

Motivation and Motor Control: Hemispheric Specialization for Motivation Reverses with Handedness

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Abstract

What is the relationship between action and emotion? People tend to perform approach actions with their dominant hand and avoidance actions with their nondominant hand. In right-handers, the left frontal lobe (which controls the dominant hand) is specialized for approach-motivational states, and the right frontal lobe (which controls the nondominant hand) for avoidance-motivational states. Are brain areas that support affective motivation functionally related to areas that support approach- and avoidance-related motor actions? If so, hemispheric specialization for motivation should covary with hemispheric specialization for motor control. Here we tested this prediction, using electroencephalography (EEG) to compare resting alpha-band power in right- and left-handers. Hemispheric asymmetries in alpha-power, which indexes neural activation, were related to Behavioral Activation System (BAS) scores, which index approach-motivational tendencies. Results show that the pattern observed in right-handers reverses in left-handers, whose right hemisphere is specialized for both approach motivation and for control of dominant-hand actions. This anatomical covariation suggests a functional link between affective motivation and motor control, and also provides information crucial for developing neural therapies for affective disorders.

Keywords: body-specificity hypothesis; EEG; emotion; handedness; hemispheric specialization; motivation.

Introduction

Emotional states are intimately linked to actions, and to the hands people use to perform them. In centuries past, sword fighters wielded the sword in the dominant hand to approach an enemy, and raised the shield with the nondominant hand to avoid attack (Pye-Smith, 1871; in Hardyck & Petrino, 1977). The tendency to *approach* with the dominant hand and *avoid* with the nondominant hand is evident in more ordinary motor actions, as well. When picking a piece of fruit from a tree, for example, people typically pull the fruit toward themselves (an approach action) using their dominant hand and push away the branch (an avoidance action) with the nondominant hand. When startled, people reflexively raise their nondominant hand to protect their face (Coren, 1992), leaving the dominant hand free for more complex actions.

In right-handers, approach- and avoidance-related motivational states are differently lateralized in the frontal lobes of the brain. The left hemisphere subserves approach emotions and the right hemisphere, avoidance emotions (Berkman & Lieberman, 2010; Harmon-Jones, Gable, &

Peterson, 2010). 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 the circuits responsible for control of the nondominant hand. This may be no mere coincidence. Approach motivation may be co-lateralized with dominant-hand motor control *because* the dominant hand is used for approach actions. Likewise, avoidance motivation may be co-lateralized with nondominant-hand motor control because the nondominant hand is used for avoidance actions (Casasanto, 2009). Here we investigated this proposed functional connection between the neural substrates of affective motivation and motor control.

If the laterality of affective motivation in right-handers results from a functional relationship between motivational states and manual motor control, then the hemispheric correlates of motivation should reverse in left-handers, for whom dominant- and nondominant-hand motor control is reversed. Alternatively, if the neural organization of motivation is functionally independent of manual motor control, a different relationship between motivation and handedness should be found. On one possibility, hemispheric specialization for motivation could be similar across most right- and left-handers, as is the case for hemispheric specialization of language (Knecht et al. 2000). Alternatively, although affective motivation appears clearly lateralized in right-handers, it could be bilaterally distributed in left-handers, as is the case for some aspects of spatial cognition (Hellige et al., 1994; Kosslyn, et al., 1989).

Laterality of emotion, then and now

In addition to dozens of studies confirming the hemispheric laterality of affective processing in right-handers (for review see Harmon-Jones, Gable, & Peterson, 2010), a few studies have investigated emotion processing in left-handers (Everhart, Harrison, & Crews, 1996; McFarland & Kennison, 1989; Natale, Gur & Gur, 1983; Reuter-Lorenz, Givis, & Moscovitch, 1983). Although results of these studies are consistent with the hemispheric reversal that we predict, two subsequent discoveries call their interpretation into question.

These studies have two characteristics in common: they all used stimuli that varied in their emotional valence, and they all relied on lateralized presentation of stimuli to the right/left ear or the right/left visual hemifield (VHF). Over the course of three decades, the fronto-temporal hemispheric

asymmetry for emotion in right-handers was firmly established, but it remained unclear to what extent the observed pattern was driven by differences in the neural locus of processing affective valence (emotional positivity or negativity) or affective motivation (the tendency toward approach or avoidance). However, based on newer research, it appears that the hemispheric correlates of valence and motivation can be dissociated, and that motivation can account for the classic fronto-temporal emotional asymmetry independent of valence (Berkman & Lieberman, 2010; Harmon-Jones, Gable, & Peterson, 2010). Therefore, previous studies that appear to show different hemispheric specialization for valence in left- and right-handers may not be informative about the hemispheric correlates of motivation.

The body-specificity of emotional valence

In light of subsequent studies, it appears that studies using lateralized stimulus presentation to compare emotion processing in left- and right-handers may not be informative about the hemispheric correlates of valence, either. According to the logic of these studies, presenting stimuli to one ear (McFarland & Kennison, 1989) or one VHF (Everhart, Harrison, & Crews, 1996; Natale, Gur & Gur, 1983; Reuter-Lorenz, Givis, & Moscovitch, 1983) caused them to be processed initially by the contralateral hemisphere, due to crossing of the auditory and visual pathways. Therefore, responses that differed as a function of the valence of the stimuli, the side of presentation, and the handedness of the participant were interpreted as evidence that valence is lateralized differently in right- and left-handers.

Yet, newer research suggests an alternative interpretation of these VHF and dichotic listening studies. The same relationship of valence, side of space, and handedness found in these studies can be observed even when hemispheric processing is not manipulated (i.e., when stimuli are not presented rapidly or unilaterally). In one study, when participants were presented with pairs of stimuli side by side on a page and asked to judge which of two products to buy, which job applicant to hire, or which of two alien creatures looks more trustworthy, right-handers tended to prefer the product, person, or creature on the right, whereas left-handers tended to prefer the one on the left (Casasanto, 2009). This was true even though stimuli were presented on a piece of paper, under no time pressure, and were presumably processed bi-hemispherically.

Children as young as 5 years old already make evaluations according to handedness and spatial location, judging animals shown on their dominant side to be nicer and smarter than animals on their nondominant side (Casasanto & Henetz, 2011). Beyond the laboratory, the association of good with one's dominant side and bad with the nondominant side can be observed in left- and right-handers' spontaneous speech and gestures (Casasanto & Jasmin, 2010).

These results support the *body-specificity hypothesis* (Casasanto, 2009), according to which people with different kinds of bodies, who interact with their environment in systematically different ways, should form correspondingly different neurocognitive representations – even when thinking about abstract things that they can never see or touch. Right-handers, who interact with the environment more fluently on the right side of space (and less fluently on the left side), come to implicitly associate *good* with *right* and *bad* with *left*, whereas the opposite is true for left-handers (Casasanto, 2009; see also Ping, Dhillon, & Beilock, 2009). This fluency-based explanation was validated in a study testing people whose dominant hand was handicapped, either long-term due to unilateral stroke, or short-term due to motor training in the lab. After a period of acting more fluently with the left hand than the right, natural right-handers implicitly associated *good* with *left*, like natural left-handers (Casasanto & Chrysikou, 2011).

A pair of experiments directly tested whether body-specific space-valence associations in memory could explain classic VHF effects for emotional faces in right- and left-handers, long interpreted as evidence for hemispheric specialization. First, in a standard VHF task, participants judged the emotional valence of faces flashed to the right or left of a central fixation. Right-handers were more likely to classify neutral faces as positive when they appeared on the right, and as negative when they appeared on the left; left-handers showed the opposite pattern, consistent with previous studies (Everhart, Harrison, & Crews, 1996; Natale, Gur & Gur, 1983; Reuter-Lorenz, Givis, & Moscovitch, 1983). Degree of handedness, as measured by the Edinburgh Handedness Inventory (EHI), correlated significantly with the strength of the body-specific effect.

In the second experiment, a new group of natural right-handers performed the same VHF task after being randomly assigned to one of two training conditions (adapted from Casasanto & Chrysikou, 2011). Half of the participants performed a 'motor fluency' task (ostensibly unrelated to the VHF task) with a bulky ski glove on their left hand, which preserved their right-hand fluency. The other half wore the glove on their right hand, which made them transiently more fluent with their left hand. For natural right-handers who had been functionally left-handed during training, face judgments revealed implicit associations of left with positive and right with negative – like natural left-handers (Brookshire & Casasanto, 2011).

Given these results, the robust emotional VHF effects observed over the past three decades can no longer be interpreted as evidence for hemispheric specialization of emotions. The side of space on which stimuli are presented can bias emotional processing even when the stimuli are processed bi-hemispherically. Induced asymmetries in motor fluency can determine the direction of space-valence associations and reverse emotional VHF effects, independent of long-term hemispheric organization. As such, previous studies leave open the question whether the

hemispheric correlates of emotion processing differ between right- and left-handers.

Does motivation lateralize with motor control?

The present study tested whether hemispheric correlates of motivation covary with hemispheric correlates of manual motor action. Given the relationship between handedness and valence found in the behavioral tasks reviewed above, it was necessary to avoid valenced stimuli and responses. Furthermore, to avoid spurious laterality effects due to language processing, visual processing, or motor action, we did not ask participants to perform any task. Instead, we measured participants' resting brain activity and correlated its asymmetry with an offline measurement known to reflect trait approach motivation.

We used EEG to examine resting power asymmetries in the alpha-band (8–12 Hz). Power in this bandwidth inversely correlates with neural excitability (Romei et al., 2007) and BOLD signal (Laufs et al., 2003; Goldman et al., 2002), and is a common index of neural activity. Left-right asymmetry ratios of alpha power at homologous frontal and temporal sites reliably relate to long-term biases in approach motivation as measured by the Behavioral Activation Scale (BAS; Carver & White, 1994).

In right-handers, higher BAS scores, which indicate stronger trait approach motivation, correlate with less left hemisphere alpha power and therefore more left hemisphere activity (Coan & Allen, 2003; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997; but see Hewig et al., 2006). If the brain areas that support approach motivation are functionally related to areas that control dominant hand actions, then the relationship between BAS and alpha-power asymmetry found in right-handers should reverse in left-handers.

Methods

Participants

Native Dutch speakers (N=48, 13 males) participated in exchange for payment. Participants had no history of psychiatric disorders or brain injury. For consistency with prior studies, we excluded 2 participants who were not strongly handed ($|EHI| \leq 25$), leaving 34 right-handers (7 male; mean EHI = 83.1±17.0) and 12 left-handers (5 male; mean EHI = -80.5±13.8).

Procedure

After providing informed consent and being fitted with the electrodes, participants were seated in a normally lit, electrically shielded room. Six resting baseline blocks were then collected in which participants were instructed to remain as still as possible. Each participant performed three blocks with their eyes closed and three with their eyes open, looking to the center of a black computer screen during the eyes-open blocks. The experimenter verbally instructed participants whether to open or close their eyes on each block. Blocks alternated between open and closed eyes, and

the order was randomized between participants. After completing the resting blocks, participants completed Dutch translations of the BIS/BAS scales (Carver & White, 1994), the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971), and several questions unrelated to the present experiment. 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 and a BrainAmps DC amplifier (Brain Products, München). The reference electrode was placed at the left mastoid and the ground at the nasion. Additionally, an electrode was placed at the right mastoid to compute an off-line linked mastoids reference, and one beneath the left eye to screen out blinks and eye movements. Signals were sampled at 500 Hz with an online 1000 Hz low-pass filter and a 10 s time constant (.016 Hz). Impedances between electrodes were reduced to 10 k Ω . The continuous EEG signals were segmented into epochs of 62 seconds, including 1 s at the beginning and end of each block.

Data Analysis

We restricted our analysis to eyes-closed blocks, which provide the most sensitive measure of the relationship between asymmetric alpha-power and BAS scores (Harmon-Jones & Allen, 1997). Because prior studies have found that asymmetrical alpha power depends on BAS and not on BIS (Coan & Allen, 2003; Harmon-Jones & Allen, 1997), we focus our analysis on BAS scores.

Analyses were performed with the FieldTrip package in Matlab (<http://www.ru.nl/fcdonders/fieldtrip/>). After recording, all signals were mathematically re-referenced to the mean of the left and right mastoids. All data was then 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. All activity for each 60-s block was then averaged for statistical analysis and natural-log transformed to normalize the values.

Linear mixed-effects regressions on the \ln -transformed average alpha-power of each eyes-closed block were used for statistical analysis. Models were fit using the *lmer* function from the package *lme4* (Bates, 2007) in the R programming environment (<http://www.R-project.org>). P-values were computed with Wald χ^2 tests comparing two models differing by one parameter at a time. In all models, subject was treated as a random-effect.

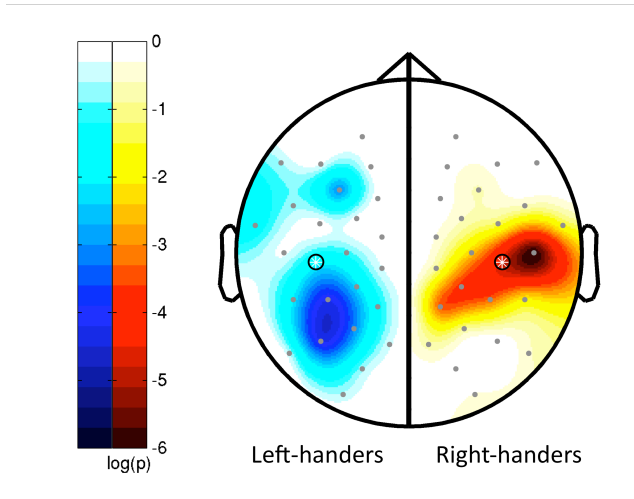


Figure 1: Scalp topography of the statistical significance of the BAS \times Hemisphere interaction, plotted separately in left-handers (left) and right-handers (right). P-values were computed independently at each electrode pair, and $\log_{10}(p)$ was plotted with dark areas denoting higher statistical significance. Because these values reflect comparisons across the left and right hemispheres, only one hemisphere was plotted for each handedness group. The electrodes used in subsequent analyses are circled.

Results

To determine whether results of this experiment replicated previous findings on the relationship between BAS and resting asymmetry, we first analyzed data from right-handers, alone. Higher BAS scores correlated with greater right-sided alpha-power at frontal, superior parietal, and temporal sites (fig. 1, right). The topography of this BAS \times Hemisphere interactions is posterior to that usually reported in emotional/motivational lateralization (Coan & Allen, 2003; Gable & Harmon-Jones, 2007; Harmon-Jones & Allen 1998; Sutton & Davidson, 1997). On the basis of prior studies and the scalp topography in right-handers, one site was chosen for comparison across handedness groups (located approximately at T3-4). All further statistical analyses were performed on alpha power recorded from this electrode pair. This allowed unbiased selection of electrodes of interest for testing the left-handers and the relationship of hemisphere, BAS, and handedness.

The 3-way interaction of Hemisphere (Right, Left) \times BAS score (continuous) \times Handedness (continuous using EHI) was highly significant ($\chi^2(1) = 14.50, p = .0001$; fig. 2), indicating that hemispheric specialization for approach motivation varies as a function of handedness. In right-handers, the BAS \times Hemisphere interaction was highly significant ($\chi^2(1) = 18.29, p = .00002$; fig. 2, right). High BAS scores predicted less alpha-power (and therefore more activity) in the left hemisphere. In left-handers, the pattern observed in right-handers was reversed: high BAS scores predicted less alpha-power in the *right* hemisphere ($\chi^2(1) = 6.08, p = .01$ fig. 2, left; topography: fig. 1, left).

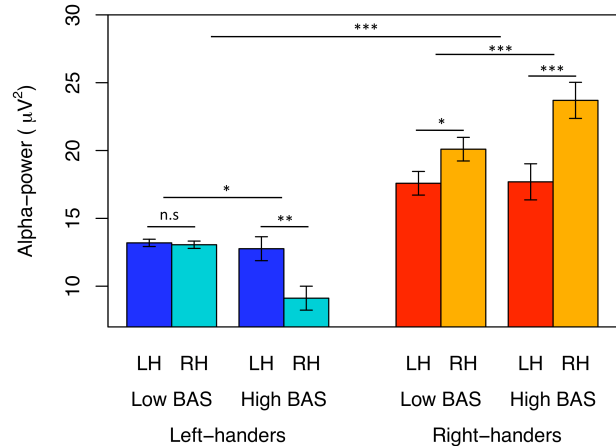


Figure 2: Mean alpha-band power in each hemisphere (LH = left hemisphere; RH = right hemisphere) for left- and right-handed participants with High and Low BAS scores. Bar heights represent power averaged across mean-split BAS score groups. Error bars indicate within-subject s.e.m. (* $p < .05$; ** $p < .01$; *** $p < .001$)

There were no main effects of BAS ($\chi^2(1) = 10^{-11}, ns$; cf. Hewig et al., 2006) or EHI-scored handedness ($\chi^2(1) = .00005, ns$). Although not relevant to the goals of this study, we found a significant main effect of the strength of handedness: higher absolute values of EHI scores were related to lower alpha-power ($\chi^2(1) = 4.40, p = .04$). This suggests that more strongly handed people have lower levels of baseline alpha-power, i.e. higher overall resting activity.

We also found an unanticipated effect of handedness on resting alpha asymmetry. Collapsing across variation in BAS scores, Handedness interacted with Hemisphere to predict alpha power ($\chi^2(1) = 7.81, p = .005$). In both right- and left-handers, the hemisphere contralateral to the dominant hand displayed less alpha-band power (and therefore greater activity) than the ipsilateral hemisphere.

Discussion

Hemispheric specialization for affective motivation reverses with handedness. As evidence of this reversal, we show here that Hemisphere, Handedness, and BAS score interact to predict resting-state neural activity in the alpha frequency band. In right-handers, approach motivational tendencies are lateralized to the left hemisphere, but in left-handers they are lateralized to the right hemisphere.

The emotional alpha-asymmetry in right-handers, which we validate here, is so well established that it has led many researchers to adopt the left-laterality of positive-approach states and the right-laterality of negative-avoidance states as facts about the brain (Kinsbourne, 1978; see also Coan & Allen, 2003; Davidson, et al., 1990; Harmon-Jones, et al., 2010), just as the left-laterality of language is an accepted fact. The finding that the alpha-asymmetry for motivation reverses with handedness calls for a substantial revision to models of emotion in the brain.

The pattern we find suggests that the hemispheric laterality of emotion is principled — not arbitrary — and may not pose an enduring mystery like the laterality of language. Specifically, we show that hemispheric specialization for motivation follows specialization for control of motor actions with the dominant hand. We predicted this relationship based on prior evidence that people tend to use their dominant hand for approach actions and their nondominant hand for avoidance actions, and evidence that they associate “good” with their dominant side and “bad” with their nondominant side. The anatomical covariation we demonstrate here provides initial support for a proposed functional relationship between the neural substrates of motivation and motor control (Casasanto, 2009; see also Davidson, et al., 1990).

Functional relationships between motivation and motor action

The data we report are correlational, so the causal relationship between the laterality of motivation and the laterality of manual motor control (i.e., of handedness) remains unknown. Broadly speaking, there are three possible relationships: 1. handedness could determine the laterality of motivation; 2. the laterality of motivation could determine handedness; 3. the laterality of both could be dependent on a third factor.

On the first possibility, it is assumed that the laterality of handedness is determined by some combination of genetic and environmental factors. Subsequently, the habit of performing approach actions with the dominant hand and avoidance actions with the nondominant hand stabilizes the locus of approach- and avoidance-motivational states.¹ On an evolutionary timescale, neural circuits that support emotional motivation could be exapted from circuits that support motor control. On a developmental timescale, motivational states could be stored as highly abstracted, covert approach- or avoidance motor plans, implemented in cortical areas neighboring (or overlapping with) the circuits that support overt action.

On the second possibility, it is assumed that the laterality of motivation is determined by some combination of genetic and environmental factors. Subsequently, having approach states lateralized to one hemisphere causes the hand controlled by ipsilateral motor circuits to be used for approach actions. If approach actions are more frequent and require more skill than avoidance actions (see note 1), this would enhance the dexterity of the ‘approach’ hand, making it dominant. Likewise, having avoidance states lateralized to

¹ This account assumes that the established links between approach-dominant and avoid-nondominant are motivated independent of genetic handedness or neural proximity. Although untested, this seems plausible: approach actions often require dexterity (e.g., picking fruit, putting a key in a lock, touching a loved one’s face). Avoidance actions such as fending off attack may require less dexterity, and may also be more dangerous (i.e., it would be adaptive to risk injuring or sacrificing the less-dexterous hand when performing avoidance actions).

the other hemisphere causes the hand controlled by its ipsilateral motor circuits to be used for avoidance actions. If avoidance actions are less frequent and require less skill than approach actions, this would decrease the dexterity of the ‘avoidance’ hand, making it nondominant.

On the third possibility, there could be no direct causal link between the evolution or development of neural circuits for motivation and manual motor action. Both could arise due to some third environmental or genetic factor, as yet unspecified. In light of the present data, in combination with behavioral data linking action, motivation, and valence, it seems unlikely that there is no causal relationship between the laterality of motivation and motor control, but this possibility awaits experimental tests that include causal interventions in which action, valence, and motivation are manipulated independently.²

How is motivation different from other lateralized functions?

Lateralization of language, the most studied asymmetrical cognitive function, only depends weakly on handedness. Like most right-handers, the majority of left-handers (73%) have language abilities lateralized to the left hemisphere (Knecht et al., 2000). Language lateralization is parametrically related to graded differences in handedness (Pujol et al., 1999), but this mostly results from increased bilaterality in left-handers: not from right-language dominance, which is rare.

Lateralization of visuospatial cognition also varies with handedness. Right-handers show a left-hemisphere advantage for processing categorical spatial relations (e.g., *under, above*) and a right-hemisphere advantage for judging analog distances (e.g., *2 cm*; Kosslyn et al., 1989). In left-handers, however, categorical and coordinate spatial relationships are not clearly lateralized in either hemisphere (Hellige et al., 1994).

The complete reversal of hemispheric specialization with handedness that we observe here sets motivation apart from most other lateralized cognitive functions. Approach motivation is not lateralized like language or spatial cognition; rather, it is lateralized like motor control of the dominant hand.

Implications for neurotherapy

The relationship between motivation and motor control has implications for neurotherapy. Several studies have demonstrated the effectiveness of transcranial magnetic stimulation (TMS) (e.g. Janicak et al., 2010) and biofeedback using EEG (Allen, Harmon-Jones, & Cavender, 2001) to decrease symptoms of depression by shifting neural activity toward the positive/approach-related left

² Possibilities 1, 2, and 3 are not mutually exclusive. Independent factors could give rise to some specification of both handedness and motivation. Through dominant-approach and nondominant-avoidance actions, then, the neural implementations of motivation and manual motor action could be mutually reinforced.

hemisphere. Effective neural therapies require an accurate picture of the emotional asymmetries in patients' brains. Based on our findings, it appears that the therapies currently in use could be detrimental to left-handers. The discovery that the hemispheric correlates of emotion are body-specific may be crucial for the development of safe, effective emotional neurotherapy.

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