

Affect and action control

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"Action readiness change is the major feature of emotion; ... the defining feature."

N. H. Frijda 1986 *The Emotions*. Cambridge Univ Press, p469

The word *emotion* suggests a conceptual link between affect and action control: etymologically, *emotion* is from the Latin *ex* (away, out) and *movere* (to move). Empirically, a link between at least some emotions and some actions is unequivocal—in facial expressions of joy, fear, sadness, for example. Emotion theorists have long posited a major role for affect in the control of behavior more generally (e.g., Frijda, 1986; Lang, Bradley, & Cuthbert, 1990; Carver, Sutton, & Scheier, 2000; Schneirla, 1959). Action-control theorists have equally noted the relevance of affect for action control, including motivation and volition (Gollwitzer, 1999). Our aim in this chapter is to show that affect is integral to action control not just in obvious examples, but in a strong sense: pervasively so and at effectively all levels of the action control hierarchy from attention to decision-making and planning. An exhaustive review would require a book; we provide a selective review, elaborating an integrated view of affect and action control, especially through a consideration of the influences of emotion on memory, decision-making, reasoning, attention, and emotion regulation. We relate them to action control within an established model of emotion in which a major end-point is action readiness (Frijda, 1986). That is, for expository purposes in this chapter, we take Frijda's model of the process of emotion and refer to it as a rough and ready model of action control, light on detail (see other chapters in this handbook) but useful for the big picture.

We review evidence suggesting that emotion and cognition interact in many ways, as revealed in behavioral, psychophysiological, and neural measures. Separate circuits and structures are responsible for more emotional versus more cognitive functions (LeDoux, 2000;

LeDoux & Armony, 1999; Panksepp, 1998). This distinction is critical for understanding psychological and emotional disorders as well as the fundamentals of healthy functioning and the nature of their interaction. We do not propose that emotion and cognition should be "blended beyond distinction" (Panksepp, 1994) but do hold to a view that they are "integrated" in the sense of being only partly—but not completely—separable (Gray *et al.*, 2002). The existence of multi-level emotion-cognition interactions suggests that these two systems are tightly integrated, constantly interacting. By biasing memory, decision making and choice behavior, reasoning, attention, and physiology, emotions influence action and action readiness in ways both strong and subtle.

But what is emotion? Contemporary views

How to understand or even simply define emotions has been debated by psychologists, neuroscientists, and philosophers over centuries (Ekman & Davidson, 1994). Ancient Greek philosophers viewed emotions as pernicious influences on judgment—and so emotions need to be controlled by the rational mind. However, a wealth of contemporary research in emotion suggests that affect is not categorically disruptive, and in fact is best understood as adaptive, i.e., functional, on balance. There are many situations where emotion may benefit cognition and decision-making, by favoring choices that encourage goal attainment, coordinating social interactions and relationships to address problems (Keltner & Haidt, 1999), and possibly by helping to resolve conflict between control dilemmas more generally (Gray, Schaefer, Braver, & Most, 2005).

Researchers have used the term *emotion* in many different senses, without a widely adopted definition (Larsen & Fredrickson, 1999). Nonetheless, action control is not merely a

consistent but a central, even defining theme in many leading accounts of emotion, though not all. Functional accounts of emotions characterize them as likely to occur in situations in which adaptive action is necessary and preceded by events that occur quickly and without warning (Davidson, 1994). According to this view, emotions are usually accompanied by autonomic activity that supports the action occurring alongside the emotion. Frijda (1986) defines emotional phenomena in terms of action readiness: "noninstrumental behaviors and noninstrumental features of behavior, physiological changes, and evaluative, subject-related experiences, as evoked by external or mental events, and primarily by the significance of such events". Action control is also central to emotion as characterized by Lang (1995), who defines emotions as "action dispositions – states of vigilant readiness that vary widely in reported affect, physiology, and behavior" which are driven by either appetitive or aversive motivation. Russell and Feldman Barrett (1999) distinguish "prototypical emotional episodes" from "core affect" by delineating specific, defining characteristics of each. A prototypical emotional episode involves a set of actions focused on an object (which can be a person, thing, or event) and at a minimum must include core affect, appropriate behavior, attention toward the object of the episode, and the experience of having an emotion. Furthermore, emotional episodes must have a beginning and end point and a specific duration. In contrast, core affect is much more general and includes basic feelings of which one may be conscious, but does not need to be directed at any particular object. These views are summarized in Table 1. Other definitions of emotion could be included here; we provide these summaries only as a basic overview of the variety of conceptions of emotion in the literature, and to point to some consensus on the importance of the control of actions.

In subsequent sections, we relate emotion-cognition interactions to components of Frijda's (1986) model, from a stimulus event and ending with action readiness (Figure 1). The structure of this model—that it is in effect a skeleton or outline, rather than fully specified model—is particularly well-suited to our exposition of how emotion-cognition interactions are directly relevant to action control, in terms of memory, decision-making, reasoning, attention, and emotion regulation. In Frijda's outline of the process of emotion (pp. 453-473; see Figure 1), the natural and useful starting point for expository purposes is the eliciting stimulus, especially as it is initially interpreted or classified by the subject's nervous system (the "analyzer"). The next stage ("comparator") computes the relevance of the stimulus for the subject, especially in terms of implications for hedonic experience. These first two stages can be influenced by attentional and perceptual biases towards or away from classes of stimuli. The third stage ("diagnoser") further evaluates the stimulus in terms of its relevance given the current context, including the ability to cope with that stimulus. In this stage, long-term memory and aspects of decision-making are important. The fourth stage ("evaluator") integrates prior information about relevance and results in an overall assessment about control precedence—the urgency, difficulty and seriousness of the event, in light of one's concerns, current situation, and ability to respond. On this basis, the next stage ("action proposer") generates an action plan or change in readiness for action, leading to both physiological changes (especially arousal) and also action generation. Throughout these stages, regulatory processes interact with processing at each stage. The process does not end there—the actions taken (and not taken) in turn influence the context and the original instigating stimulus (see Carver et al., this volume, for a control system view). Thus, Frijda's model of the emotion process also constitutes a rough-and-ready model of the process of action control. The point is not that this is the most sophisticated model

of action control (it is not), but rather that it provides a useful framework for understanding the integrated nature of emotion and action control (cf. Gray, 2001).

Emotion-cognition interactions in the service of action control:

In our view, cognition and emotion both function as control systems that regulate behavior. That is, the function of both cognition and emotion is ultimately expressed through the control of action; the functions are adaptive to the extent that the behaviors so controlled are adaptive. Contemporary studies using behavioral, psychophysiological, and neuroimaging methods have shed light on how and when emotion and cognition interact (Daggleish & Power, 1999; Drevets & Raichle, 1998). Emotion-cognition interactions occur at multiple levels of processing, and across many different types of emotional circumstances and cognitive tasks. We review studies that operationalize emotion through mood inductions, emotional priming, and the use of stimuli with overtly emotional content. The cognitive paradigms utilized measure effects on memory, decision-making, reasoning, and attention. To illustrate the bidirectionality of the emotion-cognition relation, we also review emotion regulation. Emotion regulation is a factor at all stages of Frijda's model that influences the ultimate action(s) taken (or not taken). The pervasiveness of emotion-cognition interactions at multiple levels of processing suggests that emotion and cognition are not completely separable but instead are, in a word, integrated (Gray, 2004).

Interactions revealed in performance

In this section we review results from studies in which subjects deliberate about task-relevant content during the course of the experiment with the intention of coming to some sort of conclusion or decision, as reflected overtly in some performance measure, with particular

attention to how emotion may interact with that process. Emotion-cognition interactions are seen in many cases where conflicting inputs from emotional and cognitive systems lead to conflicts that must be resolved before a decision can be made. Here we will review evidence at the information-processing level from studies of memory, emotion regulation, decision-making, and logical reasoning to demonstrate that emotion-cognition interactions influence action control.

Memory. Memory is relevant to action control in several potential ways. Long-term memory would influence the early stages (Figure 1), particularly by influencing how a stimulus is categorized or evaluated. Research on phenomena such as flashbulb memories, recovered memory, and mood-dependent memory has demonstrated that emotion often has a profound impact on memory – though the direction and nature of the influence may vary (Bohannon, 1988; Bower, 1981; Brown & Kulik, 1977; Christianson, 1992; Loftus, 1993). Behavioral conditioning paradigms using electric shock or food reward can also be construed, in cognitive terms, as emotional learning and memory.

Not only does the emotional content of a stimulus influence how it is processed and remembered, but on-going mood at the time of processing may play a major role in how information is stored and later utilized. For example, positive and negative mood inductions can lead to differential rates of false memory (Storbeck & Clore, 2005). Using the Deese-Roediger-McDermott paradigm (Roediger & McDermott, 1995), participants were instructed to memorize a list of words centered on a particular concept (e.g. bed, pillow, rest). The common concept word (in this case, sleep) is closely related in semantic meaning but is never actually presented and is thus a "lure" to test false memory. Participants who were in a pleasant mood showed higher rates of false memory for lures, while those in a negative mood state demonstrated lower lure rates. In a follow-up study, the authors determined that the affective influence occurred at

the stage of encoding rather than recall. The same paradigm was used, but during recall participants were asked to also list any related words that came to mind but were not presented in the original list. There was no interaction between recall instruction (presented versus non-presented lures) and mood group, signifying that the effect of inclusion instruction did not differ across mood groups in the production of critical lures (e.g., the differences between mood groups did not disappear with the instruction to include any words that came to mind). These results suggest that the reduced false memory rate of the negative mood group is due to a more item-specific processing strategy during encoding that made them less likely to access lures at the time of retrieval. In this case, affective state influenced cognitive information processing, biasing encoding strategies in a selective and specific way with a clear impact on memory.

Affective states also influence working memory in a variety of ways relevant to action control, especially as influencing later stages in Frijda's model (Fig 1). The ability to consider context, inhibit prepotent responses, and engage in on-the-spot problem solving and reasoning would all depend to some degree on working memory, and would be especially relevant in the diagnosis and evaluation stages; we review effects of emotion on reasoning below. Studies examining the effect of mood on working memory-related tasks have found differential influences of positive versus negative moods and suggest a possible hemispheric basis for the direction of effects (Bartolic, Basso, Schefft, Glauser, & Titanic-Schefft, 1999; Heller & Nitschke, 1997). In a study examining the influence of emotion on cognitive control, Gray (2001) found evidence for a double-dissociation of verbal and spatial working memory. After viewing videos intended to induce approach, neutral, or withdrawal states, participants completed a series of *n*-back working memory tasks with letters as stimuli (the task was to recall either the letter's identity or location). Approach-states improved verbal working memory but

impaired spatial working memory, while withdrawal states yielded the opposite pattern of results. Thus, affective state interacted with cognitive processing in a selective way, leading to specific behavioral outcomes in which some cognitive abilities were improved and others impaired, depending on the characteristics of the emotion induced.

Decision-making. The role of affect in decision-making (both the process of considering competing options as well as enacting that decision through behavior) has been of considerable research interest. Such influences of emotion on action control are strongly relevant to action control (Figure 1) as influencing evaluations of relevance, urgency, and value. Intriguing evidence for emotion-cognition interactions these processes comes from patients with damage to prefrontal regions known to be involved in decision-making and emotional processing. Using the Iowa Gambling Task (IGT), Bechara, Damasio, Damasio, and Anderson (1994) examined the decision-making behavior of patients with damage to the ventromedial prefrontal cortex (VMPFC). In the IGT, four decks of cards are presented to participants. Two of the decks offer small rewards and similarly small penalties (the "safe" decks), while the other two decks offer large rewards but also large penalties ("risky" decks). Participants are told that the game involves choosing cards from any of these decks until they are told to stop (they do not know how many selections they will be given). In the long run, the advantageous strategy is to choose from the safe decks to wind up with a net gain. Patients with VMPFC damage chose greater numbers of cards from the risky decks, while controls chose more from the safe decks. The authors suggest that due to their brain damage, these patients lack mechanisms of emotion-related feedback that healthy participants use to adaptively bias the choices they make in the IGT. Hence in the case of VMPFC patients, it appears that their decision-making abilities are impaired due to their lack of appropriate affective basis on which adaptive choices could be made.

Mood states differentially influenced decision-making related to the *endowment effect*, or the tendency for an individual's selling price for a given object to exceed the buying or choice price of the same object (Lerner, Small, & Loewenstein, 2004). Half of the individuals were given an item at the beginning of an experiment (in this case, a highlighter set) and told to hold on to it for later use. At the conclusion of the experiment participants are asked how much they would accept to sell their item (their "sell price"). The other participants are shown the item at the beginning of the experiment but it is not given to them. At the end of the study, they are asked how much money they would have to receive to forfeit the item (their "choice price"), which presumably estimates how much they value the item. The tendency for sell prices to be significantly larger than choice prices is known as the endowment effect, and is thought to reflect the increased value attributed to an item once an individual has had it in their possession.

Lerner et al. (2004) induced negative mood states in participants to determine how such states would influence decision-making behavior in a situation that normally produces an endowment effect. Participants viewed either a sad, disgusting, or neutral movie and were then asked for their sell or choice prices for the highlighter set. Following a sadness induction, individuals were willing to sell their items for less money and pay more money to obtain a different item (thought to reflect a tendency to change one's circumstances however possible when in a depressed mood). After a disgust mood induction, participants were willing to sell their items for less and would pay less to acquire new items (thought to reflect the desire to push away things when in a state of disgust). Individuals in the neutral condition replicated the robust endowment effect, showing higher sell prices than choice prices. Thus emotion selectively interacts with cognitive decision-making while individuals are processing information (here, considering their valuation of a product), such that different negatively-valenced moods elicit

distinct action tendencies. Of note, these emotional influences were global mood inductions unrelated to the task, suggesting a strong carryover effect of emotional information.

Other studies have found similarly powerful effects of affective content on decision-making. In several studies, Hsee and Rottenstreich (2004) found that exposure to emotionally-relevant stimuli influenced how participants made value judgments. Participants were primed to think either affectively or computationally by completing a questionnaire before the valuation task. In the affective condition, participants were asked to describe how they felt when hearing trigger words such as *George W. Bush* or *baby*; while in the computational condition they were asked to complete a mathematical word problems. Following the priming manipulation, subjects were asked how much they would be willing to pay for set of 5 versus 10 Madonna CDs. If participants were scope-sensitive, they would calculate their willingness to pay based on multiplying the number of discs available by an amount reflective of the cost of a single disc, with their value of 10 CDs being roughly double their value of 5 CDs. Yet participants in the affective condition showed scope-insensitivity, such that their value for 10 CDs did not increase proportionally over the value ascribed to 5 CDs. In contrast, participants primed with calculation showed a much more scope-sensitive pattern of valuation evidenced by a more linear, proportional slope. In a second study, an affect-rich object (a music book participants were asked to imagine they would enjoy a great deal) similarly elicited scope-insensitive valuations in contrast to an affect-poor object (the amount of cash the book was worth). Additionally, when participants were asked to indicate the amount they would give to a charitable cause, affective stimuli (here, photographs of endangered panda bears) again elicited scope-insensitivity. Subjects saw either 1 or 4 pandas represented as photographs or dots on a graph and were asked how much they would donate to help the pandas. Participants who saw affect-rich photographs

showed scope insensitivity in the amount they were willing to donate (e.g., donating comparable amounts for 1 versus 4 pandas), versus participants in the affect-poor condition who donated proportionally larger amounts for 4 pandas versus 1. Here, affective content influenced valuation judgments and the choices made by participants.

Reasoning. Reasoning is very relevant to action control, especially during evaluation stages when faced with unfamiliar and complex circumstances, such as contingencies that differ by context, during simulation of the consequences of potential action plans, and during emotion regulation. Emotionally-relevant semantic content appears to have a variable effect on reasoning abilities. In a study using classic logical reasoning (of modus ponens and modus tollens, e.g., "if p then q"), participants performed worse when the content of such statements contained emotionally valenced words (e.g. "If someone is in a tragic situation, then she cries") as compared to performance with neutral words (Blanchette & Richards, 2004). Participants also performed worse on statements including neutral words that had been classically conditioned to be more emotionally negative than words that had been conditioned to remain neutral. In other words, emotional words impaired logical reasoning.

In contrast, it is also the case that emotion is not always detrimental. A study using emotional recall prior to a reasoning task illustrates a facilitating role for affect in reasoning (Chang & Wilson, 2004). The reasoning task used was a version of the Wason card selection task involving the detection of potential cheaters. In the Wason task, participants are given a rule and asked to evaluate a sequence of cards concerning rule conditions. One commonly used variant of the task is a rule that involves a potential instance of an individual cheating others. Participants in the study were asked to write an autobiographical recollection of a time when they had been cheated by someone, then were asked whether writing about the event successfully evoked the

feeling they described in their story. Participants who answered affirmatively performed significantly better on this version of the task than individuals who recalled an instance of being happy or benefiting from someone's altruism, suggesting that in recalling and writing about the event, participants probably experienced emotions that adaptively biased responses such that people had an easier time detecting potential cheaters.

The apparent contradiction between these findings underscores the important distinction between task-relevant versus task-irrelevant affect in shaping action tendencies. Blanchette and Richards (2004) utilized emotional words with no connection to the reasoning problems, and as such the words likely served as distracters from the reasoning task and shifting attention away from the goal at hand. In contrast, the emotion induced by Chang and Wilson was directly applicable to the task, priming participants with emotion in a way that adaptively biased performance by facilitating action tendencies toward successful performance of the subsequent reasoning task.

Finally, affective individual differences also influence performance reasoning tasks, revealing emotion-cognition interaction. Reis et al. (in press) found that higher Harm Avoidance (HA; the degree to which an individual is cautious or careful in their daily life) predicted faster performance on a reasoning task in which participants made judgments about statements related to avoiding danger. Similarly, higher Emotional Intelligence (EI; the ability to monitor one's own and others' emotions, and to use the information to guide thinking and actions) predicted faster performance on a social reasoning task in which participants were asked to identify situations where cheating might take place (similar to the reasoning task used by Chang & Wilson, 2004). In both cases, individuals with higher ratings of the affective individual difference measures performed the related reasoning problems faster, with no loss of accuracy. The relationships

between HA and precautionary reasoning as well as between EI and social reasoning were both selective and specific, indicating a double dissociation. While affective individual differences are not equivalent to emotion inductions, these results illustrate that the interaction of emotionally-relevant personality measures with the cognitive reasoning processes bias behavior adaptively and facilitate performance. Beyond the specific example here, affective individual differences could potentially play a role in many stage in Frijda's model (Fig. 1), especially early stages of stimulus detection, classification, and relevance, as well as emotion regulation.

Emotion regulation. The process of managing one's emotional reactions has a more indirect relationship to action control than memory, decision making or reasoning, but is no less important. Emotion regulation refers to the set of processes used in response to emotional experiences and how we express our reactions to emotions (Gross, 1999). How one regulates one's emotions influences how those emotions can subsequently influence action tendencies—in fact, some forms of emotion regulation are focused on regulating specific behaviors, rather than reducing the intensity of the emotion itself. Emotion regulation strategies have a reciprocal relationship with all stages of processing in the model of emotion / action control (Fig. 1), and can determine how information, relevance, context, and urgency are evaluated. The strategies employed by individuals to interpret incoming emotional information have a substantial impact on one's experience, including memory for the information and subjective feelings. Gross's process model provides a useful framework for understanding how emotion regulation strategies may operate. One antecedent-focused cognitive strategy is *reappraisal*, where one decides in advance to interpret an emotional situation in a non-emotional framework. For example, one might choose to think about giving a talk as an opportunity to get feedback from peers instead of as a time to be evaluated; or when viewing aversive images one might determine to take the

perspective of a medical doctor trying to discern the extent of an injury. (Such antecedent-focused strategies would likely fit into the "analyzer" stage of Frijda's model.) In contrast, *suppression* is a response-focused strategy where one inhibits emotionally expressive behavior after the emotion itself is experienced. An example of suppression might involve trying to conceal the anxiety one feels while giving a talk, or putting on a "game face" or a "poker face". Suppression would be integrated into several stages of the model, including the "diagnoser" stage in which context is evaluated (here, the context being a situation where one wants to inhibit behavior) as well as the "action proposer" stage, in which action readiness changes are generated, because the strategy of suppression dictates one's behavior. These strategies of emotion regulation have important implications as they yield different behavioral, cognitive, and physiological results (also see Richards, 2004, for a review). Hence, emotion regulation strategies are an important form of emotion-cognition interactions that are highly relevant to action control.

Richards and Gross (2000) explored the influence of emotion regulation strategy on memory and subjective emotional experience. Individuals were explicitly instructed to either suppress or reappraise a negative emotional experience while viewing either a sad film or aversive images. Those in the suppression condition demonstrated poorer subsequent memory for the verbal details accompanying the stimuli in comparison with reappraisers and those in the neutral condition. Only those who were instructed to reappraise reported significantly less negative of an emotional experience. Thus the cognitive strategy employed for dealing with emotional stimuli influenced memory as well as subjective emotional experience. Because suppressors' memory was only impaired for verbal information, it is possible that suppression occurred through verbal processes (e.g. participants silently reminding themselves not to show

emotion and to continue monitoring their behavior). Furthermore, reappraisers showed better memory for non-verbal memory than other participants, although the reasons for this enhancement are unclear. Emotion regulation paradigms also demonstrate emotion-cognition interactions at the physiological and neural level, as described in later sections.

To recap, emotion can have varied influences on different aspects of cognition, including memory, decision and choice, and reasoning. In cases where the affective components are task-relevant, performance may be enhanced; yet when affect is task-irrelevant it may distract action control from the goal at hand. In this section, we reviewed influences on performance—that is, as revealed in overt action. In the next section, we review influences of emotion on covert responses and changes that potentially, albeit less directly, also influence action control.

Interactions revealed in psychophysiological responses

The interactive nature of the relationship between emotion and cognition is also evident in psychophysiological changes. In many instances, cognitive strategies bias physiological responses to emotional information. Physiological responses are also a critical component of Frijda's model of emotion, in which the end result of the evaluation and change in action readiness are both a physiological change and the generation of action (Fig. 1). Several methods are employed to assess physiological changes, with skin conductance, startle reflexes, and muscle corrugator activity among the most widely used techniques. Skin conductance responses (SCRs) are used to measure somatic state activation through an electrode adhered to the surface of the finger. The magnitude of a SCR consistently covaries with arousal levels, with greater magnitude during higher arousal. Although SCRs do not map onto pleasantness ratings, they do correlate with both interest ratings and the duration of time spent viewing a stimulus (Lang, Greenwald, Bradley, & Hamm, 1993). The startle response is elicited by a sudden, unexpected

stimulus such as a burst of white noise, and is assessed by the degree of contraction of a muscle around the eye (*orbicularis oculi*) similar to a blink. It has been well-documented that the startle blink magnitude is a sensitive index of affective modulation (Lang, Bradley, & Cuthbert, 1998; Lang et al., 1993). That is, the blink magnitude is larger when the response is elicited while the participant is subjected to a negative stimulus, and smaller when the stimulus is positive. This is likely a consequence of the fact that an unpleasant stimulus drives an aversive, more tense behavioral state (heightening the startle response), while a pleasant stimulus activates an approach-oriented state that attenuates the startle response (Lang, 1995). Similarly, electromyogram corrugator activity, measured from a facial muscle, has been consistently found to increase in a negative emotional context and decrease in pleasant conditions (Bradley, Cuthbert, & Lang, 1990). These psychophysiological methods provide additional measurements of affective state that are more accurate and time-sensitive than self-report, and therefore are useful tools with which to study emotion-cognition interactions. In this section, we review evidence from studies using memory, decision-making, and emotion regulation.

Memory. In a memory paradigm, SCR activity during an encoding period predicted how well information would be recalled at a later time (Bradley, Greenwald, Petry, & Lang, 1992). Subjects were shown a series of unpleasant or pleasant photographs that were ranked either high or low in arousal while SCRs were recorded. After a 15-minute interval, subjects were given an incidental speeded recall test and were asked to rank photographs for interest and emotion. Participants responded more quickly to slides that had been seen before and were rated high in arousal; but when slides had not been seen before, response times were significantly longer for arousing pictures (presumably due to stronger attentional capture). Participants had SCRs of greater magnitude in response to high-arousal versus low-arousal slides, and a similar pattern for

unpleasant versus pleasant slides, a finding consistent with other studies. Thus the authors propose that the psychophysiological response accompanying the emotion-cognition interaction of encoding arousing pictures into memory may have a facilitating role in later recall, since the SCR represents a component of the original event associated with the stimulus.

Decision-making. The Iowa Gambling Task has been also used to determine whether patients with VMPFC damage experienced normal physiological reactions (i.e., increased skin conductance while deliberating on and making risky choices) during a decision-making task. SCRs were measured while subjects performed the IGT (Bechara, Damasio, Tranel, & Damasio, 1997). Interestingly, during the task normal participants generated anticipatory SCRs prior to choosing a card from a risky deck throughout the experiment, even before they expressed conscious knowledge of what the pattern of decks signified (but see Maia & McClelland, 2004). At this stage of pre-conscious awareness, normal participants still chose from the advantageous decks, though they could not explain why. However, not only did patients with VMPFC damage fail to generate anticipatory SCRs prior to choosing from the risky decks, they also continued to choose from the risky decks, even at a later stage of the task when several expressed conscious knowledge of the game strategy. The generation of SCRs in anticipation to choosing from risky decks thus correlated with the ability to choose an advantageous strategy in the IGT. The intriguing finding that SCRs correlated with decision-making behavior is interpreted by the authors as evidence for "somatic markers"—nonconscious, physiological biases elicited by emotion can guide behavior even before conscious knowledge does (Bechara et al., 1997). The system proposed includes the generation of affective responses within the amygdala, the output of which is sent to the VMPFC, which then integrates the somatic information with information about current circumstances and goals (Bechara, Damasio, Damasio, & Lee, 1999). Similarly,

the authors postulate that the VMPFC signals to the amygdala when one is faced with a decision; the amygdala then sends feedback regarding somatic "markers" from previous experiences with the decision at hand (here, the deck being contemplated).

Advocates of the somatic marker hypothesis contend that VMPFC patients are unable to use emotion to guide behavior (despite being able to experience emotion), whereas amygdala patients are incapable of having a sufficiently robust emotional experience during the IGT, precluding them from experiencing the type of somatic state related to the task at hand (Bechara et al., 1999). While VMPFC patients generated SCRs in response to reward and punishment during the IGT, amygdala patients did not. Neither group demonstrated SCRs in anticipation of choosing from the risky deck. The authors interpret this finding as evidence for the amygdala's role in generating informative affective states, and the VMPFC's role in integrating somatic information with cognitive knowledge of the task. The physiological responses from the lesion patient groups in conjunction with their behavioral responses indicate there is substantial integration of emotional and cognitive information during the decision-making task, and supports the idea of discrete roles for the amygdala and VMPFC in each of these processes. Furthermore, these responses seem to have a functional role in shaping action tendencies since their presence or absence prior to the action is directly predictive of the type of behavior in which the individual engages.

One possible explanation is that patients with damage to the VMPFC are insensitive to future consequences, which drives them to choose options with immediate benefits despite possible negative outcomes later (Bechara et al., 1994; 1997). Numerous alternative interpretations have been posited to explain these tendencies. The risky and safe decks have different characteristics, as the risky decks have greater negative consequences – thus, patients

may be more risk-seeking (Sanfey, Hastie, Colvin, & Grafman, 2003). Another explanation is that patients are less able to inhibit prepotent responses driving them to choose the risky deck. Alternatives to the somatic marker hypothesis are plausible, but the role of the VMPFC in guiding decision-making behavior has robust empirical support. Whether or not this region actually provides unconscious biases, it seems essential for successful choice behavior—the ability to enact an advantageous decision. The behavior of VMPFC-damaged patients is consistently characterized by impairments in both emotion and feeling, in addition to decision-making (Damasio, 1994); hence this area is also likely to be integrally involved with emotion-cognition interactions that help guide action control and behavior.

Emotion regulation. Paradigms where emotional responses must be managed provide evidence for emotion-cognition interactions as revealed in physiological measure. Gross (1998) reported that instructions to suppress emotional responding led to subjective estimations of emotional experience comparable to similar judgments from subjects instructed to just watch the film. Importantly, however, the suppressor group demonstrated greater physiological activation in the sympathetic nervous system as measured by skin conductance, finger pulse amplitude, and finger temperature. Those instructed to reappraise showed patterns comparable to those in the watch condition, in contrast with the prediction that their physiological responses would be decreased (as were their subjective ratings of disgust). One possibility is that as a response-focused strategy (in which one must regulate a response that has already occurred) suppression was simply a more effortful strategy to pursue and placed additional demand on participants, which was manifested in physiological outcomes. However, evidence from neuroimaging, discussed below, seems to suggest that reappraisal is a comparably demanding cognitive strategy (Ochsner, Bunge, Gross, & Gabrieli, 2002).

In a related study of emotion regulation, Jackson and colleagues (2000) used different techniques to examine the consequences of regulation strategies on physiological responses. Eyeblink startle magnitude and corrugator activity were assessed at several intervals while aversive stimuli were presented. Unlike Gross (1998), Jackson et al. allowed subjects to regulate using whatever strategy they found most appropriate instead of giving them explicit instructions. Participants were presented with aversive or neutral photographs for 8 seconds. Four seconds after the onset of the photo, they were given a verbal instruction to suppress, enhance, or maintain (though no specific strategies were offered regarding how to do so). Physiological measures were taken at several points: following presentation but before instruction, after instruction, and after the photograph was removed. In this way, the paradigm examined the initial emotional response to the stimulus, the effect of the cognitive strategy utilized to regulate emotion, and the consequence of the recovery period strategy. The key finding was that instructions to suppress emotional responding led to smaller startle blink magnitudes and decreased corrugator activity relative to the maintain condition. In contrast, instructions to enhance responses led to larger startle magnitudes and increased corrugator activity in relation to maintain instructions. At first glance, these findings seem to contradict evidence by Gross (1998), who found that suppression instructions increased skin conductance yet decreased heart rate and reappraisal did not change skin conductance. However, these researchers used different instructions that most likely influenced how participants responded. While Gross characterized suppression as behaving in a way that an observer would not know one was feeling anything, Jackson et al. told participants that when suppressing, "...we would like you to decrease the intensity of disgust you feel".

Physiological changes in response to emotion-cognition interactions appear to be closely linked to generating action tendencies, as outlined in the emotion-process model (Frijda, 1986). In the case of memory and decision-making tasks, the generation of SCRs is linked to subsequent performance on the task, with this correlation suggesting the possibility that the physiological response works to bias action control by bolstering the preparatory state of the action system itself. SCR magnitude predicted subsequent recall on a memory task, and the generation of SCRs in a decision-making task predicted the likelihood of using an advantageous strategy. Furthermore, when instructed to suppress emotional reactions, participants demonstrated startle responses of lesser magnitude, again suggesting that physiological responses are closely tied to action tendencies, and may even signal a readiness for action.

Interactions revealed in neural measures

Neuroimaging studies complement performance-based, psychophysiological, and patient-based research to suggest there may be distinct neural mechanisms involved with emotion-cognition integration. Furthermore, based on reciprocal suppression of specific brain regions involved with cognitive and emotional processing (Drevets & Raichle, 1998; Gray, Braver, & Raichle, 2002), it is likely that areas engaged with these processes are tightly integrated. Responses to emotional information may also show different neural correlates depending upon the cognitive strategies implemented. Here we review evidence from studies of memory, decision-making, attention, and emotion regulation.

Memory. An fMRI study of emotion inductions and subsequent working memory performance demonstrated that emotion is integrated with higher cognition (Gray et al., 2002). That is, emotion can interact with cognition in a selective, specific way. Participants viewed positive, negative, or neutral films intended to induce brief emotional states, and were then

scanned while performing an n-back task using either faces or words to test spatial or verbal working memory. As in previous work (Gray, 2001), mild anxiety enhanced spatial working memory while impairing verbal working memory (for an independent replication see Beilock, Rydell, & McConnell, in press), with an opposite pattern holding for induced amusement. In addition, a region of the lateral prefrontal cortex showed strongest activation for face-pleasant and word-unpleasant conditions (which were behaviorally the most difficult). This area showed intermediate activity for neutral conditions and lowest activity for the easiest conditions (face-unpleasant and word-pleasant), suggesting it is sensitive to emotion-cognition integration. Moreover, because activity in this region correlated with behavioral performance, it is possible that this region might directly support cognitive-emotional integration.

The influence of emotion on the process of refreshing a word stored in memory reflects another instance of emotion-cognition interactions biasing action tendencies. In a study examining "mental rubbernecking", the process by which emotional stimuli tend to draw attention away from other cognitive processes, participants refreshed emotionally valenced words from memory faster than neutral words (Johnson, Raye, Mitchell, Greene, Cunningham, & Sanislow, 2005). In addition, refreshing a neutral word that had been presented in a set with an emotional word took longer than refreshing a neutral word in a set of neutral words or an emotional word in a mixed set, supporting the idea that the presence of an emotional word distracted attention from the task at hand. The interaction between the emotional response to the word and the refresh process biases action tendencies such that attention is briefly drawn away from the more cognitive task in order to pay attention to a potentially relevant emotional stimulus. Johnson et al. followed up this behavioral observation with an fMRI study of the process of refreshing emotionally salient words in memory and found that activity in the anterior

orbitofrontal cortex (OFC) was greater when participants refreshed neutral versus emotional items, and when items were repeated activity was greater for refreshing emotional items. These findings support the idea that the OFC region may be involved in exerting control over potentially disruptive emotional responses. In this way, the OFC may thereby influence action tendencies as it allows the individual to direct attention to the cognitive task at hand.

Decision-Making. In a study of decision-making, different neural responses were observed in response to fair versus unfair offers during the ultimatum game (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). In the ultimatum game, participants are told their partner (here, a computerized algorithm – though participants believed they were playing against real people) is given \$10 and must propose an offer to divide the \$10 between them. The partner is allowed to make only one offer, and if the participant accepts, each receives the amount proposed; but if the participant rejects the offer neither individual receives anything. Normatively, there is no reason to reject any offer since receiving any amount is preferable to receiving none. Yet participants show a reliable tendency to reject offers they believe are unfair (where the proposer receives \$8 or \$9 and the participant receives only \$2 or \$1), presumably to punish the unfair proposer.

When Sanfey et al. (2003) scanned participants during the ultimatum game, they determined that unfair offers activated areas known for involvement in both emotion (anterior insula) and cognition (dorsolateral prefrontal cortex). Interestingly, activation in the anterior insula increased for rejected offers, suggesting that in those cases emotion "overruled" cognitive processes and biased action tendencies toward a response driven by emotion more than cognition (since the decision to reject is not rational by normative standards). Of note, the response in the right anterior insula was stronger for unfair offers from a human versus unfair computer

opponents, suggesting that a slight by a real person is more emotionally upsetting than one by a computer. While at face value these results might suggest emotion is a hindrance to advantageous decision-making, the tendency to punish an unfair partner is in some sense an appropriate choice. Though participants were told their interactions with each individual were isolated interactions, punishing a perceived wrong is of significant consequence because it has several consequences. First, it establishes one's social identity and maintains one's reputation; research also indicates that individuals feel satisfaction from punishing those who violate social norms – even when punishment comes with an economic cost to the punisher (deQuervain, Fischbacher, Treyer, Schellhammer, & Schnyder, 2005; Fehr & Fischbacher, 2004). These tendencies indicate emotion-cognition interactions can influence action tendencies and behavior in adaptive ways, particularly with respect to social interactions (Keltner & Haidt, 1999).

Emotion regulation. At the neural level, selective emotion-cognition interactions are observable during periods of emotion regulation. In an fMRI study of regulation, participants viewed a series of emotionally evocative pictures with instructions to either reappraise or simply attend to their emotional response (Ochsner, Bunge, Gross, & Gabrieli, 2002). Reappraisal (in contrast to attending) activated areas including dorsal and ventral left prefrontal cortex and dorsal medial prefrontal cortex. The anterior cingulate cortex showed a positive correlation between activation and self-reported success of reappraisal strategy. Attending versus reappraising activated the left medial orbitofrontal cortex. Furthermore, the ventrolateral prefrontal cortex showed a correlation between activation during reappraisal and reappraisal-related decrease in activation in the amygdala. One possible explanation for these results is that the lateral PFC may modulate amygdala activity through the orbitofrontal cortex, which is plausible because the orbitofrontal cortex has reciprocal connections with both areas. In addition,

the prefrontal region may modulate perceptual and semantic inputs to the amygdala from occipital and parietal regions – such that when holding a reappraisal goal constant in working memory, inputs may be recognized as aversive and thus be gated from registering with the amygdala or medial orbitofrontal cortex.

Attention. Even tasks as basic as attentional matching paradigms illustrate neural mechanisms reflecting interactions between emotion and cognition. An fMRI study of attention to threat-related stimuli and anxiety revealed interesting interactions between emotion, cognitive control, and individual differences (Bishop, Duncan, Brett, & Lawrence, 2004). Participants were scanned while performing a simple matching task: they were shown a set of four photos, including 2 houses and 2 scenes, and were asked to decide whether the houses were identical or not. The two conditions were frequent- versus infrequent-threat-distracters (referring to how often the faces presented exhibited fearful expressions). Within each block, the first three stimuli ("start" trials) indicated whether the frequent distracter would be fearful or neutral in order to establish expectancy in that block. The rostral anterior cingulate cortex (rACC) showed greater activation during infrequent-threat-distracters compared with neutral distracters. Of note, no significant rACC activation was observed when participants were instructed to match faces instead of houses, suggesting that rACC plays a role in processing task-irrelevant emotional information.

Further support for emotion-cognition interactions at the neural level is seen in the relationship between state anxiety (an affective mood) and neural activity. Scores of state anxiety negatively correlated with activity during left dorsolateral PFC and ventrolateral PFC during the start trials of frequent-threat-distracter blocks (e.g., higher anxiety predicted less activity) – suggesting that affective state may reduce activity in two areas known to be involved with

attentional control. Hence negative affect may decrease cognitive ability and reduce action control tendencies supporting the underlying goal of attending to stimuli. Furthermore, higher anxiety ratings were correlated with decreased rACC activity during all types of trials – which the authors posit may explain why PFC activity is decreased in response to threat-related distracters (e.g., a decreased signal from rACC may prevent the PFC from decreasing its response to threatening stimuli and thus making the response more fear-related and thus distracting from the task). Given the extensive association of the rACC with emotional processing and regulation and its connections with the amygdala, insula, and orbitofrontal cortex (Bush, Luu, & Posner, 2000), it is plausibly involved in emotion-cognition interactions within the brain.

Top-down modulation of attention is another topic where emotion-cognition interactions clearly bias action tendencies. A number of studies have demonstrated that even when fearful faces are masked such that participants do not report conscious awareness of seeing the faces, the amygdala shows a heightened response to the stimulus (Morris, Ohman, & Dolan, 1998; Whalen, Rauch, Etcoff, McInerney, Lee, & Jenike, 1998). Such evidence has been interpreted to signify that detection of fearful stimuli by the amygdala is automatic and does not rely on cognitive processing to occur. However, other studies have found that without attention, the amygdala may not respond to fearful stimuli. Pessoa, McKenna, Gutierrez, and Ungerleider (2002) conducted an fMRI study with the hypothesis that masking techniques utilized in earlier studies had failed to fully engage attentional resources and thus did not prove the amygdala detection of fearful faces was truly independent of top-down processing. To engage attention away from the faces, participants were asked to determine whether bars in the periphery of the screen were of similar spatial orientation while a face appeared in the center of the screen. Analyses indicated that the

amygdala did not respond to fearful stimuli in the unattended condition - in both the left and right amygdala, responses were identical across stimulus types and there was no effect of valence on activation. They conclude the amygdala response is thus not automatic, but rather dependent on top-down attentional control – thus the neural response to fearful stimuli involves an emotion-cognition interaction at the level of neural processing that biases action tendencies to pay heightened attention to the appropriate stimulus.

An elegant study examining individual differences in anxiety in relation to amygdala activation to unattended, fearful stimuli adds an additional dimension to this debate – the role of individual differences in neural activity (Bishop, Duncan, & Lawrence, 2004). During an attentional matching task, the key questions were a) whether amygdala activation to fearful versus neutral faces was modulated by attention and b) whether state anxiety plays a role in the neural response. The authors found that while the left amygdala showed greater activation to attended versus unattended fearful faces, the overall amygdala response to fearful, unattended stimuli was dependent on state anxiety, an emotionally-relevant individual difference measure. Individuals with high state anxiety showed stronger activation in the amygdala to fearful faces when they were either attended or unattended; those with low state anxiety showed activation only to faces that were attended. As Bishop et al. point out, if one considers only the high-anxiety participants, one concludes that the amygdala responds to fearful stimuli independent of attention; and yet if one only examines the low anxiety participants it appears that the amygdala is sensitive to top-down attentional modulation. The ability of this study to resolve two conflicting findings underscores the importance of considering affective individual differences when interpreting emotion-cognition interactions.

Finally, the effects of emotion-cognition interactions on behavior were illustrated in an fMRI study of attention, emotion, and working memory (Dolcos & McCarthy, 2006). In a delayed-response working memory task, participants were shown a set of faces, followed by 2 distracters, then asked to determine whether a subsequent face was part of the initial set. The distracters were either emotional, neutral, or scrambled emotional images. Performance on the working memory task at a behavioral level was significantly impaired with emotional distracters in comparison to neutral and scrambled distracters, indicating that the emotional stimuli interfered with the cognitive working memory process by shifting attention to the distracter. At a neural level, activity during the distracter period varied depending on the type of distracter. Emotional distracters activated ventral regions involved in emotion processing, including the amygdala, ventrolateral PFC, and the medial PFC. In addition, emotional distracters deactivated areas involved with executive functions, such as the dorsolateral PFC, lateral PFC, and posterior cingulate cortex. Of note, participants who showed strongest activity in response to emotional distracters in the ventrolateral PFC rated the distracters as less emotional and less distracting, suggesting that the ventrolateral PFC is involved in inhibiting distracting emotions. This interpretation is consistent with the idea of the emotion-cognition interaction in this region biasing action tendencies such that cognitive resources are dedicated to inhibiting emotional responses while resources are steered away from the cognitive working memory task.

Conclusion

A relation between emotion and action control is evident not merely in trivial examples, such as facial expression, but exists throughout the action control hierarchy. In fact, the relation is so pervasive and direct that, as a reference model of action control, it is possible to a model of

the emotion process (Frijda, 1986) as a model of action control, for expository purposes. The consequences of emotion—while typically adaptive on the whole—range from the beneficial (e.g., in many social interactions) to profoundly detrimental (e.g., suicide), depending on the combination of circumstances giving rise to the stimuli, the actor's response, and the subsequent action tendencies that are elicited. We reviewed evidence for diverse emotion-cognition interactions, including memory, reasoning, decision making, and emotion regulation, with particular attention to the implications for understanding action tendencies and overt behavior. Emotion-cognition interactions are ubiquitous—they exist in many forms and under a multitude of circumstances. Emotion and cognition are both powerful control systems—with action tendencies being the ultimate target of control.

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Table 1. Selected definitions of emotion (see text for citations), many explicitly noting a role for emotion in the control of action.

Researcher	Definition of Emotion
Davidson	<ul style="list-style-type: none"> - Functional account: response to a situation where adaptive action is necessary - Situation is usually preceded by events that occur quickly & without warning - Accompanied by physiological activity that may support action
Frijda	<ul style="list-style-type: none"> - Noninstrumental behaviors and features of behavior, physiological changes, and evaluative, subject-related experiences - Evoked by external or mental events (primarily by the significance of those events)
Izard	<ul style="list-style-type: none"> - Feeling or motivational state driven by neurochemical substrates - May occur without cognition
Lang	<ul style="list-style-type: none"> - Action disposition – involves a state of readiness - May vary with respect to affect, physiology, and behavior - Driven by appetitive or aversive motivations
Russell & Feldman Barrett	<ul style="list-style-type: none"> - A set of actions focused on an object - Includes core affect, appropriate behavior, attention toward the object of focus, and the experience of having the emotion - Have clear beginning and end points, and specific duration

Figure 1. Frijda's model of the emotion process (1986, p. 454), which for expository purposes we refer to as a model of action control.

