

Neural Basis of Motivation Lateralizes with Motor Control

Geoffrey Brookshire^{1,2} & Daniel Casasanto^{1,2,3}

¹Neurobiology of Language Department, Max Planck Institute for Psycholinguistics,
Nijmegen, NL

²Department of Psychology, The New School for Social Research, New York, NY

³Donders Institute for Brain, Cognition, & Behaviour, Nijmegen, NL

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Please address correspondence to:
Daniel Casasanto
The New School for Social Research
Department of Psychology
80 Fifth Avenue, 7th Floor
New York, NY 10011
casasanto@alum.mit.edu

Abstract

According to decades of research on affective motivation in the human brain, approach motivational states are subserved by the left hemisphere and avoidance states by the right hemisphere. Here we show that hemispheric specialization for motivation reverses with handedness. This covariation provides initial support for the *Sword and Shield Hypothesis*, according to which hemispheric laterality of affective motivation is causally linked to motor control for the dominant and non-dominant hands.

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Emotional states are intimately linked to actions, and to the hands people use to perform them. *Approach* actions are usually performed with the dominant hand, and *avoidance* actions with the nondominant hand¹⁻³. In centuries past, sword fighters wielded the sword in the dominant hand when approaching an enemy, and raised the shield with the nondominant hand to avoid attack². The tendency to approach with the dominant hand and avoid with the nondominant hand is evident in more ordinary motor actions, as well^{1,3}.

In right-handers, approach- and avoidance-related motivational states are differently lateralized in the brain. The left hemisphere subserves approach emotions, and the right hemisphere avoidance emotions^{4,5}. This means that, for right-handers, approach motivation is co-lateralized with the neural circuits primarily responsible for control of the dominant hand, and avoidance motivation with circuits that control the nondominant hand. Casasanto proposed that affective motivation and motor control may co-lateralize due to a functional relationship between motivational states and approach and avoidance hand actions, established either over evolutionary or

developmental time¹. We call this the *Sword and Shield Hypothesis* (SSH). If the SSH is correct, then the hemispheric laterality of approach and avoidance motivation found previously in right-handers should reverse in left-handers, for whom cortical control of the “sword hand” (used for approach actions) and “shield hand” (used for avoidance actions) is reversed.

To test this prediction, we used electroencephalography (EEG) to compare hemispheric asymmetries in alpha-band (8-12 Hz) power between right-handers and left-handers (see **Supplementary Methods**). Alpha power was recorded during 3 minutes of resting EEG. Trait approach-motivational tendencies were measured with the Behavioral Activation Scale (BAS)⁶, and handedness with the Edinburgh Handedness Inventory (EHI)⁷. Approach motivation has been shown to correlate with reduced alpha power (indicating increased neural activity⁸) in the left hemisphere compared to the right hemisphere, for right-handers⁹. We observed this well-established pattern in right-handers (BAS Score \times Hemisphere interaction: Wald $\chi^2(1)=18.29$, $P=.00002$; **Fig. 1a, right**), but we found the opposite pattern in left-handers, for whom approach motivation was lateralized to the right hemisphere (BAS Score \times Hemisphere interaction: Wald $\chi^2(1)=6.08$, $P=.01$; **Fig. 1a, left**). Combining data from right- and left-handers, Handedness (EHI Score) interacted with Motivation (BAS Score) and Hemisphere (Left, Right) to predict alpha power (Wald $\chi^2(1)=14.50$, $P=.0001$; **Fig. 1b**), indicating that the hemispheric correlates of motivation reversed with handedness.

Stronger approach-motivational tendencies were associated with more left-hemisphere activity in right-handers, but with more right-hemisphere activity in left-handers. These results provide initial support for the SSH. Anatomical covariation between the neural substrates of affective motivation and of manual motor control is a

prerequisite for the proposed functional relationship between action and emotion in the brain¹.

Behavioral studies have shown differences between left- and right-handers for processing laterally presented positive and negative stimuli, and some authors have interpreted these data as evidence for differences in the hemispheric laterality of emotional valence^{10,11}. These studies may not be informative about the laterality of motivation, however, which is dissociable from valence^{5,12}. Furthermore, these studies may not be informative about the hemispheric laterality of emotion at all, given that subsequent studies show similar handedness-related differences for processing laterally presented positive and negative stimuli that were perceived bi-hemispherically¹.

Many cognitive functions show some variation with handedness. Aspects of language and spatial cognition that are clearly lateralized in right-handers are more bilaterally distributed in left-handers^{13,14}. The complete *reversal* of hemispheric specialization that we observe here, however, is rarely found – except in the motor system.

These findings have potential clinical implications. To decrease symptoms of depression, transcranial magnetic stimulation (TMS) is used to shift the balance of neural activity toward patients' left hemispheres, in order to stimulate approach-related emotions¹⁵. Given the hemispheric reversal we show here, however, lateralized neurostimulation therapies that are beneficial to right-handers could be detrimental to left-handers.

On the basis of the alpha-power asymmetry in right-handers shown in dozens of studies, the left-hemisphere locus of approach motivational states is widely

accepted as a fact^{5,9}. The present findings, therefore, call for a substantial revision to models of emotion in the brain.

Furthermore, these results suggest that the hemispheric laterality of emotion is principled, not arbitrary, and may not pose an enduring mystery like the laterality of language has. Affective motivation co-lateralizes with manual motor control, consistent with the way people use their right and left hands differentially to perform approach and avoidance actions.

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Author Contributions

D.C. and G.B. designed the study and wrote the manuscript. G.B. carried out the experiment and analyzed the data.

Figure caption

Figure 1 Hemispheric specialization for affective motivation depends on handedness.

(a) Scalp topography of the statistical significance of the Approach Motivation (BAS) \times Hemisphere (Right/Left) interaction on resting alpha-band power, computed and plotted separately in left-handers (left, N = 12) and right-handers (right, N = 34). P-values were computed independently at each homologous electrode pair using linear mixed-effects regressions with BAS and Hemisphere as fixed effects and Subject as a random effect. $\log_{10}(P)$ is plotted with darker areas denoting higher statistical significance. The circled electrodes, chosen on the basis of prior studies⁹ and the topography we observed in right-handers, were used for the analyses reported in the main text. **(b)** Asymmetries in alpha power at the highlighted electrode plotted for each subject as a function of BAS score. Asymmetry scores were computed as $(\text{Left-hemisphere} - \text{Right-hemisphere}) / (\text{Left-hemisphere} + \text{Right-hemisphere})$. More positive values denote higher left hemisphere alpha power (and therefore less activity in the left hemisphere than in the right hemisphere).

Supplementary Information

Methods

Participants

Dutch-speaking participants (N = 46, 12 male) were not ambidextrous ($|EHI| \geq 25$), and had no history of psychiatric disorders or brain injury (34 right-handers, 7 male, mean EHI = 83.1 ± 17.0 ; 12 left-handers, 5 male, mean EHI = -80.5 ± 13.8).

Procedure

Participants remained still during six 1-minute blocks of resting-state EEG. Each participant performed three blocks with their eyes closed and three with their eyes open, looking at a blank screen during the eyes-open blocks. Blocks alternated between open and closed eyes, with block order randomized between participants. After EEG, participants completed Dutch translations of the Behavioral activation System (BAS)¹ scale and the Edinburgh Handedness Inventory (EHI)². There was no relationship between handedness and BAS ($r = -0.004$, $P > .9$), and BAS scores were indistinguishable between the handedness groups (Right-handers: 23.2 ± 4.2 ; Left-handers: 23.0 ± 5.7).

EEG Recording

EEG was recorded with a 64-channel active electrode system, with the online reference electrode at the left mastoid and the ground at the nasion. Signals were sampled at 500 Hz with an online 1000 Hz low-pass filter and a 10 sec time constant (.016 Hz). Impedances between electrodes were reduced to 10 k Ω . Continuous EEG

signals were segmented into 62-second epochs, including 1 sec at the beginning and end of each block of resting EEG.

Data Analysis

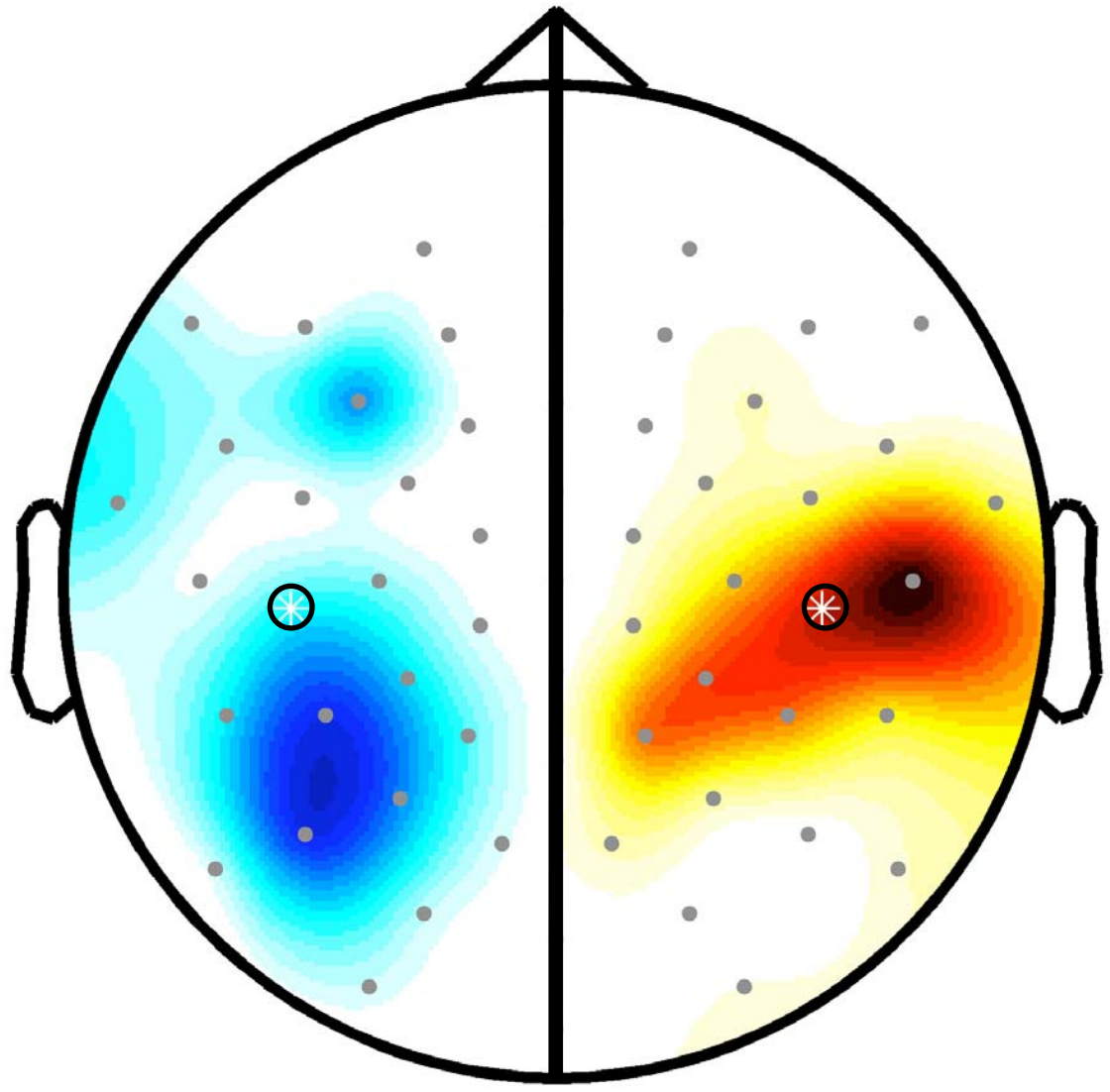
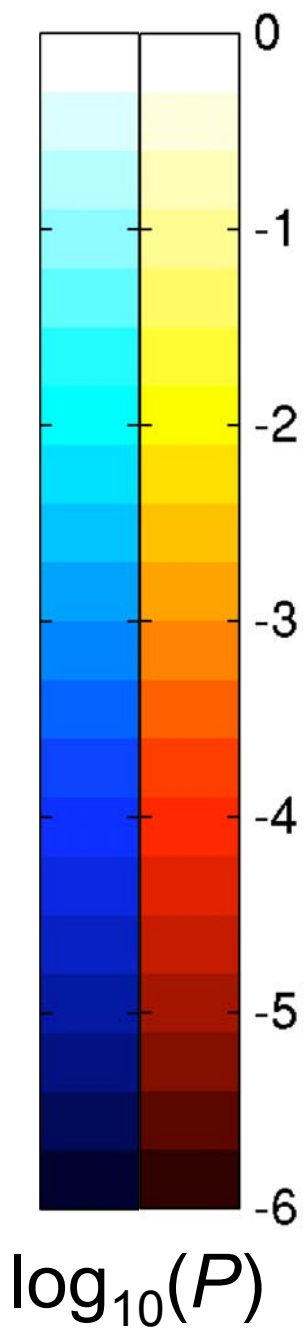
We analyzed only eyes-closed blocks, which provide the most sensitive measure of the relationship between alpha-power asymmetry and BAS³. Because prior studies have found that alpha-power asymmetry depends on BAS and not on BIS^{3,4}, we used only BAS. On the basis of prior studies^{5,6} and the scalp topography we observed in right-handers, one site was chosen for comparison across handedness groups (located approximately at T3-4). The statistical analyses reported in the main text were performed on alpha power recorded from this electrode pair (circled in **Fig. 1**). This allowed unbiased selection of electrodes of interest for testing the left-handers and the relationship of hemisphere, BAS, and handedness.

Signal processing and computation of time-frequency representations were performed using the Fieldtrip package for Matlab⁷. Offline, all signals were mathematically re-referenced to the mean of the left and right mastoids, resampled to 300 Hz, and band-pass filtered between 2 - 30 Hz. Eye movement artifacts were excluded blind to the experimental condition with a semi-automated routine using principal component analysis. Time-frequency representations were computed in time steps of 50 ms, centered around 10 Hz with 2 Hz frequency smoothing and 500 ms time smoothing. Each alpha-power value, therefore, comprised the weighted average of activity from 8-12 Hz for an epoch from 250 ms before to 250 ms after the time point, convolved with a Hanning window. Activity for each 60 sec block was averaged and normalized by natural-log transformation. The *ln*-transformed average alpha-power of each block was analyzed using linear mixed-effects regressions with

the statistical package *lme4* in the programming environment R⁸. All significance values were obtained using Wald χ^2 comparisons of model fits. In the full model, Hemisphere (Left/Right), Handedness (continuously entered with EHI scores), and Approach Motivation (continuous with BAS scores) were entered as fixed-effects, and Subject was present in all models as a random-effect.

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Left-handers

Right-handers

