

An Emotional Call to Action: Integrating Affective Neuroscience in Models of Motor Control

Rebekah L. Blakemore

*Department of Neuroscience, University of Geneva, Switzerland
Swiss Center for Affective Sciences, University of Geneva, Switzerland*

Patrik Vuilleumier

*Department of Neuroscience, University of Geneva, Switzerland
Swiss Center for Affective Sciences, University of Geneva, Switzerland
Department of Neurology, University Hospitals of Geneva, Switzerland*

Abstract

Intimate relationships between emotion and action have long been acknowledged, yet contemporary theories and experimental research within affective and movement neuroscience have not been linked into a coherent framework bridging these two fields. Accumulating psychological and neuroimaging evidence has, however, brought new insights regarding how emotions affect the preparation, execution, and control of voluntary movement. Here we review main approaches and findings on such emotion–action interactions. To assimilate key emotion concepts of action tendencies and motive states with fundamental constructs of the motor system, we underscore the need for integrating an information-processing approach of motor control into affective neuroscience. This should provide a rich foundation to bridge the two fields, allowing further refinement and empirical testing of emotion theories and better understanding of affective influences in movement disorders.

Keywords

action readiness, motive state, motor preparation, voluntary movement

Introduction

Since the pioneering writings of William James (1884, 1890), researchers investigating psychophysiological and affective processes have highlighted the intimate links between the brain, body, and actions in emotional responses. James famously noted that,

[W]e meet a bear, are frightened and run; we are insulted by a rival, are angry and strike . . . this order of sequence is incorrect . . . the more rational statement is that we feel sorry because we cry, angry because we strike, afraid because we tremble. (1890, p. 449)

This view sparked a longstanding debate that contemporary theories of emotion continue to address about the causal and

functional relationship between emotion experience and bodily responses (Sander, 2013).

Nonetheless, there is consensus among current dominant models of emotion (including basic emotion, circumplex, and appraisal theories) that emotions consist of two essential processes: emotion elicitation and an emotional response (including expression, action tendency, autonomic reaction, subjective feeling, and cognitive changes). Although both elicitation and response mechanisms can influence overt motor behaviour (see Sander, 2013, Figure 1.1), most empirical investigations in human affective neuroscience have been directed elsewhere. In particular, great strides have been made to bridge affective and

cognitive neuroscience by probing how emotions influence attention, memory, decision making, and cognitive control (Okon-Singer, Hendler, Pessoa, & Shackman, 2015; Vuilleumier, Armony, & Dolan, 2004). Despite some overlap of mechanisms underlying cognitive functions and motor action (for instance between executive control and motor inhibitory processes; or between decision making and motor programming), and despite the use of outcome measures in emotion–cognition paradigms that are often motoric in nature (e.g., response times), there has been a relative lack of effort to link affective neuroscience with *movement* neuroscience. Moreover, comparably little attention has been given to the close relationship between emotion and voluntary action—that is, the effects of emotion on movements that are goal-directed (purposive), triggered either internally or by external events though this may or may not initiate movement, and amenable to modification by learning (Krakauer & Ghez, 2000). This neglect has hampered progress in understanding emotion–motor system interactions at the behavioural and neural level, thwarting a comprehensive understanding of affective and movement disorders alike.

Accumulating evidence from psychological and neuroimaging work over the last decade has, however, provided important new insights and opened new avenues to unite these seemingly disparate fields. Here we provide an overview of this research, focussing on emotion–action interactions from a human affective neuroscience perspective. Of particular relevance to this article are two theoretical frameworks that underpin most of the research reviewed in what follows. These perspectives consider emotions respectively as action tendencies (Frijda, 1986, 2007; see also Arnold, 1960) and as motivational systems (Lang & Bradley, 2010) that strive the organism towards specific adaptive goals. Action tendency refers to the internal motivate states thought to underlie emotional feelings and overt behaviour, as epitomised by the work of Frijda (2009). These internal states, or motivational processes of action readiness, prepare and guide the body for action. Importantly, in this view, action tendencies are not limited to observable behavioural manifestations such as approach and withdrawal behaviours. They also encompass nondirectional voluntary movements and nonmotor actions (Frijda, 2009). A related framework based on motivational states as preparation for action is emphasised by Lang and colleagues, who posited that emotions are organised around two motivational systems, appetitive and defensive, evolved to avoid threat and promote survival (Lang & Bradley, 2010). These systems are implemented by specific neural circuits that mediate autonomic and somatic responses; activation of one or the other system depends on emotional valence, while the degree of motivational activation is based on emotional arousal.

With these classic models in mind, we first review research examining action arising from or directly influenced by affective information; particularly work addressing how emotional signals influence the preparation, execution, and control of action. Note that here we use the term action interchangeably with voluntary movement or motor behaviour. We then discuss considerations for future research by outlining possible strategies to align theories of emotion with those of neuromotor

control, and briefly mention neuropsychiatric pathologies where emotion–action interactions are disrupted.

How Do Emotional Processes Influence Voluntary Movement?

In the following sections we review recent empirical research explicitly addressing how emotional state modulates various parameters of voluntary motor behaviour using neuroscience tools. We therefore exclude literature simply *inferring* a relationship between emotion and action (i.e., no objective measures of a direct influence of emotion on motor control were evident). Moreover, because the focus of this review is on processes governing voluntary movement, we exclude those studies examining elementary motor phenomena modulated by emotion such as involuntary reflex responses (e.g., fear-potentiated startle; Bradley, Codispoti, Cuthbert, & Lang, 2001), as well as those examining behaviours with communicative expression value (e.g., gestures or postures; reviewed in de Gelder, de Borst, & Watson, 2015; see also Ekman, 1999; Tomkins, 1963). We include actions associated with several emotional categories (e.g., positive–negative; approach–avoidance), without specifically dissociating among these.

Emotional Effects on Performance Speed and Accuracy

To understand the appetitive and defensive motivation systems, an abundance of research has investigated how the speed of directional movements (approach and withdrawal) is affected by emotions, for example, following or during emotional priming (for a recent meta-analysis see Phaf, Mohr, Rotteveel, & Wicherts, 2014). In general, these studies showed that responses are faster to positive stimuli for movement directions towards the body (approach), while faster to negative stimuli for movements away from the body (withdrawal). Given that much attention has already been devoted to this field (including a recent special section in *Emotion Review* [Vol. 5, 2013]), an exhaustive review of this literature is outside the scope of the present article. We instead briefly review studies that delineate emotional effects on processes involved in overt movement generation, rather than those simply limited to measurement of overall response times.

Priming with emotional images can also affect the accuracy and speed of *nondirectional* motor performance. Unpleasant compared to pleasant priming was found to impair movement accuracy, but not speed, of a self-paced tracing task. However, unpleasant priming through brief exposure led to opposite effects; faster movement speed but accuracy unaffected (Coombes, Janelle, & Duley, 2005). It was suggested unpleasant stimuli facilitate movement speed (and hence preparation for action) to enhance rapid adaptive reaction to threat and survival, while they have more delayed effects on deliberative cognitive processing. These data are consistent with the motivational systems theory of emotion (Lang, Bradley, & Cuthbert, 1997), which provides an evolutionary explanation for emotional effects on motor control. However, facilitation of movement

speed to unpleasant stimuli is at odds with many studies showing response slowing in the presence of threat cues, often attributed to attentional interference (e.g., Schimmack, 2005). These negative effects on performance may be due to enhanced processing and attentional capture by negative stimuli (Vuilleumier, 2005), where attention is diverted away from the primary task or dwells longer on affect-laden stimuli. These discrepant motor effects may therefore reflect a different impact at distinct stages of emotion processing and/or motor control. Neuroscience studies using time-resolved techniques would provide valuable information to clarify the unfolding of emotion and motor information processing and thus better define the locus of their interaction.

Whether impairment or facilitation of response speed by emotions reflects alterations in the preparation and/or execution stages of movement generation remains relatively unexplored. There is some evidence for faster movement initiation times (wrist extension) to negative emotions, due, in part, to faster central motor processing time rather than peripheral motor processes (Coombes, Cauraugh, & Janelle, 2007b). Extending these findings, Coombes, Cauraugh, and Janelle (2007a) showed significantly faster initiation of extension (withdrawal) movements in response to attack relative to mutilation images. This result highlights possible differential effects of negative emotional signals on central motor processes preceding overt movement, particularly withdrawal or defensive movements. A negative affective state prior to movement onset can also affect spatial parameters of response execution. Initial trajectories of rapid reaching movements performed by spider-fearful individuals deviated away from fear-related images, indicating automatic modulation of the movement prepared before initiation and ongoing motor behaviour (Buetti, Juan, Rinck, & Kerzel, 2012).

Studies using transcranial magnetic stimulation have provided supporting evidence that emotions modulate central motor processes. Viewing affective stimuli reliably increases corticospinal motor tract excitability, though there is debate whether changes are driven by emotional arousal or negative valence (Coombes et al., 2009; Hajcak et al., 2007; Schutter, Hofman, & van Honk, 2008). Nevertheless, these findings confirm the power of emotions to directly influence the motor system, even in the absence of motor execution.

Similarly, studies using electroencephalography have reported inconsistent findings. Larger slow-wave event-related potentials (ERPs) associated with motor preparation were found for highly arousing stimuli (Perri et al., 2014; Wessa & Flor, 2007), yet reduced movement-related ERP amplitudes to aversive stimuli have also been reported (Hart, Lucena, Cleary, Belger, & Donkers, 2012), likely reflecting emotional interference. Additional research is needed to more directly link changes in preparatory cortical activity during emotion processing with motor behaviour, and to elucidate their time-course.

Inhibiting Voluntary Motor Responses in Emotional Contexts

The ability to suppress or withhold a voluntary motor response in response to emotional signals also allows for adaptive behaviour

that can promote survival. Studies examining the interaction between motor inhibition and emotional processes typically use go/no-go or stop-signal tasks. There is ongoing debate whether emotional stimuli facilitate or impair motor inhibition, and whether similar or distinct neural pathways are recruited during motor inhibition in response to emotional and nonemotional signals. The right inferior frontal gyrus (rIFG) is well known to be involved in motor and cognitive inhibition (Aron, Robbins, & Poldrack, 2014), and recent evidence supports a role of rIFG in action suppression within emotional contexts, indicating rIFG acts as a common inhibitory region across domains.

Using an emotional go/no-go task with face stimuli, Berkman, Burklund, and Lieberman (2009) suggested that intentional motor inhibition via rIFG involvement can simultaneously inhibit affective processing. Concurrent presentation of emotional faces during motor inhibition increased rIFG activity, but this enhancement was negatively correlated with amygdala responses to negatively valenced faces, indicating a dampening of affective processing through some inhibitory “spillover.” Similar findings of rIFG involvement in emotionally guided motor inhibition have been reported (Shafritz, Collins, & Blumberg, 2006), but in the latter study, the go- and no-go signals were confounded by emotional valence since participants made a key press to happy faces, but withheld their response to sad faces.

Traditional go/no-go paradigms have been criticised for not providing a direct test of emotional effects on the suppression of ongoing motor actions (Sagasse, Schwartz, & Vuilleumier, 2011). Identifying inhibition processes independent from motor execution can be addressed using stop-signal tasks. Here, the cue to withhold responding occurs after the go signal but before movement execution, allowing processes associated with cancelling an intended movement to be probed. Although both the go/no-go and stop-signal tasks require participants to withhold a response, the processes involved in inhibition may not be the same in the two paradigms (the consistency of the stimulus–stop associations in go/no-go and stop-signal tasks is fixed and varied, respectively; Verbruggen & Logan, 2008), thus the mechanisms underpinning the inhibition effects likely also differ.

Sagasse et al. (2011) integrated the presentation of fearful faces, representing task-irrelevant threat signals, into a stop-signal task. Threat information slowed response times but did not affect inhibition latencies, yet overall emotional slowing was greater when participants failed to inhibit their response. The interaction of stop and threat signals may have enhanced the “braking” effect on movement execution, thus adding up on failed attempts to stop. In contrast, when high-arousing emotional images preceded (primed) a neutral stop signal, inhibition latencies were prolonged (Kalanthoff, Cohen, & Henik, 2013; Verbruggen & De Houwer, 2007), indicating again, attentional interference effects. Moreover, emotional potency appears to differentially affect response inhibition: inhibition was improved by low-threat, but impaired by high-threat stimuli (Pessoa, Padmala, Kenzer, & Bauer, 2012).

Interestingly, neuroimaging results by Sagasse et al. (2011) showed rIFG activity was *reduced* for successful inhibition to

stop signals paired with fearful faces, highlighting that other neural mechanisms must be involved in cancelling an ongoing (already programmed) motor action in a negative emotional context. Indeed, inhibition to negative emotions was associated with activation of the amygdala, lateral orbitofrontal cortex, and supplementary motor area (SMA). Based on functional connectivity analyses, it was proposed the amygdala might inhibit motor execution in emotional contexts by modulating ongoing cortical preparatory activity through neural pathways involving SMA and rIFG. Recent imaging work using structural connectivity measures also reported evidence for direct pathways between amygdala and motor cortical areas (Grèzes, Valabrègue, Gholipour, & Chevallier, 2014). Further work is required to shed light on the role of the amygdala in integrating inhibitory and emotional processes, and to determine how amygdala output may drive changes in motor programming and execution processes.

Evidence for Freezing Behaviour in Humans

There is a growing body of literature examining how emotions modulate the control of human motor functions unrelated to direction. One example includes freezing behaviour, a passive defensive reaction observed as reduced body motion, typically evoked by threat signals (R. J. Blanchard & Blanchard, 1986). In animals, freezing immobility is one of several possible responses to threat (e.g., fight, flight) with a distinct evolutionary advantage as it facilitates orienting of selective attention to external stimuli, avoiding predator detection, and mobilising cognitive resources for overt defense (D. C. Blanchard, Hynd, Minke, Minemoto, & Blanchard, 2001).

Analogous freezing has been demonstrated in the laboratory in humans by using emotional images (Bradley et al., 2001). Viewing motivationally relevant unpleasant images can result in cardiac deceleration, greater electrodermal activity, and startle reflex attenuation. The degree of autonomic activity modulation varies with the level of defense system activation, and is thought to index enhanced perceptual processing and attention to facilitate action selection (Lang et al., 1997). Similar autonomic changes are observed in animals (Applegate, Kapp, Underwood, & McNall, 1983). Crucially, much less is known about changes in the somatic motor system itself during freezing motor behaviour. According to the defense cascade model (Bradley et al., 2001), freezing facilitates action preparation for possible fight or flight responses when the distance of threat is reduced. In this context, freezing is viewed as a preparatory processes *that precedes* initiation of overt (fight or flight) behaviour. However, others have attributed freezing behaviour to the response execution rather than response preparation stage (Wilkowski & Robinson, 2006). Thus freezing might not be limited to a state of action preparation preceding overt behaviour; it could be conceived of as one of several possible actions to threatening stimuli where an organism can switch between freezing, flight, or fight depending on the context of the threat (Fanselow & Lester, 1988).

In humans, changes in motor output associated with freezing-like responses have been demonstrated by measuring postural sway. Reduced body sway was found during viewing of

images depicting mutilation (Azevedo et al., 2005) and social threat (Roelofs, Hagens, & Stins, 2010). This is thought to reflect enhanced postural stiffness, due to increased tonic muscle activity in the lower limb. In rats, a fixed tense posture associated with freezing has also been linked to increased muscle tone (increased α -motoneurone excitability), and shown to be mediated by a dedicated neural network involving the periaqueductal gray (PAG) and cerebellum (Koutsikou et al., 2014). The PAG, and in particular the ventrolateral PAG, is critically involved in freezing behaviour during threat and stress (Brandão, Zanoveli, Ruiz-Martinez, Oliveira, & Landeira-Fernandez, 2008). Using high resolution fMRI, Satpute et al. (2013) showed distinct subregions of the human PAG are associated with different emotional experiences, mirroring neurobiological observations in nonhuman animals. Moreover, the PAG may contain different subregions that each govern specific motor patterns promoting different defense movements (Bandler, Keay, Floyd, & Price, 2000; Bandler & Shipley, 1994).

However, evidence for the role of the PAG in modulating emotional-motor control in humans is scarce. A recent fMRI study demonstrated a direct association between PAG activity and overt motor performance in a sustained isometric (precision-grip) force task (Blakemore, Rieger, & Vuilleumier, 2016). Significant attenuation of force decay during force maintenance was found when participants viewed unpleasant images compared to pleasant or neutral images. This negative valence-driven modulation of force output was associated with increased activity in a network involving rIFG, amygdala, and PAG. The degree of PAG modulation was directly correlated with the arousal-dependent modulation of force output. Together, these studies support the notion that negative emotional signals can induce a state of immobility and that action tendencies may be associated with specific emotions. Furthermore, they show that expression and involvement of PAG in defensive freezing reactions is conserved across species.

Emotion-Modulated Force Output

Further insight into how emotions can modulate motor behaviour unrelated to movement direction has been obtained by examining changes in particular action parameters, such as grip force. The control and execution of precision- and power-grip force are well characterised for healthy individuals in the motor control and neuroimaging literature, and offers a simple and elegant method to investigate the impact of emotional state on a key feature of everyday motor activities.

A series of behavioural studies have revealed that in general, arousing images, irrespective of valence, elicit a relative increase in submaximal grip force production. This was found at low and medium force levels (Naugle, Coombes, Cauraugh, & Janelle, 2012), regardless of participant gender (Coombes, Gamble, Cauraugh, & Janelle, 2008), or mood (Naugle, Coombes, & Janelle, 2010). Coombes and colleagues suggested that emotional arousal may increase force production through heightened excitation of the motor system. However, an alternative interpretation of motor immobility rather than motor facilitation has

been proposed. Blakemore et al. (2016) highlighted that the effects of pleasant stimuli on force output depend, in part, on the content of the emotional stimuli, and noted that in the studies of Coombes and colleagues (Coombes et al., 2008; Coombes, Naugle, Barnes, Cauraugh, & Janelle, 2011), the “pleasant” condition was comprised only of erotica images. Bradley et al. (2001) hypothesised that sexual stimuli represent a unique category of stimuli because motivational activation is unambiguous. That is, sexual stimuli elicit greater changes in autonomic reactivity than other similarly high-arousing stimuli (e.g., images of families, appetising food), because they are more related to species survival, and thus more strongly engage the appetitive motivation system without concurrent activation of the defensive system. Nonetheless, when taken together, the studies by Coombes and colleagues (Coombes et al., 2008; Coombes et al., 2011) and Blakemore et al. (2016) indicate that sexual stimuli can produce a distinctive impact on the motor system.

The effect of emotional signals on the variability of force output (indexed by standard deviation) is conflicting. Force fluctuations were enhanced by exposure to an aversive stressor (threat of shock; Christou, 2005; Noteboom, Fleshner, & Enoka, 2001) and negatively rated images in subclinical depression (Naugle et al., 2010) during sustained pinch-grip tasks at low forces, but not at moderate force levels (Coombes et al., 2008; Naugle et al., 2010). Variability of maximal wrist extension force was unaffected by emotion, despite larger force magnitudes during exposure to unpleasant stimuli (Coombes, Cauraugh, & Janelle, 2006). It was posited the effect of emotional state on force variability is a function of force amplitude; however modulation of force variability at low target levels in healthy controls was not replicated (Naugle, Coombes, et al., 2012).

Despite advances in understanding how emotions influence force output, the neural mechanisms underlying this interaction remain unclear. The prefrontal cortex (PFC) has been identified as a key region involved in integrating motor and emotional processes; however involvement of particular subdivisions of the PFC appears to be task-dependent, whether force is modulated by emotion or not. When force output was held constant despite change in emotional state, a functional circuit involving dorsomedial PFC and premotor cortex (PMC) was engaged during motor performance and concurrent viewing of high-arousing images (Coombes, Corcos, Pavuluri, & Vaillancourt, 2012). However, in a maximal grip force task, enhanced force output following high-arousing images was correlated with activity in primary motor cortex, while subjective ratings of arousal were underpinned by activity in ventrolateral PFC (Schmidt et al., 2009). Both studies provide new insights into brain pathways mediating emotional modulation of force production, with recruitment of different frontal areas involved in motor planning and execution for the control of stable or maximal force, respectively. However, further research is needed to first, delineate the brain mechanism underlying how emotional signals are assimilated with the executive command controlling motor output that fine-tunes muscular contraction and hence force production; and second, examine how specific to emotion such effects are relative to other cognitive influences.

Overcoming the Neglect of Action in the Neuroscience of Emotion

Despite increasing empirical support for the influence of emotions on various parameters of motor behaviour, one issue emerging from the work reviewed here is the noticeable paucity of neurophysiological evidence to account for emotion-motor interactions observed at the behavioural level. This is surprising given the explosion of interest in using sophisticated tools such as fMRI to elucidate neural mechanisms of emotional processing and (independently) the preparation and execution of motor actions; and even more surprising given that actions are central to several theories of emotions (Arnold, 1960; Damasio, 1998; Frijda, 1986; Lang et al., 1997), particularly according to the view that emotions are “causal determinants of action” (Frijda, 2010). Moreover, action readiness as an emotion-related concept draws significant parallels with similar notions in the motor control domain. As suggested by Frijda, “action readiness means preparation . . . the preparation may be merely central, or extend to the muscles” (2007, p. 40). Yet examination of central and peripheral components of the motor system that translate emotional signals into appropriate motor behaviour is still scarce in affective neuroscience. Overcoming this neglect is crucial to our understanding and hypothesis-driven empirical testing of emotion theories concerned with action.

An Information-Processing Approach to Explore Emotion–Action Interactions

Another general theme emerging from the aforementioned studies is they provide empirical support and alignment between the theories of Frijda (1986, 2007) and Lang (Lang & Bradley, 2010) that motive states prepare and guide the body for relevant action. In particular, these studies demonstrate influences of emotion on both the preparation and execution phases of voluntary movement. The debate whether it is emotional arousal or valence that influences the motor system is still difficult to reconcile given that different experimental paradigms and motor tasks are used and a limited number of emotional dimensions are often assessed (i.e., many studies only compare unpleasant with neutral stimuli). However, there is general consensus that negative affect, at least, has a significant effect on several basic parameters of motor control including response time and accuracy, movement initiation time, force generation and control, including during freezing, as well as motor inhibition.

How should future research seek to assimilate theoretical concepts from both affective and movement neuroscience to advance the understanding and experimental avenues of emotion-motor interactions? We believe that an information-processing approach to motor control (Schmidt & Lee, 2014) could provide a fruitful model to further test emotion theories. This approach has established several distinct processing stages that occur between the input of information (stimulus) and the output of a motor action (response): stimulus identification, response selection, and response programming (Figure 1). Motor preparation can begin upon presentation of the stimulus (after perceptual

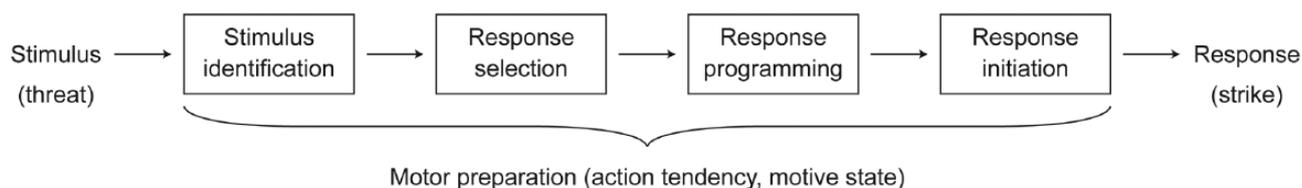


Figure 1. An information-processing approach to emotion-modulated motor control (adapted from Schmidt & Lee, 2014).

processes), indicating that actions are elicited and prepared, as least in part, prior to movement execution. In the case of an emotionally laden input signal, motor preparation could therefore directly be related to motive states.

The view that motive states in emotion represent hierarchically organised processes controlling distinct output systems is not new. Frijda (2007, p. 41) and Scherer (Grandjean & Scherer, 2009) alluded to this, though neither scholar explicitly refer to any specific theory of motor control. Such hierarchical organisation of action control is similarly reflected in the motor system where various components involved in movement generation form a highly organised, distributed network with multiple levels of control. The neuroimaging studies reviewed before showed several motor structures to be involved in emotional-motor processing, namely prefrontal cortex, including rIFG, SMA, and anterior cingulate cortex (ACC), as well as amygdala, PAG, and basal ganglia. However, there may well be other brain areas where emotion and motor signals converge, for instance cerebellum, or multimodal association cortices.

Let's borrow James's (1890) example of striking a rival. In a simplistic description, the occurrence of a relevant stimulus (a threat from a rival) is first detected and appraised by analysing incoming sensory information from the environment, in the sensory cortices, and higher level association areas (e.g., parahippocampal, posterior cingulate, prefrontal cortices), including information about the rival, and, to some extent, current context. A representation of these various components is then assembled, enabling an appropriate response to be selected among various alternatives; for instance, depending on the context, a threatening stimulus may prompt attack or fleeing behaviour. A key purpose of stimulus processing is to guide goal-directed movement. This information is subsequently processed in higher order motor centres such as the PMC and SMA, which are involved in action selection. Frijda (2007) notes that action selection critically depends on the output of appraisal processes, which ultimately drive the appropriate motive to be established (see also Moors & Scherer, 2013). When this results in the decision to attack/strike the rival, a punching response is selected among the possible action repertoire. Note that various factors might shape the available repertoire, for example, based on innate programs, past experience, context, but also hormonal factors (LeDoux, 2012). The selected motor response (limb extension for hitting) is then organised and prepared in the pre-motor cortex, but also the cerebellum and basal ganglia, by programming different parameters of the response (effectors, direction, force). The cerebellum and basal ganglia in particular are key structures that integrate signals from the limbic and

motor systems via their structural and functional multisynaptic connections with the cerebral cortex (Alexander, Crutcher, & DeLong, 1990). Both structures are also linked to motor learning, in keeping with intimate functional and anatomical relationships of emotion processes with memory mechanisms in the limbic system (as highlighted by conditioning in amygdala or reinforcement in striatum). This interplay between subcortical and cortical activity in response to emotional cues eventually leads to initiation of the constructed motor program, and finally execution of a motor response by contracting relevant muscles, via the commands sent by the primary motor cortex to the brainstem and spinal cord. The basal ganglia-thalamocortical loops are crucial for motor execution, and are also instrumental in motivational processes (Pessiglione et al., 2007), driving successful attainment of the established goal to strike. Cerebellar activity continually monitors the commenced action, fine-tuning its parameters during execution to correct errors and ensure accurate performance (Stoodley & Schmahmann, 2009). The cerebellum is also involved in emotional processing, possibly by associating sensory stimuli, particularly in fear-related contexts with their emotional significance and expression of the appropriate motor response (Timmann et al., 2010).

Thus the action tendency or the underlying motive state prepares for upcoming action through various stages that implement movement execution, each of which might potentially be influenced by emotional signals in different manners. In light of the similarities between motive states and information processing for action preparation, we propose that a more formal incorporation of motor control models (e.g., Rosenbaum, 1991) into emotion theories would allow fruitful and coherent foundations to bridge the two fields.

While evidence demonstrating that negative affect, particularly threat, may speed up motor responses is valuable (Phaf et al., 2014), an information-processing model as described before also highlights why it is likely to be insufficient to examine emotion-motor interactions in the laboratory by simply analysing response times (commonly via button presses or manipulation of levers). Facilitation of response time could be due to facilitation in one or more of these information-processing stages (decreasing the time to initiate movement) or faster performance of the movement itself. To enhance our knowledge of emotion-motor interactions at the mechanistic level, future research should take advantage of methodological tools that selectively probe motor preparation and execution processes, particularly those with precise timing characteristics. Recordings of change in muscular electrical activity using electromyography (EMG) enable, for instance, the separation

of central from peripheral effects during motor preparation (Weiss, 1965), as well as examination of agonist and antagonist muscle cocontraction, providing additional information about the locus of facilitatory effects on fear-evoked freezing behaviour. To our knowledge, only one study has used EMG for this purpose (Coombes et al., 2007b). Motor effects should also be more systematically compared with those related to perceptual and attentional changes in emotional information-processing.

At the brain level, examining ERPs related to motor preparation such as the readiness potential (Deecke, Weinberg, & Brickett, 1982; Kornhuber & Deecke, 1965) would also permit stronger inferences about how negative affect motivates and prepares the body for action. Thus far, motor ERPs have been recorded and analysed primarily in the context of exploring attention or anticipation mechanisms to emotional signals, offering only indirect evidence for modulation of motor preparatory processes per se. Similarly, fMRI studies should build on the elaborate theoretical framework and rich experimental approaches developed in the motor control literature. In doing so, continued efforts will be required to integrate innovative emotion-motor paradigms and magnetic resonance (MR)-compatible equipment to assess movement within the MR environment. Novel experiments linking brain function to simultaneously measured parameters of motor behaviour will significantly accelerate our understanding of how the brain prepares and coordinates the many muscles and joints for action in different emotional contexts. Such systematic strategies will eventually allow further refinement or elaboration of emotion theories, particularly the central role of action tendencies, such that future models may also include more details on the psychological and neural processes linking emotion elicitation with motor mechanisms controlling adaptive goal-directed behaviour.

Integrating Emotion–Action Constructs

As the bridging of affective and movement neuroscience progresses, there is the possibility for considerable confusion concerning the description of phenomena and terminology adopted from each field. Another challenge will therefore be the careful use and definition of terms applied to a united field. For instance, the term “reflex” has different connotations in the motor control and emotion literature but is often used inconsistently. In movement neuroscience, *reflexive responses*, notably spinal reflexes, are involuntary coordinated patterns of muscle contraction elicited by a peripheral stimulus in a reproducible and stereotyped manner (Krakauer & Ghez, 2000). The neural circuitry underlying the motor reflex response is entirely contained within the spinal cord, and thus its latency is short. *Emotional reflexes* on the other hand, are “physiological or behavioural reactions evoked automatically in humans by affectively evocative stimuli” (Lang & Bradley, 2009, p. 334). Eyeblink startle responses are consistent with both motor control and emotion definitions. Autonomic responses to emotional stimuli (such as fear bradycardia), however, are also considered to be reflexes; consistent with emotional reflex definitions but not with motor control terminology.

Similar confusion may result, for example, when examining emotional influences on “unintentional” or “automatic” actions (terms used synonymously with “involuntary”) in contrast to those actions that are “intentional” or “deliberative.” Indeed, spinal reflexes were traditionally viewed as automatic behaviours with a stereotyped stimulus–response relationship, whereas voluntary movements are purposive (intentional), highly adaptable, and can be generated internally or cancelled by will. Yet the terms unintentional/automatic and intentional/deliberative can all denote voluntary movement, representing ends on a continuum, in which a myriad of actions fall in between. In fact this dichotomous framework has long been a central theme of philosophical debates on the theory of action concerning beliefs, volition, agents, and will (Zhu & Thagard, 2002). A striking aspect of human motor control is our ability to carry out complicated actions in both an intentional, goal-directed manner and in an automated and effortless fashion, without moment-to-moment conscious processing (e.g., habitual responses). Indeed, recent work on instrumental behaviour has shown distinct cortico-basal ganglia networks regulating these two main categories of actions: Whereas goal-directed actions, controlled by their consequences, are underpinned by activity in the associative network involving dorsomedial striatum, habitual actions, controlled by antecedent stimuli, implicate the sensorimotor network and the dorsolateral striatum (for a review, see Yin & Knowlton, 2006). Moreover, actions elicited by emotional signals need not have intentionality (impulsive action; Frijda, 2010), yet paradoxically, “intention is central to the concept of voluntary action” (Lau, Rogers, Haggard, & Passingham, 2004, p. 1208).

Related inconsistencies are found in descriptions of freezing. Typically thought of as a stereotyped defensive reaction to threat and considered a reflexive behaviour by some (e.g., Lang, 2014), it is characterised by the cessation of ongoing motor behaviour to avoid detection, mediated by activity within cortical, subcortical, cerebellar, and brainstem structures, and can be modified by learning and experience. In addition, freezing is one among a range of possible motor behaviours that could be selected and elicited in response to threat signals (as opposed to flight, fight, etc.), combining muscular with autonomic (bradycardia) components. From a neuromotor control perspective, these are all features of voluntary rather than reflexive movement. Furthermore, the term freezing is also often used to refer to other, possibly distinct, threat responses including orienting and tonic immobility (Hagenaars, Oitzl, & Roelofs, 2014).

These examples demonstrate common emotion–action constructs need to be clearly and consistently defined with awareness of the historical frameworks and debates within each field. This approach is vital to circumvent potential misunderstandings in future research endeavours.

Beyond the Bridge: Informing Special Populations

Strengthening emotion models through the integration of affective and movement neuroscience should also help to better understand changes in motor behaviour and more generally

action control when a link in the emotion-motor processing chain is disrupted. Examination of individuals with aberrant emotion-motor processing giving rise to altered motor behaviour due to neurological or psychiatric disorder may also enable new light to be shed on emotion–action interactions at the behavioural and neural level.

For example, freezing responses have been linked to symptoms of several threat-related disorders such as conversion disorders (Vuilleumier, 2014), but also phobias and posttraumatic stress disorder (Hagenaars et al., 2014); poor inhibitory control is observed in obsessive-compulsive disorder (OCD) and schizophrenia (Kalanthoff et al., 2013), as well as disinhibition in Gilles de la Tourette syndrome (TS; Coffey & Park, 1997); psychomotor retardation with slower movement and even abnormal gait is a key feature of major depressive and bipolar disorders (Buyukdura, McClintock, & Croarkin, 2011). The notion that stress and depression negatively affects symptoms of Parkinson's disease (PD) has been extensively documented (see Metz, 2007), and was quantified in early clinical literature (Marsden & Owen, 1967). However since then, research examining affective modulation of motor function in PD patients is scarce. An association between emotional distress and motor blocks of voluntary action using rating scales in PD was recently reported (Starkstein et al., 2015), while Naugle, Hass, Bowers, and Janelle (2012) found the speed of gait initiation was enhanced in PD following viewing of aversive stimuli. In this study patients were tested *on* medication and their gait speed was not different from control participants, limiting the conclusion that can be drawn about altered emotion-motor processing in PD.

Advancements in deep brain stimulation (DBS) techniques that target basal ganglia relays have shown promising results as a therapeutic tool to ameliorate symptoms and restore motor and/or cognitive function in a number of disorders (Mallet et al., 2007). Motor complications associated with advanced PD are effectively treated with electrical stimulation of the subthalamic nucleus (STN) within the basal ganglia (Fasano, Daniele, & Albanese, 2012). However, there is growing evidence that STN stimulation has emotional side effects, for example it tends to impair recognition of negative emotional expressions in PD patients (Péron, Frühholz, Vérin, & Grandjean, 2013). Stimulation of the motor thalamus can improve motor symptoms and promote emotional stabilisation in TS (Huys et al., 2015), while several target structures for DBS, including the nucleus accumbens, ventral striatum, and STN, have shown to reduce symptom severity and enhance quality of life in treatment-refractory OCD (Kohl et al., 2014; Le Jeune et al., 2010). Together, these findings highlight the basal ganglia as key nodes involved in integrating signals for the execution of emotional and motor behaviour.

The integration of emotion and action as an emerging field will not only enhance the progress of neurosurgical approaches to PD and other movement disorders, but potentially contribute to the development of novel movement interventions that could also be applied to neurological and psychiatric disorders in a rehabilitation setting. As noted by Coombes et al. (2007b, p. 282), “manipulating affective context to alter motor function is

a promising noninvasive technique,” though to our knowledge, no intervention studies have yet been reported. Behavioural interventions might aim to optimise movement by activating emotional circuits known to speed movement responses or execute movements with greater force control. Modulating pathways controlling motive states may thus help alleviate behavioural disorders associated with slow or poor movements (Schmidt et al., 2009), or vice versa improve impulsive action control (Frijda, Ridderinkhof, & Rietveld, 2014). Moreover, interventions to facilitate motor function could equally benefit elite sportspeople or musicians who perform in highly arousing contexts, or those working in emotionally charged professions such as surgeons or pilots in which efficient, automatic, and skilful movement performance is paramount.

Conclusion

Tremendous effort has been made over the last decade to examine emotion–action interactions by uniting the disciplines of affective and movement neuroscience. Though this field is still in its infancy, we have already gained significant insights into the way in which emotions can influence several facets of motor selection and voluntary movement performance in the healthy brain, with clinical implications for affective and movement disorders. In order to more comprehensively understand this interdisciplinary field, researchers should strive to conduct multimethodological experiments. There is huge scope to combine techniques readily applied to study the preparation, initiation, and control of movement, with those used to examine emotional responses in determining how emotions can influence different temporal stages of processing. Methodological developments in neuroimaging will open opportunities to conduct further mechanistic research and exploration of the neural circuitry underlying emotion-motor processing. Additionally, further reviews of evidence for emotional modulation of reflexive, expressive, and habitual behaviours would be useful to complement the present article, providing a holistic perspective on emotion-motor interactions. Only through a collective effort across domains, will we be able to truly appreciate the significance of the interwoven nature of emotion and action.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

References

- Alexander, G. E., Crutcher, M. D., & DeLong, M. R. (1990). Basal ganglia-thalamocortical circuits: Parallel substrates for motor, oculomotor, “prefrontal” and “limbic” functions. *Progress in Brain Research*, *85*, 119–146.
- Applegate, C. D., Kapp, B. S., Underwood, M. D., & McNall, C. L. (1983). Autonomic and somatomotor effects of amygdala central N. stimulation in awake rabbits. *Physiology and Behavior*, *31*, 353–360.
- Arnold, M. B. (1960). *Emotion and personality*. New York, NY: Columbia University Press.

- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2014). Inhibition and the right inferior frontal cortex: One decade on. *Trends in Cognitive Sciences*, *18*, 177–185.
- Azevedo, T. M., Volchan, E., Imbiriba, L. A., Rodrigues, E. C., Oliveira, J. M., Oliveira, L. F., . . . Vargas, C. D. (2005). A freezing-like posture to pictures of mutilation. *Psychophysiology*, *42*, 255–260.
- Bandler, R., Keay, K. A., Floyd, N., & Price, J. (2000). Central circuits mediating patterned autonomic activity during active vs. passive emotional coping. *Brain Research Bulletin*, *53*, 95–104.
- Bandler, R., & Shipley, M. T. (1994). Columnar organization in the mid-brain periaqueductal gray: Modules for emotional expression. *Trends in Neurosciences*, *17*, 379–389.
- Berkman, E. T., Burklund, L., & Lieberman, M. D. (2009). Inhibitory spillover: Intentional motor inhibition produces incidental limbic inhibition via right inferior frontal cortex. *Neuroimage*, *47*, 705–712.
- Blakemore, R. L., Rieger, S. W., & Vuilleumier, P. (2016). Negative emotions facilitate isometric force through activation of prefrontal cortex and periaqueductal gray. *Neuroimage*, *124*, 627–640.
- Blanchard, D. C., Hynd, A. L., Minke, K. A., Minemoto, T., & Blanchard, R. J. (2001). Human defensive behaviors to threat scenarios show parallels to fear- and anxiety-related defense patterns of non-human mammals. *Neuroscience and Biobehavioural Reviews*, *25*, 761–770.
- Blanchard, R. J., & Blanchard, D. C. (1986). Defensive behaviors of laboratory and wild *Rattus norvegicus*. *Journal of Comparative Psychology*, *100*, 101–107.
- Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: Defensive and appetitive reactions to picture processing. *Emotion*, *1*, 276–298.
- Brandão, M. L., Zanoveli, J. M., Ruiz-Martinez, R. C., Oliveira, L. C., & Landeira-Fernandez, J. (2008). Different patterns of freezing behavior organized in the periaqueductal gray of rats: Association with different types of anxiety. *Behavioral Brain Research*, *188*, 1–13.
- Buetti, S., Juan, E., Rinck, M., & Kerzel, D. (2012). Affective states leak into movement execution: Automatic avoidance of threatening stimuli in fear of spider is visible in reach trajectories. *Cognition and Emotion*, *26*, 1176–1188.
- Buyukdura, J. S., McClintock, S. M., & Croarkin, P. E. (2011). Psychomotor retardation in depression: Biological underpinnings, measurement, and treatment. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *30*, 395–409.
- Christou, E. A. (2005). Visual feedback attenuates force fluctuations induced by a stressor. *Medicine and Science in Sports and Exercise*, *37*, 2126–2133.
- Coffey, B. J., & Park, K. S. (1997). Behavioral and emotional aspects of Tourette syndrome. *Neurologic Clinics*, *15*, 277–289.
- Coombes, S. A., Cauraugh, J. H., & Janelle, C. M. (2006). Emotion and movement: Activation of defensive circuitry alters the magnitude of a sustained muscle contraction. *Neuroscience Letters*, *396*, 192–196.
- Coombes, S. A., Cauraugh, J. H., & Janelle, C. M. (2007a). Dissociating motivation direction and affective valence: Specific emotions alter central motor processes. *Psychological Science*, *18*, 938–942.
- Coombes, S. A., Cauraugh, J. H., & Janelle, C. M. (2007b). Emotional state and initiating cue alter central and peripheral motor processes. *Emotion*, *7*, 275–284.
- Coombes, S. A., Corcos, D. M., Pavuluri, M. N., & Vaillancourt, D. E. (2012). Maintaining force control despite changes in emotional context engages dorsomedial prefrontal and premotor cortex. *Cerebral Cortex*, *22*, 616–627.
- Coombes, S. A., Gamble, K. M., Cauraugh, J. H., & Janelle, C. M. (2008). Emotional states alter force control during a feedback occluded motor task. *Emotion*, *8*, 104–113.
- Coombes, S. A., Janelle, C. M., & Duley, A. R. (2005). Emotion and motor control: Movement attributes following affective picture processing. *Journal of Motor Behavior*, *37*, 425–436.
- Coombes, S. A., Naugle, K. M., Barnes, R. T., Cauraugh, J. H., & Janelle, C. M. (2011). Emotional reactivity and force control: The influence of behavioral inhibition. *Human Movement Science*, *30*, 1052–1061.
- Coombes, S. A., Tandonnet, C., Fujiyama, H., Janelle, C. M., Cauraugh, J. H., & Summers, J. J. (2009). Emotion and motor preparation: A transcranial magnetic stimulation study of corticospinal motor tract excitability. *Cognitive, Affective and Behavioral Neuroscience*, *9*, 380–388.
- Damasio, A. R. (1998). Emotion in the perspective of an integrated nervous system. *Brain Research Reviews*, *15*, 83–86.
- Deecke, L., Weinberg, H., & Brickett, P. (1982). Magnetic fields of the human brain accompanying voluntary movement: Bereitschaftsmagnetfeld. *Experimental Brain Research*, *48*, 144–148.
- De Gelder, B., de Borst, A. W., & Watson, R. (2015). The perception of emotion in body expressions. *WIREs Cognitive Science*, *6*, 149–158.
- Ekman, P. (1999). Basic emotions. In T. Dalgleish & M. Power (Eds.), *Handbook of cognition and emotion* (pp. 45–60). Chichester, UK: Wiley.
- Fanselow, M. S., & Lester, L. S. (1988). A functional behavioristic approach to aversively motivated behavior: Predatory imminence as a determinant of the topography of defensive behavior. In M. D. Beecher (Ed.), *Evolution and learning* (pp. 185–212). Hillsdale, NJ: Erlbaum.
- Fasano, A., Daniele, A., & Albanese, A. (2012). Treatment of motor and non-motor features of Parkinson's disease with deep brain stimulation. *Lancet Neurology*, *11*, 429–442.
- Frijda, N. H. (1986). *The emotions*. Cambridge, UK: Cambridge University Press.
- Frijda, N. H. (2007). *The laws of emotion*. Mahwah, NJ: Erlbaum.
- Frijda, N. H. (2009). Action tendencies. In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective sciences* (pp. 1–2). New York, NY: Oxford University Press.
- Frijda, N. H. (2010). Impulsive action and motivation. *Biological Psychology*, *84*, 570–579.
- Frijda, N. H., Ridderinkhof, K. R., & Rietveld, E. (2014). Impulsive action: Emotional impulses and their control. *Frontiers in Psychology*, *5*, e518.
- Grandjean, D., & Scherer, K. R. (2009). Synchronization (and emotion). In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective sciences* (pp. 387–388). New York, NY: Oxford University Press.
- Grèzes, J., Valabrègue, R., Gholipour, B., & Chevallier, C. (2014). A direct amygdala-motor pathway for emotional displays to influence action: A diffusion tensor imaging study. *Human Brain Mapping*, *35*, 5974–5983.
- Hagenaars, M. A., Oitzl, M., & Roelofs, K. (2014). Updating freeze: Aligning animal and human research. *Neuroscience and Biobehavioural Reviews*, *47*, 165–176.
- Hajcak, G., Molnar, C., George, M. S., Bolger, K., Koola, J., & Nahas, Z. (2007). Emotion facilitates action: A transcranial magnetic stimulation study of motor cortex excitability during picture viewing. *Psychophysiology*, *44*, 91–97.
- Hart, S. J., Lucena, N., Cleary, K. M., Belger, A., & Donkers, F. C. L. (2012). Modulation of early and late event-related potentials by emotion. *Frontiers in Integrative Neuroscience*, *6*, 1–9.
- Huys, D., Bartsch, C., Koester, P., Lenzert, D., Maarouf, M., Daumann, J., . . . Kuhn, J. (2015). Motor improvement and emotional stabilization in patients with Tourette syndrome after deep brain stimulation of the ventral anterior and ventrolateral motor part of the thalamus. *Biological Psychiatry*, *79*, 392–401.
- James, W. (1884). What is an emotion? *Mind*, *9*, 188–205.
- James, W. (1890). *The principles of psychology* (Vol. 2). New York, NY: Henry Holt.
- Kalanthoff, E., Cohen, N., & Henik, A. (2013). Stop feeling: Inhibition of emotional interference following stop-signal trials. *Frontiers in Human Neuroscience*, *7*, 1–7.
- Kohl, S., Schönherr, D. M., Luigjes, J., Denys, D., Mueller, U. J., Lenartz, D., . . . Kuhn, J. (2014). Deep brain stimulation for treatment-refractory

- obsessive compulsive disorder: A systematic review. *BMC Psychiatry*, 14, 214. doi:10.1186/s12888-014-0214-y
- Kornhuber, H. H., & Deecke, L. (1965). Hirnpotentialänderungen bei willkürbewegungen und passiven bewegungen des menschen: Bereitschaftspotential und reafferente potenziale [Changes in the brain potential in voluntary movements and passive movements in man: Readiness potential and reafferent potentials]. *Pflügers Archiv*, 284, 1–17.
- Koutsikou, S., Crook, J. J., Earl, E. V., Leith, J. L., Watson, T. C., Lumb, B. M., & Apps, R. (2014). Neural substrates underlying fear-evoked freezing: The periaqueductal grey-cerebellar link. *Journal of Physiology*, 592, 2197–2213.
- Krakauer, J., & Ghez, C. (2000). Voluntary movement. In E. R. Kandel, J. H. Schwartz, & T. M. Jessell (Eds.), *Principles of neural science* (4th ed., pp. 756–781). New York, NY: McGraw-Hill.
- Lang, P. J. (2014). Emotion's response patterns: The brain and the autonomic nervous system. *Emotion Review*, 6, 93–99.
- Lang, P. J., & Bradley, M. M. (2009). Reflexes (emotional). In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective sciences* (pp. 334–336). New York, NY: Oxford University Press.
- Lang, P. J., & Bradley, M. M. (2010). Emotion and the motivational brain. *Biological Psychology*, 84, 437–450.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation and action. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97–136). Hillsdale, NJ: Erlbaum.
- Lau, H. C., Rogers, R. D., Haggard, P., & Passingham, R. E. (2004). Attention to intention. *Science*, 303, 1208–1210.
- LeDoux, J. E. (2012). Rethinking the emotional brain. *Neuron*, 73, 653–676.
- Le Jeune, F., Vérin, M., N'Diaye, K., Drapier, D., Leray, E., & Du Montcel, S. T., . . . French Stimulation dans le trouble obsessionnel compulsif (STOC) study group. (2010). Decrease of prefrontal metabolism after subthalamic stimulation in obsessive-compulsive disorder: A positron emission tomography study. *Biological Psychiatry*, 68, 1016–1022.
- Mallet, L., Schüpbach, M., N'Diaye, K., Remy, P., Bardinet, E., Czernecki, V., . . . Yelnik, J. (2007). Stimulation of subterritories of the subthalamic nucleus reveals its role in the integration of the emotional and motor aspects of behavior. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 10661–10666.
- Marsden, C. D., & Owen, D. A. L. (1967). Mechanisms underlying emotional variation in parkinsonian tremor. *Neurology*, 17, 711–715.
- Metz, G. A. (2007). Stress as a modulator of motor system function and pathology. *Reviews in the Neurosciences*, 18, 209–222.
- Moors, A., & Scherer, K. R. (2013). The role of appraisal in emotion. In M. Robinson, E. Watkins, & E. Harmon-Jones (Eds.), *Handbook of cognition and emotion* (pp. 135–155). New York, NY: Guilford Press.
- Naugle, K. M., Coombes, S. A., Cauraugh, J. H., & Janelle, C. M. (2012). Influence of emotion on the control of low-level force production. *Research Quarterly for Exercise and Sport*, 83, 353–358.
- Naugle, K. M., Coombes, S. A., & Janelle, C. M. (2010). Subclinical depression modulates the impact of emotion on force control. *Motivation and Emotion*, 34, 432–445.
- Naugle, K. M., Hass, C. J., Bowers, D., & Janelle, C. M. (2012). Emotional state affects gait initiation in individuals with Parkinson's disease. *Cognitive, Affective and Behavioral Neuroscience*, 12, 207–219.
- Noteboom, J. T., Fleshner, M., & Enoka, R. M. (2001). Activation of the arousal response can impair performance on a simple motor task. *Journal of Applied Physiology*, 91, 821–831.
- Okon-Singer, H., Hendl, T., Pessoa, L., & Shackman, A. J. (2015). The neurobiology of emotion–cognition interactions: Fundamental questions and strategies for future research. *Frontiers in Human Neuroscience*, 9, 1–14.
- Péron, J., Frühholz, S., Vérin, M., & Grandjean, D. (2013). Subthalamic nucleus: A key structure for emotional component synchronization in humans. *Neuroscience and Biobehavioural Reviews*, 37, 358–373.
- Perri, R. L., Berchicci, M., Lucci, G., Cimmino, R. L., Bello, A., & Di Russo, F. (2014). Getting ready for an emotion: Specific premotor brain activities for self-administered emotional pictures. *Frontiers in Behavioral Neuroscience*, 8, 1–9.
- Pessiglione, M., Schmidt, L., Draganski, B., Kalisch, R., Lau, H., Dolan, R. J., & Frith, C. D. (2007). How the brain translates money into force: A neuroimaging study of subliminal motivation. *Science*, 316, 904–906.
- Pessoa, L., Padmala, S., Kenner, A., & Bauer, A. (2012). Interactions between cognition and emotion during response inhibition. *Emotion*, 12, 192–197.
- Phaf, R. H., Mohr, S. E., Rottevel, M., & Wicherts, J. M. (2014). Approach, avoidance, and affect: A meta-analysis of approach–avoidance tendencies in manual reaction time tasks. *Frontiers in Psychology*, 5, 1–16.
- Roelofs, K., Hagenars, M. A., & Stins, J. (2010). Facing freeze: Social threat induces bodily freeze in humans. *Psychological Science*, 21, 1575–1581.
- Rosenbaum, D. (1991). *Human motor control*. San Diego, CA: Academic Press.
- Sagasse, P., Schwartz, S., & Vuilleumier, P. (2011). Fear and stop: A role for the amygdala in motor inhibition by emotional signals. *Neuroimage*, 55, 1825–1835.
- Sander, D. (2013). Models of emotion: The affective neuroscience approach. In J. Armony & P. Vuilleumier (Eds.), *The Cambridge handbook of human affective neuroscience* (pp. 5–53). New York, NY: Cambridge University Press.
- Satpute, A. B., Wager, T. D., Cohen-Adad, J., Bianciardi, M., Choi, J.-K., Buhle, J. T., . . . Feldman Barrett, L. (2013). Identification of discrete functional subregions of the human periaqueductal gray. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 17101–17106.
- Schimmack, U. (2005). Attentional interference effects of emotional pictures: Threat, negativity or arousal? *Emotion*, 5, 55–66.
- Schmidt, L., Cléry-Melin, M.-L., Lafargue, G., Valabrègue, R., Fossati, P., Dubois, B., & Pessiglione, M. (2009). Get aroused and be stronger: Emotional facilitation of physical effort in the human brain. *Journal of Neuroscience*, 29, 9450–9457.
- Schmidt, R. A., & Lee, T. D. (2014). *Motor learning and performance: From principles to application* (5th ed.). Champaign, IL: Human Kinetics.
- Schutter, D. J. L. G., Hofman, D., & van Honk, J. (2008). Fearful faces selectively increase corticospinal motor tract excitability: A transcranial magnetic stimulation study. *Psychophysiology*, 45, 345–348.
- Shafritz, K. M., Collins, S. H., & Blumberg, H. P. (2006). The interaction of emotional and cognitive neural systems in emotionally guided response inhibition. *Neuroimage*, 31, 468–475.
- Starkstein, S., Dragovic, M., Brockman, S., Wilson, M., Bruno, V., & Merello, M. (2015). The impact of emotional distress on motor blocks and festination in Parkinson's disease. *The Journal of Neuropsychiatry and Clinical Neuroscience*, 27, 121–126.
- Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: A meta-analysis of neuroimaging studies. *Neuroimage*, 44, 489–501.
- Timmann, D., Drepper, J., Frings, M., Maschke, M., Richter, S., Gerwig, M., & Kolb, F. P. (2010). The human cerebellum contributes to motor, emotional and cognitive associative learning. A review. *Cortex*, 46, 845–857.
- Tomkins, S. S. (1963). *Affect imagery consciousness: The negative affects* (Vol. 2). New York, NY: Springer.
- Verbruggen, F., & De Houwer, J. (2007). Do emotional stimuli interfere with response inhibition? Evidence from the stop signal paradigm. *Cognition and Emotion*, 21, 391–403.
- Verbruggen, F., & Logan, G. D. (2008). Automatic and controlled response inhibition: Associative learning in the go/no-go and stop-signal paradigms. *Journal of Experimental Psychology (General)*, 137, 649–672.
- Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, 9, 587–594.

- Vuilleumier, P. (2014). Brain circuits implicated in psychogenic paralysis in conversion disorders and hypnosis. *Clinical Neurophysiology, 44*, 323–337.
- Vuilleumier, P., Armony, J., & Dolan, R. J. (2004). Reciprocal links between emotion and attention. In R. S. J. Frackowiak, K. J. Friston, C. D. Frith, R. J. Dolan, C. J. Price, S. Zeki, . . . W. D. Penny (Eds.), *Human brain function* (pp. 419–444). San Diego, CA: Academic Press.
- Weiss, A. D. (1965). The locus of reaction time change with set, motivation, and age. *Journal of Gerontology, 20*, 60–64.
- Wessa, M., & Flor, H. (2007). Failure of extinction of fear responses in posttraumatic stress disorder: Evidence from second-order conditioning. *American Journal of Psychiatry, 164*, 1684–1692.
- Wilkowski, B. M., & Robinson, M. D. (2006). Stopping dead in one's tracks: Motor inhibition following incidental evaluations. *Journal of Experimental Social Psychology, 42*, 479–490.
- Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience, 7*, 464–476.
- Zhu, J., & Thagard, P. (2002). Emotion and action. *Philosophical Psychology, 15*, 19–36.