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Motor Asymmetries Predict Neural Organization of Emotion

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Abstract

According to decades of research in affective neuroscience, approach and avoidance motivation are supported by the left and right hemispheres, respectively. With the Sword and Shield Hypothesis (SSH), we challenge this conclusion, and propose a novel principle underlying the organization of emotion in the brain: the hemispheric lateralization of motivation depends on the neural locus of motor control for the dominant hand (used preferentially for approach actions) and the non-dominant hand (used preferentially for avoidance actions). The SSH predicts that the laterality of approach motivation should vary continuously with the laterality of circuits used for planning and executing approach-related actions. To test this prediction, we measured mood before and after 5 sessions of tDCS applied bilaterally to DLPFC in right- and left-handers. Results in right-handers show that positive emotions increased after left-excitatory stimulation, but decreased after right-excitatory stimulation. In non-right-handers, however, the opposite pattern was found: Positive emotions decreased after left-excitatory stimulation, but increased after right-excitatory stimulation. These findings reveal continuous covariation between the neural systems for action and emotion, supporting the SSH.

Keywords: Emotion; motivation; motor control; handedness; hemispheric specialization, tDCS.

Introduction

A cornerstone of cognitive-affective neuroscience is the robust finding that the left hemisphere is specialized for approach motivation and the right hemisphere for avoidance motivation (reviewed in Harmon-Jones, Gable, & Peterson, 2010). Although temporal and parietal areas have been implicated in affective motivation (Amodio, Master, Yee, & Taylor, 2008; Brookshire & Casasanto, 2012), studies suggest that this asymmetry centrally involves dorsolateral prefrontal cortex (DLPFC): Approach motivation recruits left DLPFC, and avoidance motivation recruits right DLPFC (Berkman & Lieberman, 2010).

Approach/avoidance asymmetries can also be observed in behavior. People tend to perform approach actions with the dominant hand, and avoidance actions with the non-dominant hand (Casasanto, 2009). The dominant hand, for example, is preferred when eating. In contrast, people reflexively protect their faces with the non-dominant hand when startled (Coren, 1992). Sword-fighters in centuries past approached their enemies with a sword held in the dominant hand, and avoided incoming blows with a shield in the non-dominant hand (Harris, 2010).

In right-handers, therefore, the left hemisphere is involved both in approach motivation and in coordinating actions with the hand preferred for approach actions. Casasanto (2009) proposed that this correspondence may result from a functional relationship between affective motivation and manual motor control for approach and avoidance actions. We call this the Sword and Shield Hypothesis (SSH; Brookshire & Casasanto, 2012). The SSH suggests that the lateralization of approach/avoidance motivation is functionally linked to the way we use our hands to perform approach and avoidance actions, and offers a new principle to predict and explain the neural organization of emotion.

The SSH predicts that differences in how people use their hands for approach and avoidance actions should correspond to differences in the neural organization of affective motivation. Left-handers tend to perform approach actions with their left hands and avoidance actions with their right hands (Coren, 1992; Harris, 2010). Accordingly, approach motivation in left-handers should be lateralized to the right hemisphere, the reversal of the pattern found in right-handers.

To test this prediction, Brookshire and Casasanto (2012) examined resting activation asymmetries in EEG as a function of manual motor asymmetries and trait approach motivation. As in previous studies (Sutton & Davidson, 1997), higher approach motivation in right-handers correlated with greater leftward activation asymmetries. This pattern reversed in left-handers, however. Consistent with the SSH, increased approach motivation in left-handers correlated with greater rightward activation asymmetries (Brookshire & Casasanto, 2012).

Causal role of frontal asymmetry

Frontal asymmetries are widely believed to play a causal role in determining emotional experience (Harmon-Jones et al., 2010). Supporting this idea, patients with left hemisphere lesions are prone to depression, whereas those with right hemisphere lesions are prone to mania and indifference to their injuries (Robinson, Boston, Starkstein, & Price, 1988). Similarly, deactivating the right hemisphere with sodium amobarbital causes laughter and elation, whereas deactivating the left hemisphere causes crying and negative affect (Lee, Loring, Meader, & Brooks, 1990). These data underscore the necessity of the two hemispheres in emotion, but they are limited by low spatial resolution (constrained to the level of hemisphere), and by the extremity of processing disruptions used (completely deactivating a neural area). Would subtler, more spatially restricted manipulations of activation asymmetries influence emotional processing?

Allen, Harmon-Jones, and Cavender (2001) used biofeedback in EEG to train participants to induce rightward or leftward frontal activation asymmetries. Participants trained to produce leftward asymmetries experienced greater positive, approach-oriented emotions than those with rightward training. However, it is possible that participants used strategies to complete the biofeedback task (e.g. rehearsing approach-motivated memories), complicating inferences about a causal role of frontal activation in producing emotions. Activation asymmetries may have been a consequence—not a cause—of changes in emotional state.

Subsequent work has addressed the causal role of frontal asymmetries using transcranial direct current stimulation (tDCS). In tDCS, a weak, constant electrical current is passed between two conductive electrodes on the scalp. After 5–20 minutes of stimulation, neurons beneath the anodal electrode are transiently excited, and those beneath the cathode are inhibited (Nitsche & Paulus, 2000).

Several studies have used tDCS to intervene on activation asymmetries in DLPFC, but many of these fail to find support for a causal involvement of frontal asymmetries in emotional experience. Specifically, tDCS applied in a single session to DLPFC had no effect on self-reported mood or trait motivational tendencies (Koenigs, Ukueberuwa, Campion, Grafman, & Wassermann, 2010; Plazier, Joos, Vanneste, Ost, & De Ridder, 2011; Nitsche et al., 2012).

Studies of the causal role of frontal asymmetries on more implicit emotional processing have yielded mixed results. Nitsche et al. (2012) found that anodal tDCS over left DLPFC facilitated identification of both positive and negative facial expressions, but that the effect was stronger for positive expressions. Penolazzi et al. (2010) examined memory for emotional pictures after bilateral tDCS over DLPFC. Anodal tDCS almost invariably improves memory performance (for review see Jacobson, Koslowski, & Lavidor, 2011). Surprisingly, however, left-anodal/right-cathodal stimulation facilitated recall of unpleasant pictures, and right-anodal/left-cathodal stimulation facilitated recall of pleasant pictures. Although this experiment seems to suggest a causal role of frontal asymmetries in emotional memory, the fact that left-excitatory tDCS improved recall of negative pictures, and right-excitatory of positive pictures, is inconsistent with a great deal of research in right-handers linking positive emotions with the left hemisphere (Harmon-Jones et al., 2010).

Researchers noting the clinical potential of neurostimulation have begun using repeated sessions of tDCS to treat major depressive disorder, with somewhat more consistent results than the single-session studies reviewed above. Left-anodal tDCS often ameliorates symptoms of depression (reviewed in Murphy, Boggio, & Fregni, 2009). However, these treatment-oriented studies did not include all of the experimental conditions needed to support the conclusion that induced activation asymmetries play a causal role in emotional experience: Researchers delivered only left-excitatory and sham stimulation, but never right-excitatory stimulation. Thus, it is not possible to conclude that increasing activity in the left hemisphere relative to the right was responsible for the positive effects of neurostimulation of mood. Perhaps multiple sessions of tDCS may boost positive mood regardless of stimulation montage. To determine whether frontal activation asymmetries play a functional role in determining emotional states, experiments must apply both left- and right-excitatory stimulation. Furthermore, in order for the findings to be generalizable beyond a clinical population, relationships between lateralized stimulation and mood would need to be shown in healthy participants.

Parametric covariation in brain and behavior

According to the SSH, there is a functional relationship between the neural circuits for motivation and manual motor asymmetries. In addition to predicting a reversal in approach/avoidance lateralization in left-handers, the SSH predicts that parametric variation in manual motor asymmetries should correlate with graded differences in the lateralization of motivation. Strong right-handers, that is, should show stronger left-lateralization of approach motivation than weak right-handers. Previous work has not tested this prediction.

The present experiment

In this study, we measure mood before and after 5 sessions of tDCS applied bilaterally to DLPFC. We analyze changes in emotional state as a function of participants' manual motor asymmetries, and whether they received left-anodal/right-cathodal or right-anodal/left-cathodal stimulation. In doing so, we test for a causal role of frontal activation asymmetries in determining emotional state. Furthermore, we test for the graded relationship between motor control and the lateralization of affective motivation predicted by the SSH.

Method

Participants

Participants (N = 30) were recruited from the New School community, postings to the website www.craigslist.org/, and a database of participants who have taken part in other studies in our lab. To ensure that the sample included participants with the full range of handedness asymmetries, we selectively contacted left-handed and ambidextrous participants from the database. These participants were not aware that they were being contacted based on their handedness.

Several exclusion criteria were followed to ensure participants' safety. Respondents were not included in the study if they indicated that they were pregnant, had ever experienced an epileptic seizure, had ever sustained a stroke or other brain injury, or were taking any psychoactive drugs or medications. Additionally, we did not test anyone who reported ever having been diagnosed with depression, bipolar disorder, anxiety disorder, or schizophrenia.

One participant was canceled during the first session when a low impedance could not be obtained. Four additional participants did not complete the study (Right-excitatory stimulation, N = 2; Left-excitatory stimulation, N = 2), one of whom returned to complete the final day of data collection. Data were analyzed from the remaining 25 participants (Right-handers, EHI $\geq$ 40: N =17; Non-right-handers, EHI $<$ 40: N = 8). Demographics such as age and gender were not collected.

Procedure

This study took place over five consecutive days (Monday–Friday). Informed consent was obtained at the beginning of each session, and participants were payed at the end of every session. On day 1, participants completed an untimed, computerized version of the Positive and Negative Affect Scale (PANAS; Watson & Clark, 1994). Emotion words appeared on the screen one at a time, and participants rated the degree to which they had experienced that emotion "during the past few days" on a scale of one ("very slightly or not at all") to five ("extremely") by pressing the numbers 1–5 on a computer keyboard. To assess handedness, participants completed the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). This scale offers a continuous measurement of handedness, in which scores vary from strongly left-handed (-100) to strongly right-handed (100).

On days 2–4, tDCS was applied after ensuring that participants had not experienced any discomfort after the previous sessions. After applying tDCS on day 5, the same tests were performed as on day 1. After the first cohort of 7 participants, we began collecting EHI at day 5. Participants also completed a brief adverse effects questionnaire. Upon completing the study, participants were debriefed and encouraged to contact the experimenter if they had any further questions or experienced any discomfort.[1]

Transcranial Direct Current Stimulation

Direct current stimulation was delivered using a battery-powered stimulator (Soterix Medical, New York) with two 5×7 cm saline-soaked sponges covering the electrodes. New sponges were used for each session. In each session, a current was applied at 2 mA for 20 min. To minimize discomfort, the current slowly ramped between 0 and 2 mA when powering on and off. Stimulation was delivered bilaterally above DLPFC at F3-4 in the 10-20 system (DaSilva, Volz, Bikson, & Fregni, 2011). An experimenter was in the room with the participant at all times to ensure that stimulation remained comfortable.

Stimulation was delivered double-blindly in two between-subjects conditions. Before beginning the study, a confederate set a polarity-blinding box to either reverse the polarity of the outgoing wires, or leave polarity unchanged, and then sealed the box. This allowed both the experimenter and the participant to remain blind to the stimulation condition. Participants were randomly assigned to one of the two conditions.

In one condition, the anode was placed above F3 and the cathode above F4, exciting left frontal areas while inhibiting right frontal areas (Left-excitatory). In the second condition, the anode was placed above F4 and the cathode above F3, exciting right while inhibiting left frontal areas (Right-excitatory). Stimulation condition remained the same across all 5 sessions. Of the participants retained in the final analysis, $N = 10$ were given right-excitatory stimulation, and $N = 15$ left-excitatory stimulation.

Results

Adverse effects

One participant canceled the study due to a persistent headache, and three further participants requested that the intensity be reduced for several minutes in one session. Of the four participants reporting discomfort, two had received left-excitatory stimulation, and two right-excitatory stimulation. No other subjects reported significant discomfort.

Manual motor asymmetries

To examine whether tDCS altered manual motor asymmetries, we compared EHI scores before and after stimulation. EHI scores on days 1 and 5 were strongly correlated ($r = .98$). Change in EHI scores did not significantly depend on tDCS polarity (Welch's $t(12.3) = -1.50, p = .16$).

Emotional state

PANAS responses were analyzed using linear mixed-effects regressions fit by maximum likelihood in R (R Core Team, 2012) with the `lmer()` function in the `lme4` library (Baayen, Davidson, & Bates, 2008). Change in each emotion (day 5 – day 1) was modeled as a function of valence (Positive; Negative), tDCS polarity (Left-excitatory; Right-excitatory), and handedness (entered continuously using EHI score collected on day 1). Random intercepts were included for Subjects and Items (i.e. emotion words). All categorical predictors were entered using deviation coding. Unless otherwise noted, p-values and 95% Highest Posterior Density intervals (HPD) of the parameter estimates were estimated using Markov chain Monte Carlo (MCMC) sampling with 20,000 samples using the `pvals.fnc()` function in the `languageR` library.

Of primary interest, handedness, valence, and tDCS polarity interacted to predict change in PANAS ratings ($\beta = -0.015, \text{HPD} = [-0.022, -0.009], p = .0001$). As evident from Figure 1, this interaction was driven primarily by strong effects of handedness and polarity on positive emotions, but not on negative emotions. Separate mixed-effects regressions with positive and negative items support this conclusion.

Change in negative emotions did not significantly depend on handedness, tDCS polarity, or their interaction (all ps $> .5$; Fig. 1a). In contrast, handedness significantly interacted with tDCS polarity to predict change in the intensity of positive emotions ($\beta = -0.016, \text{HPD} = [-0.021, -0.010], p = .0001$; Fig. 1b). In participants receiving left-excitatory stimulation, stronger right-handedness correlated with greater increases in positive emotions ($\beta = 0.011, \text{HPD} = [0.0064, 0.016], p = .0001$). In those receiving right-excitatory stimulation, the opposite pattern

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[1] Three additional tasks were performed on days 1 and 5. To measure trait motivational tendencies, participants completed the Behavioral Activation System / Behavioral Inhibition System scales (BIS/BAS; Carver & White, 1994). Participants also completed a finger-tapping task as a performance-based measure of manual motor asymmetries. Finally, an N-back task was performed as a measure of working memory. Results from these tasks do not bear on mood, and have not been analyzed.

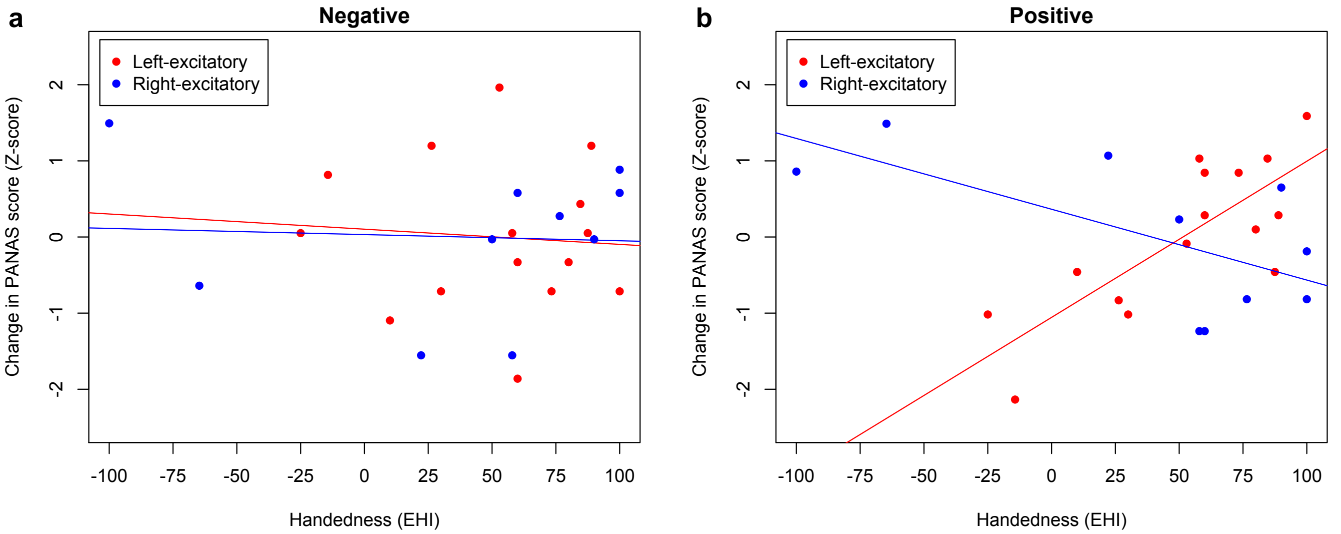

Figure 1: Change in **(a)** negative and **(b)** positive emotion from day 1 to day 5 as a function of manual motor asymmetries (EHI). Each point illustrates Z-transformed average change across all PANAS items for a single participant. Best-fit lines are plotted for each stimulation condition. Left-excitatory = anode left, cathode right; Right-excitatory = cathode left, anode right.

was observed: stronger right-handedness correlated with decreases in positive emotions ($\beta = -0.0044, \text{HPD} = [-0.0080, -0.0006], p = .02$).

By defining handedness categorically, we examined differences between right- and non-right-handers in the effects of tDCS on emotional state. For right-handers, left-excitatory tDCS led to more positive emotions than with right-excitatory tDCS ($\beta = -0.21, \text{HPD} = [-0.41, -0.012], p = .04$). For non-right-handers, the opposite pattern emerged: left-excitatory tDCS caused *decreases* in positive emotions compared with right-excitatory tDCS ($\beta = 0.55, \text{HPD} = [0.19, 0.89], p = .006$).

These regression analyses leave open the question of whether parametric variation in handedness corresponds to graded differences in the hemispheric lateralization of emotion; significant parameter estimates in linear regressions can be caused by either continuous covariation or a step-function. Rank-order tests, however, can be used to discriminate between categorical and continuous relationships. A significant Spearman's correlation revealed that stronger right-handedness was continuously related to greater increases in positive emotions in participants who received left-excitatory stimulation ($\rho(13) = 0.71, p = .003$). In those who received right-excitatory stimulation, this correlation was marginally significant in the opposite direction: stronger right-handedness continuously predicted greater reductions in positive emotions ($\rho(8) = -0.56, p = .09$).

Discussion

The effects of tDCS on mood depend upon the hemisphere to which excitatory stimulation is applied and the handedness of the participant. In right-handers, five sessions of left-excitatory (left-anodal, right-cathodal) tDCS led to increased positive emotions, whereas right-excitatory (left-cathodal, right-anodal) tDCS led to decreased positive emotions. Non-right-handers, by contrast, showed the opposite pattern, with right-excitatory tDCS increasing positive emotions and left-excitatory tDCS decreasing them. Furthermore, we find graded, parametric variation between manual motor asymmetries and emotion in the brain. Stronger motor asymmetries correlate with more strongly lateralized circuits for emotion. These results demonstrate a functional relationship between activation asymmetries in the frontal lobes and the experience of positive emotions, and show that the laterality of positive emotion covaries continuously with the laterality of manual motor control.

According to the motivational model of hemispheric specialization for emotion, approach motivation is lateralized to the left hemisphere and avoidance to the right (Harmon-Jones et al., 2010). In conflict with this model, we show that neural regions specializing in approach motivation are co-lateralized with circuits that control the dominant hand. This finding is consistent with the SSH, which proposes a functional relationship between motivation and manual action.

Manual motor asymmetries predict the way approach motivation is distributed across the two hemispheres. For the right-handed majority, this appears as left-lateralized approach motivation. Does this mean that the classic motivational model is mostly correct—that it is right for the approximately 90% of people who are right-handed, and only wrong for the other 10%? We suggest the answer is no: As a field, we have arrived at incorrect generalizations about the cortical basis of emotions. It is not the case that "anterior regions of the left and right hemispheres are specialized for approach and withdrawal processes, respectively" (Davidson, 1992, p. 127). It is only incidentally true that the left hemisphere is specialized for approach motivation in most of the people who have been tested. This specialization is not due to any functional properties of the left hemisphere, per se. It appears that any theory that assigns a privileged role to the left hemisphere in processing approach motivation is incorrect.

These findings may help to elucidate an enduring mystery in affective neuroscience: What role do activation asymmetries play in motivation? Although no clear consensus has emerged, some researchers believe that leftward asymmetries may reflect "expression of approach-related emotions" (Harmon-Jones, 2004, p. 55) or "approach-related, goal-directed action planning" (Davidson, 2004, p. 225). By highlighting the close connection between action and emotion, our findings suggest that leftward asymmetries are closely linked to performance of approach actions.

Causal links between frontal asymmetries, motivation, and hand action

To our knowledge, these findings provide the first unequivocal evidence that frontal activation asymmetries casually influence emotional experience in healthy participants. However, this study leaves open the question of the causal relationship between neural circuits for motivation and for motor control of the hands. We consider three possibilities.

First, handedness could determine the laterality of motivation. In this case, handedness is assumed to be set by some combination of genetic and environmental influences. If approach actions require greater dexterity than avoidance actions, then habits could develop in which approach actions are performed by the more adept dominant hand. These habits could then stabilize on an evolutionary or a developmental timescale, causing cortical areas involved in planning actions with the dominant hand to specialize in approach actions.

Second, the laterality of motivation could determine handedness. In this case, the laterality of motivation is assumed to be determined by genetic and environmental factors. Manual action circuits ipsilateral to regions specializing in approach motivation may subsequently come to be used preferentially for approach actions. If approach actions are more frequent or require more skill than avoidance actions, then dexterity may be enhanced in the hand used to perform them.

Third, handedness and the laterality of motivation could be determined by a common factor. In this case, there would be no direct causal link between the lateralization of neural circuits of motivation and manual motor control. Any proposed third factor would need to account for the close covariation we observe.

Valence and motivational direction

We find that positive emotions are strongly modulated by induced frontal activation asymmetries, whereas negative emotions are unaffected. If negative emotions are assumed to be the mirror image of positive emotions, this result seems incongruous. This apparent contradiction resolves when examining the motivational direction of the words in the positive and negative PANAS subscales.

The left and right hemispheres appear to be differentially specialized for motivational direction, not valence (Berkman & Lieberman, 2010; Harmon-Jones et al., 2010). Although these dimensions are highly correlated, they can also be dissociated. Induced frontal asymmetries, then, should alter the motivational direction—but not necessarily the valence—of participants' mood.

The emotions comprising the positive PANAS subscale uniformly involve strong approach motivation (active, alert, attentive, determined, enthusiastic, excited, inspired, interested, proud, strong). The negative subscale, on the other hand, is more varied. Some items seem to involve avoidance motivation (afraid, scared, ashamed), some approach motivation (hostile, irritable), and some do not have any clear motivational direction (nervous, jittery, guilty, upset, distressed).

In summary, we find that an emotion category with a consistent motivational direction (the positive subscale) is influenced by manipulations of frontal activation asymmetries, whereas a more heterogenous emotion category (the negative subscale) is not affected. Further studies must determine if avoidance motivation can be similarly modulated by induced activation asymmetries.

Clinical implications

Neurostimulation techniques such as tDCS and transcranial magnetic stimulation (TMS) are currently in use as treatments of major depressive disorder (Murphy et al., 2009). By increasing activation in left frontal areas, clinicians hope to augment positive, approach-oriented emotions, alleviating depression. This treatment is predicated on the assumption that the left hemisphere is specialized for approach motivation. We provide evidence against this assumption. Hemispheric specialization for motivation reverses in many people, including left-handers (see also Brookshire & Casasanto, 2012), who are at increased risk for depression (Denny, 2009).

Systematic differences in the neural organization of motivation may have urgent consequences for the success and safety of neurostimulation therapies. We show that positive affect is reduced after anodal tDCS to the hemisphere that controls the non-dominant hand. This result suggests that FDA-approved treatments involving anodal tDCS to left-DLPFC may exacerbate depression in non-right-handers.

Conclusions

Accepted theories of emotion in the brain hold that the left hemisphere is specialized for approach motivation, and the right for avoidance motivation. We provide evidence against this "motivation model" and in support of the SSH. Hemispheric lateralization for emotion covaries with manual motor asymmetries, consistent with a causal relationship between motivation and motor control. The SSH proposes a principle by which the hemispheres become specialized for approach and avoidance states, and may lead not only to a better understanding of *how* motivation is organized in the cerebral cortex, but also of *why* it is organized that way.

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