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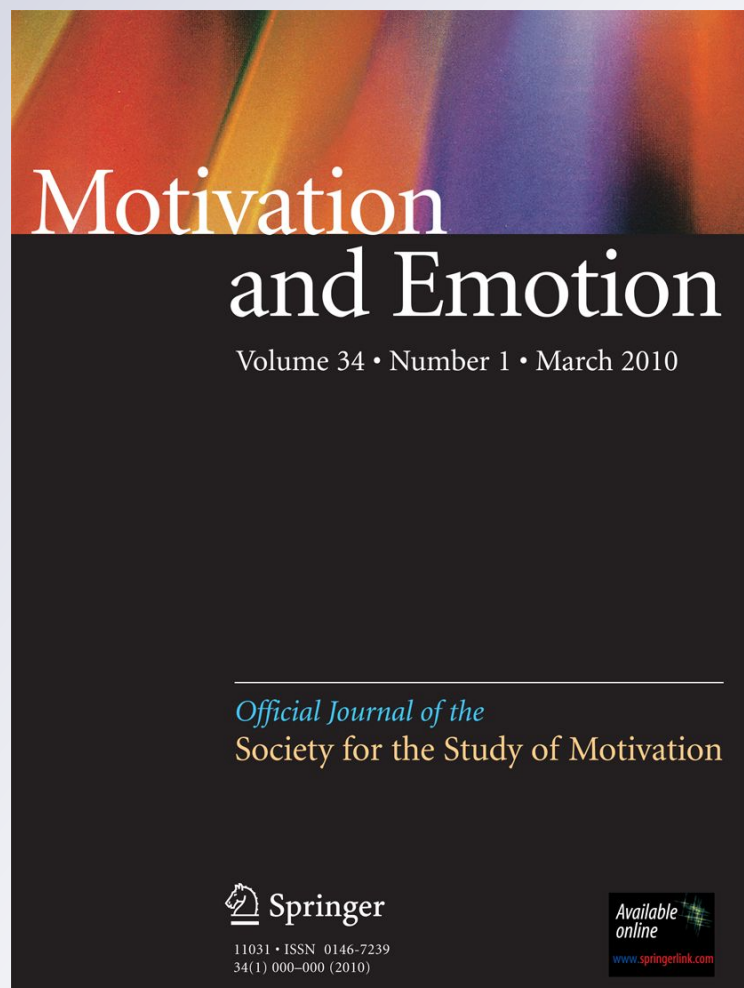
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The emotive neuroscience of embodiment

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Abstract Embodiment in psychological research and theory often refers to the idea that the body plays a crucial role in emotive, motivational, and cognitive processes. We review past and recent embodiment research, focusing on neuroscientific work. In particular, we review a growing body of evidence supporting the notion that manipulated facial expressions, hand contractions, and changes in physical posture influence physiological activity related to approach motivation or the inclination to move toward a stimulus. Several other perspectives are also considered, such as work related to facial-feedback theories of emotion, theories of grounded or embodied cognition, and mirror neuron research. Ultimately, we conclude that bi-directionality may exist between certain bodily movements and other components of approach- or avoidance-related emotions. Avenues for new research are considered given these implications.

Keywords Embodiment · Emotion · Motivation · Neuroscience · Asymmetric frontal cortical activity · Startle eyeblink response · Late positive potential

Introduction

The English word “emotion” is derived from the French word “émouvoir,” which is based on the Latin word “emovere,” where *e-* (variant of *ex-*) means ‘out’ and *movere* means ‘move’. The term “motivation” is also derived from “*movere*.” Thus, the terms emotion and motivation, in lay definitions, are rooted in terms that mean

to move and the body rarely acts without movement. We run toward dear friends we have not seen in a long while and run away from things we fear. We grimace at the sight of something disgusting, and grin from ear-to-ear when we experience something extremely pleasant.

In this review, we discuss work indicating that bodily manipulations influence self-reported emotions and motivational processes. Then, we review research attempting to uncover physiological mechanisms underlying these behavioral effects. Finally, we review research linking bodily movements with approach or avoidance inclinations. Based on this research, we arrive at three conclusions: (1) manipulated facial expressions, hand contractions, as well as body postures influence relative left frontal cortical activity, a physiological correlate of approach motivation; (2) postural manipulations also influence physiological correlates of motivated attention, sub-cortically driven processes, and neuroendocrine levels; and (3) manipulated postures may prompt approach or avoidance behaviors.

Bodily manipulations influence self-reported emotions and motivational processes

For over a century, scientists have been curious about outward displays of emotion. For example, the innateness and universality of certain facial expressions was recognized by Charles Darwin (1872). The idea that these expressions share inherent connections with emotions was proposed by William James (1890). Building upon these earlier theoretical arguments, the facial feedback hypothesis (Laird 1974) suggests that manipulated facial expressions of emotion cause self-reported changes in emotions (for a review of the classical theoretical arguments, see

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Adelmann and Zajonc 1989). Support for this hypothesis has traditionally come from experiments that manipulate participants' facial expressions with instructions or non-obtrusive methods, such as having them hold a pen between their teeth to facilitate smiling. Afterwards, participants are often presented with a stimulus and asked to give their self-reported emotional reactions. For example, facilitating as compared to inhibiting smiling has been found to increase self-reported positive reactions toward cartoons (Strack et al. 1988). More recent experiments have also demonstrated that inhibiting muscle movements interferes with emotional processes. For example, denervating facial muscles with botulinum toxin-A (BTX) has been found to slow the reading of emotional passages (Havas et al. 2010) and decrease amygdala activation during intentional facial mimicry (Hennenlotter et al. 2009).

Research on this topic, however, has come to involve many other bodily manipulations aside from facial expressions. For example, past work has indicated that nodding one's head up and down, as compared to shaking one's head from side to side, leads to the formation of positive attitudes toward neutral objects (Tom et al. 1991) as well as more agreement with persuasive messages (Wells and Petty 1980). Furthermore, arm movements associated with the acquisition of desired stimuli, flexion, relative to arm movements not associated with such actions, extension, have been found to influence judgments of neutral ideographs; participants judged these ideographs more positively when they engaged in arm flexion relative to arm extension poses (Cacioppo et al. 1993).¹

Researchers have also found that these arm movements are associated with motivational responses, such as the urge to approach or avoid a stimulus. Arm flexion, relative to arm extension, has been associated with more of an approach-motivated response (Rotteveel and Phaf 2004). For example, an experiment by Van Peer et al. (2007) demonstrated that administering cortisol versus placebo to highly anxious individuals influences their behavioral and physiological responses to threatening angry-face stimuli. In this experiment, participants with high and low trait anxiety were presented with approach-oriented happy and threat-oriented angry faces. Participants were asked to indicate, as quickly and accurately as possible, whether a presented face was happy or angry. Participants made these responses by pressing one of three buttons, which were arranged vertically; the top button was physically further away from the participant as compared to the second. The

bottom button was physically closer to the participant. Thus, when pressing the top button, participants made an arm-flexion pose indicative of pulling something toward them (approach). When pressing the bottom button, however, participants made an arm-extension pose indicative of pushing something away (avoidance). In addition, participants were either told congruent (press the top button to indicate a happy face and the bottom to indicate an angry face) or incongruent (the reverse) instructions for the task.

Results indicated that participants were faster to respond to happy faces with approach as compared to avoidant arm movements. In addition, participants were faster to respond to angry-threat faces with avoidant as compared to approach arm movements. Highly anxious participants given cortisol versus placebo, additionally, were slower to respond to angry faces with approach as compared to avoidant movements. These results suggest that a combination of trait and state dependent factors influence how individuals physically react to emotional stimuli. Motivational direction (approach or avoidance) also underlies these types of effects, which have been conceptually replicated in additional experiments (van Peer et al. 2009, 2010).

Other bodily manipulations have also been found to influence motivational processes. For example, a series of experiments by Riskind and Gotay (1982) examined if different postures influence motivational behaviors. In two experiments, participants were assigned, in an ostensibly unrelated biofeedback study, to adopt a slumped/helpless posture or an upright/expansive posture. Then, participants completed a series of insoluble puzzle tasks measuring task persistence. Results indicated that participants who adopted the slumped posture persisted less on the insoluble tasks as compared to participants who adopted the upright posture.²

Manipulated facial expressions influence physiological correlates of emotion

Scientists have proposed that, in part, the mechanism that allows facial expressions to influence self-reported emotions has to do with how the movement of facial muscles influences other physiological processes (Zajonc et al. 1989). Consider the downward movement of the corrugator supercilii muscle (furrows the brow) that is often associated with negative expressions (e.g., anger, disgust). Zajonc et al. (1989) theorized that downward movement of

¹ Other research has indicated that the context (positive or negative) of the presented stimuli can influence these arm-flexion and arm-extension effects (Centerbar and Clore 2006). Furthermore, the meaning attributed to these types of motor actions is also an important factor (Eder and Klauer 2009).

² Riskind (1984) went on to clarify that situational contexts (success or failure) can influence these posture effects as well. Context, it should be noted, is an important thing to consider with any bodily manipulation effect.

the corrugator muscle might reduce air-intake into the nasal cavity, cause more mouth as compared to nose breathing, and raise the temperature of blood entering the brain. Furthermore, Zajonc et al. (1989) hypothesized that a rise in facial temperature due to downward corrugator activity would be associated with the experience of negative affect. Contrastingly, contraction of the zygomatic major muscle (moves the cheeks up and back to form a smile) was theorized to open the nasal cavity, improve nose breathing, and reduce the temperature of blood entering the brain. It was also hypothesized that a reduction in facial temperature due to contraction of the zygomatic muscle would be associated with the experience of positive affect. These predictions were based on the notion that thermoregulation of brain areas such as the hypothalamus could influence hedonic states and associated neurotransmitter (e.g., nor-epinephrine) activity.

In order to test these ideas, Zajonc et al. (1989) had participants recite neutral stories containing a high frequency of the German letter *ü*, or neutral stories without words containing this letter (Study 1). Reciting the German letter *ü* contracts the corrugator muscle downward while extending the zygomatic major muscle. *Ü* stories, therefore, were predicted to be less liked and raise facial temperature more so than the no-*ü* stories. Results were in line with these predictions. Several other important findings were uncovered: story comprehension was not necessary as these effects were observed in both German and non-German speaking participants (Study 2), simply repeating the letter *ü* relative to a control letter led to similar effects (Study 3), and repeating vowels (e, ah) that contracted the zygomatic muscle led to a reduction in facial temperature and a greater liking for the recitation of these vowels (Study 4). Finally, participants enjoyed the sensation of cool air entering their nasal cavities', thus reducing overall facial temperature (Study 5). Subsequent research directly manipulated hypothalamic cooling versus heating and found that cooling caused more feeding in rats but not more hedonic reactions to taste. These results led the researchers to conclude that hypothalamic cooling may increase the attractiveness of the food without modulating taste pleasure (Berridge and Zajonc 1991).

Thus, facial expressions might influence thermoregulation of the hypothalamus which, subsequently, can influence an organism's motivational state. Other researchers, however, have theorized that moving the face in certain ways leads to innate, parallel physiological changes in heart rate, skin conductance, and other measures of autonomic nervous system (ANS) activity (Ekman et al. 1983). These physiological changes, therefore, might influence self-reported emotions as well.

To test this idea, Levenson et al. (1990) had participants make several emotional facial expressions while their heart

rate, skin conductance, finger temperature, and forearm muscle tension were recorded. Participants self-reported emotions' were also recorded. Results across several experiments indicated that patterns of heart rate and finger temperature were specific to manipulated facial expressions, in particular between negative expressions of anger, disgust, and fear. For example, heart rate acceleration was larger for anger as compared to disgust. In addition, heart rate acceleration was larger for fear as compared to disgust. Heart rate acceleration was also larger for sadness as compared to disgust. Lastly, finger temperature increased more for anger as compared to fear. The fact that different expressions required different muscle movements could not account for these differences in ANS activity; autonomic distinctions among emotions did not parallel the number of muscles used to create each emotional expression. In addition, participants reported experiencing the target emotion after making the associated facial expression. Furthermore, these differences in ANS activity and self-reported emotions were more pronounced when participants produced facial configurations that closely resembled the associated emotional expressions. Several other important findings were uncovered: similar results were seen for theater actors (Study 1), college students (Study 2), and participants from the general population (Study 3). Results were also similar when participants could see their facial expressions (Study 1) and when they could not see their expressions (Study 2). Studies that followed these original studies, which were conducted with American samples, revealed that many of these findings replicated with men of the Minangkabau from West Sumatra (Levenson et al. 1992).

These results, therefore, suggest that facial expressions might have direct effects on ANS activity. One might question how the body transforms ANS signals (or temperature changes resulting from facial muscle movements) into subjective emotional states, however. In other words, how do we perceive the feelings from our bodies? Researchers have proposed that projections from the brainstem (which carries sympathetic and parasympathetic bodily signals) to nuclei within the anterior insular cortex and the anterior cingulate cortex are likely involved in this process (for a review, see Craig 2002). Several studies have demonstrated that subjective ratings of temperature (Craig et al. 2000) and pain (Kong et al. 2006) correlate with activity in the anterior insular cortex, whereas the objective intensity of these bodily signals is associated with more posterior activity of this brain region. These results suggest that the anterior insular cortex might be the primary neural mechanism for the integration of bodily signals and subjective emotional experiences (Craig 2009). The somatosensory cortex, furthermore, has also been implicated in these processes (Damasio 1993).

As we have alluded to, however, emotional states are also associated with motivational urges to approach or avoid environmental stimuli. Below, we review research testing whether bodily manipulations influence asymmetric frontal cortical activity, a pattern of activity that relates to the motivational direction, approach or withdrawal, of emotional states.

Bodily manipulations influence physiological correlates of approach motivation

Past observational studies indicated that lesions to the right orbitofrontal cortex are often associated with the onset of mania symptoms (Starkstein et al. 1988). Damage to the left dorsolateral prefrontal cortex, on the other hand, has been associated with depression symptoms (Turner et al. 2007). In addition, asymmetric frontal cortical activity measured with electroencephalographic (EEG) neuroimaging techniques has been associated with the motivational direction of emotions (Harmon-Jones 2003; Harmon-Jones et al. 2010). Relative right frontal activity has been associated with withdrawal-oriented emotions, such as fear and disgust (Davidson et al. 1990; Jones and Fox 1992). Relative left frontal activity, on the other hand, has been associated with approach-oriented emotions, such as joy (Davidson and Fox 1982) and anger (Harmon-Jones 2004; Harmon-Jones and Allen 1998; Harmon-Jones and Sigelman 2001; Harmon-Jones et al. 2003, 2004; Verona et al. 2009). Approach and withdrawal states have also been found to activate left and right prefrontal cortices as measured with functional magnetic resonance imaging (Berkman and Lieberman 2010). Research utilizing repetitive transcranial magnetic stimulation (rTMS) has also indicated that electrically deactivating the left pre-frontal cortex reduces participants' approach-oriented attention to angry faces (van Honk and Schutter 2006). Work has also been conducted with bodily manipulations to further demonstrate that asymmetric frontal cortical activity relates to the motivational direction (approach or withdrawal) of emotional states, as we review below.

Facial expressions

Manipulated facial expressions, for example, influence relative left frontal cortical activity. In one of the first experiments to demonstrate this, Ekman and Davidson (1993) instructed participants to form one of two smiles during an EEG recording session. Genuine smiles often involve Duchenne's marker, that is, movement of zygomatic major (cheek) but also orbicularis oculi (underneath the eye) muscles. Less genuine smiles, however, often involve movement of zygomatic muscles only (Ekman

et al. 1988). Ekman and Davidson (1993) found that when participants were instructed to form genuine smiles with Duchenne's marker, as compared to less genuine smiles without this marker, they had greater relative left frontal cortical activity.

More recent experiments have also investigated how manipulated facial expressions influence relative left frontal cortical activity. For example, facial expressions indicative of anger and joy, approach-oriented emotions, cause greater relative left frontal cortical activity, whereas facial expressions indicative of fear and disgust, withdrawal-oriented emotions, cause less relative left frontal activity (Coan et al. 2001).

Unilateral muscle contractions

Researchers have suggested that there are close connections between the motor and frontal cortex (Harmon-Jones 2006; Schiff and Lamon 1989, 1994). Thus, voluntarily moving the body and increasing cortical activity in the motor cortex may, through spreading of activation, increase activity in frontal areas. Furthermore, given that sensory and motor pathways are crossed (Rinn 1984), unilaterally moving the right side of the body may lead to an increase in left hemispheric activation, whereas moving the left side of the body may lead to an increase in right hemispheric activation.

Based on these ideas, Harmon-Jones (2006) demonstrated that left and right hand contractions influence right and left hemispheric activation in the frontal cortex, respectively. In this study, right-handed participants squeezed a ball with either their right or left hand for two 45s periods and again while they listened to a mildly positive, approach-oriented pilot radio broadcast concerning apartment living options for the participants. As predicted, right-hand contractions compared to left-hand contractions caused greater relative left frontal activation. Similar effects also occurred over the motor cortex. Furthermore, right-hand contractions caused greater self-reported approach affect as indexed by scores on the Positive and Negative Affect Schedule (PANAS; Watson et al. 1988). Thus, manipulating regional brain activity with hand contractions has been found to influence self-reported emotions as well.

Extending this earlier work, Peterson et al. (2008) demonstrated that unilateral hand contractions influence behavioral responses. In this experiment, right-handed participants wrote an essay on a controversial topic (e.g., war in Iraq). Next, they received insulting feedback on their essays from another participant. In actuality, every participant received the same insulting feedback; the other participant did not actually exist. However, prior to receiving feedback, participants squeezed a ball with either

their right or left hand in order to increase relative left or right frontal cortical activity, respectively. Then, participants were told they would play a reaction time game against the other participant who had given them insulting feedback. In this modified version of Taylor's (1966) aggression game, participants were able to aggress against the other player with noise blasts. Results indicated that participants who made right-hand contractions gave longer and louder noise blasts during the reaction time game compared to participants who made left-hand contractions. Also, these aggressive behavioral responses were correlated with greater relative left frontal cortical activation in the right-hand contraction condition. Further analyses suggested that right- and left-hand contractions differentially affected coherence between the motor cortex and other areas of the brain. Right-hand contractions caused more coherence between the motor cortex and frontal regions, whereas left-hand contractions caused greater coherence between the motor cortex and posterior regions.

Thus, unilateral movements of the body can influence asymmetric frontal brain activity as well as approach behavior; in the previous experiment, right-hand contractions and greater relative left frontal cortical activity led to more aggressive, approach-oriented responses in the form of longer and louder noise blasts. These findings clarify one way in which bodily manipulations might influence motivational processes.

Manipulations of whole body posture

Past work has shown that whole-body manipulations also change motivational processes, such as task persistence (e.g., Riskind and Gotay 1982). The effects of posture, whole-body manipulations, may also play a significant role in neuroimaging studies investigating emotive processes. Some, but not all, functional magnetic resonance imaging (fMRI) studies have failed to find a connection between anger and relative left frontal activity (Tomarken and Zald 2009). In contrast, several EEG and rTMS studies have found an association between anger and relative left frontal activity (Carver and Harmon-Jones 2009; van Honk and Schutter 2006). One difference between these two neuroimaging techniques is that most current fMRI scanning procedures require participants to be in a supine or reclining body posture. Participants normally sit upright for EEG and rTMS studies. Thus, the supine posture required by most current fMRI scanners may reduce, but not necessarily eliminate, the relative left frontal cortical activity associated with approach motivation.

To test whether reclining postures reduce relative left frontal cortical activation associated with approach-motivated anger, Harmon-Jones and Peterson (2009) had participants write an essay on a controversial topic under the

guise that another ostensible participant would evaluate it. Prior to receiving feedback, participants either remained upright in their chair or reclined backward. All participants in the reclining condition and half the participants in the upright condition received insulting feedback. The remaining half of the participants in the upright condition received neutral feedback. Results replicated previous research in that greater relative left frontal cortical activity was found in the insult-upright condition compared to the neutral-upright condition. The insult-upright condition also produced greater relative left frontal cortical activity than did the insult-reclined condition.

Reclining backward relative to sitting upright, therefore, might reduce brain activity associated with approach-motivated anger. As previously stated, however, simply manipulating the face without an emotion eliciting stimulus can influence relative left frontal cortical activity (Coan et al. 2001). In order to extend this work on body posture, Price and Harmon-Jones (2010) created multiple postures hypothesized to be associated with different levels of approach motivation. Reclining backward was hypothesized to be associated with low approach motivation; reclining often occurs following the acquisition of a desired goal, such as after eating a delicious meal. Leaning forward was hypothesized to be associated with higher approach motivation; leaning forward often occurs during goal acquisition, such as leaning towards a delicious meal. Finally, sitting upright was hypothesized to be associated with a level of approach motivation somewhere between reclining backward and leaning forward. In this experiment, participants assumed one of these three postures while EEG was recorded for 1 min. Results indicated that reclining backward caused participants to have less relative left frontal cortical activity as compared to leaning forward. Sitting upright fell between these two conditions, as predicted.

In a follow up experiment, Harmon-Jones et al. (2011) examined if changes in physical posture would influence relative left frontal activity to appetitive emotional stimuli. Participants in this experiment leaned forward or reclined backward while viewing appetitive dessert and neutral rock pictures used in prior investigations of approach motivation (Gable and Harmon-Jones 2008). Consistent with the hypothesis that leaning forward increases approach motivation, leaning participants had greater relative left frontal activity to dessert as compared to neutral rock pictures, whereas reclining participants did not demonstrate this difference. Thus, posture influenced relative left frontal cortical activity to appetitive pictures, but not neutral pictures.

One might question the lack of an effect of body posture on responses to neutral pictures, because these postures have been found to influence relative left frontal cortical

activity during a resting, baseline or “neutral” state (Price and Harmon-Jones 2010). One interpretation is that in a resting, baseline state where there are no other obvious stimuli to process, such as neutral pictures, the posture itself might have a stronger influence on asymmetric frontal cortical activity. When a neutral stimulus is presented, however, the neutral stimulus might override the effect of posture. Thus, the postural effects observed in a resting, baseline state might be subtle.

Given these findings, simply leaning forward might increase a person's inclination to move toward something desirable, but not toward something neutral. In each of the experiments reviewed in this section, however, the physiological measure was always relative left frontal activity. In the next section, we review recent research demonstrating that postural manipulations also influence neural activity related to motivated attention and reflexive responses to emotional stimuli.

Postural manipulations influence late positive potentials to emotional stimuli

The late positive potential (LPP), an event-related brain potential (ERP) starting approximately 300 ms after stimulus onset and lasting for several 100 ms, has been associated with motivated attention (for a review, see Hajcak et al. 2011). For example, LPPs are larger to erotic images compared to positive pictures less associated with basic motivational impulses, such as exciting sports scenes (Briggs and Martin 2009). In addition, mothers have larger LPPs to pictures of their own children's faces relative to pictures of familiar children, unfamiliar children, familiar adults, and unfamiliar adults (Grasso et al. 2009). Individuals who are currently in love with another person, furthermore, evince larger LPPs to pictures of that person relative to pictures of a friend or a beautiful but unknown person of the opposite sex (Langeslag et al. 2007). LPPs are also larger to scenes of mutilation and threat compared to scenes of contamination and loss (Schupp et al. 2004). Functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) studies have revealed multiple neural generators of the LPP, such as the occipitotemporal and parietal cortex (Keil et al. 2002; Sabatinelli et al. 2007).

To examine if postural manipulations influence this physiological correlate of motivated attention to emotional stimuli, Price et al. (2011) manipulated participants' posture while they viewed highly arousing positive (erotic images) and neutral pictures (images of persons). Participants viewed these pictures while leaning and reclining in a counterbalanced within-subjects design. Results indicated that leaning forward relative to reclining backward caused

participants to have larger LPPs to the arousing positive pictures. On the other hand, posture did not influence LPPs to neutral stimuli.

Postural manipulations influence startle responses to emotional stimuli

In addition, Price et al. (2011) found that these postural manipulations also influenced the sub-cortically driven startle reflex. The magnitude of the startle eyeblink reflex is another physiological measure reliably modulated by the emotive significance of stimuli (Bradley et al. 2001; Lang et al. 1990; Vrana et al. 1988). This reflex causes the orbicularis oculi muscle around the eye to contract to sudden aversive events, protecting the eye from potential harm. The startle response is typically induced by loud (100 db) bursts of white noise with instantaneous rise time (Blumenthal et al. 2005). When these startle probes are presented during the viewing of affective pictures, the magnitude of startle eyeblinks is potentiated by arousing negative pictures and attenuated by arousing positive pictures. This effect is explained by the response-matching hypothesis, which postulates that the startle eyeblink is a defensive reaction that is responsive to the presence of affective cues. Aversive cues, such as arousing negative pictures, exacerbate the congruent avoidant motivation elicited by the startling sound and lead to larger startle blinks. Appetitive cues, such as arousing positive pictures, contrast the avoidant motivation of the startling sound and these inconsistent motivational states lead to smaller startle blinks. Smaller startle responses, therefore, are considered more appetitive responses. Animal models, furthermore, have clarified the neural pathways involved in the acoustically-elicited startle response and found that nuclei within the amygdala play a critical role in the affective modulation of this response (Davis 2006).

Consistent with the response-matching hypothesis, the startle response has been linked with a person's motivational disposition. High trait behavioral approach system (BAS) sensitivity, measured with Carver and White's (1994) scale, is correlated with smaller startle responses during arousing positive pictures (Hawk and Kowmas 2003). Furthermore, trait emotions associated with approach motivation (e.g., anger, enjoyment, surprise) are correlated with smaller startle responses during arousing positive pictures (Amodio and Harmon-Jones 2011). In addition, positive approach-motivated pictures (e.g., erotic images) are associated with smaller startle responses than positive pictures lower in basic motivational impulses (e.g., sports scenes; Gard et al. 2007).

Price et al. (2011) examined if postures varying in approach motivation would causally influence startle

responses to arousing positive stimuli. In this experiment, participants leaned forward or reclined while viewing erotic and neutral people stimuli. Startle probes were presented at 3.5 or 4 s after picture onset for 60% of the erotic and neutral pictures within a condition. Replicating much past research, results indicated that picture type influenced startle eyeblink responses, with startle eyeblink responses being smaller during the viewing of arousing positive pictures than during the viewing of neutral pictures. In a novel extension of past research, results indicated that leaning forward compared with reclining caused even smaller startle responses during arousing positive pictures. Posture did not influence startle responses to motivationally less relevant neutral stimuli. Converging evidence, therefore, supports the idea that leaning forward is associated with heightened approach motivation relative to reclining backward, which may be associated with less approach motivation.

Postural manipulations influence neuroendocrine levels

Researchers have also examined the effects of postural manipulations on feelings of power and neuroendocrine (e.g., testosterone and cortisol) changes (Carney et al. 2010). In this experiment, participants were randomly assigned to display two low-power or two high-power body postures for 1 min each. Low-power body postures contained contractive positions with closed limbs (e.g., standing and sitting in slumped positions), whereas the high-power body postures were expansive positions with open limbs (e.g., sitting with feet up and standing widely over a table). Saliva samples were collected 10 min before, and 17 min after the body posture manipulation. As predicted, high-power posers had an increase in testosterone compared to low-power posers. High-power posers also reported feeling more “powerful” and “in charge” and took greater risks in a gambling task compared to low-power posers. Furthermore, contractive low power positions resulted in increases in cortisol, whereas the high power positions resulted in decreases in cortisol.

Theories of grounded or embodied cognition and emotion

In this section, we attempt to meld some of our findings with recent research investigating theories of grounded cognition. It is important to note, however, that bodily manipulation research is different from research directly supporting theories of grounded cognition. Each of these lines of inquiry may nevertheless complement one another.

Theories of grounded or embodied cognition rely on the non-dualist assumption that cognitions (e.g., memories) are specific types of neural activations. More specifically, when an object is encountered, people acquire sensory information (e.g., smells, sounds, tactile sensations) about it that presumably gets stored in sensorimotor areas within the brain. When the object is no longer present and the person thinks about it, these sensory signals are re-experienced or partially activated because they were stored for later use (Barsalou 1999). Mental imagery is a common example of how cognitions reflect the re-activation of modality (e.g., tactile, auditory, but in this case especially visual) specific sensations (Barsalou 2008).

Conceptual knowledge about emotion is also thought to lead to a partial activation of modality specific sensations previously associated with relevant emotional experiences. One interesting prediction from theories of grounded cognition is that conceptual knowledge can also influence more overt changes in behavior, such as outward bodily changes (Barsalou et al. 2003). Thus, generating information about emotions may lead to outward changes in bodily states. Consistent with the idea that failure and disappointment are often associated with a slumped body posture (e.g., Riskind and Gotay 1982), research has demonstrated that generating disappointment-related words causes participants to stoop down more so than generating pride-related words (Oosterwijk et al. 2009). In this experiment, participants verbally produced single words or phrases related to failure/disappointment and success/pride. Neutral conditions (e.g., generating information about kitchens) were also included before each of the experimental conditions. Each condition lasted 90 s and was counterbalanced in a within-subjects design. Changes in physical posture were recorded every 2 s during a specific condition. Results indicated that participants decreased their height along a vertical dimension more while generating disappointment-related as compared to pride-related words. Thus, generating conceptual information about disappointment led to the partial activation of the associated slumped or defeated body posture.

The research reviewed with posture and frontal cortical asymmetry demonstrates that manipulating a persons' posture influences approach-related brain activity. Thus, bodily manipulation research and research investigating theories of grounded cognition are distinct from one another. However, they may be similar in that they represent two-sides of the same process. It remains to be seen if postural manipulations (e.g., leaning, reclining) influence the extent to which a person can generate approach- or avoidance-related conceptual knowledge; the research reviewed here would support this prediction.

The mirror neuron system

But how do sensory signals get stored in the brain for later use? One possible neural mechanism is the mirror neuron system. Numerous studies have indicated that non-human primates have similar patterns of brain activity while performing certain actions and seeing others performing the same actions (Rizzolatti and Craighero 2004). This process involves the firing of mirror neurons, that is, cells within a complex frontoparietal network that enable the integration of sensory signals and motor actions (Iacoboni and Dapretto 2006). These researchers have also devised neural models to explain several forms of imitation-based learning in humans. It may very well be that seeing, feeling, and performing certain actions are related processes. The initial neural mechanism that makes this possible, furthermore, may be imitation-based learning established via the mirror neuron system.

One interesting theory is that the mirror neuron system is associated with far more than simple mimicry. Some work has suggested that mirror neurons not only code actions, but also the intentions of those actions in humans (Iacoboni and Dapretto 2006) and non-human primates (Rizzolatti et al. 2001). For example, seeing someone grasp a cup by the handle to drink, as compared to grasping it by the rim to clean, causes greater inferior frontal mirror neuron activity (Iacoboni et al. 2005). Other research, in addition, has supported the notion that the mirror neuron system is not only associated with motor-mimicry; it might also be responsive to the affective connotations of related actions. For example, individuals have similar patterns of facial muscle movements while unconsciously viewing emotional facial expressions (Dimberg et al. 2000) as well as emotional postures (Tamietto et al. 2009). The mirror neuron system, therefore, might be similarly activated by positive facial expressions as well as postures indicative of positive emotional states. Based on this research, it would be interesting to further investigate if the mirror neuron system is capable of coding the motivational direction (approach or withdrawal) of observed actions as well.

Revisiting the idea “what is bodily feedback?”

Adelmann and Zajonc (1989) asked this question—“What is bodily feedback?”—over two decades ago. They later tested that facial expressions influence facial temperature alongside self-reported emotions. They theorized that these temperature changes could influence the subsequent release of different neurotransmitters involved in emotional experiences (Zajonc et al. 1989). As the authors stated, however, this is unlikely the sole physiological mechanism responsible for facial-feedback effects. Additionally, this

line of work did not investigate other bodily manipulations. The evidence reviewed here suggests that bodily movements such as facial expressions (Coan et al. 2001; Ekman and Davidson 1993), hand movements (Harmon-Jones 2006; Peterson et al. 2008), and changes in physical posture (Harmon-Jones and Peterson 2009; Harmon-Jones et al. 2011; Price and Harmon-Jones 2010) indicative of approach or avoidance influence asymmetric frontal brain activations associated with these motivational inclinations. Furthermore, changes in physical posture also influence sub-cortically driven emotive processes (Price et al. 2011) as well as changes in neuroendocrine levels (Carney et al. 2010). Thus, these types of whole bodily manipulations likely influence multiple emotion-related physiological processes occurring throughout the brain and body.

A daunting task for future researchers, however, may not be looking for additional mechanisms but, rather, developing methods that study the integration of already known neural mechanisms associated with embodiment. We have suggested that there may be a relationship between seeing and performing actions with the body, as well as feeling certain ways. What is the relationship between the underlying neural mechanisms associated with these processes? More specifically, what is the relationship between mirror neuron, anterior insula, and somatosensory activity? Work examining this notion will, hopefully, provide an over-arching model that explains the neural connection between seeing, doing, and feeling.

Conclusions

In short, due to the complexity of these processes, more work is necessary. EEG methodologies may assist in these endeavors. fMRI techniques may assist as well. It is important to remember, however, that current fMRI techniques have participants in a supine posture. This, in and of itself, is an embodiment manipulation that has been found to reduce (but not eliminate) approach motivation (Harmon-Jones and Peterson 2009; Harmon-Jones et al. 2011; Price and Harmon-Jones 2010; Price et al. 2011). Nevertheless, future researchers should consider the motivational consequences of these postures and other bodily manipulations. In doing so, more complete theories addressing the mind–body connection are likely to develop.

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