can in some cases scale to the aggregate level and far into the future. Additional research will be needed to replicate and extend these findings and to determine whether they will generalize to choices of other consumable goods (e.g., luxury products versus practical products).

Other predictions

Investigators have begun to use neuroimaging data to predict choices that extend beyond the realm of consumer goods, both at the individual level and at the group level. For instance, increased anterior cingulate cortex activity and MPFC activity during peoples' contemplation of their future identities and plans predicts the extent to which they value future monetary rewards (Ersner-Hershfield et al. 2009; Mitchell et al. 2011; Peters and Büchel 2010). Further, increased MPFC activity in response to advertisements and appeals can predict individual differences in future healthy behavior (e.g., increased sunscreen use, reduced smoking; Falk et al. 2010; Chua et al. 2011; Falk et al. 2011), and may even extend to aggregate responses to health-related appeals (Falk et al. 2012). In the context of consumer research, these findings suggest that the neural focus of predictive activity may depend on abstractness of the choice under consideration. Specifically, as individuals increasingly integrate dimensions of value within options, across options, and even across time, predictive neural activity may shift upward along the medial wall of the prefrontal cortex. Thus, integration of more abstract values may recruit increasingly ascending frontostriatal circuits (Haber and Knutson 2009).

Improving predictions

Although neuroimaging designs and analyses had historically been optimized to identify neural activity correlated with input, using neural data to predict output raises new methodological challenges. Continued progress will therefore require innovations in experimental design and analysis. Specifically, investigators might wish not only to predict future behavior but also to interpret which neural circuits predict that behavior. Thus, designs should ideally be structured to elicit temporally specific, strong, and reliable brain activity before behavioral output. Output models also will require investigators to use many correlated neural features to try to predict a few behavioral outcomes; the "$p >> n$ problem" is also prevalent in genetics. Thus, analytic techniques designed to deal with massive correlated predictors of limited outputs must be developed. For instance, a regression technique called GraphNet can induce sparsity, clustering, and structured priors on multivariate data to automatically select neural features that optimally classify associated outcomes (Grosenick et al. 2013).

Applied to neuroimaging data, these models can select out neural activity in space and time that predicts choice. For instance, in the case of fMRI data acquired during purchasing (i.e., in the SHOP task) these techniques increased the prediction of choice from 60 percent observed using volume of interest methods to 74 percent (a level approaching that of self-report variables collected after the scan), but also revealed which features predict purchasing and when they do so (Grosenick et al. 2008, 2013). Consistent with original predictions, these models verified that NAcc responses to products and MPFC responses to prices separately predict purchasing, but additionally implicated the posterior cingulate's response to prices in purchasing. (See figure 9.2.) Although not previously recognized, the predictive power of posterior cingulate activity may reflect greater visuospatial attention to products that would eventually be purchased. Thus, beyond validating and improving predictions, output analyses can identify novel features for future functional characterization. Eventually, as research accumulates, behavioral prediction benchmarks may be established and improved, promoting reliable and incremental scientific advances. Ultimately, mediation models may help investigators to understand not only which neural features predict output, but also which can connect input to output (Wager et al. 2008). All these developments lie on the near horizon for neuroimaging research, but further innovations in multilevel design

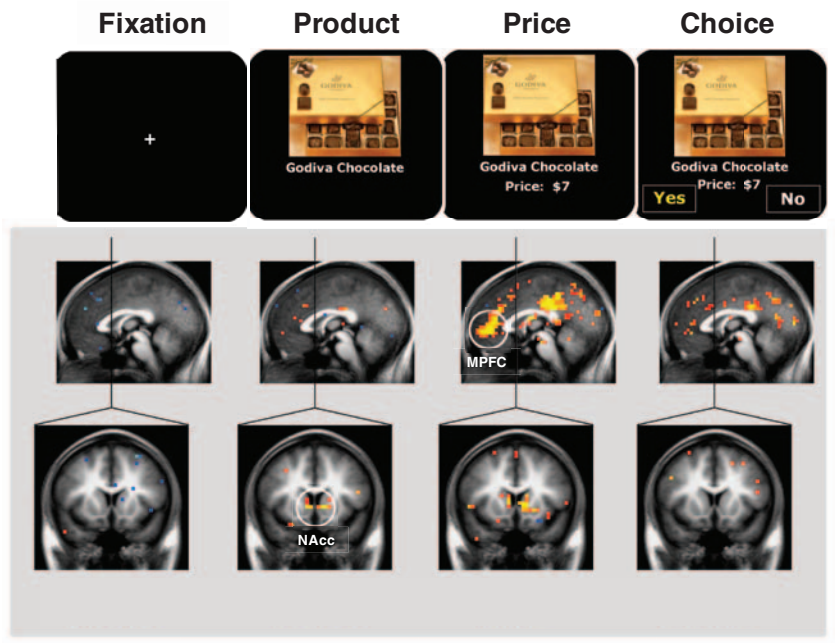

Figure 9.2
Spatiotemporal features that predict consumer choice identified with GraphNet (adapted from Grosenick et al. 2013). When subjects see a product, ventral striatal activity predicts choice; when an associated price appears, MPFC, dorsal striatal, and posterior cingulate activity predict choice. (Note the relative absence of predictive features during the fixation and choice periods.)

and analyses may be necessary to scale from individual to aggregate predictions.

Implications

Since the turn of the twenty-first century, research has consistently and coherently implicated mesolimbic circuitry in human reward processing. Within this circuit, although subcortical NAcc and VTA activity may be more associated with appetitive processes, cortical MFPC and NAcc activity may be more associated with integrative or consummatory processes. Prediction studies further indicate that NAcc activity and sometimes MPFC activity can predict choice and purchasing of consumer products, both in the near future and in the distant future, within and across individuals.

Since NAcc activity specifically increases during reward anticipation, "appetitive" signals from this circuit may best predict choice and subsequent consumption. Remarkably, in only ten years scientists have advanced from asking *whether* brain activity can be used to predict consumption to determining *how well* brain activity can be used to predict consumption. (See also the chapter by Plassmann and Wager.)

Other circuits may also play major roles in predicting choice and consumption, but contexts that evoke their input have not yet been delineated. For instance, anterior insula activity may also predict choice when potential losses are at stake (Knutson and Greer 2008; see also the chapter by Rick), and MFPC activity may also predict choice when multiple dimensions of the same options or different options are under consideration (Haber and Knutson 2010). Dorsal medial frontal activity may play more prominent roles when self-relevance and extended time scales are at stake (Peters and Büchel 2010). Together, these findings fit into and extend a framework for value-based decision making in which primary anticipatory affective responses initially guide choice, which can then be subsequently modulated by more integrative and distal considerations (Knutson and Greer 2008). The current neuroimaging evidence is consistent with the notion that decision making involves a hierarchical multi-component process that unfolds dynamically and flexibly.

The current rate of progress suggests that in the next ten years methods will further improve prediction of behavior from brain signals. Some advances will result from technological enhancements in spatial and especially temporal resolution (e.g., more rapid and homogenous image acquisition due to simultaneous acquisition of multiple slices). Even more significant advances may result from conceptual innovations (e.g., more sophisticated and efficient predictive designs and analyses). Neural prediction of choice and consumption may soon surpass predictions derived from more conventional sources such as self-report, particularly when people are unaware of, unsure of, or reluctant to share their reactions. Though these improved predictions may raise ethical questions related to the neuroimaging of "hidden" information (Ariely and Berns 2010), it is unlikely that anyone will ever be scanned against his or her will, since obtaining interpretable data requires subject cooperation (i.e., minimal motion). Even more promising, some individual predictions may scale to the group level. Investigators will have to clarify the conditions under which this "scaling"

can occur (e.g., to which groups, at which time scales, and under which conditions). Most important, neuroimaging findings should feed back on and inform decision theory, clarifying which accounts correctly predict choice at both the individual and the aggregate level and which do not (and therefore deserve revision or retirement).

Epilogue

More than 100 years after its conception, the early ethological ethological distinction between appetitive and consummatory reward processing has held up well. Beyond animal research, human neuroimaging research now indicates that appetitive and consummatory circuits can be distinguished in space and time. Findings also suggest that the appetitive component motivates positive arousal and approach towards both primary and secondary rewards. Additional findings not reviewed here (see, e.g., Knutson and Greer 2008) suggest that appetitive circuits can be distinguished from aversive circuits and that their activity does not depend on sensory input or motor output. Mounting evidence implies that activity in appetitive circuits can predict eventual choice and consumption, both in the near future and in the distant future. These findings thus have implications not only for decision theory but also for applications to predicting choice in the context of consumer preference and product marketing.

As the unfortunate fate of the hungry ghosts suggests, appetitive and consummatory phases of reward processing may be linked. Consistent with the modern notion of a "reward prediction error" (Schultz et al. 1997), consummatory circuits may eventually calm appetites. When the two become disconnected, however, appetitive behavior may grow excessive, disrupting the rhythm of life and threatening mental stability. Brain lesions or excessive drug use may imbalance these circuits, but so might experiential factors that include learning, social influence, and even cultural values (Tsai et al. 2006; see also the chapter by Whybrow, the chapter by Kringelbach, the chapter by Robinson, Robinson and Berridge, and the chapter by Plassmann and Wager). Thus, mapping the appetitive and consummatory circuits that support reward processing may eventually improve the knowledge of how they dynamically interact with and balance each other, with long-term implications for health and well-being.

Table 9.1
Studies using neural (fMRI) activity to predict consumer choice.

Study	Region labels	Consumable good	Targeted, or whole brain?	Sooner, or later?	Individual, or group?
Knutson et al. 2007	NAcc, MPFC, Ains(-)	Products	Targeted*	Sooner (seconds)	Individual
Tusche et al 2010	VStr*, MPFC, Ains(?)	Cars	Whole	Sooner (minutes–hours)	Individual
Lebreton et al. 2009	NAcc, MFPC	Images (faces, houses, paintings)	Targeted?	Sooner (minutes–hours)	Individual
Levy et al. 2011	VStr, MPFC	Products	Targeted	Sooner (minutes–hours)	Individual
Smith et al. 2010	VStr*, MPFC	Images (faces)	Targeted?	Sooner (minutes–hours)	Individual
Demos et al. 2012	NAcc	Food, sex	Targeted	Later (6 months)	Individual
Salimpoor et al. 2013	NAcc	Songs	Targeted	sooner (minutes–hours)	Individual
Berns and Moore 2011	NAcc	Songs	Targeted?	Later (3 years)	Group

*With corrections for small volumes.

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