The emotive nature of conflict monitoring in the medial prefrontal cortex

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ABSTRACT

The detection of conflict between incompatible impulses, thoughts, and actions is a ubiquitous source of motivation across theories of goal-directed action. In this overview, we explore the hypothesis that conflict is emotive, integrating perspectives from affective science and cognitive neuroscience. Initially, we review evidence suggesting that the mental and biological processes that monitor for information processing conflict—particularly those generated by the anterior midcingulate cortex—track the affective significance of conflict and use this signal to motivate increased control. In this sense, variation in control resembles a form of affect regulation in which control implementation counteracts the aversive experience of conflict. We also highlight emerging evidence proposing that states and dispositions associated with acceptance facilitate control by tuning individuals to the emotive nature of conflict, before proposing avenues for future research, including investigating the role of affect in reinforcement learning and decision making.

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1. Introduction

Monitoring performance for goal conflicting thoughts, feelings, and behaviours underlies flexible responding in complex, unpredictable environments. During smoking cessation, for example, quickly detecting impulses (e.g., the desire to smoke) or actions (e.g., picking up a cigarette) that conflict with the goal to quit can signal the need to control behaviour, safeguarding goal progress. Beyond unwanted temptations, conflict is evoked across diverse explanatory frameworks, ranging from high-level dissonant states that emerge when individual's hold multiple inconsistent ideologies, to seemingly lower-level conflicts that occur when stimulus dimensions cue mutually incompatible responses (e.g., Stroop conflict). Underscoring the theoretical ubiquity of conflict, detecting and overcoming some internal conflict or discord is fundamental to multiple seminal perspectives in western philosophy, psychology, and neuroscience (e.g., Baumeister et al., 2007; Botvinick et al., 2001; Carver and Scheier, 1990; Descartes, 1647/1982; Dollard and Miller, 1950; Jung, 1939; Festinger, 1962; Freud, 1913; Proulx et al., 2012). Here, conflict is typically viewed as a crucial motivational signal, stimulating the organism to engage remedial control processes (e.g., focusing attention, becoming more cautious).

In these traditions, emotion and control are often conceptualised as parallel processes that are at odds with each other, creating states of inner turmoil that must be resolved to achieve our goals (see also Heatherton and Wagner, 2011; Kahneman, 2011; Metcalfe and Mischel, 1999). Contrasting this dualism, the present overview synthesizes evidence from multiple psychological and physiological perspectives indicating that conflict is emotive. By using the portmanteau *emotive*, we emphasize our view that conflict has both emotional and motivational properties. That is, conflict triggers a negatively valenced affective state, and the degree of this aversive experience motivates the upregulation of cognitive control to avoid further negative experiences.

Drawing from multiple levels of analysis, we focus on conflict monitoring signals that are putatively generated in the brain's anterior midcingulate cortex (aMCC), exploring the hypothesis that this region tracks the affective valence of conflicts as they arise. We then highlight evidence suggesting that this neural response acts as a motivational input to control, with the behavioural expression of control varying systematically with the extent to which the aMCC tracks the aversiveness of conflict. For the sake of brevity, the current overview specifically emphasises research exploring the relationship between transient negative evaluations of conflict and the immediate upregulation of cognitive control. Conversely, we do not explicitly address how control might be related to positive affect (cf., Chiew and Braver, 2011); how negative task experiences (e.g., fatigue) can promote task disengagement and the shifting of priorities (cf., Carver, 2015; Inzlicht, Schmeichel, and Macrae, 2014); or how the interplay between motivation and task engagement might be critically moderated by difficulty (Gendolla, 2000).

In addition to providing an up-to-date view on the integration of conflict monitoring and negative affect, however, we intend this overview to be generative. In latter sections we discuss promising research

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arising from social and affective neuroscience exploring processes through which cognitive control might be improved, and end by highlighting less investigated areas. In these later sections, we focus on three areas specifically, including the coupling between physiological responses to conflict; the role of negative affect in conflict-driven reinforcement learning; and conflicts that arise during value-guided decision making. In each section, we present our view that the field psychophysiology is well poised to comprehensively address the functional integration of negative affect, motivation, and cognitive control.

2. Neural conflict monitoring and cognitive control

Cognitive control allows us to flexibly calibrate attention, cognition, and action in a goal-directed manner, particularly in novel and unpredictable environments (Banich, 2009; Botvinick et al., 2001). Behaviourally, control is often investigated using conflict paradigms (e.g., the Stroop task) that require habitual, pre-potent responses to be overridden (Cohen et al., 1990; Kerns et al., 2004) or by studying remedial control processes that occur after mistakes (i.e., post-error slowing; Rabbitt and Rodgers, 1977) or conflict (conflict adaptation; Gratton et al., 1992; Kerns et al., 2004; Stürmer et al., 2002).

A dominant goal in cognitive neuroscience in the past two decades has been to identify the neural processes that monitor the fluctuating need for control. Perhaps one of the most replicable results in all of cognitive neuroscience is that goal-conflicting events are associated with increased activation in the aMCC (Botvinick et al., 2001; Ullsperger et al., 2014; van Veen et al., 2009). In the response-locked event-related potential (ERP), similar performance monitoring processes have been operationalised as the amplitude of the error-related negativity (ERN; see Fig. 1): a sharp negative deflection observed within 100 ms after errors at frontocentral electrode sites (Falkenstein et al., 1991; Gehring, Goss, Coles, Meyer, and Donchin, 1993). Given the ERN's temporal proximity to control demanding events (i.e., mistakes), its topographical

distribution, and a number of dipole source localization results, this component is widely thought to reflect neural monitoring processes arising from the aMCC (Dehaene et al., 1994; van Veen and Carter, 2002; Yeung et al., 2004).

The aMCC and the ERN putatively reflect performance monitoring processes that signal to other brain areas (e.g., the dorsolateral prefrontal cortex) the need to increase top-down control (Cavanagh et al., 2009; Kerns et al., 2004; Ridderinkhof et al., 2004). More controversial is the precise computational basis of this monitoring process. According to the conflict monitoring account, the aMCC is sensitive to the co-activation of mutually exclusive response alternatives arising either from conflicting stimuli (i.e., incongruent Stroop targets) or when representations of an executed erroneous response and the should-have-been executed response are active simultaneously (Botvinick et al., 2001; Yeung et al., 2004). Further accounts link performance monitoring to error-specific processes and activity in the mesolimbic dopamine system (Brown and Braver, 2005; Holroyd and Coles, 2002). While early research aimed to differentiate between these accounts, recent frameworks have posited their reconciliation by suggesting that conflict itself is demanding/costly, registering as a negative reward prediction error (cf., Botvinick, 2007).

These cognitive neuroscience accounts have provided great insights into the computational and neural underpinnings of cognitive control. Rather than assuming that the brain "knows" when to exert control, these models specify the processes that detect the fluctuating need for control in mathematically tractable terms (Danielmeier, Wessel, Steinhauser, and Ullsperger, 2009; Yeung et al., 2004). In parallel to these accounts, however, affective neuroscience has revealed that conflict elicits many of the hallmark features of emotion, including valence judgements, physiological arousal, and subjective emotional experiences (Dreisbach and Fischer, 2015; Etkin et al., 2011; Inzlicht et al., 2015; Koban and Pourtois, 2014; Pessoa, 2009; Shackman et al., 2011), proposing a degree of integration between control and emotion that is virtually ignored by computational accounts.

3. The emotive nature of conflict monitoring

Before specifically addressing the emotive nature of conflict, any integrative account requires a clear working definition of emotion. While no universal gold-standard definition of emotion exists, consensus among theorists suggests that emotional episodes comprise valence judgements (i.e., positive or negative?) in response to an internal (e.g., thought) or external (e.g., a snake) stimulus, in addition to changes in physiological arousal (e.g., sweating, heart rate, pupil dilation), expressions (e.g., facial, verbalizations, posture), behaviours promoting wellbeing or survival, and the subjective experience of an emotional feeling state (e.g., anger, happiness, fear, anxiety; Barrett, 2006; Frijda and Scherer, 2009; Gross, 1998; Gross and Barrett, 2011; Russell, 2003).

Beyond this accord, theories deviate regarding the mechanisms that give rise to emotion, existing on a continuum between so-called basic theories to psychological constructivist accounts (Gross and Barrett, 2011). Basic theories propose that specific emotions (e.g., happiness, sadness, fear, anger, etc.) arise from dedicated circuits that produce specific expressions, actions, and patterns of physiological arousal (e.g., Ekman and Cordaro, 2011; Izard, 1993; Panksepp, 1998). These locationist theories, and the resultant partitioning of the brain into cognitive and affective regions (see also Bush et al., 2000), are unable to integrate emotion and control by their very definition. Conversely, psychological constructivism proposes that complex experiential states—including emotions—emerge from dynamic interactions between domain-general mechanisms (e.g., valence, attention, action, interoception, appraisal, meta-cognition; Barrett, 2006, 2013; Russell, 2003, 2009). Given this domain generality, we have suggested that constructivist accounts are well suited to handle the integration of cognitive control and emotion (cf., Inzlicht et al., 2015; Saunders and Inzlicht, 2016).
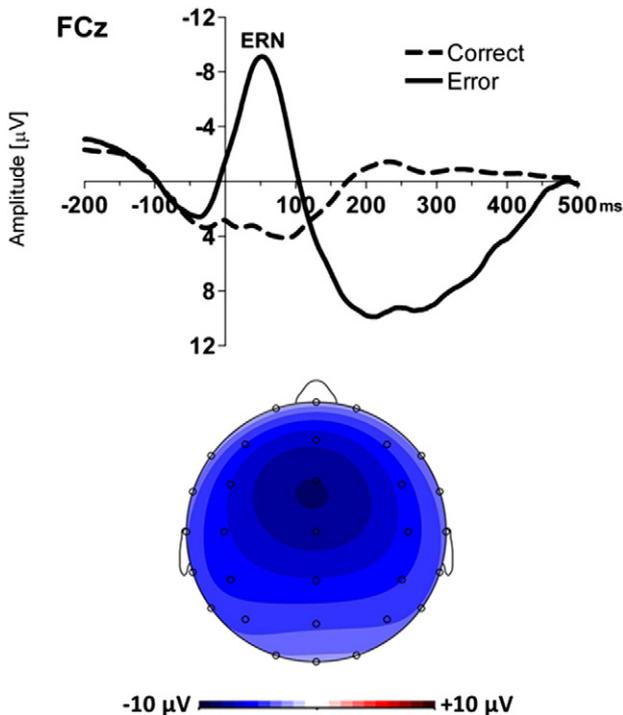

Fig. 1. The error-related negativity (ERN) at electrode FCz during an inhibitory control task (see Saunders et al., 2015a). The ERN is depicted both as a continuous waveform as a function of correct and error trials, and also as a topographic map with negative amplitudes reflected by increasing blue tone in a 50 ms window around the peak of the difference ERP (error – correct).

One central feature of constructivist models is the suggestion that emotion-space can be represented by *core affect*: a circumplex arising from orthogonal dimensions of pleasure (positive affect vs. negative affect) and activation (high arousal vs. low arousal; Russell and Barrett, 1999). Here, anxiety, frustration, and anger, for example, reflect negative states of increased activation, while lower arousal negative states are felt as sadness or fatigue.

But why would the seemingly benign types of conflicts encountered during cognitive control lead to changes in valence and arousal? (cf., Fig. 2). Why, for example, might viewing the word "red" written in blue ink feel worse than viewing the word "blue" written in blue ink?

Conflict arises when competing possibilities are simultaneously activated: typically one goal congruent option (e.g., colour-naming; refusing a cigarette) and another option that is inconsistent with this goal (e.g., the automatic semantic processing of words; the habit to smoke with your friend). Thus, conflict indicates that action tendencies are being drawn in incompatible directions, with negative affect likely arising from the resulting goal confusion, inability to act, and/or the increased likelihood of mistakes (Brown and Braver, 2005; Dreisbach and Fischer, 2016; Dollard and Miller, 1950; Harmon-Jones et al., 2009).

Second, resolving conflict usually involves effortful top-down control (e.g., suppressing automatic word reading; overriding the urge to smoke; Ach, 2006; Kerns et al., 2004). Existing research suggests that effort is particularly aversive, typically prompting effort avoidance when all else is equal (Brehm and Self, 1987; Hull, 1939; Kool et al., 2010; Westbrook et al., 2013). Thus, the close coupling between conflict and cognitive labour might give conflict a negative tone (Botvinick, 2007).

Theories emphasizing the integration of emotion and control require unambiguous evidence that even seemingly benign conflict tasks (e.g., the Stroop) trigger canonically affective reactions. As the combined dimensions of valence and arousal (i.e., core affect) are a hallmark feature of emotion (Larsen and Diener, 1992; Russell and Barrett, 1999; Watson et al., 1988), failure to provide robust evidence for the involvement of valence and arousal in cognitive control would critically undermine this integration.

3.1. Affective priming

Affective priming refers to the phenomenon where a valenced prime (e.g., the word "DEATH") either facilitates subsequent processing of a target with congruent valence (e.g., the word "BOMB"; Fazio et al., 1986) or transfers its valence to previously neutral stimuli (Payne et al., 2005). Suggesting that conflict is aversive, negative words are categorized more quickly and accurately if they are preceded by incompatible relative to compatible Stroop stimuli (e.g., Dreisbach and Fischer,

2012; Pan et al., 2016; Schouppe et al., 2015) and mistakes (Aarts et al., 2012, 2013). Similarly, neutral words are rated more negatively if they are preceded by incompatible relative to compatible Stroop trials (Fritz and Dreisbach, 2015).

These affective priming effects are also short-lived. Conflict-driven affective priming occurs when stimulus-onset asynchronies between prime and target are brief (e.g., ~200–600 ms), and dissipates—or even reverses—when these intervals become longer (~> 800 ms; Aarts et al., 2012; Fritz and Dreisbach, 2015). These results suggest that conflict-related negative affect is transient, and is perhaps even actively counter-regulated over time (Fritz and Dreisbach, 2015).

3.2. Peripheral nervous system arousal to conflict

Peripheral nervous system activation, including changes in heart rate, skin conductance, body temperature, pupil response, and muscle tone, are implicated across theories of emotion (Gross, 1998; Frijda and Scherer, 2009). When scared, we might notice our heart racing, increased sweat, and muscle tension. Despite this theoretical ubiquity of such bodily arousal in affective science, few physiological responses directly map onto specific emotions or valence (Cacioppo et al., 2000; Stemmler, 2004; Quigley and Barrett, 2014). For example, increased skin conductance and pupil dilation occur to both positive and negative stimuli, suggesting that autonomic arousal reflects the non-valenced preparation to act (i.e., motivational significance), rather than an evaluative judgement (Bradley, 2009). Therefore, evidence that conflict and errors are associated with changes in heart rate (Danev and De Winter, 1971; Hajcak et al., 2003; Wessel et al., 2011), skin conductance (Hajcak et al., 2003; O'Connell et al., 2007), and pupil dilation (Critchley et al., 2005; van Steenbergen and Band, 2013; Wessel et al., 2011) indicates that conflict and errors increase arousal, rather than negative affect per se.

Electromyographic (EMG) recordings of the facial musculature can provide more direct evidence for the aversive nature of conflict. The corrugator supercilii, for example, is a small pyramidal muscle located above the medial eyebrow, and is the primary facial muscle involved in frowning. The corrugator supercilii has been implicated in negative experiences in general, rather than specific emotional experiences such as frustration, anger, or sadness (Cacioppo et al., 1986; Prkachin, 1992). As such, activation of the corrugator muscle putatively reflects the bipolar valence dimension (positive-negative) that is central to core affect (Larsen et al., 2003). Supporting the emotive nature of conflict, recent event-related EMG studies report corrugator supercilii activation is reliably increased for erroneous compared to correct actions within 100 ms of the response Elkins-Brown et al., 2016; Lindström et al., 2013), see Fig. 3.

Although consistent with the negative valence of conflict, alternate accounts propose that the corrugator muscle tracks cognitive demand (de Morree and Marcora, 2010; van Boxtel and Jessurun, 1993). Therefore, because conflict is tightly coupled with effort, error-related corrugator engagement might reflect demand, rather than affect. While this caveat undermines the specificity of error-related corrugator activity, negative affect and effort are also perhaps not strictly dissociable. Effort is often perceived as aversive (Kool et al., 2010; McGuire and Botvinick, 2010; Schouppe et al., 2014), and, as such, negative appraisals are perhaps inherent and inseparable from demanding tasks, perhaps explaining why corrugator is engaged by effort.

In addition to corrugator activation, the startle reflex is widely regarded as a psychophysiological marker of defensive motivation and aversive arousal (Blumenthal, 2015; Bradley et al., 1990). Startle occurs rapidly after the onset of intense or threatening stimuli, and is associated with defensive movements (e.g., closing eyelids, raising shoulders) that serve to protect sensitive body parts (e.g., eyes, neck; Eaton, 1984) and interrupt current information processing (Blumenthal, 2015). In humans, startle is frequently operationalized as EMG blink
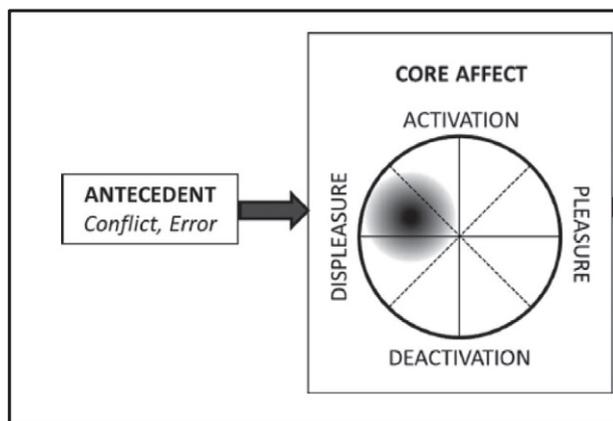
Fig. 2. Depiction of the emotive nature of conflict as mapped onto the dimensions of core affect. Here, goal conflict is an emotional antecedent event that triggers a state of core affect characterized by increased negative affect and elevated arousal, as depicted by the shaded area in this figure. Copied with permission from Saunders and Inzlicht (2016).
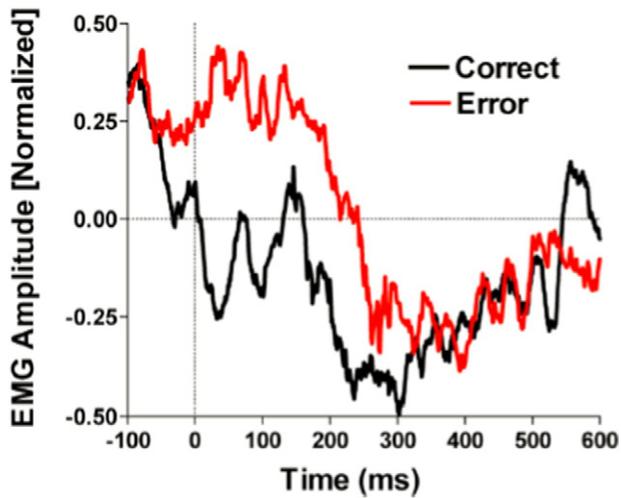
Fig. 3. Figure depicting continuous EMG activity recorded over the corrugator supercilii following correct (black) and error (red) responses. Here, statistically significant increases in corrugator activity were observed 0–300 ms following errors relative to correct responses. Copied with permission from Elkins-Brown et al. (2016).

magnitude over the orbicularis oculi, and is typically increased after the presentation of negative stimuli (e.g., Grillon and Davis, 1997).

Important for current concerns, startle is potentiated after errors (Hajcak and Foti, 2008; Riesel et al., 2013), further suggesting that erroneous actions prime negative affect. As with the corrugator responses to mistakes, caveats remain in the interpretation of the startle reflex as a direct measure of negative affect. Startle response is increased, for example, following cues warning about both upcoming positive (erotic) and negative (phobic) images during a pre-stimulus interval (Sabatinelli et al., 2001). These results suggest that pre-stimulus startle might be sensitive to arousal more broadly, rather than negative affect. As error-related startle potentiation tends to occur after the stimulus (i.e., after the formation of an internal representation of the mistake), it might well be argued that these error effects represent a valenced response analogous to that observed during the viewing of affective images (Bradley, 2009; Sabatinelli et al., 2001). However, further research should clarify if startle responses to mistakes directly reflect negative affect.

Together, then, evidence from EMG studies of facial musculature are consistent with proposals that conflict is aversive, notwithstanding the need for more precise clarification regarding the phenomenological correlates of these facial responses. Combined with other changes across the autonomic nervous system (e.g., heart-rate deceleration, increased skin conductance, pupil dilation) and evidence from affective priming studies, converging evidence indicates that conflict triggers a state of core affect that is negatively valenced and accompanied by increased arousal (see Fig. 2).

3.3. The neural integration of control and emotion

Akin to studies of peripheral arousal, little evidence suggests that isolated brain structures are specifically related to discrete emotional states (Fitzgerald et al., 2006; Lindquist et al., 2012). In the present context, conflict monitoring signals have been observed in several brain regions classically implicated in emotion, such as the amygdala (Koban and Pourtois, 2014; Pourtois et al., 2010) and anterior insula (Klein et al., 2007; Ullsperger et al., 2010). Furthermore, overlapping regions of the aMCC are not only sensitive to conflict and performance monitoring, but are also implicated in negative affect, pain, and emotional disorder (Mayberg, 1997; Shackman et al., 2011; van Tol et al., 2010). These results suggest considerable neuroanatomical convergence between the

neural structures recruited during prototypical emotional episodes and conflict monitoring.

This integration is irreconcilable with locationist accounts of emotion that propose a dedicated correspondence between brain regions and psychological process (e.g., amygdala ➔ fear), but is consistent with psychological constructivist views where complex psychological states emerge from domain-general processing dynamics (Barrett, 2013; Coan, 2010; Russell, 2003). That being said, process integration also raises its own questions. Foremost, if several distributed neural structures (amygdala, insula, aMCC) reflect common, domain-general processes during both cognitive control and emotion, what is the nature of these processes, and how do these processes differ between brain regions?

Affective neuroscience has taken strides towards addressing some questions in regard to the functional significance of these brain regions in control (see Ullsperger, Harasay, Wessel, and Ridderinkhof, 2012; Koban and Pourtois, 2014 for discussions regarding the role of the insula and amygdala). In what follows, we focus specifically on conflict monitoring signals in the aMCC and related electrical brain activity.

3.4. The aMCC and valenced responses to conflict

Several recent accounts have postulated that the aMCC might track the unpleasantness of events during goal-directed action. Spurred by the co-localization of cognitive control, negative affect, and pain to the aMCC cortex, the Adaptive Control Hypothesis (Shackman et al., 2011) posits that the aMCC integrates information about aversive events from multiple neural loci, steering performance to avoid these aversive events. Other views similarly propose that the aMCC monitors the affective significance of actions along a valence dimension (cf., Koban and Pourtois, 2014; Inzlicht et al., 2015). Critically, these views do not necessarily suggest that the aMCC causally generates affective reactions—affect is more likely generated by subcortical 'hedonic hotspots'(Berridge and Kringelbach, 2013). Instead, the aMCC putatively integrates affective information with action and control related signals to bias behaviour away from aversive demands (Botvinick, 2007; van Steenbergen et al., 2014).

Studies combining the affective priming paradigm (e.g., Dreisbach and Fischer, 2012) with cognitive neuroscience have provided strong evidence that conflict signals in the aMCC track the negative valence of conflict. In one study, the amplitude of the ERN was associated with the extent to which mistakes prime the processing of negative, but not positive, words (Aarts et al., 2013). In a conceptually similar fMRI study, reduced aMCC response to negative images occurred after conflicting Stroop trials, while aMCC responses to positive images was reduced after congruent trials (Braem et al., 2016). These findings suggest repetition suppression—where the presentation of a given stimulus category (e.g., cognitive conflict) leads to reduced neural reactivity to the subsequent presentation of a similar stimulus (e.g., negative images). Together, these results propose that the aMCC represents the affective valence of conflict during cognitive control.

Another classic feature of emotional episodes is that they can be deliberately regulated (Gross, 1998, 2015). Disgust in response to distressing stimuli, for example, can be reduced by viewing the eliciting scene from a cold, analytical, and emotionless perspective (Gross, 1998). Therefore, if neural monitoring signals reflect the valence of conflict, this affect also be amenable to emotion regulation. Indeed, ERN amplitudes are reduced by a number of emotion regulation strategies, including cognitive reappraisal (Hobson et al., 2014), the misattribution of arousal (Inzlicht and Al-Khindi, 2012; however, see Rodilla, Beauducel, and Leue, 2016 for recent non-replication), and the anxiolytic effects of alcohol (Bartholow et al., 2012). Reduced mediofrontal performance monitoring signals are also observed when trials are interspersed with spontaneous rewards (van Steenbergen, Band, and Hommel, 2012) or humorous cartoons (van Steenbergen et al., 2014). In this later investigation, cingulate activation to conflict was inversely

related to activation in subcortical regions implicated in hedonic reactivity (i.e., ventral striatum and ventral pallidum; van Steenbergen et al., 2014).

Conversely, the ERN is increased when errors are punished (Riesel et al., 2012; Saunders et al., 2015a), when performance is derided (Wiswede et al., 2009), if participants are placed under social stress (Hajcak et al., 2005), or when instructions guide attention towards momentary affect (Saunders et al., 2016). These results strongly suggest that neural conflict monitoring is systematically moderated by factors that vary the intensity of affect.

4. The emotive nature of conflict and control implementation

Central to emotion is the urgency to act in ways that deal with immediate challenges, opportunities, or threats (Frijda, 1988; Levenson, 1999). And through these ties to changes in action, conflict can be considered emotive. Here, while motivation might broadly reflect a general urge or willingness to act, valence can give motivation the direction to either approach or avoid an event or situation (Bradley, 2009). Evaluating conflict as negative appears to trigger increased avoidance motivation, reflecting the desire to reduce these aversive experiences (Botvinick, 2007; Dignath and Eder, 2015; Inzlicht et al., 2015; Schouppe et al., 2012). In this sense, subsequent remedial control adjustments can be viewed as a form of adaptive emotion regulation driven to maintain positive hedonic homeostasis (Saunders et al., 2015b). This idea resembles the concept of emotion auto-regulation, where the actions brought about by an emotional elicitor (i.e., conflict) can terminate or modify the nature of the emotional episode (Kappas, 2011).

One clear hypothesis arising from this functional perspective is that factors that moderate the affective significance of conflict should be accompanied by concomitant variation in the expression of control. Indeed, increased top-down control is implemented if performance is incentivised or punished (Chiew and Braver, 2013; Riesel et al., 2012; Saunders et al., 2015a; Stürmer et al., 2011), when threatening images signal the need to inhibit a pre-potent response (Senderecka, 2016), after negative mood inductions (Kuhbandner and Zehetleitner, 2011; van Steenbergen et al., 2010, 2012), and when conflicting trials are preceded by perceptually disfluent (i.e., aversive; Winkielman et al., 2003) rather than fluent (i.e., non-aversive) targets (Dreisbach and Fischer, 2011).

A lessening of control is observed when the aversiveness of conflict is counteracted. Sequential adjustments after conflict are reduced when spontaneous rewards (van Steenbergen et al., 2009, 2012), positive feedback signals (Saunders and Jentzsch, 2012), or humorous cartoons (van Steenbergen et al., 2014) are presented between trials, presumably because positive signals counteract the negative hedonic impact of conflict. Similarly, emotion regulation strategies that have been shown to reduce neural reactivity to errors are also directly or indirectly (i.e., through their impact on reduced neural monitoring) accompanied by the reduced cognitive control (Bartholow et al., 2012; Hobson et al., 2014; Inzlicht and Al-Khindi, 2012).

Affective neuroscience accounts of control also predict that awareness of internally generated emotional states should moderate control. Alexithymia reflects individual differences in the ability to detect and describe self-generated emotion (Taylor et al., 1999). Recent investigations suggest that increasing alexithymia predicts reduced neural conflict monitoring (i.e., reduced ERN amplitudes; Maier et al., 2016) and poorer behavioural regulation of conflict (de Galan et al., 2014). While these results should be confirmed in larger samples, they support the idea that conflict-driven control relies partially on sensitivity to internally generated affective states.

Further neuropsychological evidence for the convergence of affect and conflict-driven control has been reported in a recent lesion study (Tolomeo et al., 2016). Patients who received bilateral anterior cingulotomy for treatment resistant depression demonstrated impairment both in the identification of negative facial expressions and in

conflict control on the Stroop task, relative to comparable lesion-free patients. Perhaps most remarkably, these deficits scaled the extent that these lesions overlapped with the co-localization of emotion and conflict monitoring identified by a prior neuroimaging meta-analysis (i.e., Shackman et al., 2011). These findings causally implicate overlapping portions of the aMCC in the processing of negative affect and cognitive control, strongly supporting the functional integration of these processes.

Finally, if cognitive control itself can be understood as a form of emotion regulation (cf., Saunders et al., 2015b), successful control implementation should induce positive affect. Extending previous findings that conflict primes negative affect (e.g., Aarts et al., 2012; Dreisbach and Fischer, 2012), successfully overcoming conflict appears to facilitate the subsequent categorization of positive stimuli (Schouppe et al., 2015). These findings complement studies where increased activity in reward-related brain regions—the ventral striatum—is observed after unrewarded accurate performance (e.g., Satterthwaite et al., 2012). These results support the idea that successfully resolving conflict via control implementation can satisfy homeostatic drives to maintain pleasant states.

5. Anxiety, acceptance, and improving cognitive control

Considering the functional integration of negative affect and cognitive control, it is noticeable that our view deviates from established views that hot, emotional processes have an antagonistic relationship with colder cognition (Baumeister and Heatherton, 1996; Heatherton and Wagner, 2011; Hofmann et al., 2009; Iordan et al., 2013; Kahneman, 2011; Metcalfe and Mischel, 1999). From this, the obvious question arises: How can different models of control provide such opposing roles for affect?

Answering this question requires a nuanced understanding of how and why emotions can be both helpful and harmful. No single emotion—positive or negative—is adaptive or maladaptive across all times and situations. Emotions might be helpful or harmful depending on multiple factors, including their intensity, duration, and suitability to the current context (Gross and Jazaieri, 2014). Extreme emotions have a high capacity to capture and occupy attention, suggesting intense emotion might distract attention from the task at hand (Padmala et al., 2011). Similarly, ruminative or catastrophic emotional reactions might interfere with ongoing performance through a failure to disengage from negative feelings (e.g., Elliott et al., 1997; Holmes and Pizzagalli, 2010).

Investigations of cognitive control in samples with anxious psychopathologies illustrate this apparent dark side of emotion. A significant body of research indicates that several psychopathologies (e.g., generalized anxiety disorder, obsessive compulsive disorder) are associated with increased neural reactivity to conflict (Cavanagh and Shackman, 2015; Moser et al., 2013; Weinberg et al., 2012)—an effect that is particularly associated with increased worry in these samples (Zambrano-Vazquez and Allen, 2014). However, these disorders are seldom associated with enhanced cognitive control. Interestingly, a recent study found that while worry was associated with increased neural reactivity to conflict, this anxiety was not associated with enhanced connectivity (i.e., theta phase synchrony; Cavanagh and Frank, 2014) between medial and lateral electrode sites (Moran et al., 2015). This latter finding suggests that despite reacting more strongly to conflict, anxious individuals are less able to use this signal to improve control.

Conversely, other states and traits may allow the constructive use conflict-related affect. Emerging research from social affective neuroscience has investigated the psychological processes (e.g., self-affirmation and mindfulness) that potentially facilitate improvements in control by promoting measured evaluations of conflict. These highly learnable processes have the potential to inform strategies and interventions to improve control (Inzlicht et al., 2014).

5.1. Affirming the self and the non-defensive reactivity to conflict

In general, we are motivated to view ourselves as positive, good, and worthwhile (Cohen and Sherman, 2014). These motivations are broadly adaptive, however, the drive to preserve self-integrity can produce defensive responses to self-referential negative feedback (e.g., denying or ignoring health risks associated with unprotected sex; Sherman et al., 2000). Self-affirmation theory (Steele, 1988) posits that this defensiveness can be counteracted when individuals reflect positively on their core values, which, in turn, increases openness to negative feedback (see also Trope and Pomerantz, 1998).

Cybernetic models of control consider conflict is a source of negative self-referential feedback (Carver and Scheier, 1990; Inzlicht et al., 2014). Therefore, it might be hypothesised that self-affirmation should increase receptivity to conflict signals. In one such study, a self-affirmation manipulation—writing about a personally relevant value was associated with increased neural reactivity to conflict (ERN amplitude) and improved inhibitory control (Legault et al., 2012). These results suggest that affirming the self can increase the adaptive use of internally generated aversive signals that arise during cognitive control. Crucially, while these initial results are promising, on-going work should test the replicability and strength of this effect. Indeed, the efficacy of self-affirmation has recently been questioned in educational settings (Hanselman et al., 2016), underscoring the need to rigorously test the effects of self-affirmation on cognitive control.

5.2. Mindfulness and emotional acceptance

Mindfulness has recently been identified as a route to enhance cognitive control (Teper et al., 2013). Arising from Buddhist traditions, mindfulness comprises increased awareness and acceptance of momentary experiences, including thoughts, emotions, and bodily sensations (Bishop et al., 2004; Kabat-Zinn, 1994). Largely antithetical to anxiety, mindfulness allows the close tracking of present-moment affective experiences without elaboration, defensiveness, or catastrophization (Farb et al., 2007).

Thus, mindfulness might facilitate cognitive control by allowing individuals to track conflict-related affect with fidelity, and use this information to adjust performance. Supporting this hypothesis, one cross-sectional study reported that the duration of mindfulness experience was associated with increased ERN amplitudes and reduced Stroop errors (Teper and Inzlicht, 2013). Specifically implicating an affective mechanism, these control enhancements were mediated by self-reported emotional acceptance.

Further support for the relationship between mindful attention and control has been provided by a recent experimental study (Saunders et al., 2016). Here, participants first performed a baseline go/no-go task, followed by a brief (<15 min) mindfulness meditation that non-judgmentally focused momentary attention towards either thoughts or feelings, depending upon group assignment. Interestingly, specifically focusing on momentary feelings enhanced ERN amplitudes on a post-induction go/no-go task relative to baseline measures. Additionally, emotion-focused participants did not show the fatigue-like performance detriment (i.e., increased impulsiveness) that became apparent over time in the thought-focused group. These results provide experimental support for suggestions that emotive aspects of mindfulness specifically drive the up-regulation of cognitive control.

The effects of mindfulness on cognitive control should be considered with the caveat that two investigations using brief mindfulness meditations failed to find increases in ERN amplitudes (Bing-Canar et al., 2016; Larson et al., 2013). These findings motivate continued, well-powered research to assess the relationship between mindfulness and control.

To summarize, results emerging from studies of mindfulness and self-affirmation suggest that conflict-related affect is most effective not when it is used to chastise or derogate the self, but is instead met with openness and acceptance.

6. Emerging directions and unanswered questions

In this overview, we have investigated the emotive nature of conflict. We now focus on current controversies and less studied areas in the field with the goal to stimulate ongoing research.

6.1. The integration and function of physiological signals during control

Conflict signals arise across distinct aspects of the central and peripheral nervous system, including startle responses, frowning, sweating, heart-rate deceleration, and pupil dilation, as well as neural activation of the aMCC, anterior insula, and amygdala (cf., Critchley et al., 2005; Hacjak, 2012; Inzlicht et al., 2015; Klein et al., 2007; Koban and Pourtois, 2014; Lindström et al., 2013). As these components vary in their temporal and spatial characteristics, ongoing research must determine the functional similarities and differences among these correlates of control.

The ERN, for example, arises early after responses (0–100 ms), and is puatatively sensitive to valence (Aarts et al., 2013; Inzlicht and Al-Khindi, 2012). In contrast, the ERN seems insensitive to error awareness (Nieuwenhuis et al., 2001; O'Connell et al., 2007), subjective feelings that arise during cognitive control (Saunders et al., 2015a), or non-valenced autonomic responses to conflict (Hajcak et al., 2003). Thus, a reasonable working theory of the ERN is that this ERP reflects an initial—if rudimentary—evaluation of actions (i.e., "something bad has gone wrong"), without reflecting a full-blown emotion.

If the ERN reflects the valence of actions, however, it should be expected that this component will correlate with other valenced physiological responses. However, while some initial results suggested positive associations between error-potentiated startle and ERN amplitude (Hajcak and Foti, 2008), recent analyses attribute this effect either to the influence of statistical outliers (see Moser et al., 2014) or is limited to individuals with particularly large ERNs (Riesel et al., 2013). Similarly, while error-related corrugator activity coincides temporally with the ERN (both 0–100 ms; Elkins-Brown et al., 2016; Lindström et al., 2013), one existing study found no strong evidence for an association between error-related corrugator activity and the ERN (Elkins-Brown et al., 2016). As such, ongoing research should clarify the relationship between the ERN and other physiological signals that are sensitive to aversive evaluations. One fruitful approach to achieve these goals might be the increased use of single-trial within-subjects analyses that have better resolution to detect trial-specific relationships and higher statistical power than the individual difference studies (Blankertz et al., 2011; Cavanagh and Shackman, 2015).

6.2. Negative affect and reinforcement learning

Beyond signalling the immediate need for adjustment, errors are important learning events. Detecting a wrong note during a music recital, for example, might help to stamp this error into memory and reduce the chance of similar future mistakes. As emotional memoranda are often learned with greater strength than neutral items (cf., Dolan, 2002; O'Doherty et al., 2001), avoidance learning might be facilitated by affective reactivity to errors.

Avoidance learning is typically studied using probabilistic learning paradigms in which positive and negative feedback is used to guide choices towards one of several stimuli (e.g., Cools et al., 2002; Frank et al., 2005). Here, negative learning, defined as the propensity to learn from mistakes, can be differentiated form positive learning, inferred from the ability to learn by approaching rewards (Frank et al., 2005). Suggesting that biases towards negative learning is facilitated by increasing the affective significance of conflict, increased depressive symptomatology has been associated with increased neural reactivity to negative feedback and enhanced negative learning (Cavanagh et al., 2011a; analogous results have also observed under social evaluative stress, Cavanagh et al., 2011b). Thus, unlike studies of psychopathology

observed in conflict control paradigms (cf., Weinberg et al., 2012), results from probabilistic learning suggest that stress and emotional reactivity alters the behavioural expression of reinforcement learning (however, see Zambrano-Vazquez and Allen, 2014).

While increased negative learning in depression might arises from harmful hypersensitivity to aversive signals, the ability to learn from errors itself is quite advantageous. One future research goal will be to investigate and establish factors that promote increased learning from errors without adversely impacting on wellbeing. A fruitful approach is to test if psychological factors that promote more accepting and non-judgemental responses to negative affect also enhance the ability to learn from mistakes.

6.3. The emotive nature of conflict and decision making

Conflict can also arise during value-guided decision making when there is no objectively correct response (i.e., when choice is based on subjective preference). During temporal discounting, for example, choosing between a desirable reward now (e.g., $15 today) and an appealing delayed reward (e.g., $30 in two weeks) is more conflicting than choosing between the same distal reward and a smaller immediate return (e.g., $1 today). While subjective conflicts differ in important ways from that which arises in classic conflict tasks, neuroimaging suggests that decision conflicts are also tracked by the aMCC (e.g., Blair et al., 2006; Kitayama et al., 2013; Pochon et al., 2008; Shenhav and Buckner, 2014). Furthermore, as with ERP investigations of cognitive control, a negative deflection in the response-locked ERP called the conflict negativity (CN[1]) peaks over frontocentral electrode sites, showing maximal amplitudes for high-conflict compared to low-conflict choice decisions (Di Domenico et al., 2016; Nakao et al., 2010), see Fig. 4. These results are consistent with the idea that a common monitoring system resides in the aMCC and tracks conflict across multiple domains (Botvinick et al., 2001).

If the aMCC facilitates adaptive control by tracking the aversiveness of conflict (cf., Botvinick, 2007; Koban and Pourtois, 2013; Shackman et al., 2011), decision-related conflict signals should also be associated with negative affect. Supporting this idea, one recent study found that choosing between two highly desirable prizes (e.g., a digital camera or a smartphone?) increased aMCC activation, and this activity correlated with subjective anxiety felt towards these win-win conflicts (Shenhav and Buckner, 2014). Furthermore, decision conflict has been shown to engage the autonomic nervous system (e.g., pupil dilation; Cavanagh et al., 2014), suggesting that decision conflicts are also arousing. Thus, like other forms of conflict, preliminary evidence indicates that decision conflicts also triggers a state of aversive arousal.

Future research can further investigate the affective correlates of decision conflict. Studies measuring the CN, for example, can utilize the temporal resolution of ERPs to test the time-course of decision-related anxiety and its relationship with peripheral arousal. Similarly, as a number of emotion-regulation strategies have been shown to reduce neural reactivity to conflict (Bartholow et al., 2012; Hobson et al., 2014; Inzlicht and Al-Khindi, 2012), it should also be tested if these moderators also attenuate neural reactivity to decision conflict (i.e., CN amplitude). Finally, one further benefit of decision making paradigms is that neural monitoring can be studied using choice stimuli that are reflective of the personal conflicts experienced in our day-to-day lives (e.g., healthy

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[1] Note that the CN is highly comparable to an ERP identified as the Correct Response Negativity (CRN) in regard to both its temporospatial profile (i.e., negative ERP 100 ms after the response at frontocentral electrodes) and its sensitivity to experimental manipulations of conflict (c.f., Bartholow et al., 2005). Indeed, we suspect that the ERN, CRN, and CN all likely reflect the activity of a common neural conflict monitoring system. During value guided decision making, however, responses are guided by subjective preference rather than objective accuracy. As such, the term "correct response negativity", we believe, is potentially misleading when identifying ERP responses that arise in contexts lacking an objectively correct answer. As such, we prefer to use CN to refer to this component during subjective decision making.
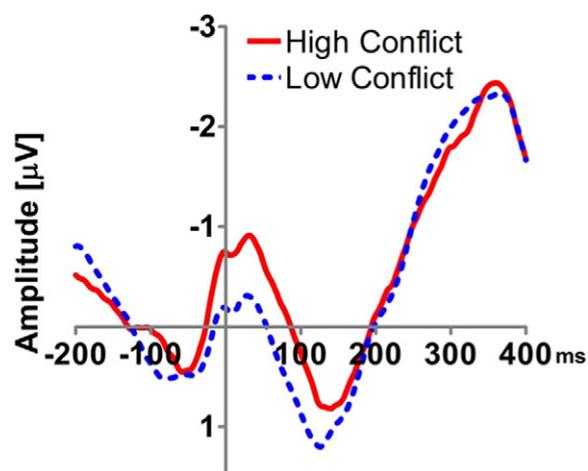

Fig. 4. ERP waveform depicting the conflict negativity (CN) at electrode Cz to high- and low-conflict choice items during value-guided decision making. ERPs were created for illustrative purposes from an unpublished neuroeconomic study of decision making (Peterson et al., 2016).

vs. unhealthy foods; immediate vs. delayed rewards). Beyond generally increasing ecological validity, the flexibility inherent to decision making paradigms allows for bespoke tests of self-control conflicts that are characteristic of individual differences, such as addiction, problem gambling, or dieting.

7. Concluding remarks

Considerable converging evidence from affective psychophysiology, cognitive neuroscience, and social and personality psychology now indicates that conflict is aversive. Contrasting accounts in which control and emotion are seen as separable but interacting phenomena, this emerging consensus suggests that affect and cognition are functionally integrated (Inzlicht et al., 2015; Koban and Pourtois, 2014; Pessoa, 2009; Shackman et al., 2011). It is our hope that this overview will be generative, with ongoing research in affective neuroscience not only helping to uncover the affective nature of cognitive control, but also to investigate the contribution of emotive responses to conflict outside the range of phenomena typically studied in conflict paradigms. It is our belief that psychophysiological research is well positioned to comprehensively address these future research goals.

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