

Emotional State and Initiating Cue Alter Central and Peripheral Motor Processes

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Evidence indicates that voluntary and involuntary movements are altered by affective context as well as the characteristics of an initiating cue. The purpose of this study was to determine the contribution of central and peripheral mechanisms to this phenomenon. During the presentation of pleasant, unpleasant, neutral, and blank images, participants ($N = 33$) responded to auditory stimuli (startle, 107 dB startle or 80 dB tone) by initiating a bimanual isometric contraction of the wrist and finger extensor muscles. Analyses of electromyography and force measures supported the hypothesis that exposure to unpleasant images accelerates central processing times and increases the gradient of slope of peripheral movement execution. In addition, startle cues as compared with tone cues accelerated and magnified all temporal and amplitude indices. Collectively, these findings have noteworthy implications for (a) those seeking to facilitate the speed and force of voluntary movement (i.e., movement rehabilitation), (b) understanding the higher incidence of motor difficulty in individuals with affective disorders, and (c) those seeking to regulate emotional input so as to optimize the quality of intended movements.

Keywords: EMG, startle, force, affect, motor function

Understanding how emotion modulates overt action is critical for at least three primary reasons. First, activating emotional circuits that predispose humans to execute motor actions faster and with more force may be an effective method to forge new pathways between intention and movement for those suffering motor impairment (e.g., stroke and Parkinson's disease). Second, within a wide range of performance contexts, movements have to be executed during dynamic states of emotional flux. Given that emotions are considered to be action dispositions (Lang, Bradley, & Cuthbert, 1998), delineating the central and peripheral mechanisms that contribute to emotion-modulated movement may also serve those seeking to regulate emotional input so as to optimize the quality of intended movements. Finally, mounting evidence has indicated a higher propensity for motor dysfunction among individuals suffering from various affective disorders (e.g., Caligiuri & Ellwanger, 2000; Lepicard et al., 2003; Schmahmann, 2004; Wassermann, Greenberg, Nguyen, & Murphy, 2001). Clearly, evaluating the mechanisms that underlay emotion-modulated motor actions has broad theoretical and pragmatic implications.

The biphasic theory of emotion (Lang, Bradley, & Cuthbert, 1997; Lang et al., 1998), in addition to being broadly embraced by the affective sciences, readily lends itself to the study of emotion as it applies to movement (Coombes, Cauraugh, & Janelle, 2006; Coombes, Janelle, & Duley, 2005; Hillman, Rosengren, & Smith, 2004; Marsh, Ambady, & Kleck, 2005). Biphasic theory posits that the broad array of emotions experienced and displayed by human

beings can be organized according to valence (i.e., appetitive or defensive) and intensity (i.e., arousal level). In addition to numerous self-report and psychophysiological indices that have consistently indexed the ebb and flow of emotion during exposure to affective stimuli (e.g., skin conductance, heart rate, event-related potentials, startle blink; see Bradley, 2000, for a summary), motor activation has been implicated as a helpful measure in indexing the overt behavioral consequences of emotion (Heilman & Gilmore, 1998). When engaged, appetitive or defensive systems affect the functioning brain, priming physiological adaptation and specific representations, associations, and action programs that correspond to the environmental context that has elicited the given emotion. In short, although a primary function of emotion is the preparation for action (Schupp, Junghofer, Weike, & Hamm, 2003), little is known concerning the manner by which emotions influence subsequent voluntary action (Ledoux, 1998).

Emotion-Modulated Movement: Behavioral Evidence

In addition to affective modulation of the startle blink reflex (Hillman, Hsiao-Weckler, & Rosengren, 2005; Lang, Bradley, & Cuthbert, 1990), attempts to understand the transition from emotional reaction to emotional action have independently emerged across a broad range of disciplines. For example, the association between emotion and limb position was addressed by Cacioppo et al. (1993), who required participants to execute isometric arm flexion or extension¹ while making attitudinal judgments. Increased pleasant emotion (i.e., activation of appetitive circuitry) was reported when participants were placed in a postural set with arms flexed, and increased unpleas-

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¹ Flexion/extension is a bending/straightening movement around the joint, decreasing/increasing the angle between the bones of the limb at the joint and resulting—in the Cacioppo et al. (1993) study—with the proximal bone being drawn toward/away from the body.

ant emotion (i.e., activation of defensive circuitry) was reported when participants assumed postural sets with their arms extended.

Supplementing these findings, recent psychophysiological and behavioral evidence has indicated that exposure to aversive stimuli results in avoidance-driven alterations in posture in female participants (Hillman et al., 2004) and a freezing postural response in male participants (Azevedo et al., 2005). In addition, Chen and Bargh (1999) exposed participants to stimulus words and instructed one group of participants with incongruent instructions by requiring them to push a lever away from them (avoidance behavior) if the stimulus word presented was pleasant (activation of appetitive circuitry) and to pull the lever toward them (approach behavior) if the stimulus word was unpleasant (activation of defensive circuitry); the second group received opposite, congruent instructions. Results indicated that faster pulling of the lever coincided with pleasant initiating cues, whereas unpleasant initiating cues were associated with significantly faster responses when pushing the lever. In a second experiment, participants were exposed to pleasant and unpleasant stimuli and were instructed to only pull (Group 1) or push (Group 2) the lever at the onset of each valenced cue. Again, results confirmed that unpleasant stimuli resulted in faster pushing movements, and pleasant stimuli led to significantly quicker pulling movements.

These findings have been replicated with stimuli consisting of novel words rather than familiar words, corroborating the notion that emotions can and will differentially affect movement speed and direction (Duckworth, Bargh, Garcia, & Chaiken, 2002). Furthermore, we have previously demonstrated that the speed and accuracy of a non-direction-specific square tracing task is altered by unpleasant affective contexts, with faster movement time and greater movement error emerging following short and long exposure periods, respectively (Coombes et al., 2005). In addition, Marsh, Ambady, and Kleck (2005) recently reported that exposure to faces experiencing threat results in speeded flexion rather than extension movements, indicating that unpleasant contexts do not exclusively speed extension movements.

Finally, using a non-direction-specific task, Noteboom, Fleshner, and Enoka (2001) demonstrated that relative to a cognitive manipulation that increased arousal and a control condition, increases in arousal caused by exposure to an unpleasant stressor lead to a reduction in steadiness of a pinch grip task, again a non-direction-specific task. The notion that unpleasant contexts will only accelerate extension movements and pleasant contexts will only accelerate flexion movements remains open to debate. As such, understanding emotion and movement in terms of exclusively matching flexion and extension movements with pleasant and unpleasant cues may not be helpful. Thus, the motor system appears to be primed in a non-direction-specific manner, given that unpleasant contexts may require approach (attack) or withdrawal (escape) movements. Consequently, indexing overall movement time, movement direction, and movement error do not determine how or where within the motor system emotions modulate movement.

Indexing Central and Peripheral Motor Processes

Fractionating reaction time (RT) into central and peripheral components is a key technique to understanding the motor system (Weiss, 1965) and how the various components of the motor

system are altered by emotion. Fractionated RT provides two separate components that represent the location of the timing delay as it relates to the perceptual, response selection, and motor stages of movement production (Botwinick & Thompson, 1966; Ito, 1997). Premotor RT (PRT) represents perceptual and cognitive processing time, reflecting the temporal duration necessary to perceive a target initiating stimulus (in this case, an acoustic probe) and formulate the appropriate motor action (in this case, extension of the wrists and fingers). PRT, therefore, represents the time interval between the onset of the initiating cue and the onset of electromyography (EMG) activity. Specifically, the offset of PRT is marked by EMG activity in the corresponding muscle(s) surpassing a predetermined amplitude above baseline (i.e., double the baseline value). Thus, PRT is a reflection of central processing (Basmajian & De Luca, 1985; Latash, 2000).

The time point demarcating the end of PRT to the beginning of overt movement (i.e., force onset) is termed *motor reaction time* (MT) and reflects the elapsed time associated with impulse propagation along the motor pathways and motor unit recruitment necessary for execution of the response (Li, Stevens, Kamper, & Rymer, 2005). According to Basmajian and DeLuca (1985), this later delay represents the inherent delay in the muscular system overcoming limb mass and the peripheral mechanism of voluntary actions. Delayed total reaction times (PRT + MT) due to variations in task complexity (Ma & Trombly, 2004) and preparatory period are predominantly reflected in PRT (Weiss, 1965).

In addition to temporal delays preceding the onset of overt movement, speed and amplitude measures reflect the characteristics of overt movement. Specifically, peak EMG and force amplitude provide insight into the global patterning of action potentials within the muscle of interest and a measure of the force produced by the corresponding discharging of action potentials in the muscle, respectively. Because target forces were not manipulated in the present study to prevent confound from task constraints, EMG and force risetime and slope were included to determine the impact of emotion on the relationship between the speed and amplitude with which overt movements were executed (Moore, Drouin, Gansneder, & Shultz, 2002).

Previous studies have reported global indices concerning the manner by which emotional contexts alter movement (e.g., total movement time; Chen & Bargh, 1999; Duckworth et al., 2002; Marsh et al., 2005), but researchers have not fractionated RT and provided comprehensive process-oriented detail concerning where within the motor system (central or peripheral) the observed modulation occurs. Without determining how emotions alter specific movement processes, researchers will be unable to delineate the likely cortical, subcortical, and peripheral contributions to movement modulation. Pragmatically, therefore, the efficacy of strategies to regulate the influence of emotion on movement and to use emotion to facilitate movement rehabilitation will remain limited.

Movement Parameters Influenced by Characteristics of the Initiating Cue

To date, protocols addressing emotion and voluntary movement have not varied in the intensity of an initiating cue. A growing body of literature, however, has indicated that preplanned voluntary movements initiated to a startle cue are significantly more rapid than movements initiated to tone cues (Carlsen, Chua, Inglis,

Sanderson, & Franks, 2004a, 2004b; Cressman, Carlsen, Chua, & Franks, 2006; Rothwell, 2006; Valls-Solé, Rothwell, Goulart, Cossu, & Munoz, 1999; Valls-Solé et al., 1995). Interpreting these findings, Valls-Solé et al. (1999) have proposed the subcortical triggering hypothesis, which suggests that preplanned movements may be stored and then initiated from the subcortex by a startling stimulus.

Given the inherent aversive nature of startling stimuli, researchers continue to query whether startle cues may elicit direction-specific reflexive behaviors (i.e., postural flexion; Hillman et al., 2005) in addition to expediting voluntary movement times. Whereas aversive affective contexts have been associated with extension movements of limbs, startle cues have been linked with postural flexion. In consequence, postural and limb movements may not respond in a similar fashion (i.e., flexion, extension) to similar cues. To further investigate the relations among these factors, in the present study we combined affective context, startle cue, and preplanned voluntary extension movements of the wrists and fingers.

Present Study

Understanding how emotions modulate specific components of the nervous system has advanced in recent years. To date, however, the impact of central and peripheral processes that summate to emotion-modulated overt movement has not been evaluated. Likewise, although consistent findings demonstrate that variations in the intensity of an initiating stimulus modulate the characteristics of overt movement, variations in the initiating cue have not been coupled with manipulations of affective context. To build on previous findings and to address their limitations, the purpose of the current study was to merge previously established emotion and movement protocols with psychophysiological and behavioral measures to index emotion and initiating cue-driven variations in central and peripheral motor processes.

During the presentation of affectively valenced images, acoustic stimuli were presented as cues to initiate preplanned voluntary extension movements of the upper limbs. EMG and force production measures were collected during each trial. Onset of EMG and force production served as indices of central processing time. Peak amplitude, risetime, and slope of EMG and force indexed the speed and magnitude of peripheral activation. Driven by previous evidence and inferences derived from the affective and movement sciences, we predicted that unpleasant contexts and startle initiating stimuli would independently result in (a) accelerated central processes (PRT and force onset) and (b) accelerated and magnified peripheral processes (peak EMG, peak force amplitude and risetime, and slope), relative to other conditions. As an ancillary hypothesis, we also predicted that central processes would be fastest and peripheral processes accentuated when aversive contexts were paired with startle initiating stimuli.

Method

Participants

Thirty-three undergraduate students (19 women and 14 men) from the University of Florida participated in this study for extra course credit. Participants ranged in age from 18 to 27 years ($M =$

21.09 years, $SD = 1.83$) and reported no hearing loss or central nervous system disorders that would affect movement. Written informed consent was obtained from all participants before beginning the study. All participants were right-hand dominant and reported normal hearing. One male participant and 1 female participant were removed from all analyses because of technical issues (e.g., equipment malfunction), and all left-handed participants (2 men) were excluded from the analyses to prevent a potential handedness confound. In addition to the 4 participants excluded, data points 3 standard deviations from the mean were considered extreme scores and were removed before analysis. The repeated measures analyses were such that participants missing one (or more) scores were completely removed from each separate analysis. In summary, all 29 eligible participants were included in the EMG slope, EMG risetime, and peak force latency analyses. Twenty-eight participants were included in each of the remaining five analyses.

Affective Stimuli

Participants viewed a total of 24 digitized photographs selected from the International Affective Picture System (National Institute of Mental Health Center for the Study of Emotion & Attention, 1999), representing three affective categories that were matched or polarized according to valence and arousal norms (eight pleasant, eight unpleasant, eight neutral²). Categories were differentiated according to valence (pleasant: $M = 7.22$, $SD = 1.75$; unpleasant: $M = 2.50$, $SD = 1.61$; neutral: $M = 4.99$, $SD = 1.31$), and pleasant and unpleasant categories were matched for arousal and chosen so as to distinguish valenced categories from neutral (pleasant: $M = 5.25$, $SD = 2.20$; unpleasant: $M = 5.72$, $SD = 2.11$; neutral: $M = 3.17$, $SD = 1.94$). Six blank images were also presented to act as a nonscene control condition. The total number of images viewed was limited to 30, in an effort to prevent fatigue and to avoid habituation to the startle probe. All pictures were visible for 6 s.

Task

While viewing a picture, participants were required to respond as quickly as possible to an acoustic stimulus by initiating an isometric bimanual contraction of the wrist and finger extensor muscles against two independent load cells (left/right limb; see Figure 1).

Acoustic Stimuli

Created with custom-built LabVIEW software (version 7.1; National Instruments, Austin, Texas), the tone cue consisted of a 50-ms tone delivered at 80 dB with near instantaneous risetime. In contrast, the startle cue stimulus was a 50-ms burst of white noise delivered at 107 dB with near instantaneous risetime. Acoustic stimuli were presented binaurally through a set of calibrated headphones (Radio Shack digital sound-level meter 33-2055; Fort Worth, Texas). Acoustic stimuli were presented randomly 2–4 s

² The International Affective Picture System images used were as follows: pleasant: 2160, 2360, 2550, 2501, 4641, 4658, 4659, and 8180; unpleasant: 2590, 2700, 3220, 3230, 3266, 3350, 6250, and 6550; neutral: 2210, 2383, 2485, 2570, 2580, 2830, 7000, and 7009.

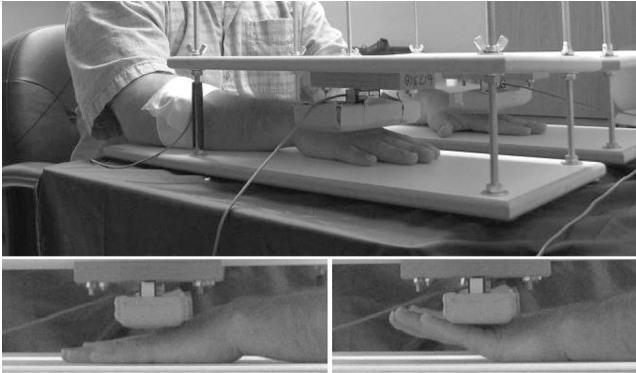


Figure 1. Experimental setup. Top: postures of trunk, arms, and forearms before and during the bimanual task. Bottom left: posture of hands relative to load cells during movement preparation and intertrial interval. Bottom right: posture of hands relative to load cells during ballistic movement execution.

after picture onset and were equally represented within each picture category (three startle/tones per category). To prevent habituation and anticipation, catch trials (no sound) occurred twice within each valence category. Intertrial intervals varied from 6 to 10 s. Each picture was matched with an acoustic condition (startle, tone, silence), and the same combination was presented to every participant. However, the order of the pairings was randomized and manipulated to ensure that the same valence category and sound condition were not presented more than twice in succession.

Instrumentation

Participants were prepared for measurement in accordance with the Society for Psychophysiological Research guidelines (Putnam, Johnson, & Roth, 1992). EMG surface electrodes (silver–silver chloride electrodes, 1 cm in diameter and 2 cm apart with an epoxy-mounted preamplifier) were placed over the extensor communis digitorum and extensor carpi ulnaris muscles of the left and right arms. To index force generation during each isometric wrist/finger extension, two 34.1-kg load cells embedded in cushioned platforms were altered in height to accommodate individual hand sizes. Upper limb EMG (bandpass filter 1–500 Hz) and force data were amplified with a gain of 5,000 and collected at 1,000 Hz via Biopac software (version 3.7.3; Biopac Systems Inc., Goleta, California).

Trial onset and offset and visual and auditory stimulus presentation were controlled via a custom LabVIEW program that simultaneously sent 5-V digital markers into the physiological trace to indicate picture onset and acoustic stimulus onset, respectively. Each separate 10-s trial (2-s baseline, 6-s picture presentation, 2-s buffer) was streamed to disk for offline analyses.

Procedure

After all questions had been answered and informed consent had been obtained, participants were seated in a comfortable chair positioned 1.0 m from an 18-in. (45.72-cm) LCD presentation screen. Next, height of the force platforms was adjusted, load cells were calibrated, and EMG sensors were attached. Following cal-

ibration, participants were familiarized with the protocol via a six-trial practice session (all neutral images: two startle, two tone, and two catch trials).

Participants were instructed to (a) “look at each picture for the entire time it is on the screen,” (b) “consider picture onset as a cue to prepare to make the required wrist and finger extension,” and (c) “respond as quickly as possible to an acoustic stimuli by initiating a short duration bimanual isometric contraction of the wrist and finger extensor muscles.” Following picture offset, participants were instructed to continue viewing the blank screen as the next image would appear after a short break. At the conclusion of all trials, hands were removed from the customized force platform, EMG sensors were removed, and the participants were debriefed. From participant arrival to departure, the experiment lasted approximately 30 min.

Data Reduction

EMG and force data were analyzed offline via a custom LabVIEW program. EMG signals were rectified and filtered with a 25-Hz lowpass elliptic filter (Carlsen et al., 2004b). Baseline EMG and force scores were calculated for each trial (mean score during the 150 ms preceding acoustic stimulus onset). Nine dependent measures were calculated for each trial: (a) PRT, (b) MT, (c) force onset (F_{onset}), (d) EMG amplitude (EMG_{amp}), (e) force amplitude (F_{amp}), (f) force risetime (F_{risetime}), (g) EMG risetime (EMG_{risetime}), (h) force slope (F_{slope}), and (i) EMG slope (EMG_{slope} ; see Figure 2 for specific details and calculations). For each trial for each limb, the semiautomated analysis program superimposed force and filtered EMG data over the digital trigger signal. Visible on a computer monitor, the program automatically identified and then inserted cursors at F_{amp} and EMG_{amp} locations

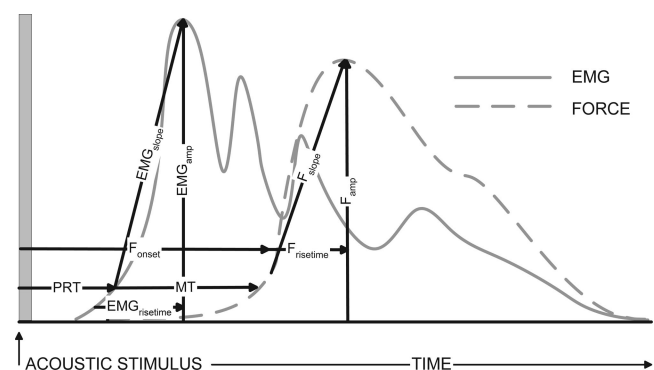


Figure 2. Calculation of dependent variables: premotor reaction time (PRT), delay between acoustic stimulus onset and EMG threshold; motor reaction time (MT), delay between acoustic stimulus onset and EMG onset; force onset (F_{onset}), delay between acoustic stimulus onset and force onset; EMG amplitude (EMG_{amp}), peak amplitude within a 40- to 500-ms window following acoustic stimulus onset; force amplitude (F_{amp}), peak amplitude within a 40- to 800-ms window following acoustic stimulus onset; EMG risetime (EMG_{risetime}), latency between EMG onset and peak; force risetime (F_{risetime}), latency between force onset and peak; EMG slope (EMG_{slope}), EMG amplitude change from threshold to peak, divided by time from threshold to peak; force slope (F_{slope}), force amplitude change from threshold to peak, divided by time from threshold to peak; EMG = electromyography.

within specified windows after acoustic stimulus onset (EMG, 40–500 ms; force, 40–800 ms). Baseline corrected normalized F_{amp} and EMG_{amp} T scores were calculated for each trial within each participant's data before statistical analysis. Onset of muscle contraction was identified by locating the first time point where EMG signal amplitude was greater than double the baseline value (Wong & Ng, 2005). Likewise, onset of force production was identified as the first time point at which force data exceeded double the force baseline value (see Figure 2). Given the strictness of the detection algorithm, coupled with intermittent intermediary EMG and/or force noise between stimulus onset and movement onset, the location of each of these threshold locations was visually verified and manually adjusted if necessary. Because of excessive noise and/or no visible peak in EMG or force within the specified windows, a total of 19 trials were removed from 9 participants' data sets (range = 1–4 trials per participant; 97.8% of the trials were included in the analysis). For each participant, no more than 1 trial was removed from each acoustic stimulus by valence condition. Summary statistics were created by averaging left and right limb data for each dependent variable.

Statistical Analyses

Each dependent variable was analyzed in separate 2 (acoustic stimulus: startle, tone) \times 4 (valence: pleasant, unpleasant, neutral, blank) analyses of variance with repeated measures on both factors. For analyses involving valence, if the sphericity assumption was violated, then Greenhouse-Geisser (1959) conservative degrees-of-freedom adjustments were applied and critical p values were corrected (Winer, Brown, & Michels, 1991). Follow-up analyses were conducted using simple effects tests and Tukey's Honestly Significant Difference procedure for significant interactions and main effects, respectively. Probability was set at $p < .05$ for all analyses.

Results

PRT

A main effect of acoustic stimulus indicated that when movements were initiated following startle relative to tone cues, PRTs were accelerated, $F(1, 27) = 28.59, p < .001$. In addition, follow-up analyses of a significant valence effect, $F(2.27, 61.14) = 6.27, p = .002$, evidenced that PRTs were fastest during exposure to unpleasant and neutral stimuli relative to pleasant and blank stimuli (see Figure 3). An Acoustic Stimulus \times Valence interaction was not evidenced.

MT

A main effect of acoustic stimulus was evidenced, indicating that MT was shorter when movements were executed following startle relative to tone cues, $F(1, 28) = 33.02, p < .001$. The main effect of valence and the Acoustic Stimulus \times Valence interaction were not significant.

Force Onset Latency

Significant effects of acoustic stimulus and valence were noted for force onset latency (see Figure 3). Specifically, the temporal

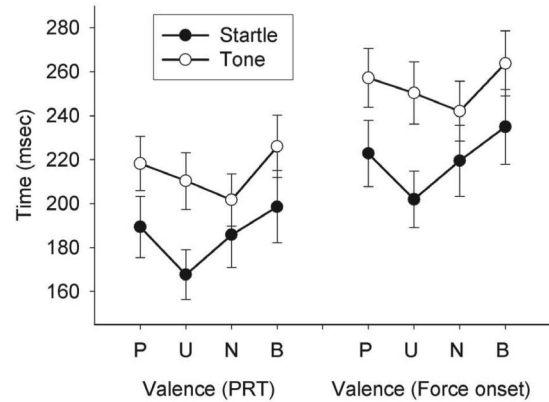


Figure 3. Mean premotor reaction time (PRT) and force onset latency (± 1 SE) averaged across limb for startle and tone cues across all valence categories. PRTs and force onsets were faster when movements were initiated following startle relative to a tone cues. Central processing times were faster during exposure to unpleasant and neutral images relative to pleasant and blank images. P = pleasant; U = unpleasant; N = neutral; B = blank.

delay between acoustic stimulus presentation and force onset was attenuated when movements were initiated (a) following startle relative to tone cues, $F(1, 27) = 37.72, p < .001$, and (b) during exposure to unpleasant and neutral categories relative to pleasant and blank categories, $F(2.24, 60.38) = 5.55, p = .005$. The Acoustic Stimulus \times Valence interaction was not significant.

EMG Peak Amplitude

A main effect of acoustic stimulus was found, indicating that peak EMG was greater to startle relative to tone cues, $F(1, 27) = 55.56, p < .001$. Neither the main effect of valence, nor the acoustic stimulus interaction reached significance (see Figure 4).

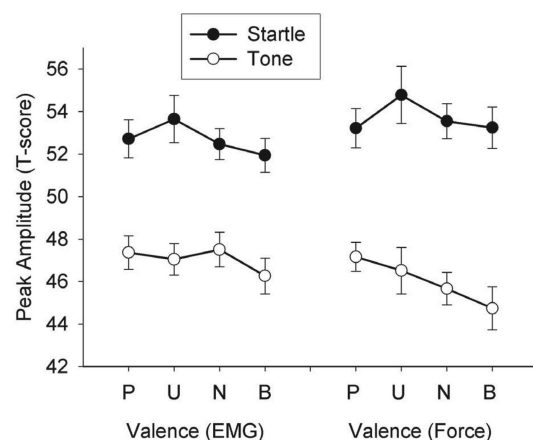


Figure 4. Mean peak EMG and force amplitude T scores (± 1 SE) averaged across limb for startle and tone trials for each valence category. For each dependent measure, peak amplitudes were larger when movements were executed following startle relative to tone cues. No effects of valence on EMG or force were evidenced. P = pleasant; U = unpleasant; N = neutral; B = blank; EMG = electromyography.

Peak Force Amplitude

Analysis of normalized peak force amplitude scores evidenced a main effect of acoustic stimulus, $F(1, 28) = 91.53, p < .001$, indicating that peak force amplitude was greater to startle as compared with tone stimuli (see Figure 5). The main effect of valence and the interaction between acoustic stimulus and valence were nonsignificant.

Peak EMG Risetime

The duration between EMG onset (PRT) and peak EMG amplitude was significantly altered by acoustic stimulus, $F(1, 27) = 17.07, p < .001$, such that latencies were faster to startle ($M = 64.18, SE = 2.91$) relative to tone cues ($M = 74.05, SE = 3.93$). No other main effects or interactions were identified.

Peak Force Risetime

Similar to modulation of peak EMG risetime, analysis of peak force risetime revealed a significant main effect of acoustic stimulus, $F(1, 28) = 14.15, p = .001$. The corresponding means indicated that risetimes were shorter when movements were initiated to startle cues ($M = 221.05, SE = 18.21$) as compared with tone cues ($M = 240.69, SE = 19.99$). The effect of valence was not significant, and, likewise, acoustic stimulus and valence did not interact to modulate peak force risetime.

EMG Gradient

An effect of acoustic stimulus was evidenced on peak EMG slope, $F(1, 28) = 44.54, p < .001$. Inspection of the means indicated that slopes were significantly steeper when movements were initiated following startle rather than tone cues. Neither the valence main effect nor the Acoustic Stimulus \times Valence interaction reached significance.

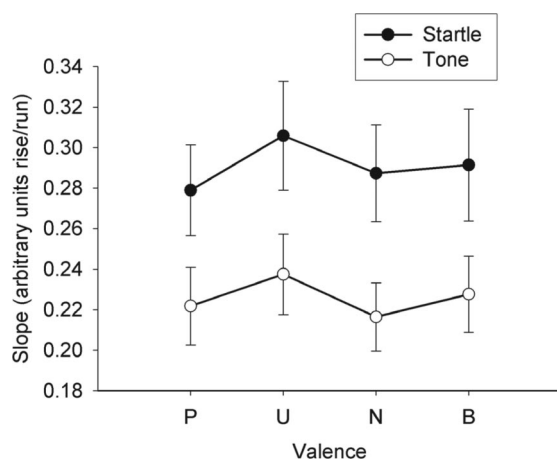


Figure 5. Mean slope of force (± 1 SE) averaged across limb for startle and tone conditions for all valence categories. Main effects of acoustic stimuli and valence evidenced steeper slopes when movements were (a) initiated following presentation of a startle cue and (b) during exposure to unpleasant relative to pleasant and neutral images. P = pleasant; U = unpleasant; N = neutral; B = blank.

Force Gradient

The gradient of slope between force onset and peak force was significantly altered by acoustic stimulus, $F(1, 27) = 48.16, p < .001$, and valence, $F(3, 81) = 3.10, p = .039$ (see Figure 5). Follow-up analyses indicated that steeper slopes coincided with all startle conditions relative to tone conditions, and steeper slopes were evidenced during exposure to unpleasant relative to pleasant and neutral images. An interaction effect of acoustic stimulus and valence on force gradient did not reach significance.

Discussion

In line with predictions, central and peripheral voluntary motor processes were modulated by affective context and initiating cue. The current findings corroborate as well as extend the hypothesis that active defensive circuitry alters voluntary movement. Specifically, we demonstrated that exposure to unpleasant images (i.e., activation of defensive circuitry) expedites PRT preceding voluntary movement and increases the gradient of slope of peripheral movement execution (Chen & Bargh, 1999; Coombes et al., 2005; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Marsh et al., 2005).

In addition, our startle-related hypotheses were comprehensively supported for central and peripheral measures, corroborating prior startle-triggered PRT findings (Carlsen et al., 2004a, 2004b; Rothwell, 2006; Valls-Solé et al., 1999; Valls-Solé et al., 1995). That is, PRT was shorter following startle relative to tone initiation cues. The present results extend previous startle-related work by demonstrating that, relative to tone cues, startle cues resulted in shorter MTs, force onsets, and risetimes (force and EMG), as well as increasing peak magnitude (force and EMG) and gradient of slope (force and EMG). Although visual inspection of our data suggested a trend that startle stimuli interacted with aversive contexts to alter movement (see Figure 3), this interaction was not statistically supported. Nevertheless, significant effects of valence and acoustic stimulus on central as well as peripheral processes offer substantial insight concerning how movements are altered by emotion and initiating cue.

Central Processes

Consistent with Hypothesis 1, PRTs and force onset latencies were faster during exposure to unpleasant images relative to pleasant and blank exposure periods. Furthermore, PRT and force onset latencies were faster when movements were executed to startle relative to tone cues. Although force onset requires a level of peripheral activation, PRT and force onset followed a similar pattern across experimental conditions, with a delay of approximately 40 ms separating the corresponding measures (PRT < force onset). Consequently, we discuss force onset with PRT as a central process.

Two prominent findings emerged from these data. First, although the arousal rather than the valence qualities of emotional stimuli have been shown to dictate the magnitude of interference on a button-press discrimination task (Schmuck, 2005), our data support the notion that emotional valence modulates voluntary ballistic motor function above and beyond the effects of emotional arousal. Previous reports have contended that the emotional system

has been shaped by evolution such that it primes organisms to respond to contexts in a fashion that promote survival (Öhman, Hamm, & Hugdahl, 2000; Öhman & Soares, 1998); we corroborate and specify this position by demonstrating that the central processing times that precede voluntary movement are expedited in unpleasant relative to pleasant and blank contexts. Given that previous reports have indicated that direction-specific (Chen & Bargh, 1999; Duckworth et al., 2002; Marsh et al., 2005) and direction-nonspecific (Coombes et al., 2005) movement times are accelerated during or following exposure to unpleasant or aversive contexts, our findings suggest that speeded movement times can be attributed in part to faster centrally driven processes. Expedited response execution under these conditions offers organisms an advantage in aversive contexts. Extrapolating this finding to contemporary society, we suggest that activating defensive emotional circuitry could facilitate the speed of movement initiation in cases in which this effect is desirable (e.g., in rehabilitation contexts for those suffering from motor impairment).

Second, central processing times during exposure to neutral images were not distinguishable from unpleasant conditions, with neutral conditions also leading to faster times relative to corresponding pleasant and blank conditions. Potentially driven by faster initiation times to tone cues in neutral contexts (see Figure 3), these findings dictate that caution be exercised before accepting a purely valence-driven interpretation of our data. Indeed, similar behavioral responses to snake and neutral pictures have been reported elsewhere. Schimmack (2005), for example, elegantly pitted arousal, general negativity, and evolutionary threat hypotheses against each other within an interference protocol. Participants were required to solve a math problem (Study 1) and detect the location of a line (Study 2) during the simultaneous presentation of varying emotional images. Findings indicated that although arousal was a significant predictor of response latency, no significant differences in response latencies between neutral and snake pictures were evidenced in either study. Schimmack suggested that a threat detection system (in our case, the subsequent behavioral response) may not be hardwired, but may be under voluntary control and open to the influence of learning experiences. Indeed, a flexible system that is open to learning would certainly be more consistent with functional theories of emotion (Nelson, Shelton, & Kalin, 2003) and would be functionally adaptive.

Although our visual stimuli included a range of unpleasant stimuli preventing specific emotional categories (and therefore hypotheses) to be compared and contrasted, our findings indicate that overt movements during exposure to single unpleasant and neutral images may not always be differentiated. Given that explanations are lacking and previous protocols addressing emotion and movement have not yielded data from neutral conditions (Chen & Bargh, 1999; Duckworth et al., 2002), comparing motor function during exposure to matched arousal but polarized valenced contexts is a necessary future research direction and is elaborated below. To this point, however, neither the arousal hypothesis, evolutionary hypothesis, nor negativity hypotheses appear to be adequate in offering a comprehensive interpretation of the relationship between emotion and central processes that precede overt motor behavior.

As noted above, expectations were confirmed with regard to startle stimuli expediting PRTs and force onset times (Carlsen et al., 2004a, 2004b; Valls-Solé et al., 1999; Valls-Solé et al., 1995).

Two complementary explanations are offered to account for the impact of acoustic stimulus on movement: (a) subcortical triggering and (b) stimulus intensity. The reticular formation has been implicated as a central structure within the startle circuit (Grillon & Baas, 2003), ensuring rapid overt behavioral responses to abrupt startling stimuli (i.e., startle blink response). In addition to the role of the reticular formation in the manifestation of involuntary movements, emerging evidence has indicated that neurons within the reticular system are sensitive to voluntary motor planning and initiation (Buford & Davidson, 2004). As such, although our PRTs were not fast enough to rule out cortical processing (cf. Carlsen et al., 2004a; Valls-Solé et al., 1999), subcortical initiation cannot be discarded.

Compared with previous reports of rapid PRTs (Carlsen et al., 2004a, 2004b; Valls-Solé et al., 1999; Valls-Solé et al., 1995), our times were markedly slower. To bridge the affective and motor literature, we presented startle cues at a volume of 107 dB through headphones (within the common range of that used in the emotion-startle blink literature, e.g., Lang et al., 1990; Stanley & Knight, 2004) rather than the 124 dB presented through speakers behind the participant's head (as used by Carlsen et al., 2004a; Valls-Solé et al., 1999), which may have slowed response times. Increasing the intensity of a startling stimulus typically leads to a corresponding increase in the amplitude of the associated startle response (Davis, 1984), a finding that has, at the subcortical level, been positively correlated with the activation of neurons within the reticular formation (Yeomans & Frankland, 1996). We infer that this finding also holds true in the voluntary motor domain and consequently, given the comprehensive effect of initiating cue, stimulus volume is the most likely explanation to account for our slower PRTs.

In summary, it remains tenable that lengthier PRTs masked rather than eliminated subcortical triggering of motor responses. Furthermore, active emotion circuits appear to alter voluntary movements in a similar fashion (although to a different degree) regardless of the characteristics of the initiating cue. Recent reports have suggested that a startle paired with a prepared voluntary movement can facilitate motor function of the paretic limb of patients following stroke (Rothwell, 2006). Consequently, the subcortical triggering hypothesis continues to gain support and remains a promising explanation. Further investigating control and clinical populations with protocols that couple startle cues with affective manipulations is an exciting direction for future research. Likewise, whether a rapid startle-elicited response is expedited within higher or lower brain structures and whether the response is the result of strengthened synaptic connections or a decreased threshold between neurons remains to be seen (Carlsen et al., 2004a).

Peripheral Processes

The magnitude and speed of peripheral motor activity was indexed via MT, peak EMG and force amplitude, risetime, and slope. The effect of stimulus intensity was comprehensive, with larger peaks, shorter MTs, risetimes, and steeper slopes evidenced following startle relative to tone probes. The lack of a significant interaction between emotion and initiating cue again demonstrates that stimulus intensity does not alter the impact of emotion on peripheral motor processes. However, in a similar fashion to

central processes, we posit that an increase in stimulus intensity alters the functional activation of peripheral control processes (i.e., motor unit size, number of motor units recruited, firing rate of motor units) that at present remain independent from the variations driven by emotional processes.

The modulation of peripheral processes due to affective context offered mixed support for Hypothesis 2. Contrary to prediction, analyses did not reveal significant effects of valence on peak EMG, force amplitude, or risetime. Lang and colleagues (1990) have reported that peak EMG of the startle blink response is potentiated during exposure to unpleasant images. Similarly, we have previously found that exposure to unpleasant images increases peak force production of a sustained muscle contraction (Coombes et al., 2006). Within our current protocol, participants were instructed to “respond as quickly as possible to an acoustic stimulus” as opposed to being instructed to respond to the initiation cue by executing and then sustaining a maximum voluntary contraction (Coombes et al., 2006). Hence, although ballistic and sustained contractions may be dissimilarly altered by emotion, the most plausible explanation for these contrasting findings is that in each case participants were required to concentrate on different aspects of movement production (i.e., speed vs. magnitude). In future ballistic movement studies, this discrepancy could be controlled by requiring a second group of participants to execute forceful movements rather than speeded movements to the initiation cue.

The temporal findings evidenced in central processes were not replicated in peripheral processes, with MT and risetime latencies to peak EMG and force immune to effects of valence. These findings demonstrate that previous accounts of speeded motor responses to varying affective cues are most probably the result of expedited central rather than peripheral processes (Chen & Bargh, 1999; Coombes et al., 2005; Marsh et al., 2005). Our final measure of peripheral activation, however, offered partial support for the hypothesis that emotion alters peripheral motor processes, with steeper force slopes during exposure to unpleasant relative to pleasant and neutral exposure periods. An effect of emotion on EMG slope was not evidenced, however, suggesting that although EMG and force are each altered by a combination of similar parameters (i.e., motor unit size, number of active motor units, motor unit firing frequency; Moritz, Barry, Pascoe, & Enoka, 2005), the collective processes that control speed and magnitude of force generation were dissimilar from those that alter EMG peak, risetime, and slope.

Because peak force amplitude was not accentuated and peak force risetime was not accelerated when averages were created for all unpleasant exposure periods, we posit that peripheral activation patterns during exposure to unpleasant images must have varied across unpleasant trials. As such, during exposure to unpleasant images (a) larger peaks were reached more rapidly, (b) smaller peaks were reached more rapidly, and (c) larger peaks were reached within a similar time period. Although averaging across these patterns likely contributed to our peak amplitude and risetime findings, collapsing each of them into a measure of gradient ensured that important effects of emotion on peripheral activation patterns were not missed.

The comparatively steeper force slopes noticed under unpleasant conditions are indicative of speed and magnitude alterations that index acute peripheral processes, thereby offering organisms an evolutionary advantage in such contexts (Öhman & Soares, 1998). With risetime and peak magnitude ruled out in the present

case, understanding which unpleasant images mediated which peripheral motor patterns is an obvious avenue for future research. In addition, the association between specific emotional contexts and corresponding peripheral motor patterns could be evaluated.

Summary and Conclusion

To index the impact of emotion and initiating cue on voluntary movement, participants executed extension movements of the wrist and finger muscles to startle and tone acoustic cues while being exposed to images differing in emotional arousal and valence. The present findings demonstrate that exposure to unpleasant images (i.e., activation of defensive circuitry) accelerates central processing times and increases the gradient of slope of peripheral movement execution. In addition, startle cues compared with tone cues accelerated and magnified all temporal and amplitude indices.

Two unexpected issues emerged in the present study: (a) the similarity between neutral and unpleasant conditions in mediating central processing times and (b) the lack of an effect of emotion on peak EMG and force production. Methodological factors may account for these disparate findings relative to previous work. Manipulating specific emotional category, motivational direction, and the delay between emotional cue onset and movement initiation have been demonstrated to alter affective asymmetry (Wacker, Heldmann, & Stemmler, 2003) and subsequent movement patterns (Marsh et al., 2005; Stanley & Knight, 2004). Indeed, recent reports have documented that inhibition or potentiation of physiological systems and their impact on voluntary and involuntary movement are dependent on the affective intensity and thematic content of emotional cues (i.e., erotica vs. adventure, Bernat, Patrick, Benning, & Tellegen, 2006; anger vs. fear, Marsh et al., 2005; threat vs. disgust, Stanley & Knight, 2004) and the time interval between picture onset and movement onset (early 300 ms vs. late 2,000–5,000 ms; Stanley & Knight, 2004). By replicating and extending this protocol to take into account Stanley and Knight's and Marsh et al.'s findings, we posit that polarizing emotional categories and requiring flexion and extension movements at varying but specific time intervals following picture onset will help delineate arousal- and valence-driven alterations in central and peripheral motor processes.

In conclusion, manipulating affective context to alter motor function is a promising noninvasive technique that may serve to help those suffering motor deficits (e.g., bradykinesia, such as in stroke, Parkinson's disease, and affective disorders). In addition, for those striving to regulate the impact of emotion (e.g., surgeons, police officers, military personnel), these data highlight the innate disposition of the human to move more rapidly in aversive contexts, strengthening the notion that innate movement dispositions may not always be congruent with intended movement plans. With continued empirical effort, researchers will be able to provide recommendations to harness the benefits and alleviate the costs associated with emotion-modulated movement.

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Correction to Waller et al. (2006)

In the article “Intramuscular Electrical Stimulation of Facial Muscles in Humans and Chimpanzees: Duchenne Revisited and Extended” by Bridget M. Waller, Sarah-Jane Vick, Lisa A. Parr, Kim A. Bard, Marcia C. Smith Pasqualini, Katalin M. Gothard, and Andrew J. Fuglevand (*Emotion*, 2006, Vol. 6, No. 3, pp. 367–382), the address provided for the on-line supplemental materials was incorrect. The correct address at which the supplemental materials can be viewed is the following:
<http://dx.doi.org/10.1037/1528-3542.6.3.367.supp>

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