QUESTION 13

How Are Emotions Integrated into Choice?

13.1 HOW CAN AFFECT INFLUENCE CHOICE?

Brian Knutson and Mirre Stallen

BACKGROUND

In their more existential moments, scientists might wonder whether they have added anything new to the store of human knowledge, or just recycled earlier ideas and findings. To directly address this question with respect to the influence of emotion on choice, we revisited the first edition of this volume (i.e., *The Nature of Emotion* from 1994, which represented the cutting edge of emotion research at the time), and were surprised to find no chapters on this topic, and few explicit mentions of any connection between emotion and choice. Even commentary about the neural substrates of emotion was sparse (although Panksepp and LeDoux did consider connections between brain activity and emotional experience) (Ekman & Davidson, 1994). A decade later (in 2004), little had changed. For instance, a respected editor (i.e., for *Nature Neuroscience*) then correctly noted that neuroscientists were "not yet close to explaining or predicting human decision-making in the real world. . . ." Over 20 years later, however, the state of the science has drastically shifted. Not only have affective neuroscientists associated neural activity with anticipation of good and bad outcomes, but also with different types of affective experience. Furthermore, this neural activity both precedes and can be used to predict choice. These discoveries have stimulated the birth and growth of new fields of inquiry (including affective neuroscience, social neuroscience, decision neuroscience, neuroeconomics, neuromarketing, neurofinance, and others). While a full neural account of the influence of emotions on choice is yet to be resolved, we argue that new techniques and concepts have already begun to connect affect to choice.

To highlight these recent advances, we reframed our originally posed question "How are *emotions integrated* into choice?" as "How does *affect influence* choice?" Beyond focusing on underlying neural substrates with the question "how," the reframing implies two additional assumptions. First, by targeting basic affective dimensions (e.g., valence, arousal) rather than more complex emotional categories (e.g., anger, happiness, fear, sadness), researchers might most efficiently identify neural correlates of affective experience (which could then inform subsequent work on emotions). Second, by examining how affect influences rather than is integrated into choice, researchers might more rapidly characterize affective states and neural activity that predict and causally alter choice, rather than those that occur after choice. At the turn of the twenty-first century, two key developments turned researchers' attention towards "anticipatory" affective states. First, the technological development of functional magnetic resonance imaging (or FMRI) allowed researchers to visualize second-to-second changes in the activity of deep and small human brain circuits previously implicated in affective experience in animal models (Panksepp, 1998). Second, conceptual accounts began to emphasize how affect might prospectively influence rather than merely consequentially respond to choice (Bechara et al., 1996), and might even overshadow more cognitive calculations (Finucane et al., 2000; Loewenstein et al., 2001). These technological and conceptual advances implied that researchers might use neuroimaging to link anticipatory affect to choice (Knutson & Greer, 2008). Unlike previous accounts, which distinguished affect, emotion, and mood based on different targets and time scales (Ekman & Davidson, 1994), anticipatory affect accounts instead imply an underlying continuum that connects affect, emotion, and mood, based on common neural mechanisms and experiential qualities (in line with early conceptual schemes proposed by Wundt, 1897; Figure Q13.1.1).

FINDINGS

Initial studies sought to identify neural markers of anticipatory affect. Beginning around 2000, functional magnetic resonance imaging (fMRI) studies advanced from mapping neural correlates

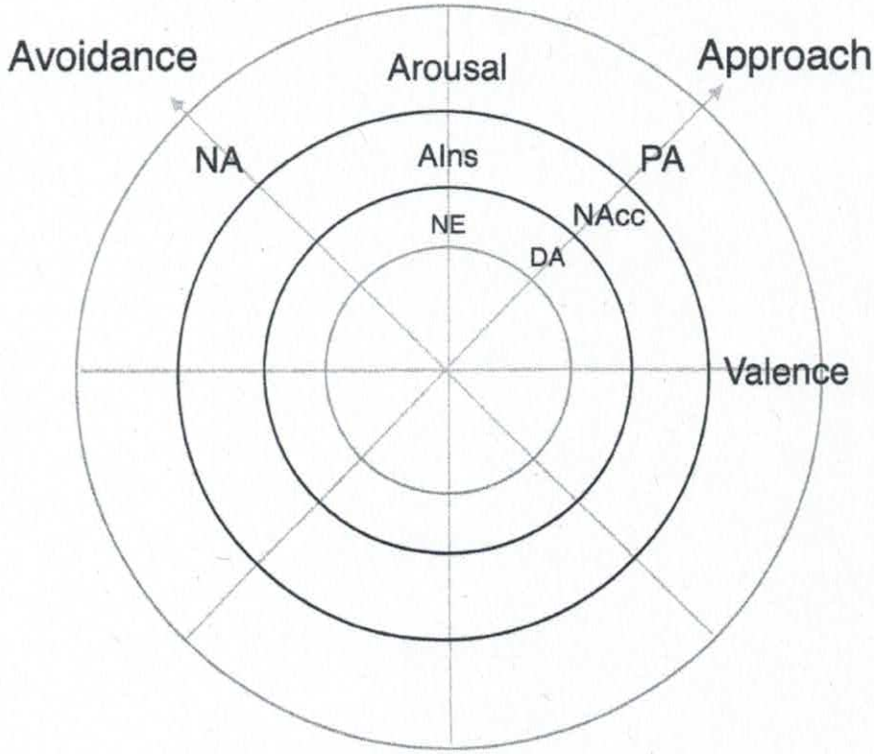

FIGURE Q13.1.1 *Proposed links across levels of analysis.* Concentric circles represent levels of analysis extending from molecular (inner) to molar (outer). These depict neurochemistry (DA = dopamine; NE = norepinephrine), circuit activity (NAcc = nucleus accumbens; AIns = anterior insula), affect (PA = positive arousal; NA = negative arousal), and behavior. Lines trace potential links between levels (adapted from Knutson et al., 2014).

of sensory input (e.g., primary visual cortex responses to flickering checkerboards) and motor output (e.g., primary motor cortex responses to finger tapping) to examining neural responses to affective stimuli (e.g., anticipation and receipt of sweet versus bitter tastes or monetary gains versus losses). While earlier neuroimaging studies (e.g., with Positron Emission Tomography) had explored neural responses to positive and negative emotional stimuli (e.g., standardized sets of affective pictures), many of these studies could not control for sensory input, motor output, arousal, expectancy, or individual variability in affective responses to stimuli. FMRI researchers soon learned, however, that they could control these confounds through timed delivery of positive and negative outcomes. For instance, neural responses to monetary gain and loss cues (i.e., signaling the possibility of gains or losses) could be distinguished from responses to outcomes (i.e., actually receiving gains or losses). FMRI findings indicated that anticipation of gains elicited proportional nucleus accumbens (NAcc), medial caudate, and anterior insula (AIns) activity, whereas anticipation of losses only elicited proportional medial caudate and anterior insula activity (Knutson et al., 2001). Some of this activity correlated with anticipatory affect elicited by incentive cues—for instance, NAcc activity correlated with positive arousal, while anterior insula activity instead correlated either with negative arousal or with general arousal. These robust and replicable findings thus implied deep neural targets for predicting choice (Knutson & Greer 2008; Bartra et al., 2013; Clithero & Rangel, 2014), based on the notion that positive arousal promotes approach while negative arousal instead promotes avoidance (Larsen et al., 2001; Watson et al., 1999; Bradley et al., 2001).

Moving beyond localization, subsequent studies began to use anticipatory brain activity to predict choice. By 2005, fMRI researchers began to realize that brain activity in affective circuits might predict choice on a trial-to-trial basis. In the context of risky choices that require balancing uncertain gains against uncertain losses, an anticipatory affect account implies that NAcc activity should promote approach and predict risk seeking, whereas AIns activity should promote avoidance and predict risk aversion. Indeed, in an investing task, elevated NAcc activity predicted both optimal and suboptimal increases in risk taking, whereas elevated AIns activity predicted decreases in risk-taking, and even after controlling for external information related to expected value and variance (Kuhnen & Knutson, 2005). Activity in these circuits also predicted acceptance versus rejection of risky gambles (Knutson et al., 2008a; Hampton & O'Doherty, 2007). Furthermore, these neural predictions extended to other types of choices (e.g., purchases). For instance, NAcc activity in response to products predicted purchasing, but AIns activity to associated prices predicted not purchasing (Knutson et al., 2008b; Knutson et al., 2007). Interestingly, mere exposure to products can also activate these circuits and predict later decisions to purchase (e.g., after the experiment), suggesting that immediate choice is not necessary (Lebreton et al., 2009; Smith et al., 2010; Levy et al., 2011; Salimpoor et al., 2013). Activity in these circuits in response to unattended products also predicted subsequent purchasing, suggesting that attention is not necessary (Tusche et al., 2010). Together, these findings supported earlier psychological arguments that affect might unconsciously influence choice (Zajonc, 1980).

While these neural predictions aligned with traditional finance theories in which people balance reward against risk to inform choice (Preuschoff et al., 2006; Knutson & Huettel, 2015), the proposed mediating role of anticipatory affect suggested new predictions. First, neural activity might predict choice biases unexplained by traditional theories, such as responses to extreme outcomes. Specifically, people tend to prefer lottery-like (or positive-skewed) gambles that pair small probabilities of gaining large amounts with large probabilities of losing small amounts. Neuroimaging evidence now indicates that increased NAcc activity can account for preferences for these lottery-like gambles (Wu et al., 2011). Second, even when caused by irrelevant stimuli, activity in these circuits still might influence choice. Accordingly, neuroimaging results now suggest that viewing positively arousing images (e.g., exciting sexual images) prior to gambles increases risky choices, and this effect is mediated by increased NAcc activity (Knutson et al., 2008a). Third, neural predictions of risky choice might generalize from finance to other domains, including social interaction. Indeed, enhanced NAcc activity predicts increased sharing of resources with strangers in the context of charitable giving (Genevsky et al., 2013), as well as in repeated trust games (Rilling et al., 2002; Rilling et al., 2004; King-Casas et al., 2005), which involve risk when partners' intentions are unclear. Social variables might also incidentally influence risky choice through affect, since the presence of peers can increase teens' choices to drive recklessly (e.g., to run stop lights), while concomitantly increasing NAcc activity (Chein et al., 2011). Thus, neural activity associated with anticipatory affect might explain choices that violate as well as conform to traditional choice theories.

More recent studies have begun to examine whether neural activity can be used to predict not only individual but also group choice. Since 2010, researchers have attempted to use brain activity to forecast group choice (e.g., the fates of funding appeals in an internet market). While some accounts of group choice imply "no scaling," such that individual choices cannot scale to the aggregate (e.g., due to all individuals having and using the same information), other accounts imply "total scaling," such that all individual choices directly scale to the aggregate (e.g., by directly multiplying individual choice). An intermediate account might imply "partial scaling," such that some components of individual choice scale to the aggregate more than others. These more generalizable components could include anticipatory affect.

In an initial demonstration of the ability of brain activity to forecast aggregate choice, researchers found that teens' NAcc activity in response to music samples correlated with song downloads over two years later, but their liking ratings did not (Berns & Moore, 2012). Subsequent researchers reported that group NAcc activity correlated with the emergence of bubbles in experimental markets, but individual differences in AIns activity predicted who would bail out before those markets "crashed" (Smith et al., 2014). Researchers have also used group NAcc activity to forecast which microlending appeals would succeed in garnering funding on the Internet—even better than the actual choices of the group studied (Genevsky & Knutson, 2015). Group NAcc activity has also been used to forecast market responses to advertisements (e.g., price elasticity in response to ads) (Venkatraman et al., 2015), but group medial prefrontal cortex (MPFC) activity may forecast responses to other types of appeals (e.g., calls in response to antismoking advertisements) (Falk et al., 2012). While it is currently unclear why MPFC rather than NAcc activity forecasts responses to some types of appeals, this may depend upon their content (e.g., since some emphasize potential harms, rather than benefits). Together, these promising new findings suggest that predictions based on neural affective responses can in some cases generalize to forecast aggregate choice, and so might bridge previously unconnected fields like psychology and economics.

IMPLICATIONS

In summary, since the first edition of this volume, researchers have made rapid progress towards establishing that affect can influence choice. These advances arose due to a convergence in conceptual predictions and technical improvements in neuroimaging resolution. Resulting findings have the potential to feed back on and inform theory. Thus, scientists have moved beyond the question of *whether* affect can influence choice to questions about *how and when* affect influences choice.

Traditionally, theorists have often attempted to provide "broad" characterizations of affective phenomena within a single level of analysis (e.g., the experiential level). These recent developments, however, point towards an alternative "deep" approach that identifies critical nodes in adjacent levels of analysis and then attempts to link them (e.g., activity in affective circuits to affective dimensions of experience; Figure Q13.1.1). While such a "deep science" approach may miss details at a given level of analysis, identified links across levels of analysis may more rapidly highlight new questions and promising avenues for translational research (Knutson, 2016). For example (Figure Q13.1.1), at the physiological level, new optogenetic tools now allow researchers to directly test causal predictions that dopamine release can increase fMRI activity in the striatum (including the NAcc) (Samanez-Larkin & Knutson, 2015), which correlates with subsequent approach behavior (Ferenczi et al., 2016). At the experiential level, NAcc activity generally predicts approach behavior, but it also varies dynamically, implying that future research might provide a more continuous readout of latent "affect dynamics" (Knutson et al., 2014). At the behavioral level, machine-learning techniques have validated and improved neural predictions of choice, and continuing advances may supersede established benchmarks (Grosenick et al., 2013). And finally, at the group level (not depicted in Figure Q13.1.1), while brain activity can be used to forecast some market outcomes, the added value and limits of these predictions remains to be characterized.

Together, these findings suggest that affect centrally drives choice, rather than being peripherally integrated into choice. New neuroimaging markers may allow investigators to track affect dynamics and delineate how and when affect influences choice. Beyond alleviating existential concerns, these advances may soon unleash affective neuroscience's potential for improving human health and welfare.

13.2 EMOTIONS THROUGH THE LENS OF ECONOMIC THEORY

Agnieszka Tymula and Paul Glimcher

THE PSYCHOLOGY AND BIOLOGY OF EMOTION

During the 1970s, both psychologists and biologists had largely come to view emotion as a primitive, inefficient, and evolutionarily ancient system for the control of behavior. Driven largely by the work of MacLean (1952), emotional mental states and emotional behavior were seen as the product of a set of brain structures common to nearly all mammals, and christened "the limbic system." Importantly, MacLean was dually trained as an early neurobiologist and as a Freudian psychologist. His work was aimed at testing, at a biological level, Freud's hypothesis that human behavior was driven by three distinct modules: the *id*, the *ego*, and the *super-ego* (Freud, 1923). Simplifying quite a bit: Freud had argued that the id was the most ancient and primitive element of the human cognitive architecture and that it was concerned with what he considered simple, primitive urges and desires. The id, he proposed, was restrained in some sense by the more advanced ego—which was capable of detailed linguistic-rational analysis. The ego was, he argued, very self-regarding, and it was in turn regulated by the super-ego. This mental element was, in Freud's analysis, the most advanced of the three; it was strongly driven by prosocial (or in the language of modern economics, "other-regarding") preferences.

In his widely read and hugely influential work, MacLean argued for a similar (although not identical) parceling of the human brain into three subcomponents, a divisional structure he referred to as the "triune" brain (MacLean, 1985). Drawing on Freud and other sources, MacLean argued that the structures of the limbic system (which at that time was thought to be composed of the cingulate cortices, the hippocampus, portions of the

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Fundamental Questions

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