Frequency Asymmetries in Vision and Action

Owen P. Morgan (opm6@cornell.edu) and **Daniel Casasanto (casasanto@cornell.edu)**
Cornell University, Department of Psychology
Martha Van Rensselaer Hall, Ithaca, NY 14853

Abstract

According to a large body of research, the left and right cerebral hemispheres are specialized for different frequencies, in vision and audition, but the cause of this specialization is unknown. Here, we tested whether hemispheric asymmetries in visual perception can be explained by asymmetries in people's tendency to perform high- and low-frequency actions with their dominant and nondominant hands, respectively (the Action Asymmetry Hypothesis [AAH]). In a large, preregistered, online study, participants ($N = 1008$) judged low- and high-frequency shapes presented in the left and right visual hemifields. Overall, the typical hemispheric asymmetry for high vs. low visual frequencies, which we found in right handers, was significantly reduced in left handers. Hemispheric asymmetries for high-spatial-frequency stimuli were completely reversed between right and left handers. These results provide initial support for the AAH: Frequency asymmetries in perception may be explained by frequency asymmetries in action.

Keywords: action; vision; frequency specialization; handedness; hemispheric asymmetry

Introduction

According to decades of research, the cerebral hemispheres in humans are specialized for different frequencies in both vision and audition (see Christman, 1989; Flevaris & Robertson, 2016; and Ivry & Robertson, 1998 for reviews). In vision, relatively low-frequency information is processed more quickly when it is presented to the left visual field (LVF), which the retinas project directly to the right hemisphere; conversely, relatively high-frequency information is processed more quickly when it is presented to the right visual field (RVF), which the retinas project directly to the left hemisphere. For example, when participants are asked to discriminate the frequency of sine-wave gratings, they respond faster for low frequency gratings in the LVF, and high frequency gratings in the RVF (e.g., Christman et al., 1991; Kitterle et al., 1990, 1992; Kitterle & Selig, 1991; Proverbio et al., 1997; but see Proverbio & Zani, 2021). Likewise, in audition when participants are asked to discriminate relatively high- and low-frequency tones presented to the left and right ears (assumed to project information primarily to the contralateral auditory cortices), they respond faster when low-frequency tones are presented to the left ear and high-frequency tones to the right ear (Ivry & Lebby, 1993).

Dozens of studies using a range of tasks have documented the hemispheric asymmetry for high and low frequencies in vision. Beyond spatial frequency grating discrimination tasks, hemispheric specialization has been found in frequency-filtered images of natural scenes (Brederoo et al., 2019; Brederoo et al., 2020; Peyrin et al., 2003, 2006a, 2006b) and faces (Perilla-Rodríguez et al., 2013, Sergent, 1985), as well as in "flanker" tasks, where large (low spatial-frequency) stimuli are flanked by small (high spatial-frequency) stimuli (Chokron et al., 2000).

The hemispheric specialization for frequency has been tested most often using hierarchically constructed visual stimuli: large (low spatial-frequency) "global" letters, shapes, or objects, built out of small (high-spatial frequency) "local" letters, shapes or objects (Navon 1977). In these tasks, subjects may be asked to attend to both levels at once ("divided attention"), to one level per block ("focused attention"), or to a level cued before each trial ("selective attention"). Frequency specialization has been found in all of these varieties of tasks using hierarchically constructed letter stimuli, with divided attention (Blanca et al., 1994; Brederoo et al., 2017, 2019; Christie et al., 2012; Hübner et al., 2007; Kéïta et al., 2014; Sergent, 1982; Weissman & Banich, 1999; Yovel et al., 2001; but see Arnau et al., 1992; Blanca Mena, 1992), selective attention (Hübner, 1997; Hübner & Malinowski, 2002; Hübner & Kruse, 2011; Volberg & Hübner, 2004; Wendt et al., 2007; but see Hübner et al., 2007), and focused attention (Aiello et al., 2018; Evans et al., 2000; Evert & Kmen, 2003; Han et al., 2002; Hübner, 1997; Hübner & Kruse, 2011; Martin, 1979; Martinez et al., 1997; Robertson et al., 1993; Yovel et al., 2001; but see Alivisatos & Wilding, 1982; Blanca & López-Montiel, 2009; Boles, 1984; Boles & Karner, 1996; Han et al., 2002; Jiang & Han, 2005; Lux et al., 2004; Proverbio et al., 1998; Tsvetanov et al., 2013; Van Kleeck, 1989). Frequency specialization has also been found using hierarchically constructed objects (Brown & Kosslyn, 1995; but see Kéïta & Bedoin, 2011) and shapes (Brederoo et al., 2017; Kimchi & Merhav, 1991).

Meta-analyses suggest that frequency specialization in hierarchical stimulus tasks is reliable (Van Kleeck, 1989; Rezvani et al., 2020). Behavioral studies confirm that processing global vs. local stimuli in these tasks requires attention to spatial frequency (see Flevaris & Robertson, 2016 for a review). Finally, lesion studies (e.g., Lamb et al., 1989) and neuroimaging (see Kauffmann et al., 2014 for a review) confirm that frequency specialization in behavioral tasks (i.e., visual hemifield manipulations) corresponds to hemispheric processing asymmetries in the brain.

Hemispheric specialization for frequency represents an organizing principle of perception, across modalities (Christman et al., 1991; Flevaris & Robertson, 2016; Ivry & Robertson, 1998). Furthermore, frequency asymmetries have been invoked as explanations for other neural and cognitive processes, ranging from the hemispheric laterality of language to the spatial organization of number in infants' minds (Felisatti, Laubrock, et al., 2020). Yet, the cause of this hemispheric specialization has remained unknown. Here we review the hypotheses that have been considered to date, and report the first test of a new hypothesis that may explain hemispheric specialization for frequency.

Theories of hemispheric specialization for frequency in perception

Why are the cerebral hemispheres specialized for different frequencies? On one proposal, which we will call the "Brain Development Hypothesis" (BDH), frequency specialization comes about because of an asymmetry in early brain development (Hellige, 1993; Ivry & Robertson, 1998). This proposal starts with the observation that, in utero, some perceptual brain areas may mature earlier in the right hemisphere (e.g., Chi et al., 1977; see Dehaene-Lambertz & Spelke, 2015 for a review). Across neuroimaging studies of human fetuses (Habas et al., 2012) and infants (Hill et al., 2010; G. Li et al., 2014), the superior temporal sulcus and parieto-occipital sulcus, landmarks linked to auditory and visual processing, develop earlier in the right hemisphere. In audition, newborn babies have more experience with low-frequency sounds because the womb acts as a low-pass filter (Ivry & Robertson, 1998). If the right hemisphere develops with more low-frequency input than the left hemisphere, this disparity could lead to the typical pattern of frequency specialization. In vision, human babies are most sensitive to low-frequency information, and have low acuity for high-frequency features of objects such as faces (e.g., Leat et al., 2009). If right hemisphere visual areas develop earlier than left hemisphere homologues, then the right hemisphere will develop with more low-frequency input, leading to the typical pattern of frequency specialization observed in adults. Therefore, the BDH offers a plausible account of how frequency asymmetries might develop, in both vision and audition. To our knowledge, however, this hypothesis has not been directly tested. Furthermore, research that emerged in the decades following the proposal of the BDH suggests that the Sylvian fissure, near important auditory and visual areas, may develop earlier in the *left* hemisphere (e.g., G. Li et al., 2014; Hill et al., 2010 see Bisiacchi & Cainelli, 2022 for a review), calling into question the assumptions about the laterality of brain development that motivated the BDH.

On a second proposal, which we will call the "Language Asymmetry Hypothesis (LAH)," frequency specialization is caused by the brain's asymmetry in language processing. In most people, left hemisphere brain areas are specialized for processing high-frequency components of language, such as written word forms (e.g., Cohen & Dehaene, 2004)

and phonemes, according to dichotic listening tests (e.g., Packheiser et al., 2020). Could the fact that these language functions are lateralized to the left hemisphere explain why the left hemisphere is specialized for high frequency information, beyond language? LAH offers a second plausible explanation for frequency specialization (e..g, Piazza & Silver, 2017). But to our knowledge, this theory has not been tested directly. Furthermore, the opposite relationship between hemispheric specialization for frequency and for language has also been proposed: In principle, frequency specialization could explain the laterality of language, not vice versa (e.g., Felisatti, Aagten-Murphy, et al., 2020).

Here we propose that systematic asymmetries in hand actions might lead to hemispheric specialization for frequency (the "Action Asymmetry Hypothesis" (AAH)). In performing many actions, people use their dominant hand to manipulate objects (e.g., to swing a hammer; to write with a pen), and use their nondominant hand to stabilize objects (e.g., to position the nail, to hold the piece of paper steady). Because manipulating an object tends to require actions with higher spatio-temporal frequency than stabilizing an object, there is an asymmetry in the frequency of the actions that people perform with their dominant and nondominant hands. This frequency asymmetry in action could lead to frequency asymmetries in vision and audition, via one of two mechanisms. First, having motor areas in the left and right hemispheres specialized for relatively high and low frequency actions could cause ipsilateral perceptual areas to develop the same relative frequency specialization, over evolutionary or developmental time. Coordinating percepts and actions requires reciprocal connections between perceptual and motor areas, and these connections may form more efficiently within hemispheres than between hemispheres (e.g., Hommel et al., 2001). Second, performing actions at different spatio-temporal frequencies with the dominant and nondominant hands could create systematic asymmetries in people's visual and auditory experiences of these actions. In right handers, for example, performing high frequency actions with the dominant hand is likely to create high-frequency visual and auditory events in right hemispace; the visual and auditory cortices that first receive input from right hemispace could therefore become specialized for relatively high frequencies. Via either (or both) of these mechanisms, AAH could provide a functional explanation for hemispheric specialization for frequency.

Does handedness predict hemispheric specialization for frequency in vision?

We aimed to test these competing hypotheses concerning the origin of hemispheric asymmetries for frequency by testing whether handedness predicts the strength of the frequency asymmetry. Whereas many studies have investigated frequency specialization in right handed participants, to date, only one study has tested whether left handers show reduced frequency asymmetry (Brederoo et al., 2020 found a null result in a sample with 53 left handers). Here, we tested for a correlation between handedness and visual hemifield biases

in the perception of higher and lower spatial frequencies, in a large online sample of right and left handers.

The BDH does not predict any difference between right and left handers' frequency asymmetries, because (to the best of our knowledge) no difference in right and left handers' rates of hemispheric maturation in perceptual areas has been proposed or found. Does the LAH predict a difference between right and left handers? If it were the case that hemispheric specialization for language typically reverses between right and left handers, then the LAH could in principle predict a difference in hemispheric specialization for frequency. However, the longstanding belief that hemispheric specialization for language varies with handedness has been largely overturned. In a large neuroimaging study of language lateralization (n = 297), Mazoyer et al. (2014) found that the correlation between handedness and language laterality was "barely above the chance level" (pg. 8). Consistent with this finding, a large study (n = 1554) focusing on language lateralization for phonemes (a high-frequency component of language) found a weak relationship between handedness and the laterality of phoneme perception that was "barely in line with the notion that there is a link between language lateralization and handedness." (Packheiser et al., 2020, pg. 6). Packheiser and colleagues' (2020) Bayesian analyses found evidence in favor of the null hypothesis, corroborating the conclusion that language lateralization and handedness are *unrelated*. Because there is no clear evidence that hemispheric specialization for high-frequency components of language varies with handedness, the LAH does not predict that frequency specialization should differ systematically between left and right handers. By contrast with these earlier theories, the AAH predicts that left handers, who perform high frequency actions with their left hand (and often on their left side of space), should show reversed or reduced frequency specialization compared to right handers.

Method

Participants

1,008 participants were recruited through the online data collection platform Prolific, and 844 met all inclusion criteria: 378 right handers (EHI >= +40), 135 mixed handers (EHI > -40 and < +40), and 331 left handers (EHI < -40). Participants' mean age was 29.08 years (*SD* = 6.03), and years of education, 14.38 (*SD* = 2.48). 441 participants described their sex as male, 391 as female, and 12 as something else. Left-, right- and mixed- handed participants did not differ significantly in age, education, or sex (all $p > .05$).

Recruitment and pre-screening We first recruited a pilot sample of 112 right handers, 103 of whom met inclusion criteria. This pilot sample was used to determine which dependent variable (reaction time or accuracy) would be treated as primary in the full study, and to estimate the sample size needed for 90% power to detect an interaction of field by level by handedness, if strong left handers were to show an interaction of field by level (reaction time) half that of right

handers. Guided by this power analysis, we recruited participants in batches until the sample yielded at least 302 left handers (EHI < -40) and 302 right handers (EHI > +40) meeting inclusion criteria. We used Prolific's pre-screening tool to target left and right handers in roughly equal proportion, first recruiting 336 participants who had responded "Right-handed" and 336 who had responded "Left-handed" or "Ambidextrous" to the pre-screening question, "Are you left or right-handed?" This sample yielded 171 left (EHI < -40) and 372 right handers (EHI > +40) who met preregistered inclusion criteria. We then recruited 336 more participants who had responded "Left-Handed" or "Ambidextrous" to the pre-screener, yielding a total of 331 left handers who met inclusion criteria. Additionally, participants were pre-screened for English fluency (so they could read the instructions), US nationality (to simplify demographics collection), Age (18 - 40 years, to reduce variability in peripheral vision acuity), and Prolific approval rate (98% minimum). Each participant was compensated $3.00usd (median $14.10/hr) for attempting the study.

Exclusion criteria Following preregistered criteria, a participant's data were excluded if they (1) reported living in a country other than the US, (2) reported an age below 18 or over 40, (3) reported having done the task before; if they (4) did not complete the EHI questionnaire or (5) did not complete all 160 experimental trials; or if, within either 80-trial block, (6) their accuracy was below 60% (48/80 trials correct), (7) they responded "go" in 78/80 or more trials, or (8) their median reaction time was greater than 1500ms or (9) lower than 200ms. Additionally, participants were excluded if their EHI scores did not match their pre-screening responses ("Left handed" with EHI > 0; "Ambidextrous" with EHI of -100 or +100; or "Right handed" with EHI < 0). We added these exclusion criteria after noticing that a large number of recruited "Left handed" participants had EHI scores indicating right handedness.

Materials and Procedure

Stimuli Stimuli were hierarchical shapes: global shapes made of local shapes (Navon, 1977). All stimuli were "incongruent": the shape at the global level was always different from the shape at the local level. Target shapes were circles and squares; distractors were diamonds and triangles. Global stimulus arrangements were based on 4x4 square or triangular grids of local stimuli. Following Yovel et al. (2001), relative stimulus sizes were chosen to make the global and local levels roughly equally salient: the height of each local stimulus was approximately 1/7 the height of each global stimulus.

Following Brederoo et al. (2020), stimuli were always presented in bilateral pairs, with one hierarchical shape on the left side of the screen and one on the right, at the same time. Because bilateral presentation requires participants to attend to stimuli in both hemifields at the same time, we reasoned that this mode of presentation would increase the chances that participants focus on the center of the screen, and there-

fore perceive target stimuli in their peripheral field, where global/local effects are strongest (Navon, 1977). Choosing parameters that encourage subjects to fixate on the center of the screen may be especially important in online studies, where participants are not under in-person social pressure to fixate throughout the experiment.

Each stimulus had its centermost edge at a distance of 1.5% screen width from the central fixation point, and each stimulus had a width of 9% screen width. These distances were chosen to produce a distance from central fixation of 0.5 degrees, and stimulus width 4.5 degrees, on a 14" diagonal laptop viewed from 47.3cm (the mean viewing distance found by Q. Li et al. (2020), who used a "virtual chinrest" to estimate viewing distance in an online sample). All possible bilateral combinations of stimuli were used, with the constraints that the same hierarchical stimulus never appeared on both sides at once, and that no more than one target could be present on the screen.

Procedure Participants completed a divided attention go-nogo detection task with two 80-trial blocks. A divided attention task was used because previous work suggests that frequency specialization may be more robust for divided than focused attention (Hübner et al., 2007; Yovel et al., 2001). Participants were asked to fixate on the cross in the center of the screen, and press a button whenever they saw one of the two target shapes, at either the global or the local level (go-nogo). The fixation cross was presented for 600ms, and the bilateral stimuli were presented for 134ms, followed by a 256ms blank screen, a 134ms mask (a grid of "#") and another blank screen. If participants did not press the response button within 2000ms of stimulus offset, their response was recorded as "nogo." After a "go" response or "nogo" time-out, participants were prompted to advance to the next trial by pressing spacebar.

Bilateral stimulus pairs were pseudo-randomized for each subject such that 128 (80%) trials included a target (exactly one target, at one level in one visual field): 32 included a global square, 32 a global circle, 32 a local square, and 32 a local circle. To balance response hand, each participant responded with the "z" button (on the left of the keyboard) with their left index finger in one block, and the "/" button (on the right of the keyboard) with their right index finger in the other block. The response button for the first block varied pseudo-randomly between participants.

After reading initial instructions, participants were shown examples of target-present and target-absent trials, with written explanations. Then, participants answered four multiple choice questions that assessed their understanding of the task. Before each experimental block, participants completed a practice block of 16 trials (8 target-present, 8 target-absent), getting feedback after each trial (a green check if correct, a red *X* if incorrect).

The task was programmed and administered using Inquisit Web (version 6.6.1).

Veale Edinburgh Handedness Inventory After the lateral hierarchical shapes task, participants completed the 4-item Veale Edinburgh Handedness Inventory (Veale, 2014). They were shown the question"Which hand do you prefer to use for each of the following actions and tools?", followed by the four prompts, "Writing," "Throwing," "Toothbrush," and "Spoon." The prompts had five possible responses: "Always left," Usually left," "Both equally," "Usually right," and "Always right." A laterality quotient ranging from -100 (strongly left handed) to +100 (strongly right handed) was calculated for each participant following Oldfield (1971).

Analysis procedure

Planned analyses On the basis of our pilot study, and consistent with previous studies (e.g., Evert and Kmen, 2003), we identified reaction time as our primary dependent variable of interest. (Accuracy is also reported as an exploratory variable, below.) In our primary preregistered analysis, we tested the effect of handedness on the interaction of field by level as measured by reaction time (time to respond "go" to present targets). We used linear mixed models to test this interaction, first with handedness as a categorical predictor, and then with handedness as a continuous predictor. In the categorical analysis, we tested whether left handers (EHI <= -40) showed a significantly reduced LVF global>local bias compared to right handers (EHI >= 40). In the continuous analysis, we tested whether hand preference, as measured continuously by the EHI, correlated with the strength of LVF global>local bias, in the direction of reduced LVF global>local bias for left handers. Additionally, we tested whether right handers showed a two-way interaction of field by level in the predicted direction (LVF global>local bias), and whether left handers showed an interaction of field by level in either direction. We used one-sided inferential tests for directional predictions.

Exploratory analyses To test AAH's prediction that the effect of handedness on the laterality of frequency should be strongest in participants with the strongest handedness, we tested the categorical interaction effect in participants with the most extreme EHI scores. Additionally, we explored whether target shape (square vs. circle) influenced the 2-way interaction of field by level, and the 3-way interaction of field by level by handedness.

Finally, we tested for the interaction of field by level by handedness on accuracy (odds of correct vs. incorrect response to targets) using binomial mixed models.

Statistical analyses were run using R 4.2.2 (R Core Team, 2022) with the lme4 (Bates et al., 2015) and emmeans (Lenth, 2022) packages. Data and analysis code, along with stimuli, experiment scripts, and preregistration, are available at https://osf.io/fpk6m.

Results

Exclusions

Of the 1,008 recruited participants (451 right handed [EHI >= 40], 160 mixed handed [-40 < EHI < +40], and 349 left

handed), 164 were excluded: 82 showed EHI scores that did not match their pre-screening responses (51 pre-screened as "Left handed" but with EHI scores > 0; 29 "Ambidextrous" with EHI of -100 or +100; and 2 "Right handed" with EHI <= 0); 47 did not complete the task phase of the experiment; 12 showed low accuracy (below 60% on any block); 12 pressed "go" almost every time (78 or more trials out of 80 on either block); 11 reported having done the task before; 8 had fast reaction times (median < 200ms); 5 had slow reaction times (median > 1500ms); 2 reported being from a Non-US country; 1 reported an age over 40 years; and 1 did not complete the EHI. Of these 164 excluded participants, 14 met multiple exclusion criteria.

Reaction time analyses

Continuous handedness: planned analyses With handedness treated as continuous, we found that degree of left handedness predicted reduction in LVF global>local bias (0.067ms per EHI unit, 95% CI [0.003, 0.13], p = .02, one-sided). Estimated LVF global>local bias for EHI +100 (strong right handers) was 28.14ms (95% CI [20.31, 35.98]), and for EHI -100 (strong left handers), 14.72ms 14.82ms (95% CI [6.48, 23.17]), a difference of 13.32ms. (See Figure 1.)
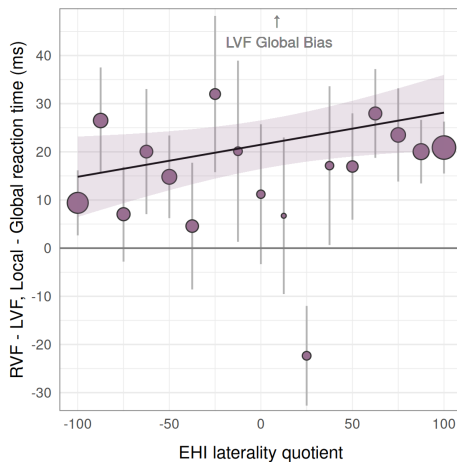

Figure 1: Hemifield frequency bias by handedness (continuous). Dots and vertical error lines show subject-level means and *SEM*. The shaded area shows 95% CI around the model-estimated line of best fit.

Categorical handedness: planned analyses For reaction time, LVF global>local bias was significantly reduced in left handers (n = 331, EHI <= -40) compared to right handers (n = 378, EHI >= +40; difference between groups = 11.67ms, 95% CI [0.65, 22.69], p = .019, one-sided). Both groups showed significant LVF global>local bias: for right handers, the effect size was 27.31ms (95% CI [19.80, 34.81], p = < .001, one-sided); for left handers, 15.56ms (95% CI [7.61, 23.67], p < .001, two-sided. (See Figure 2.)

Within local stimuli, right and left handers showed reversed hemifield bias, in the direction predicted by AAH: right handers responded faster to local stimuli in the RVF than LVF by 12.28ms (95% CI [6.93, 17.63], p <.001, two-sided), whereas left handers responded faster to local stimuli in the LVF than RVF by 9.65ms (95% CI [3.91, 15.39], p = .001, two-sided; difference = 21.93ms, 95% CI [4.01, 14.09], p <.001]).
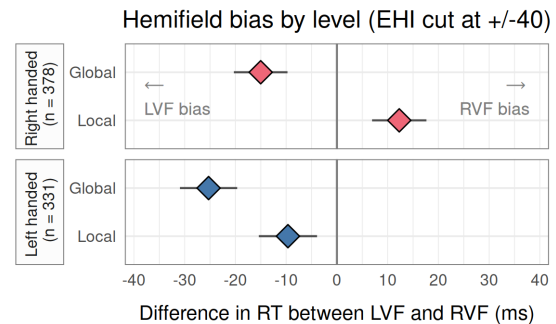

Figure 2: Hemifield frequency bias by level by handedness (categorical). Diamonds show mixed-effects model point estimates, with 95% CI.

Categorical handedness: exploratory analyses Limiting analysis to strong left and right handers with EHI scores of +/-100, the effect of field by level by handedness was 23.51ms (95% CI [7.10, 39.92], p = .0025, one-sided). Strong right handers (n = 182, EHI = +100) showed significant LVF global>local bias (28.10ms (95% CI [17.34, 38.86], p < .001, one-sided). Strong left handers' (n = 138, EHI = -100) hemifield bias did not differ significantly from zero (4.59ms (95% CI [-7.80, 16.98], p = .47, two-sided).

Within right handers, target shape influenced the LVF global>local bias effect: the effect was greater for squares (37.66ms, 95% CI [27.00, 48.32]) than for circles (18.14ms, 95% CI [7.72, 28.56]; difference = 19.52ms, 95% CI [4.61, 34.43], p = .01, two-sided). Additionally, for both right and left handers, shape influenced the degree of global bias, across visual fields: for squares, right handers' global bias was higher by 40.68ms (95% CI [33.21, 48.15], p < .001, two-sided), and left handers' global bias was higher by 36.01ms (95% CI [28.01, 44.00], p < .001, two-sided). Because global precedence effects may be stronger under perceptual uncertainty (e.g., Navon, 1977), these observed effects of shape could be due to the circles being more visible or distinct from the distractor shapes. Supporting this explanation, in the full sample, reaction times were faster for circles than for squares, at both the local level (difference = 66.71ms, 95% CI [62.81, 70.60], p < .001, two-sided) and the global level (difference = 24.53ms, 95% CI [24.53, 32.20], p < .001, two-sided).

Testing whether the less visible circles may have added noise to the critical three-way interaction of field by level by handedness, we observed a marginal interaction of shape by field by level by handedness (15.89ms, 95% CI [-5.99, 37.76],

$p = .08$, one-sided). The interaction of field by level by handedness was significant for squares (19.76ms, 95% CI [4.11, 35.40], $p = .006$, one-sided), but not for circles (3.87ms, 95% CI [-11.41, 19.16], $p = .31$, one-sided). For circle targets, the estimated LVF global>local bias for right handers was 18.14ms (95% CI [7.70, 28.58], $p < .001$, one-sided); for left handers, 14.27ms (95% CI [3.10, 25.43], $p = .01$, two-sided). For square targets, the estimated LVF global>local bias for right handers was 37.66ms (95% CI [26.98, 48.34], $p < .001$, one-sided); for left handers, 17.90ms (95% CI [6.47, 29.33], $p = .002$, two-sided).
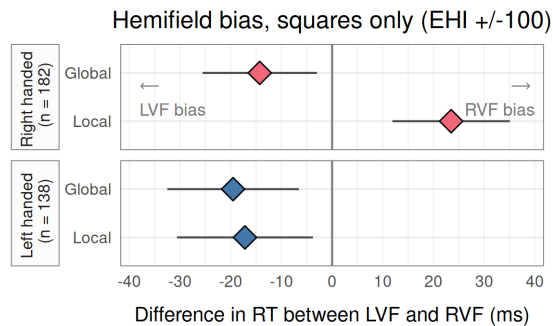

Figure 3: Hemifield frequency bias by level by handedness (EHI +/-100), for square targets only. Diamonds show mixed-effects model point estimates, with 95% CI.

To explore the relationship between handedness and frequency asymmetry further, we limited the analysis to squares (the target shape that carried the statistically significant 3-way interaction) and participants with EHI scores of +/-100 (the participants who were predicted to produce the strongest effects of handedness). In this subset of the data, the difference between right and left handers' LVF global>local bias was 34.68ms (95% CI [11.35, 58.01], $p = .002$, one-sided). Strong right handers showed significant LVF global>local bias of 37.13ms (95% CI [21.86, 52.4], $p < .001$, one-sided); strong left handers' hemifield global bias did not differ significantly from zero (2.45ms (95% CI [-15.18, 20.09], $p = .79$, two-sided; see Figure 3).

Accuracy analyses

Categorical handedness: exploratory analyses For accuracy, we observed no significant interaction of field by level by handedness ($OR = 0.90$, 95% CI [0.70, 1.16], $p = .42$, two-sided). Both groups showed LVF global>local bias: the relative odds of correct/incorrect responses for global/local, LVF/RVF stimuli for right handers was 1.77 (95% CI [1.49, 2.10], $p < .001$, one-sided); for left handers, 1.95 (95% CI [1.62, 2.35], $p < .001$, two-sided).

Continuous handedness: exploratory analyses With handedness treated as continuous, we found that degree of left handedness did not significantly predict degree of LVF global>local bias (accuracy; $\beta = .0002$ log(odds) units per EHI unit, 95% CI [-0.001, 0.002], $p = .40$, one-sided).

Discussion

Hemispheric specialization for spatial frequency in vision differed significantly between left and right handers. The effect seen in right handers (EHI >40) was reduced by an estimated 43% in all left handers (EHI <-40), and by 84% in the most extreme left handers (EHI +/-100). These results challenge the Brain Development Hypothesis and the Language Asymmetry Hypothesis, neither of which predicts that frequency specialization should depend on handedness, and provide initial support for the Action Asymmetry Hypothesis: Frequency asymmetries in vision may be explained by frequency asymmetries in action.

AAH proposes that frequency specialization is due to asymmetries in action that, in the strongest cases, may reverse completely between right- and left-handers (e.g., using the left vs. right hand to write); on the basis of such actions, AAH appears to predict a *reversed* direction of frequency specialization between strong left and right handers—not a reduction of lateralization, as the overall results show here. One explanation for why frequency specialization in left handers might not perfectly mirror right handers' is that many artifacts are designed for the right-handed majority: left handers often need to use their nondominant hand to type on the number pad of a standard computer keyboard, use a can opener, or cut with standard (right-handed) scissors. Left handers' experience performing common actions as if they were right handers could potentially explain why their frequency specialization is reduced but not reversed. Furthermore, we note that frequency specialization *did* reverse completely for judgments of high-frequency (i.e., local) stimuli: We found a LVF bias in left handers but a RVF bias in right handers. Because the dominant hand is important for high-frequency manipulation actions, whereas either hand can be used for low-frequency stabilizing actions, AAH most clearly predicts that specialization should reverse for high-frequency stimuli. Future studies of visual and auditory frequency processing will test whether a full reversal of hemispheric specialization is found for all stimuli, or selectively for high-spatial-frequency stimuli, as we found here.

Could LAH explain the reduction we observed in left handers' frequency specialization? If the rate of atypical language laterality were higher in our left handers than our right handers, then in principle this difference could explain a reduction in frequency specialization. But it is implausible that language laterality would *reverse* in a majority of our left handers (e.g., Packheiser et al., 2020); therefore, language laterality cannot explain the hemispheric reversal we found for high-frequency stimuli. In order to discriminate definitively between the predictions of LAH and AAH, future studies will measure both the laterality of language (e.g., via dichotic listening) and of frequency specialization in vision (e.g., via hierarchical shape judgments) to determine whether handedness predicts frequency specialization independent of language lateralization.

Acknowledgments

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