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Approach motivation in human cerebral cortex†

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Different regions of the human cerebral cortex are specialized for different emotions, but the principles underlying this specialization have remained unknown. According to the *sword and shield hypothesis*, hemispheric specialization for affective motivation, a basic dimension of human emotion, varies across individuals according to the way they use their hands to perform approach- and avoidance-related actions. In a test of this hypothesis, here we measured approach motivation before and after five sessions of transcranial direct current stimulation to increase excitation in the left or right dorsolateral prefrontal cortex, in healthy adults whose handedness ranged from strongly left-handed to strongly right-handed. The strength and direction of participants' handedness predicted whether electrical stimulation to frontal cortex caused an increase or decrease in their experience of approach-related emotions. The organization of approach motivation in the human cerebral cortex varies across individuals as predicted by the organization of the individuals' motor systems. These results show that the large-scale cortical organization of abstract concepts corresponds with the way people use their hands to interact with the world. Affective motivation may re-use neural circuits that evolved for performing approach- and avoidance-related motor actions.

This article is part of the theme issue 'Varieties of abstract concepts: development, use and representation in the brain'.

1. Introduction

Emotions are a paradigm case of abstract concepts. You can never see *happiness*, even if you can see a smile, or touch *anger*, even if you can feel your face get flushed. Yet, people's abstract emotions appear to be grounded in their concrete interactions with the physical world in multiple ways [1]. Here, we show that the cerebral organization of affective motivation, a basic dimension of human emotions, is predicted by the way people use their hands to perform approach and avoidance actions.

Affective motivation is the predisposition to approach or avoid physical or social stimuli. According to more than a hundred studies, left fronto-temporal cortex subserves approach-related emotions like happiness and anger, whereas right fronto-temporal cortex subserves avoidance-related emotions like disgust and fear [2–7]. Although this pattern is well supported by data, the functional principles that give rise to the observed cortical specialization for emotions have remained unclear. Links between action and emotion suggest a possible organizing principle.

People often use their dominant hand for approach actions, and their non-dominant hand for avoidance actions [8–10]. For instance, people tend to use the dominant hand to grab a small ball (an approach action), but raise the non-dominant hand reflexively to protect themselves if a ball is thrown at them unexpectedly (an avoidance action, [10]). In an iconic illustration of these action tendencies, swordsmen in centuries past wielded the sword in their dominant hand to attack the enemy (an approach action) and raised the shield with their non-dominant hand to fend off attack (an avoidance action).

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Putting together this 'sword and shield' pattern of hand actions with the results of numerous studies of motivation in the brain, we observed that, for right-handers, the hemisphere that controls the hand preferred for approach actions is also specialized for approach motivation, and the hemisphere that controls the hand preferred for avoidance actions is specialized for avoidance motivation. This may be no mere coincidence.

According to the *sword and shield hypothesis* [8], affective motivation in the cerebral cortex depends on neural systems for planning and performing motivated actions with the dominant and non-dominant hands. Specifically, we hypothesized that the cortical substrates of approach motivation overlap functionally and anatomically with cortical circuits for performing approach actions, and the cortical substrates of avoidance motivation with circuits for performing avoidance actions. In previous studies (see [6] for a review), approach-related cortical activity may have been found in the left hemisphere not because the left hemisphere is inherently specialized for approach motivation, but rather because almost every study has tested exclusively right-handed subjects, who tend to perform approach actions with their right hand (i.e. their 'sword hand') and avoidance actions with their left hand (i.e. their 'shield hand'). This proposal predicts that the well-established pattern of hemispheric specialization for approach emotions may only obtain for strong right-handers, and that individual differences in manual motor control should correspond to differences in cortical specialization for motivation.

In a previous study [8], we tested the sword and shield hypothesis using electroencephalography (EEG). Experiments in right-handers have shown that people with stronger trait approach motivation have relatively higher left-hemisphere activation at rest [11–13]. We predicted that this relationship should reverse in left-handers. Consistent with this prediction, we found that stronger approach motivation corresponded to greater left-hemisphere activity in right-handers, but corresponded to greater right-hemisphere activity in left-handers. A significant difference in the laterality of approach motivation in left- versus right-handers was observed robustly, at 10 different pairs of homologous right- and left-hemisphere electrodes, including a pair of superior frontal electrodes (near F3–F4) where approach-related EEG asymmetries have been observed most frequently in right-handers [8].

The current study tested whether the lateralization of approach motivation varies continuously with the strength and direction of individuals' handedness. If there is a functional relationship between the cortical substrates of approach motivation and of motor control for approach-related actions, which are performed preferentially with the dominant hand, then: (i) the hemispheric laterality of approach motivation should reverse between strong left-handers and strong right-handers, as in our earlier EEG study, and (ii) graded differences in handedness should correspond to graded differences in the lateralization of approach motivation.

To test these predictions, we measured approach motivation before and after five daily 20-min sessions of transcranial direct current stimulation (tDCS). In tDCS, a weak electrical current is passed through the cortex by electrodes on the scalp, leading to modulations in excitability of neurons beneath the electrodes [14]. In a double-blind procedure, we used tDCS to increase neural excitability in either the left or right frontal cortex for each participant. We analysed changes in self-reported approach motivation as a function of participants' handedness (measured continuously) and of the polarity of tDCS stimulation they received (left-anodal/right-cathodal or right-anodal/left-cathodal).

2. Material and methods

(a) Participants

Participants ($N = 30$) were recruited from The New School university community, postings to the website www.craigslist.org/, and a database of participants who had taken part in other studies in our laboratory. This sample size was determined on the basis of previous studies that used similar tDCS methodology to test the effect of frontal cortex stimulation on emotion; in particular, we followed Boggio *et al.* [15] who concluded on the basis of a power analysis that '20 [participants] (10 in each group) were needed to detect group difference'. By recruiting 30 participants, we ensured that there were at least 10 participants in each group.

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. All participants were paid in exchange for their participation. All procedures were approved by the Institutional Review Board at The New School (New York, NY, USA).

To ensure participants' safety, we excluded respondents from participation 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 excluded during the first session when low scalp impedance could not be obtained. Four additional participants did not complete all five sessions of the study (right-excitatory stimulation, $n = 2$; left-excitatory stimulation, $n = 2$) and were excluded. Data were analysed from the remaining 25 participants (right-handers, Edinburgh Handedness Inventory (EHI) > 40: $n = 17$; non-right-handers, EHI < 40: $n = 8$). Age and gender demographics were not collected.

(b) Materials and procedure

(i) Overview

This study took place over five consecutive days (Monday–Friday). Informed consent was obtained at the beginning of each session. Participants were paid at the end of every session, with a bonus at the fifth session.

On day 1, participants completed a battery of pre-stimulation tests, including two questionnaires measuring motivation and two continuous measures of handedness (see below). Participants also completed a working memory task that is not relevant to the present study. After participants finished these tasks, we applied the first session of tDCS. On days 2–4, we applied tDCS after ensuring that participants had not experienced any discomfort after the previous sessions. On day 5, participants underwent tDCS and then performed the same tasks as on day 1. Participants also completed a brief adverse effects questionnaire. Upon finishing the study, participants were debriefed and encouraged to contact the experimenter if they had any further questions or experienced any discomfort.

(ii) Measuring state approach motivation

Participants completed an untimed, computerized version of the Positive and Negative Affect Scale (PANAS-X) [16]. Emotion words (e.g. 'interested') 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. We measured approach motivation using the approach-affect subscale [16], which included the following items: *enthusiastic*, *active*, *interested*, *strong*, *excited*, *determined*, *inspired*, *alert*, *proud*.

We focused on approach motivation for two reasons. First, there is disagreement among theorists as to whether 'avoidance motivation' refers to the tendency to *not act* [17] or the tendency to act so as to withdraw or defend oneself [2]. The latter meaning of 'avoidance' is relevant to our experimental hypothesis, but we are not aware of any validated, non-clinical scales that measure avoidance motivation in this sense of the tendency to perform avoidance-related actions. Second, previous studies have found that approach motivation is more reliably associated with asymmetric cortical activation than avoidance motivation ([2,11,12]; but see [18]). Therefore, here we only tested associations between EHI and the hemispheric laterality of approach motivation, as in our previous EEG study [8].

(iii) Measuring trait approach motivation

In addition to the PANAS, participants completed the Behavioral Activation System/Behavioral Inhibition System (BIS/BAS) scales [19] as a measure of dispositional trait motivation. Because the BIS/BAS scales measure stable personality traits, we did not expect that short-term tDCS would influence responses on these scales.

(iv) Handedness

Participants completed the EHI as an index of manual motor asymmetries [20]. This scale provides a continuous measurement of handedness, with scores varying from strongly left-handed (−100) to strongly right-handed (100). EHI was collected in only the first session for the first seven participants, and in both the first and final sessions for the remaining 18 participants.

In addition, all participants completed a finger-tapping task as a measure of simple performance differences between the hands. Participants tapped with one index finger on the spacebar of a computer as quickly they could for 10 s. Participants performed three trials with each hand for six trials total, alternating hand on each trial. Starting hand was randomly assigned. Asymmetry scores were calculated as R–L, where R and L are the total taps produced with the right and left index fingers in all blocks.

(v) 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, direct 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 dorsolateral prefrontal cortex (DLPFC) at F3–F4 in the 10–20 system [21]. Because the current is likely to spread diffusely into the cortex, we do not assume that stimulation was restricted to DLPFC, but that a range of frontal areas were affected. An experimenter was in the room with the participant at all times to ensure that stimulation remained comfortable.

Stimulation was delivered using a double-blind procedure in two between-subjects conditions. Before beginning the study, a polarity-blinding box was set to either reverse the polarity of the outgoing wires, or leave polarity unchanged. 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 (left) and the cathode above F4 (right), exciting left frontal areas while inhibiting right frontal areas (left-excitatory).[1] In the second condition, the anode was placed above F4 (right) and the cathode above F3 (left), exciting right while inhibiting left frontal areas (right-excitatory). Stimulation condition remained the same across all five sessions for each participant. Of the participants retained in the final analysis, 10 received right-excitatory stimulation and 15 received left-excitatory stimulation.

3. Results

We analysed changes in approach emotional state as a function of tDCS polarity and the participants' EHI scores. We computed the mean of each participant's responses in the approach subscale, separately for the pre-stimulation and post-stimulation sessions. We then computed the change in approach motivation as the difference between sessions (Session 2 − Session 1). A first set of analyses treated handedness as categorical, for comparison with previous EEG results. Of primary interest, a second set of analyses treated handedness as continuous. Following these main analyses, further analyses were conducted to confirm that tDCS had no effect on trait motivational tendencies or on handedness.

(a) Effects of transcranial direct current stimulation on motivation with handedness coded categorically

Lateralized tDCS changed participants' experience of approach-motivated emotions and had opposite effects on right-handers and non-right-handers, according to a two-way ANOVA predicting the change in approach motivation as a function of tDCS polarity (right-excitatory and left-excitatory) and handedness (right-handers and non-right-handers) ($F_{1,21} = 35.1$, $p = 0.000007$, $\eta^2 = 1.34$, figure 1*a*). In right-handers, approach emotions increased after left-excitatory stimulation relative to right-excitatory stimulation ($t_{11.5} = 2.6$, $p = 0.02$, $d = 1.32$). Non-right-handers showed the opposite pattern: approach emotions increased after right-excitatory stimulation but decreased after left-excitatory stimulation ($t_{4.44} = -7.8$, $p = 0.001$, $d = 4.97$). This categorical between-group difference is consistent with the results of an EEG study, showing that greater approach motivation correlated with more left-hemisphere activity during rest in right-handers, but with more right-hemisphere activity during rest in left-handers [8].

(b) Effects of transcranial direct current stimulation on motivation with handedness coded continuously

For our main analysis of interest, we used linear regressions with handedness coded continuously (from −100 to 100 EHI) to test for covariation between manual motor asymmetries and the hemispheric lateralization of approach motivation. The effects of left- versus right-hemisphere tDCS on the experience of approach emotions covaried continuously with the individual participants' strength of handedness ($\beta = -0.14$, s.e. $= 0.03$, $t = -5.1$, $p = 0.00004$; figure 1*b*). After left-excitatory stimulation, stronger right-handedness was correlated with a greater increase in approach emotions and stronger left-handedness with a greater decrease in approach emotions ($\beta = 0.10$, s.e. $= 0.02$, $t = 4.7$, $p = 0.0004$). By contrast, after right-excitatory stimulation stronger left-handedness was correlated with a greater increase in approach emotions, and stronger right-handedness with a greater decrease ($\beta = -0.04$, s.e. $= 0.02$, $t = -2.3$, $p = 0.05$).

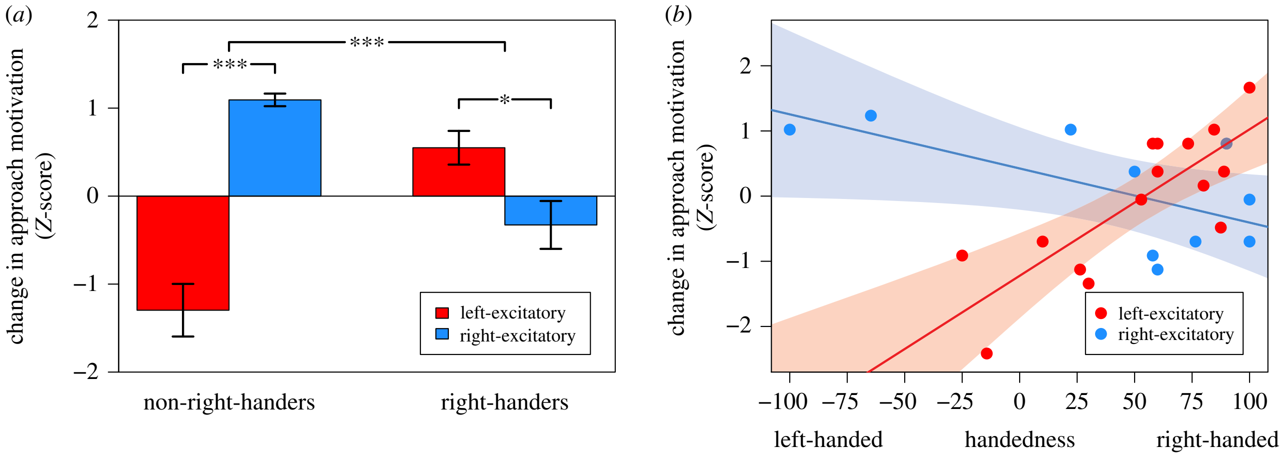

Figure 1. The laterality of approach motivation covaries with manual motor asymmetries. (*a*) Change in approach motivation (last day − first day) plotted separately for right- and non-right-handers, and for left- and right-excitatory tDCS. Error bars show standard error of the mean for responses averaged by subjects. *$p < 0.05$, ***$p < 0.001$. (*b*) Change in approach motivation plotted for each participant as a function of their handedness, measured continuously. Each point shows the *Z*-transformed change in approach motivation for one participant. Best-fit regression lines are plotted separately for participants who received left-hemisphere excitatory stimulation and right-hemisphere excitatory stimulation, with 95% confidence intervals on the regression lines shown as shaded areas.

To ensure that our findings were not driven unduly by a small number of strong left-handers, we performed additional analyses using robust regressions with Huber weights. Significance was determined with robust *F*-tests using the 'f.robftest' function in the *sfsmisc* library in R. Robust regression analyses supported the conclusions from the previous analyses. As in the standard regression analyses, robust regressions revealed a significant effect of handedness on approach emotions after left-excitatory stimulation ($t = 4.69$, $F = 22.042$, $p = 0.0004$), a marginally significant effect of handedness on approach emotions after right-excitatory stimulation ($t = -2.05$, $F = 4.30$, $p = 0.07$) and a significant interaction of handedness and tDCS polarity ($t = -4.88$, $F = 23.99$, $p = 0.00008$).

(c) Effects of transcranial direct current stimulation on trait motivation

As expected, trait approach motivation was not influenced by tDCS. No stimulation-by-handedness interaction emerged in either BAS or BIS ($p > 0.9$). This indicates that a single week of tDCS influenced only state approach motivation (measured by the PANAS scale, reported in the main analyses of the paper), but not trait approach motivation, which is believed to be a stable aspect of personality [16].

(d) Effects of transcranial direct current stimulation on handedness

As expected, tDCS had no measurable effect on participants' handedness. EHI scores were almost identical between the two testing sessions ($r = 0.98$, $n = 18$ participants with EHI collected at both sessions), overall, and differences in stimulation polarity did not cause differential changes in EHI scores between sessions ($t_{12.3} = -1.5$, $p = 0.16$). Finger-tapping asymmetries were more variable ($r = 0.56$), but were similarly unaffected by stimulation polarity ($t_{22.8} = 0.28$, $p = 0.78$). Participants' day-1 finger-tapping asymmetries did not correlate with their day-1 EHI scores ($n = 25$, $r = -0.05$, $p = 0.8$). EHI was used for all hypothesis testing, because it was more reliable than finger tapping and has been used more widely in previous studies.

(e) Adverse effects

The study was terminated prior to completion for one participant who reported a headache. Three other participants requested that the stimulation intensity be reduced for several minutes in one session; all three completed the study. Of these, four participants reporting discomfort, two had received left-excitatory stimulation and two right-excitatory stimulation. No other subjects reported notable discomfort.

4. Discussion

By manipulating asymmetries in cortical excitability with five sessions of tDCS, we showed that hemispheric specialization for approach motivation covaries with specialization for motor control of the dominant hand. This relationship was found both when we coded handedness categorically and when we coded it continuously. In strong right-handers, left-excitatory tDCS led to increased approach motivation, whereas right-excitatory tDCS led to decreased approach motivation. In non-right-handers, by contrast, we found the opposite pattern: right-excitatory tDCS increased approach motivation and left-excitatory tDCS decreased it. Furthermore, we found continuous covariation between hand dominance and motivation in the brain: stronger motor asymmetries corresponded to stronger lateralization of motivation. These results support the sword and shield hypothesis [8], showing that the laterality of approach motivation covaries continuously with the laterality of manual motor control, and suggesting a functional relationship between cortical circuits for action and emotion.

These results provide a conceptual replication of our earlier EEG study, showing that approach motivation was lateralized to the left hemisphere in right-handers and to the right hemisphere in left-handers [8]. Taken together, these studies provide a novel explanation for a large body of previous data showing a left-hemisphere bias for approach motivation [2–7,24]. This bias may have emerged in previous studies because the cortical organization of motivation reflects the organization of the motor system, and because most previous studies tested only strong right-handers for whom motor control of the 'sword hand', which is used preferentially for approach actions, is strongly lateralized to the left hemisphere.

The laterality of motivation typically observed in strong right-handers has been interpreted as indicating that the left hemisphere is specialized for approach motivation. However, continuous variation in the effects of tDCS across individual subjects (figure 1*b*) supports the conclusion that *neither hemisphere* is inherently specialized for approach motivation. Rather, approach motivation is distributed across both cerebral hemispheres, with the strength and direction of lateralization varying as a function of the consistency with which individuals tend to perform approach- and avoidance-related actions with their right and left hands.

(a) What other cognitive functions reverse with handedness?

The complete reversal of hemispheric specialization between strong left- and right-handers sets motivation apart from other lateralized cognitive functions. Lateralization of language depends only weakly on handedness. Like most right-handers, the majority of left-handers (approx. 75%) also have language lateralized to the left hemisphere [24–26]. According to one large-scale fMRI study ($N = 297$), the correlation between handedness and language laterality is 'barely above the chance level' [26]. According to another large-scale study using transcranial Doppler imaging ($N = 310$), 'degree of hand-preference [does] not mirror degree of language lateralization' [27].

The long-standing belief that left-handers tend to have reversed language dominance has been largely debunked. Therefore, previous proposals that have linked the cerebral laterality of approach actions or emotions to the laterality of language cannot explain the present data [7,28]. Like language, some aspects of visuospatial cognition that are clearly lateralized in right-handers are more variable in left-handers [29,30], but neither the laterality of language nor of visuospatial cognition *reverses* with handedness. By contrast, the laterality of dominant-hand motor control does reverse and, accordingly, so does the laterality of approach motivation.

(b) Previous links between action and affective motivation

Some connections between affective motivation and action tendencies have been proposed previously [28], and two previous links between motivation and hand actions have been found [19,31]. Importantly, however, these previous proposals do not predict or explain the pattern of data shown here.

Cacioppo *et al.* [31] found that ideographs presented during arm flexion movements were judged to be more positive in valence than those presented during arm extension movements. The authors predicted this result on the basis of an association between action and motivation: people tend to make flexion movements when performing approach-related actions (e.g. eating something desirable), and extension movements when performing avoidance-related actions (e.g. rejecting something undesirable). Although these findings are important for a full understanding of connections between action and emotion, they cannot explain the cerebral laterality of motivation (nor were they intended to do so). In the original study by Cacioppo *et al.* [31] and many follow-ups, participants made flexion and extension movements with *both hands* simultaneously, presumably activating both hemispheres. Cacioppo and co-workers [32] trace the neural basis of the flexion–extension effect to bilateral spinal motor neurons, not to the cerebral hemispheres. The flexion-approach/extension-avoidance code appears to be a different link between action and motivation, separate from the action–motivation link posited by the sword and shield hypothesis.

Of greater relevance, Harmon-Jones [19] showed that unilateral hand contractions increased contralateral frontal activity, and that right-hand contractions increased approach-related emotions relative to left-hand contractions. In closing, Harmon-Jones speculated that 'perhaps basic approach motivational movements are accomplished more often and/or efficiently via the right hand or right side of the body', consistent with the sword and shield hypothesis. However, Harmon-Jones's study did not test for effects of handedness and was not predicated on any differential hand use for approach versus avoidance actions, but rather on the assumption that approach motivation is generally lateralized to the left hemisphere—an assumption challenged by the sword and shield hypothesis and by the data we present here.

(c) Evolution of neural systems for action and emotion

The sword and shield hypothesis may clarify not only *how* motivation is organized in the cerebral cortex, but also provide a potential explanation for *why* it is organized this way: neural circuits for affective motivation may be built upon neural circuits that control approach- and avoidance-motivated actions. Approaching or avoiding stimuli is perhaps the most basic of all behaviours, found even in single-celled organisms that are unlikely to form affective states or intentions as humans do. We posit, therefore, that approach and avoidance actions are ontologically prior to approach and avoidance motivational states, and that neural circuits for affective motivation may re-use neural circuits that evolved primarily for performing motor actions. Affective motivational states may consist in highly abstracted motor plans, which indicate a state of readiness to perform either approach- or avoidance-related actions.

(d) Caveats and future studies

One caveat in interpreting the results of this experiment concerns the sample size. Because neurostimulation studies carry some potential risk for subjects (and potential discomfort), sample sizes for (multi-session) tDCS studies tend to be smaller than samples for purely behavioural studies. Our sample size was consistent with established standards for this literature, however, and multiple aspects of the results suggest that this sample size was sufficient. Chiefly, a complex pattern of data was predicted *a priori*, and all of the predicted effects (i.e. two contrasting simple effects and a particular interaction) were statistically significant, no matter whether we analysed the data using a categorical or a continuous coding of handedness.

To elaborate, the effect of left-excitatory stimulation, and the difference between the effects of left- and right-excitatory stimulation, remained highly significant under all three analysis strategies we used: ANOVA with categorical coding of handedness, regression with continuous coding of handedness and robust regression with continuous coding of handedness. The effect of right-excitatory stimulation was significant under the first two analyses, and marginally significant under the third ($p = 0.07$), due to the small sample size in the right-excitatory group. Importantly, the sample size in this group was equal to the minimum sample size indicated by a previous tDCS study by Boggio *et al.* [15], which we adapted. Validating Boggio *et al.*'s recommendation, this sample size was sufficient to allow us to detect highly significant differences between treatment groups (i.e. left- versus right-excitatory stimulation groups) in the predicted direction, in all analyses.

Ideally, increasing the sample size would allow us to report a highly significant effect in the right-excitatory group in all analyses as well, and to fill in segments of the handedness continuum where the data were sparse (due to our double-blind procedure). We elected not to increase the sample size, however, for two reasons. First, *all predicted effects were statistically significant in the planned sample*, by ANOVA and by standard regression analyses. Second, increasing excitability in the 'shield' hemisphere caused a *decrease* in participants' experience of positive, approach-related emotions, as predicted by the sword and shield hypothesis. For example, left-excitatory stimulation caused non-right-handers' experience of approach emotions to decrease by about a standard deviation, on average (figure 1*a*, left). In short, our treatment made about half of our participants feel worse. Given this finding, it would be unethical to increase the sample size without strong justification; because all of the predicted effects were significant in the planned sample, we do not believe we had any such justification.

Consistent with current statistical practices, we do not rely on the statistical significance of these results alone to gauge our confidence in them, but also on their effect sizes [33]. The observed effects were large. In our categorical analysis, for example, the partial η^2 value for the critical interaction was 1.34: much greater than the conventional threshold for a 'large' effect, which is 0.14. Likewise, the Cohens's d value for the simple effects in right-handers and non-right-handers was 1.32 and 4.97, respectively: much larger than the conventional threshold for a 'large' effect, which is 0.80 [34].

All statistical measures aside, the best indication of reliability is widely agreed to be replication [35,36]. Overall, the pattern of results we show here is a conceptual replication of our previous EEG study testing the sword and shield hypothesis [8]. Our effect of left-excitatory stimulation on emotion in right-handers is a conceptual replication of previous tDCS results in right-handers [15]. Finally, because our two stimulation conditions show complementary effects of handedness and hemisphericity on emotion, our right-excitatory stimulation condition can be considered a conceptual replication of our left-excitatory stimulation condition: two statistically independent tests of the sword and shield hypothesis. Future studies should seek to generalize these findings to a new sample of healthy participants (with proper oversight from a clinician) and also to extend them to a clinical population.

Future studies could also consider whether the relationships predicted by the sword and shield hypothesis extend to non-human animals. Many non-human animals tend to perform motivation-related actions on particular sides of their bodies [37]. For example, chicks tend to use their right eye to search the ground for food (an approach-motivated action) while their left eye scans the sky for predators (an avoidance-motivated action) [38]. Such behavioural asymmetries—whether or not they involve differential use of the *hands*—may correlate with the lateralization of approach motivation in non-human animals' brains.

(e) Potential clinical implications of the body-specific organization of motivation

Our results support the body-specificity hypothesis: individuals with different kinds of bodies, who interact with the environment in systematically different ways, develop corresponding differences in their brains and minds [39]. In addition to addressing basic scientific questions, our findings raise questions about clinical treatments for psychiatric disorders.

Individual differences in the neural organization of motivation may have urgent implications for the safety and success of neural therapies for anxiety disorders and depression. Clinicians use tDCS or transcranial magnetic stimulation (TMS) to stimulate left frontal areas in order to promote positive, approach-related emotions [15,40–42]. Yet, this treatment is predicated on the assumption that the left hemisphere is specialized for approach motivation. Our results indicate that this assumption may be false for non-right-handed people, who constitute approximately 40–50% of the general population (depending on how handedness categories are defined) [43]. Given that the present study tested only healthy non-clinical volunteers, conclusions about clinical treatments would be premature. Nevertheless, these results suggest that neurostimulation treatments that benefit strong right-handers could be ineffective or detrimental for everyone else, and that neural therapies for common psychiatric disorders should be tailored to the specifics of people's bodies.

Data accessibility. Data can be found at https://osf.io/zp5nt.

Authors' contribution. G.B. and D.C. designed the study and wrote the paper. G.B. and C.G. collected the data, and G.B. analysed the data.

Competing interests. We declare we have no competing interests.

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Endnote

[1] Although cathodal tDCS is often assumed to be inhibitory, 2 mA cathodal stimulation has also been found to have an effect that either is no different from sham stimulation [22] or is excitatory [23]. Our study does not rely on the assumption that cathodal stimulation is inhibitory, only on the assumption that anodal stimulation will be *more* excitatory than cathodal stimulation. If anodal and cathodal stimulation were equally excitatory, then the treatment we performed would be ineffective in changing the balance of neural excitability across hemispheres, and we could not find the predicted results.

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