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Frequency Asymmetries in Vision: The Action Asymmetry Hypothesis

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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). In two large, preregistered, online studies, participants judged low- and high-frequency shapes presented in the left and right visual hemifields. Overall, the typical hemispheric asymmetry for high versus low visual frequencies, which we found in right handers, was significantly reduced in left handers. Across experiments, hemispheric asymmetries for high-spatial-frequency stimuli were completely reversed between strong right and left handers. A third experiment testing dichotic listening suggests that this reversal cannot be explained by differences in language laterality. These results provide initial support for the action asymmetry hypothesis: Frequency asymmetries in perception may be explained by frequency asymmetries in action.

Public Significance Statement

This study seeks to explain a fundamental principle of perception in brain and behavior: Sights and sounds in the left and right perceptual fields are processed differently depending on their spatiotemporal frequencies (how fine-grained, or fast-changing, they are). Beyond perception, these asymmetries could potentially help explain the organization of language and the origin of the mental number line. Yet, the cause of these asymmetries has remained mysterious. To test a new explanation for these phenomena, we recruited from a group of people who have been underrepresented in cognitive neuroscience: left handers. In a series of three preregistered experiments, we find evidence that frequency asymmetries in vision may arise from asymmetries in how people use their hands to perform everyday actions.

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

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; Ivry & Robertson, 1998, for reviews). This frequency specialization provides an organizing principle for perception in the brain across modalities (Christman et al., 1991; Flevaris & Robertson, 2016; Ivry & Robertson, 1998), and it has been invoked as an explanation 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 frequency specialization has remained unknown. Here we report the first tests of a new hypothesis that seeks to explain frequency specialization in perception in terms of patterns of motor action.

In vision, relatively low-spatial-frequency information is processed more quickly when it is presented to the left visual field (LVF), which is projected to the right hemisphere via anatomical connections from both retinas; conversely, relatively high-spatial-frequency information is processed more quickly when it is presented to the right visual field (RVF), which is projected to the left hemisphere (see Ivry & Robertson, 1998, for a review). For example, when participants are asked to discriminate the spatial frequency of sine-wave gratings, they respond faster for low-frequency gratings in the LVF and high-frequency gratings in the RVF (Christman et al., 1991; Kitterle et al., 1990; Kitterle & Selig, 1991; Kitterle et al., 1992; Proverbio et al., 1997; but see Proverbio & Zani, 2021). Likewise, in audition, when participants are asked to

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A preliminary version of this research was presented at the 45th Annual Conference of the Cognitive Science Society, in July 2023. Data and analysis code are available at https://osf.io/mc5gy.

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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 have been found to 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, 2020; Peyrin, Chokron, et al., 2006; Peyrin et al., 2003; Peyrin, Mermillod, et al., 2006) 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 & Kruse, 2011; Hübner & Malinowski, 2002; 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; Gerlach, 2023; Gerlach & Poirel, 2020; 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 (Rezvani et al., 2020; Van Kleeck, 1989). Behavioral studies confirm that processing global versus 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.

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 "Fetal Asymmetry Hypothesis" (FAH), 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 than in the left 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 FAH 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 FAH suggests that the Sylvian fissure, near important auditory and visual areas, may develop earlier in the *left* hemisphere (e.g., Hill et al., 2010; G. Li et al., 2014; see Bisiacchi & Cainelli, 2022, for a review), calling into question the assumptions about the laterality of brain development that motivated the FAH.

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? The LAH offers a second plausible explanation for frequency specialization (e.g., Piazza & Silver, 2017). But to our knowledge, like the FAH, the LAH 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 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 article steady). Because manipulating an object tends to require movements with higher spatiotemporal frequency than stabilizing an object, there is an asymmetry in the spatial and temporal frequency of the movements 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, respectively, 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., Stephan et al., 2000). In line with this proposal, experiments on visuomotor representation of numerosity have demonstrated a link between frequency of hand tapping and sensitivity to frequency of visually presented stimuli (Anobile et al., 2024). Second, performing actions at different spatiotemporal 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, the AAH could provide a functional explanation for hemispheric specialization for frequency.

An additional benefit of the AAH is that it may explain why different kinds of frequency are lateralized similarly across different sensory modalities. In vision, the "frequency" that is lateralized is spatial frequency; in audition, the "frequency" that is lateralized is temporal (or spectral) frequency. In bimanual action, the left and right hands are specialized for movements that differ in both their spatial and temporal frequencies. Therefore, frequency specialization in action can potentially explain the link between spatial and temporal frequency specialization, across sensory modalities.

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 frequency asymmetries in vision. Whereas many studies have investigated frequency specialization in right-handed participants, to date, only three studies have tested frequency specialization in left handers, with inconclusive results: Goodarzi et al. (2005) found reversed frequency specialization in a sample with 70 left handers, Brederoo et al. (2020) found a null result in a sample with 53 left handers, and Veetil et al. (2023) found a null result in a sample of 104 participants with a uniform distribution of handedness scores. Here, in Experiments 1 and 2, we tested for a correlation between handedness and visual hemifield biases for higher and lower spatial frequencies, in large samples of right and left handers.

The FAH 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. To the extent that language laterality varies with handedness, the LAH could predict a difference between left and right handers' hemispheric specialization for frequency, in principle. 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" (p. 8). Consistent with this finding, a large study ($n = 1{,}554$) 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, p. 6). Packheiser et al.'s (2020) Bayesian analyses found evidence in favor of the null hypothesis, corroborating the conclusion that language lateralization and handedness are *unrelated* (but see Karlsson et al., 2023). 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. In contrast to the earlier theories (the FAH and LAH), 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, even when statistically controlling for language laterality (Experiment 3).[1]

Experiment 1: Does Handedness Predict Frequency Specialization?

In Experiment 1, we tested whether handedness predicts frequency specialization, as measured in a preregistered task in which shapes with high- and low-frequency components were presented to the left and right visual hemifields, in a large, online sample with approximately equal numbers of left and right handers.

Method

Participants

Participants ($N = 1{,}008$) were recruited through the online data collection platform Prolific, and 844 participants met all inclusion criteria: 378 right handers (Edinburgh Handedness Inventory [EHI] score $\geq +40$), 135 mixed handers (EHI > -40 and $< +40$), and 331 left handers (EHI < -40; see Figure 1 for the distribution of EHI scores). Participants' mean age was 29.08 years ($SD = 6.03$) and years of education, 14.38 ($SD = 2.48$). Four hundred forty-one 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 $p > .05$). Six hundred six participants reported their race as White, 82 Black or African American, 76 multiple races, 69 Asian, five American Indian or Alaska Native, three Native Hawaiian or Other Pacific Islander, and three as something else; 100 reported Hispanic ethnicity.

Recruitment and Prescreening. 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

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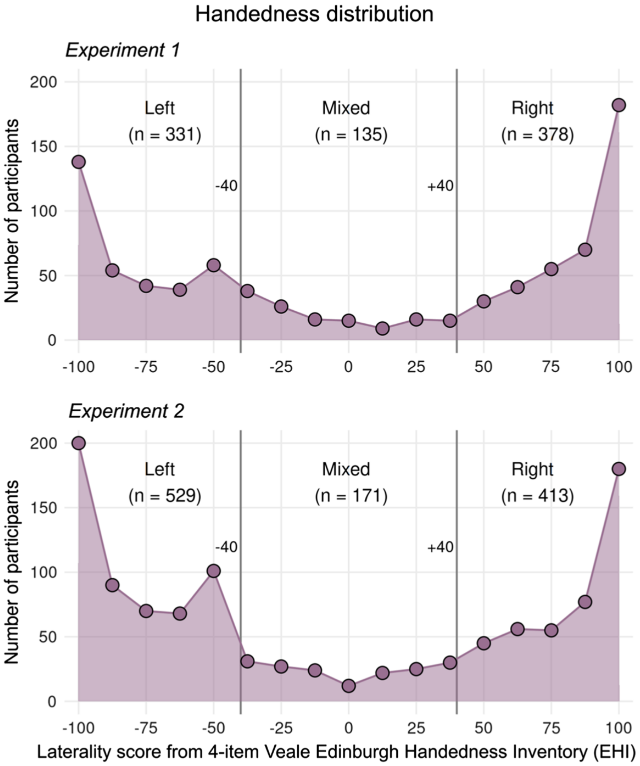
[1] A reviewer raised the question of what the action asymmetry hypothesis might predict in the case of congenitally uni-manual people. Because people with one hand use their hand for manipulating movements more than their contralateral limbs, the AAH might predict that they would show high-frequency specialization for their dominant side of space (and contralateral hemisphere). In principle, one-handed people might have greater asymmetry in the neural control of manipulating actions; under one of AAH's proposed mechanisms, this greater asymmetry in neural specialization could lead to greater hemispheric specialization for frequency than in two-handed people. This speculative proposal could be tested empirically.

Figure 1

Distribution of Handedness Scores of Participants in Experiments 1 and 2



Note. Vertical lines and counts show the bins used to define right and left handers in primary categorical analyses (EHI ± 40). See the online article for the color version of this figure.

(reaction time [RT] 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 × 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 prescreening 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 prescreening question, "Are you left or right-handed?" This sample yielded 171 left (EHI < −40) and 378 right handers (EHI > +40) who met inclusion criteria. We then recruited 336 more participants who had responded "left-handed" or "ambidextrous" to the prescreener, yielding a total of 331 left handers who met inclusion criteria. Additionally, participants were prescreened for English fluency (so they could read the instructions), U.S. nationality (to simplify demographics collection), age (18–40 years, to reduce variability in peripheral vision acuity; e.g., Collins et al., 1989), and Prolific approval rate (98% minimum). Each participant was compensated $3.00 USD (median $14.10/hr) for attempting the study, which was approved by Cornell's Institutional Review Board (IRB0007462 [1709007462]). All participants gave informed consent via an online form.

Exclusions. Of the 1,008 recruited participants, 164 were excluded, leaving 844. Following preregistered criteria, participants were excluded if they reported living in a country other than the United States (*n* = 2); reported an age below 18 or over 40 (*n* = 1); reported having done the task before (*n* = 11); did not complete the EHI questionnaire (*n* = 1); did not complete all 160 experimental trials (*n* = 47); had accuracy below 60% (48/80 trials correct) within either 80-trial block (*n* = 12); responded "go" to 78 or more trials in any 80-trial block (*n* = 12); or had a median reaction time greater than 1,500 ms (*n* = 5) or less than 200 ms (*n* = 8) within either 80-trial block. Additionally, participants were excluded if their EHI scores did not match their prescreening responses (*n* = 82: 51 prescreened as "left handed" but with EHI scores >0; 29 "ambidextrous" with EHI of −100 or +100; and 2 "right handed" with EHI ≤ 0). We added this exclusion criterion after noticing that some of the recruited "left-handed" participants had EHI scores indicating right handedness. Of the 164 excluded participants, 14 met multiple exclusion criteria.

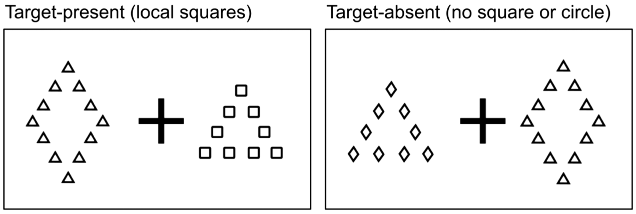
Materials and Procedure

Stimuli. Stimuli were hierarchically constructed shapes: global shapes made of local shapes (Navon, 1977; see Figure 2 for example stimuli). All stimuli were "incongruent," meaning that 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 a target could appear on either side of the screen (and never both sides at once), we reasoned that bilateral presentation would require participants to attend to both hemifields at the same time, increasing the chance that participants would focus on the center of the screen, and therefore

Figure 2

Example Stimuli



Note. The left example screen shows a target-present trial, with local squares present on the right side of the screen. The right example screen shows a target-absent trial, with no squares or circles present. (In Experiment 1, the target shapes were squares and circles; in Experiment 2, the target shapes were squares and rectangles.) Stimuli and fixation cross are not shown to scale; in the experiment, each hierarchical stimulus had a width of only 9% screen size.

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° and stimulus width of 4.5°, on a 14″ diagonal laptop viewed from 47.3 cm (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 (see Figure 2 for example stimuli).

Procedure. Participants completed a divided attention go–nogo detection task with two 80-trial blocks. Participants were asked to fixate on the cross in the center of the screen and to press a button whenever they saw one of the two target shapes, at either the global or the local level. This 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). The fixation cross was presented for 600 ms, and the bilateral stimuli were presented for 134 ms, followed by a 256-ms blank screen, a 134-ms mask (a grid of “#”), and another blank screen. If participants did not press the response button within 2000 ms of stimulus offset, their response was recorded as “nogo.” After a “go” response or “nogo” timeout, participants were prompted to advance to the next trial by pressing spacebar (see Figure 3 for an example trial).

Bilateral stimulus pairs were pseudorandomized 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 pseudorandomly between participants. The lateral buttons “z” and “/” were used, rather than a central button, in order to increase the chances that participants used the expected hand, given that their behavior could not be directly observed by experimenters (e.g., if we had asked participants to use the spacebar for responses, they may default to their dominant hand, even if instructed to switch hands).

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 (eight target-present, eight 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 (2022).

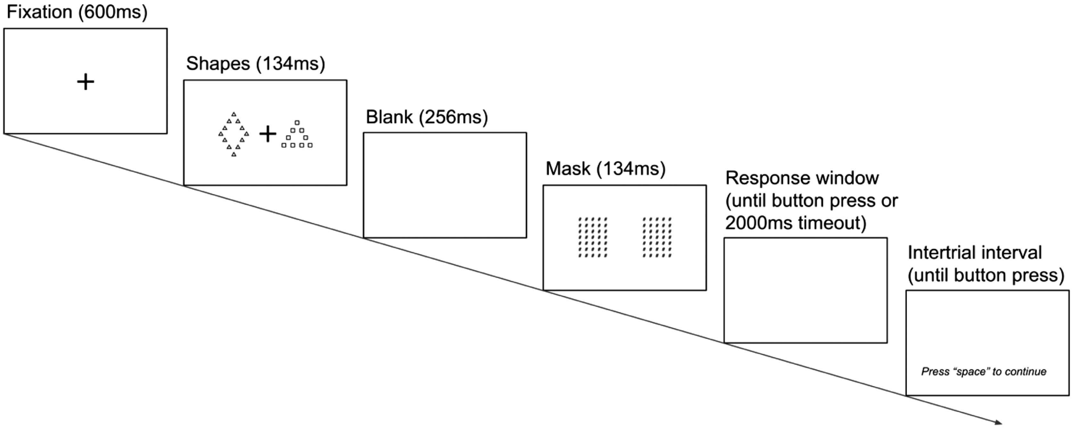
Veale Edinburgh Handedness Inventory. After the lateral hierarchical shapes task, participants completed the four-item Veale Edinburgh Handedness Inventory (EHI; Veale, 2014). They were shown the question “Which hand do you prefer to use for each of the following actions and tools?” followed by the four 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 score was calculated for each participant as the mean of their responses, coded as −2 (“always left”) to +2 (“always right”) scaled linearly to a range of −100 (*strongly left handed*) to +100 (*strongly right handed*). For categorical analyses, *left handers* and *right handers* were defined as those with scores of less than −40 or greater than +40; *strong left handers* and *strong right handers* were defined as those with scores of exactly −100 or +100. The four-item EHI was used in order to minimize the time burden on participants, and because it has been found to have high reliability, and may capture mixed handedness more accurately than longer inventories (Veale, 2014).

Analysis Procedure

Primary Analyses. On the basis of our pilot study and consistent with previous studies (e.g., Evert & Kmen, 2003), we identified reaction time as our primary dependent variable of interest. (Accuracy is also reported as an exploratory variable, in the

Figure 3

Example Target-Present Trial



Appendix.) 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 RVF local > global 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 RVF local > global bias, in the direction of reduced RVF local > global bias for left handers. Additionally, we tested whether right handers showed a two-way interaction of field by level in the predicted direction (RVF local > global bias) and whether left handers showed an interaction of field by level in either direction.

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 two-way interaction of field by level and the three-way interaction of Field by Level × Handedness.

Finally, we tested for the interaction of Field by Level × Handedness on accuracy (odds of correct vs. incorrect response to targets) using binomial mixed models. The results of these exploratory analyses are reported in the Appendix.

Statistical analyses were run using R 4.2.2 (R Core Team, 2023) with the lme4 (Bates et al., 2015) and emmeans (Lenth, 2022) packages. Inferential statistics for top-level interaction effects were calculated using likelihood ratio tests, comparing lme4 models with and without the interaction term, using base R's anova() function. Inferential statistics for lower order interactions and marginal effects were calculated with emmeans using Satterthwaite's approximation (Satterthwaite, 1941). Confidence intervals for all effect sizes were calculated using emmeans. All reported p values are two-sided.

Transparency and Openness. All experiments in the present study were preregistered using *AsPredicted* (https://aspredicted.org), with Registration Numbers 115434 (Experiment 1; https://aspredicted.org/yc8g2.pdf), 132650 (Experiment 2; https://aspredicted.org/3t8j-gq3y.pdf), and 133012 (Experiment 3; https://aspredicted.org/m4qh-23b2.pdf). Data, analysis code, stimuli, and experiment scripts are available at https://osf.io/mc5gy (Morgan & Casasanto, 2025).

Results

Primary Analyses

Reaction Time: Does Handedness (Continuous) Predict Frequency Specialization? With handedness treated as continuous, left handedness predicted reduced RVF local > global bias (0.067 ms per EHI unit, 95% CI [0.003, 0.130]), $\chi^2(1) = 4.25$, $p = .039$. Estimated RVF local > global bias for EHI + 100 (strong right handers) was 28.14 ms (95% CI [20.31, 35.98]) and for EHI − 100 (strong left handers), 14.82 ms (95% CI [6.48, 23.17]), a difference of 13.32 ms (see Figure 4).

Within the local level, left handedness predicted reversed RVF bias (0.123 ms per EHI unit, 95% CI [0.078, 0.168]), $t(101, 766.6) = 5.34$, $p \leq .0001$. Strong right handers (EHI = +100) showed estimated RVF bias of 14.96 ms (95% CI [9.38, 20.53]); by contrast, strong left handers (EHI = −100) showed estimated LVF bias of 9.61 ms (95% CI [−1.88, 8.43]), a difference of 24.57 ms.

Reaction Time: Does Handedness (Categorical) Predict Frequency Specialization? For reaction time, RVF local > global bias was significantly reduced in left handers ($n = 331$, EHI ≤ -40) compared to right handers ($n = 378$, EHI $\geq +40$); difference between groups = 11.67 ms (95% CI [0.65, 22.69]), $\chi^2(1) = 4.31$, $p = .038$. Both groups showed significant RVF local > global bias: For right handers, the effect size was 27.31 ms (95% CI [19.78, 34.83]), $t(85, 499.1) = 7.11$, $p < .0001$; for left handers, 15.64 ms (95% CI [7.60, 23.69]), $t(85, 499.4) = 3.81$, $p = .001$; see Figure 5.

Within the local level, right and left handers showed reversed hemifield bias, in the direction predicted by AAH: Right handers responded faster to local targets in the RVF than LVF by 12.28 ms (95% CI [6.93, 17.63]), $t(85, 499.3) = 4.50$, $p < .0001$, whereas left handers responded faster to local targets in the LVF than RVF by 9.65 ms (95% CI [3.91, 15.39]), $t(85, 499.7) = 3.30$, $p = .001$; difference = 21.94 ms (95% CI [14.01, 29.79]), $t(85, 499.5) = 5.48$, $p < .0001$.

Exploratory Analyses

Reaction Time: EHI Extremes (±100). Limiting analysis to strong left and right handers with EHI scores of ±100, strong left handers' RVF local > global bias was reduced by 23.52 ms (95% CI [7.10, 39.93]), $\chi^2(1) = 7.89$, $p = .005$. Strong right handers showed significant RVF local > global bias (28.10 ms, 95% CI [17.34, 38.86]), $t(38, 617.45) = 5.12$, $p < .0001$, whereas strong left handers showed no significant interaction of field by level (4.59 ms, 95% CI [−7.81, 16.98]), $t(38, 617.6) = 0.73$, $p = .47$; see Figure 5.

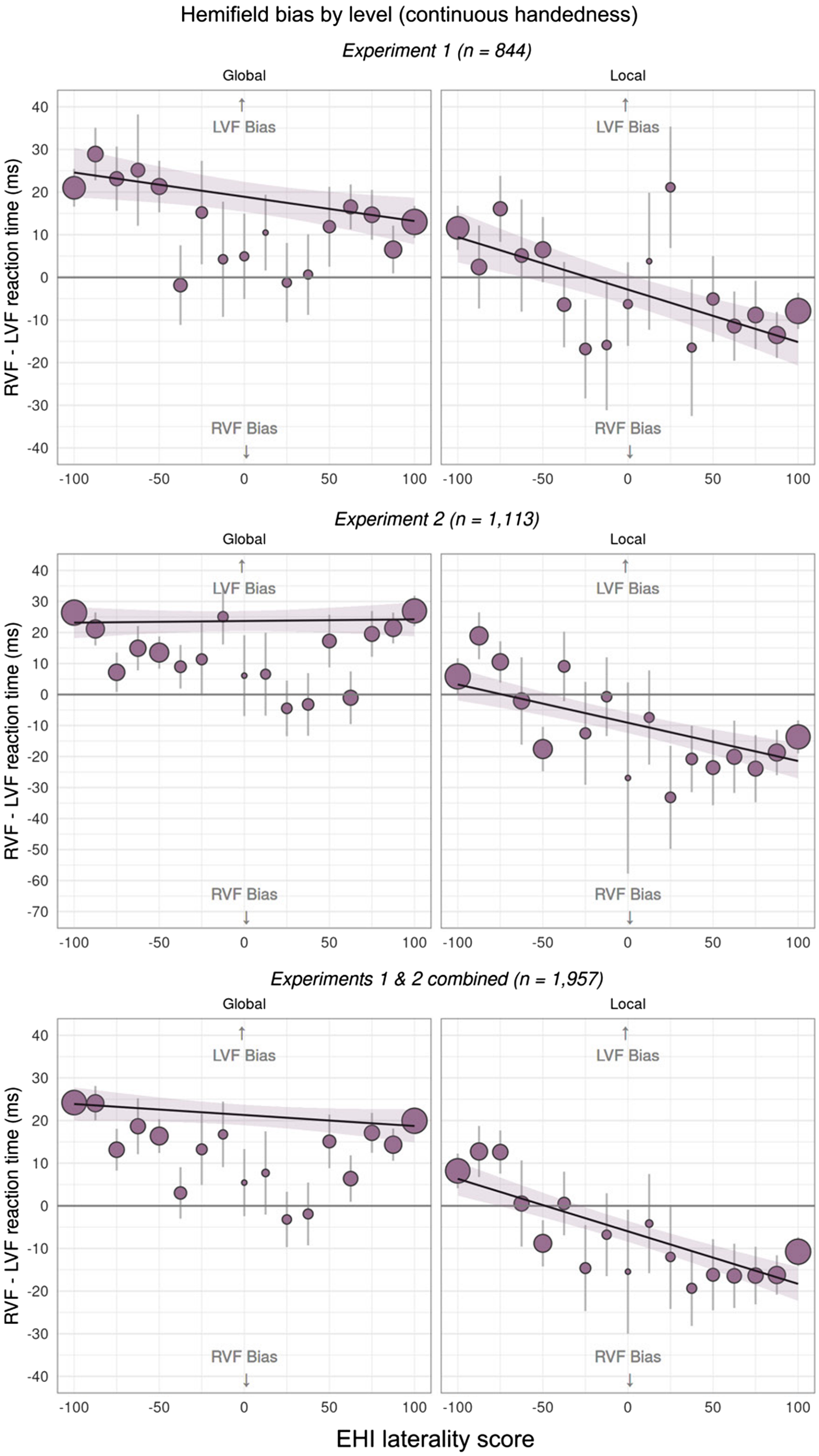
Within the local level, strong left handers showed reversed hemifield bias: Strong right handers responded faster to local targets in the RVF than LVF by 13.56 ms (95% CI [5.90, 21.22]), $t(38, 617.6) = 3.47$, $p = .0005$, whereas strong left handers responded faster to local targets in the LVF than RVF by 18.09 ms (95% CI [9.25, 26.93]), $t(38, 617.69) = 4.01$ $p < .0001$; difference = 31.65 ms (95% CI [19.96, 43.35]), $t(38, 617.67) = 5.30$, $p < .0001$.

Reaction Time: Effect of Target Shape. Some pilot participants reported that the circle targets were relatively easy to see compared to the square targets, and indeed, reaction times were faster for circles than for squares, at both the local level, difference = 66.71 ms (95% CI [62.81, 70.61]), $t(85, 494.1) = 14.49$, $p < .0001$, and the global level, difference = 28.36 ms (95% CI [24.53, 32.20]), $t(85, 491.0) = 14.49$, $p < .0001$. Because global precedence effects may be stronger under perceptual uncertainty (Navon, 1977), the circles' high visibility could lead to lower global precedence and potentially weaken the interaction of field by level. Indeed, participants showed greater global precedence for squares, by 40.68 ms for right handers (95% CI [33.21, 48.15]), $t(85, 492.1) = 10.67$, $p < .0001$, and 36.01 ms for left handers (95% CI [28.01, 44.00]), $t(85, 492.9) = 8.83$, $p < .001$. Within right handers, the interaction of field by level was greater for squares (37.66 ms, 95% CI [26.97, 48.34]), $t(85, 491.4) = 6.91$, $p < .0001$, than for circles (18.14 ms, 95% CI [7.70, 28.58]), $t(85, 490.6) = 3.41$, $p = .0007$; difference = 19.52 ms (95% CI [4.58, 34.46]), $t(85, 490.9) = 2.56$, $p = .01$.

Although target shape did not have a significant effect on the interaction of Field by Level × Handedness (15.89 ms greater for squares, 95% CI [−5.99, 37.76]), $\chi^2(1) = 2.03$, $p = .16$, the

Figure 4

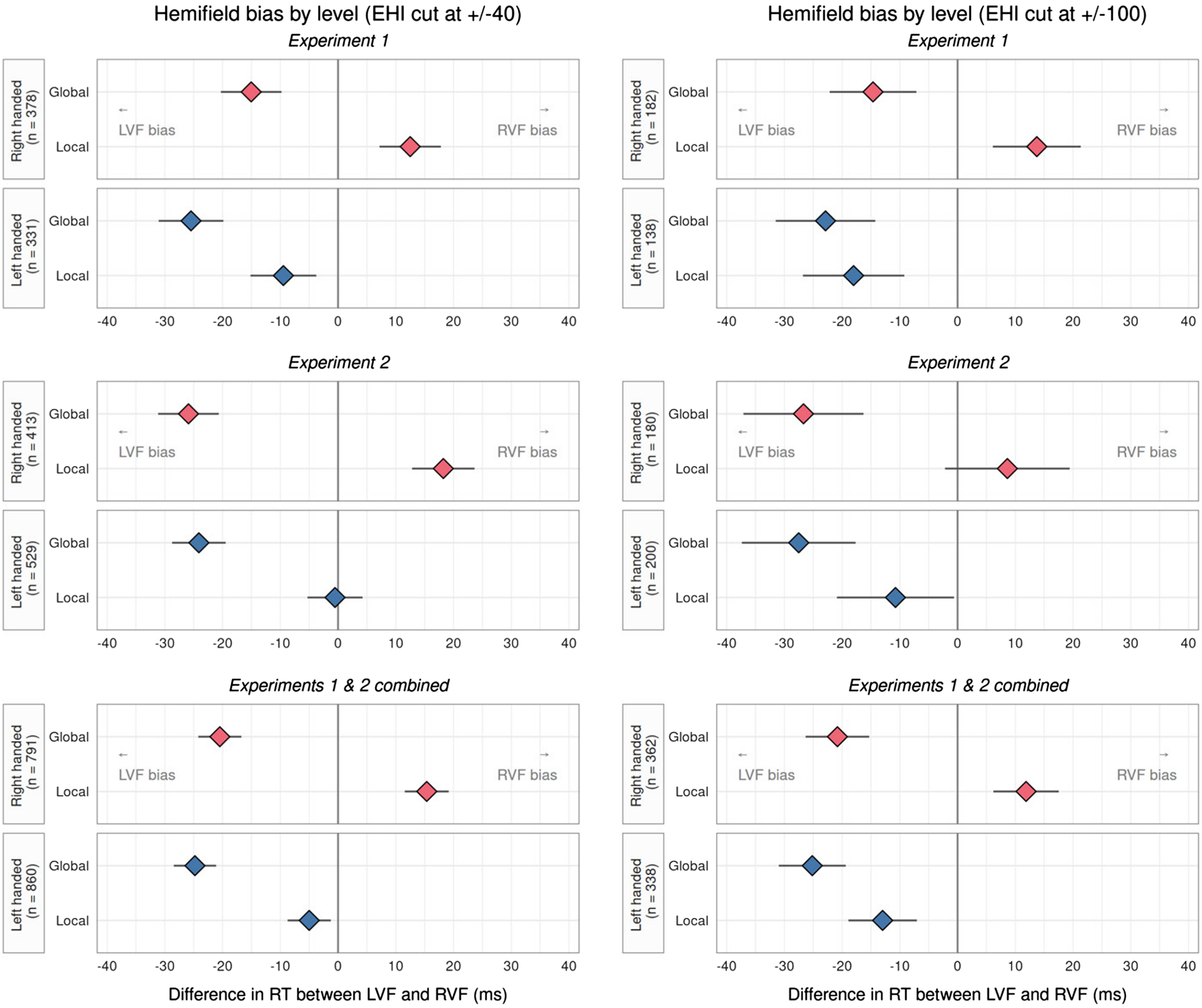
Hemifield Frequency Bias by Handedness (Continuous)



Note. Dots and vertical error lines show subject-level means and standard error of the mean. The shaded area shows 95% confidence interval around the model-estimated line of best fit. EHI = Edinburgh Handedness Inventory; RVF = right visual field; LVF = left visual field. See the online article for the color version of this figure.

Figure 5

Hemifield Frequency Bias by Handedness (Categorical)



Note. Plots in the left column compare right and left handers, with handedness binned at EHI > 40 (right handed; red) and EHI < −40 (left handed; blue). Plots in the right column compare strong right handers (EHI = 100; red) to strong left handers (EHI = −100; blue). The horizontal axes represent response time to stimuli in the right versus left visual field. Diamonds show mixed-effects model point estimates for responses to global and local targets, with 95% confidence interval. EHI = Edinburgh Handedness Inventory; RVF = right visual field; LVF = left visual field. See the online article for the color version of this figure.

interaction of Field by Level × Handedness was significant for squares (19.76 ms, 95% CI [4.11, 35.40]), $t(85, 491.5) = 2.48$, $p = .013$, but not for circles (3.87 ms, 95% CI [−11.41, 19.16]), $t(85, 490.62) = 0.50$, $p = .62$. On the basis of this exploratory analysis of the different stimulus shapes, we modified the stimuli for Experiments 2 and 3.

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), and hemispheric specialization for high-spatial frequencies was reversed. These results challenge the fetal and language asymmetry hypotheses, neither of which predicts that frequency specialization should depend on handedness, and they provide initial support for the AAH: Frequency asymmetries in vision can be predicted by frequency asymmetries in action.

Experiment 2: Replicating Experiment 1

In Experiment 2, we replicated Experiment 1 in a second large, online sample. The design was identical except that rectangle targets replaced the circle targets that had been used in Experiment 1, with the aim to ensure that all targets were equally difficult to identify. Additionally, participants completed the dichotic listening task analyzed in Experiment 3. Experiment 2 analyses aimed to closely replicate the analyses of Experiment 1, using the same inclusion criteria.

Method

Participants

One thousand four hundred fifty participants were recruited through the online data collection platform Prolific, and 1,113 met all inclusion criteria: 413 right handers (EHI $\geq$ +40), 171 mixed handers (EHI > −40 and < +40), and 529 left handers (EHI < −40; see Figure 1 for the distribution of EHI scores). Participants' mean age was 29.62 years (*SD* = 5.85) and years of education, 14.74 (*SD* = 2.54). Five hundred ninety-five participants described their sex as male, 500 as female, and 18 as something else. At the time of participation, 615 participants lived in the United States and 498 in the United Kingdom. Eight hundred thirty-one participants reported their race as White, 96 Black or African American, 90 multiple races, 84 Asian, seven American Indian or Alaska Native, three Native Hawaiian or other Pacific Islander, and two as something else; 99 reported Hispanic ethnicity. Left handers in this sample had a mean age of 29.2 years (*SD* = 5.7), whereas right handers had a mean age of 30.57 years (*SD* = 5.81); difference = 1.37 years (95% CI = [0.62, 2.12]), $t(940) = 3.63$, $p = .0003$. Left handers also had, on average, 14.94 years of education (*SD* = 2.35), whereas right handers had 14.48 (*SD* = 2.35); difference = 0.46 years (95% CI [0.13, 0.79]), $t(936) = 2.72$, $p = .007$. Additionally, left handers were more likely to be female (*OR* = 1.75, 95% CI [1.35, 2.27], $z = 4.15$, $p < .0001$). These differences may be accounted for by demographic differences in the pool of Prolific participants from the United States and the United Kingdom. Exploratory analyses evaluated the potential effect of sex on frequency asymmetry and its relation to handedness, in part to ensure that primary analyses were not confounded by this demographic difference.

Recruitment and Exclusions. Participants were recruited in batches until the sample yielded at least 375 participants in each group (yielding greater than 90% power to replicate all effects of interest). The recruitment procedure and exclusion criteria were identical to Experiment 1, except that participants from the United Kingdom were included, to enable timely recruitment of a sufficient number of left-handed participants. Each participant was compensated $3.00 USD (median $14.06/hr) for attempting the study, which was approved by Cornell's Institutional Review Board. All participants gave informed consent via an online form.

Of the 1,450 recruited participants, 307 were excluded, leaving 1,113. Following preregistered criteria, participants' data were excluded if they reported living in a country other than the United States or the United Kingdom ($n = 4$), reported an age below 18 or over 40 ($n = 4$), reported having done the task before ($n = 12$), did not complete the EHI questionnaire ($n = 5$), did not complete all experimental trials ($n = 90$), had accuracy below 60% (48/80 trials correct) within either 80-trial block ($n = 19$), responded "go" to 78 or more trials in any 80-trial block ($n = 44$), or had a median reaction time greater than 1,500 ms ($n = 11$) or less than 200 ms ($n = 14$) within either 80-trial block. Additionally, 139 participants were excluded for having EHI scores that did not match their prescreening responses (79 prescreened as "left handed" but with EHI scores >0; 55 "ambidextrous" with EHI of −100 or +100; and five "right handed" with EHI $\leq$ 0). Of the 307 excluded participants, 29 met multiple exclusion criteria.

Materials and Procedure

Participants completed a bilateral hierarchical shapes task identical to that in Experiment 1, except that target shapes were squares and rectangles, instead of squares and circles. We made this change because the circles used in Experiment 1 were highly visible, which may have reduced sensitivity to global precedence effects. Participants also completed the dichotic listening task described in Experiment 3. Half of all participants completed the dichotic listening task first, and half completed the hierarchical shapes task first. Participants filled out the four-item Veale Edinburgh Handedness Inventory (described in Experiment 1) after completing both the hierarchical shapes and dichotic listening tasks.

Analysis Procedure

To test the reliability of the results of Experiment 1, we replicated all primary analyses, as well as the exploratory analyses with strong right and left handers (EHI ± 100). Additionally, we repeated primary analyses in the combined sample of participants from both experiments.

Results

Primary Analyses

Reaction Time: Does Handedness (Continuous) Predict Frequency Specialization? With handedness treated as continuous, left handedness predicted reduced RVF local > global bias (0.13 ms per EHI unit, 95% CI [0.06, 0.19]), $\chi^2(1) = 17.88$, $p < .0001$. Estimated RVF local > global bias for EHI + 100 (strong right handers) was 45.61 ms (95% CI [37.73, 53.48]) and for EHI − 100 (strong left handers), 19.92 ms (95% CI [12.72, 27.12]), a difference of 25.69 ms (see Figure 4).

Within the local level, left handedness predicted reduced RVF bias (0.12 ms per EHI unit, 95% CI [0.07, 0.18]), $t(131, 342.5) = 5.65$, $p \leq .0001$. Strong right handers (EHI = +100) showed estimated RVF bias of 21.36 ms (95% CI [15.70, 27.01]), and strong left handers (EHI = −100) showed estimated LVF bias of 3.28 ms (95% CI [−1.88, 8.43]).

Reaction Time: Does Handedness (Categorical) Predict Frequency Specialization? For reaction time, RVF local > global bias was significantly reduced in left handers ($n = 529$, EHI ≤ -40) compared to right handers ($n = 413$, EHI $\geq +40$), difference between groups = 20.51 ms (95% CI [10.45, 30.57]), $\chi^2(1) = 15.98$, $p < .0001$. Both groups showed significant RVF local > global bias: For right handers, the effect size was 44.09 ms (95% CI [36.54, 51.63]), $t(111, 144.6) = 11.46$, $p \leq .0001$; for left handers, 23.57 ms (95% CI [16.92, 30.23]), $t(111, 144.1) = 6.94$, $p < .0001$; see Figure 5.

Within the local level, left handers showed reduced hemifield bias, in the direction predicted by AAH: Right handers responded faster to local targets in the RVF than LVF by 18.16 ms (95% CI [12.75, 23.57]), $t(111, 145.9) = 6.58$, $p < .0001$, whereas left handers responded faster to local targets in the LVF than RVF by 0.56 ms (95% CI [−4.21, 5.33]), $t(111, 145.6) = 0.23$, $p = .82$;

difference = 18.72 ms (95% CI [11.51, 26.83]), $t(111, 145.78) = 5.09$, $p < .0001$.

Exploratory Analyses

Reaction Time: EHI Extremes (±100). Limiting analysis to strong left and right handers with EHI scores of ±100, left handers' RVF local > global bias was reduced by 17.44 ms (95% CI [1.50, 33.38]), $\chi^2(1) = 4.60$, $p = .032$. Both groups showed significant RVF local > global bias: For right handers, the effect size was 36.96 ms (95% CI [25.36, 48.56]), $t(44, 479.7) = 6.25$, $p < .0001$; for left handers, 19.52 ms (95% CI [8.58, 30.45]), $t(44, 479.0) = 3.50$, $p = .0005$.

Within the local level, left handers showed reversed hemifield bias: Right handers responded faster to local targets in the RVF than LVF by 9.97 ms (95% CI [1.61, 18.32]), $t(44, 479.9) = 2.34$, $p = .019$, whereas left handers responded faster to local targets in the LVF than RVF by 7.98 ms (95% CI [0.14, 15.83]), $t(44, 479.4) = 2.00$ $p = .046$; difference = 17.95 ms (95% CI [6.48, 29.41]), $t(44, 479.7) = 3.07$, $p = .002$.

Experiments 1 and 2: Combined Results

Participants

One thousand nine hundred fifty-eight combined participants (860 left handers, 307 mixed handers, and 791 right handers) met inclusion criteria for Experiments 1 or 2. To summarize, Experiments 1 and 2 differed in the following respects: (a) Target shapes in Experiment 2 were squares and rectangles, rather than squares and circles; (b) participants in Experiment 2 completed the dichotic listening task described in Experiment 3, either before or after the Navon task; and (c) all participants in Experiment 1 were based in the United States, whereas Experiment 2 included participants from both the United States and the United Kingdom. Exploratory analyses on the effect of sex were conducted with the combined sample, in order to maximize statistical power to detect potential differences.

Reaction Time: Does Handedness (Continuous) Predict Frequency Specialization? Combining experiments, left handedness predicted reduced RVF local > global bias (0.097 ms per EHI unit, 95% CI [0.054, 0.141]), $t(233, 104.7) = 4.39$, $p < .0001$. Strong right handers (EHI = +100) showed estimated RVF local > global bias of 37.03 ms (95% CI [31.47, 42.58]), $t(233, 104.9) = 13.06$, $p < .0001$, and strong left handers (EHI = −100) showed estimated RVF local > global bias of 17.54 ms (95% CI [12.02, 23.07]), $t(233, 104.5) = 6.22$, $p < .0001$. The interaction of Field by Level × Handedness did not differ significantly between Experiments 1 and 2, difference = 0.063 ms per EHI unit (95% CI [−0.024, 0.15]), $\chi^2(1) = 1.99$, $p = .16$; see Figure 4.

Within the local level, left handedness predicted reversed hemifield bias (0.123 ms per EHI unit, 95% CI [0.092, 0.154]), $t(233, 106.3) = 7.76$, $p < .0001$. Strong right handers (EHI + 100) showed estimated RVF local bias of 18.31 (95% CI [14.34, 22.28]), $t(233, 106.6) = 9.03$, $p < .0001$, whereas strong left handers (EHI − 100) showed estimated LVF local bias of 6.33 ms (95% CI [2.38, 10.28]), $t(233, 106.1) = 3.14$, $p = .002$. The effect of handedness on local hemifield bias did not differ between Experiments 1 and 2, difference = 0.00 ms per EHI unit (95% CI [−0.063, 0.062]), $t(233, 106.2) = 0.01$, $p = .99$.

Reaction Time: Does Handedness (Categorical) Predict Frequency Specialization? Combining experiments, RVF local > global bias was significantly reduced in left handers ($n = 860$, EHI ≤ −40) compared to right handers ($n = 791$, EHI ≥ +40); difference between groups = 16.01 ms (95% CI [8.58, 23.51]), $t(196, 641.1) = 4.21$, $p < .0001$. Right handers showed 35.84 ms RVF local > global bias (95% CI [30.51, 41.16]), $t(196, 641.2) = 13.19$, $p < .0001$, and left handers showed only 19.79 ms RVF local > global bias (95% CI [14.55, 25.03]), $t(196, 641.0) = 7.41$, $p < .0001$. The interaction of Field by Level × Handedness did not differ significantly between Experiments 1 and 2, difference = 9.0 ms greater in Experiment 2 (95% CI [−5.92, 23.96]), $t(196, 642.0) = 1.18$, $p = .24$; see Figure 5.

Within the local level, left handers showed reversed hemifield bias, in the direction predicted by AAH: Right handers responded faster to local targets in the RVF than LVF by 15.36 ms (95% CI [11.55, 19.17]), $t(196, 642.6) = 7.91$, $p < .0001$, whereas left handers responded faster to local targets in the LVF than RVF by 5.00 ms (95% CI [1.26, 8.74]), $t(196, 642.4) = 2.62$, $p = .009$; difference = 20.36 ms (95% CI [15.02, 25.69]), $t(196, 642.5) = 7.47$, $p < .0001$. The effect of handedness on local hemifield bias did not differ significantly between Experiments 1 and 2, difference = 3.20 ms greater in Experiment 1 (95% CI [−7.47, 13.88]), $t(196, 642.5) = 0.59$, $p = .56$.

Reaction Time: EHI Extremes (±100). Limiting analysis to strong left and right handers with EHI scores of ±100, left handers' RVF local > global bias was reduced by 20.49 ms (95% CI [9.05, 31.93]), $t(83, 094.7) = 3.51$, $p = .0005$. Both groups showed significant RVF local > global bias: For right handers, the effect size was 32.68 ms (95% CI [24.78, 40.57]), $t(83, 095.0) = 8.11$, $p < .0001$; for left handers, only 12.19 ms (95% CI [3.90, 20.47]), $t(83, 094.4) = 2.88$, $p = .004$. The interaction of Field by Level × Handedness did not differ significantly between Experiments 1 and 2, difference = 6.03 ms greater in Experiment 1 (95% CI [−16.86, 28.92]), $t(83, 094.7) = 0.52$, $p = .61$; see Figure 5.

Within the local level, left handers showed reversed hemifield bias: Right handers responded faster to local targets in the RVF than LVF by 11.86 ms (95% CI [6.21, 17.51]), $t(83, 095.4) = 4.11$, $p < .0001$, whereas left handers responded faster to local targets in the LVF than RVF by 12.99 ms (95% CI [7.06, 18.91]), $t(83, 094.9) = 4.30$ $p < .0001$; difference = 24.85 ms (95% CI [16.66, 33.04]), $t(83, 095.2) = 5.95$, $p < .0001$. The effect of handedness on local hemifield bias did not differ significantly between Experiments 1 and 2, difference = 13.78 ms greater in Experiment 1 (95% CI [−2.61, 30.16]), $t(83, 095.1) = 1.65$, $p = .10$.

Exploratory Analyses

Sex and Frequency Specialization. In principle, higher levels of the sex hormones estradiol or progesterone in females could lead to reduced hemispheric specialization for spatial frequency (Hausinger & Pletzer, 2021) by increasing interhemispheric communication (Hausmann, 2017). However, studies that have tested whether hemispheric specialization for spatial frequency depends on sex have found conflicting results. Using frequency-filtered natural scenes, Peyrin, Chokron, et al. (2006) found greater hemispheric specialization (in the direction of RVF high-spatial-frequency bias) in males, with no significant hemispheric specialization detected in females. In contrast, Perilla-Rodríguez et al. (2013) found greater hemispheric specialization in females and no significant hemispheric specialization in males, when identifying frequency-filtered face images. Hausinger and Pletzer (2021) found no significant effect of sex on hemifield asymmetry in a hierarchical letter task. (All three of these studies included only right-handed participants.) Does sex influence hemispheric specialization for frequency, in either direction? And, does the effect of handedness on frequency specialization hold across male and female participants?

Within right-handed participants, the typical effect of field by level was present in both males (38.28 ms, 95% CI [31.20, 45.36]), $t(193, 708.4) = 10.60$, $p < .0001$, and females (32.26 ms, 95% CI [23.89, 45.36]), $t(193, 710.3) = 7.55$, $p < .0001$, with no significant difference between groups, difference = 6.01 ms greater in males (95% CI [−4.95, 16.98]), $t(193, 709.5) = 1.08$, $p = .282$. The effect of handedness on frequency specialization held in both male (13.37 ms, 95% CI [3.15, 23.59]), $t(193, 708.5) = 2.57$, $p = .01$, and female (17.58 ms, 95% CI [6.29, 28.86]), $t(193, 709.8) = 3.05$, $p = .002$, participants, with no significant difference between groups, difference = 4.20 ms greater in females (95% CI [−11.02, 19.43]), $t(193, 709.8) = 0.54$, $p = .59$; see Figure 6. In summary, we find no significant sex differences in hemispheric specialization for frequency or in the relationship between handedness and hemispheric specialization for frequency.

Discussion

Experiment 2 replicated the effect of handedness on hemispheric specialization for spatial frequency. Combining Experiments 1 and 2, left handers showed a reduced interaction of field by level and reversed hemispheric specialization for high-spatial frequencies, supporting the AAH.

Experiment 3: Can Language Laterality Explain the Effect of Handedness on Frequency Specialization?

In Experiment 3, we tested whether language laterality, as measured in a dichotic listening task, could explain away the effects of handedness on frequency specialization observed in Experiments 1 and 2. To do this, we tested whether handedness predicted language laterality and whether the effect of handedness on frequency specialization persisted when language laterality was taken into account. AAH predicts that the effect of handedness on frequency specialization will remain significant when statistically controlling for language laterality and when limiting analysis to participants with left-hemisphere language dominance.

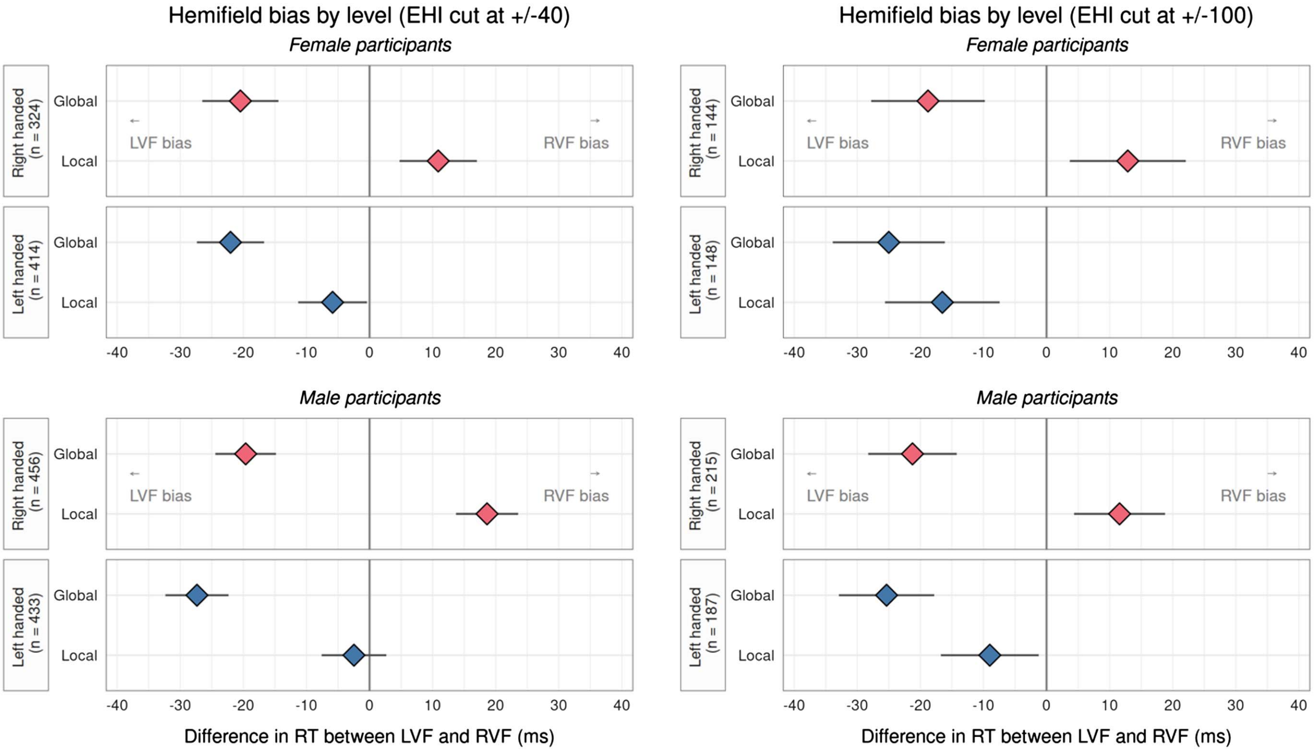
Method

Participants

We administered Experiment 3's dichotic listening task to all participants of Experiment 2, in the same session. Of the 1,450 participants recruited, 734 met inclusion criteria for Experiment 3: 293 right handers (EHI ≥ +40), 99 mixed handers (EHI > −40 and < +40), and 342 left handers (EHI < −40; see Figure 1 for the distribution of EHI scores). Participants' mean age was 29.67 years

Figure 6

Hemifield Frequency Bias by Handedness (Categorical), by Sex (Combining Experiments 1 and 2)



Note. Diamonds show mixed-effects model point estimates, with 95% confidence interval. EHI = Edinburgh Handedness Inventory; RT = reaction time; RVF = right visual field; LVF = left visual field. See the online article for the color version of this figure.

(*SD* = 5.84) and years of education, 14.65 (*SD* = 2.50). Four hundred sixteen participants described their sex as male, 305 as female, and 13 as something else. At the time of participation, 422 participants lived in the United States and 312 in the United Kingdom. Five hundred fifty-seven participants reported their race as White, 53 Black or African American, 63 multiple races, 54 Asian, six American Indian or Alaska Native, 0 Native Hawaiian or other Pacific Islander, and one as something else; 68 reported Hispanic ethnicity.

Exclusions. Of the 1,450 recruited participants (the same pool as Experiment 2), 1,330 fully completed both the Navon and dichotic listening tasks; of these, 596 were excluded based on preregistered criteria. Participants' data were excluded if they reported living in a country other than the United States or United Kingdom ($n = 4$), reported an age below 18 or over 40 ($n = 4$), reported having done the task before ($n = 12$), did not complete the EHI questionnaire ($n = 5$), did not complete all experimental trials ($n = 90$), had accuracy lower than 5/6 trials correct in the headphone check ($n = 410$) or the stereo audio check ($n = 115$), had accuracy lower than 75% in mono dichotic listening (the 24 trials with the same sound played to each ear; $n = 78$), or had below 60% accuracy in stereo dichotic listening (the 120 trials with different sounds played to each ear; $n = 39$). Additionally, 139 participants were excluded for having EHI scores that did not match their prescreening responses (79 prescreened as "left handed" but with EHI scores >0; 55 "ambidextrous" with EHI of −100 or +100; and five "right handed" with EHI ≤ 0). According to our preregistered criteria, participants were eligible for inclusion in analyses of the simple correlation between handedness and dichotic listening, even if they did not meet inclusion criteria for the hierarchical shapes task described in Experiment 2 (whereas they would need to meet criteria for both tasks for all analyses correlating data from both tasks). However, very few participants ($n = 26/760$) met criteria for the dichotic listening task but not the hierarchical shapes task. To simplify reporting, participants were only included in Experiment 3 analyses if they met inclusion criteria for both tasks. Of the 596 excluded participants, 198 met multiple exclusion criteria.

Materials and Procedure

Participants completed a consonant–vowel dichotic listening task that has previously shown to be reliable when administered by smartphone (Bless et al., 2013) and online (Parker et al., 2021). This task follows many of Westerhausen's (2019) recommendations for dichotic listening task design, including use of 120 or more trials, one stimulus pair per trial, pseudorandomization of stimulus order, and consonant–vowel stimuli which are likely to perceptually "fuse." The task was implemented in Inquisit with the aim of reproducing the online task administered by Parker et al. (2021) as closely as possible.

Stimuli. The dichotic listening stimuli were identical to those used by Karlsson et al. (2019) and Parker et al. (2021), comprising the six consonant vowel syllables: *ba*, *da*, *ga*, *pa*, *ta*, and *ka*. In each trial, a single pair of these syllables was presented, one syllable to each ear, for a total of 36 unique stereo stimuli.

Procedure. Before the dichotic listening task, participants completed two screening tasks which were meant to ensure they were wearing headphones (or earphones), with the expected sound channel on each ear. First, they completed a headphone check in which they judged which of three stereo sounds was quietest: These sounds were engineered to have perceptibly different volumes when heard with headphones, but to be very difficult to distinguish without headphones, because of phase cancellation (see Woods et al., 2017, for a detailed explanation). Second, participants completed a stereo audio check in which they were played a series of sounds, each played to only one sound channel, and reported in which headphone they heard each sound.

Then, participants completed a training phase in which they were presented each of the target stimuli, in mono, while being shown the text label for each sound (e.g., they heard the syllable *ga* while seeing the text label "ga"). These text labels would later be used for responses during the task phase. Participants could click "play" as many times as they liked to familiarize themselves with each sound. Once participants had listened to every sound, they advanced to the task phase.

In the task phase, participants completed four blocks each with the full set of 36 stimulus trials, for a total of 144 trials: 120 experimental trials with distinct phonemes in each ear and 24 catch trials with the same phoneme played to each ear. Participants were instructed to report which sound they heard most clearly on each trial: "Your goal is to indicate the sound that you heard. Sometimes you might hear two sounds. If you hear two sounds, you should select the sound that was clearest." Participants reported which sound they heard most clearly by clicking one of six text labels on the bottom of the screen, which were always presented in the same, alphabetical, order. For each participant, a language laterality score was calculated based on the number of responses correctly reporting right ear (RE) and left ear (LE) stimuli using the following formula:

$$\text{Language laterality} = \frac{\text{RE} - \text{LE}}{\text{RE} + \text{LE}} \times 100. \tag{1}$$

This formula yielded laterality scores ranging from −100 (strong left ear preference, right hemisphere dominance) to 100 (strong right ear preference, left-hemisphere dominance).

Participants were not instructed to use a particular hand to make their responses. After the task phase, participants were asked which hand they had used: "During the task you just completed (clicking to report which sounds you heard), which hand did you use to click the mouse or trackpad?" Participants could respond with the same options as on the Veale Edinburgh Handedness Inventory (always left, usually left, both equally, usually right, or always right), and their responses were scaled from −100 (*always left*) to 100 (*always right*).

As described in Experiment 2, participants completed the dichotic listening task and sound checks either before or after the bilateral shapes task, pseudorandomly, such that half of participants completed the shapes task first, half dichotic listening first. Participants completed the Veale Edinburgh Handedness Inventory after completing both the shapes and dichotic listening tasks.

Analysis Procedure

In primary analyses, we tested whether handedness predicts language laterality, in a simple linear model, and when statistically controlling for dichotic listening response hand. For comparison with previous studies, we estimated the effect of handedness on dichotic listening measured continuously and categorically (i.e., the proportion of right and left handers who showed right and left ear preference). In exploratory analyses, we tested whether the effect of handedness on frequency specialization persisted when accounting for language laterality, by including language laterality as a covariate, and by limiting analyses to participants with left-hemisphere language laterality.

Results

Primary Analyses

Does Handedness (Continuous) Predict Language Laterality? Consistent with previous literature (e.g., Karlsson et al., 2023; Packheiser et al., 2020), handedness correlated weakly with language laterality, slope = 0.063 dichotic listening score units per EHI unit (95% CI [0.031, 0.095]); $\rho(732) = .14$, 95% CI [.07, .21], $p = .0001$; see Figure 7. However, because participants were free to respond using whichever hand they preferred during the task, there is reason to suspect this estimate may be inflated by a possible response-hand congruity effect. If responding with your right hand increases your bias toward right ear preference, participants who responded with their right hand would have greater right ear preference, as a group. Because right handers may be more likely to click with their right hand, response-hand congruence could result in spurious correlation between right handedness and right ear bias. Indeed, degree of right-handedness correlated with click hand, $\rho(732) = .38$, (95% CI [.31, .44], $p < .0001$), and click hand correlated with language laterality in the expected direction, $\rho(732) = .13$ (95% CI [.06, .20], $p = .0005$). Accordingly, statistically controlling for click hand should yield a more accurate estimate of the effect of handedness on dichotic listening laterality.

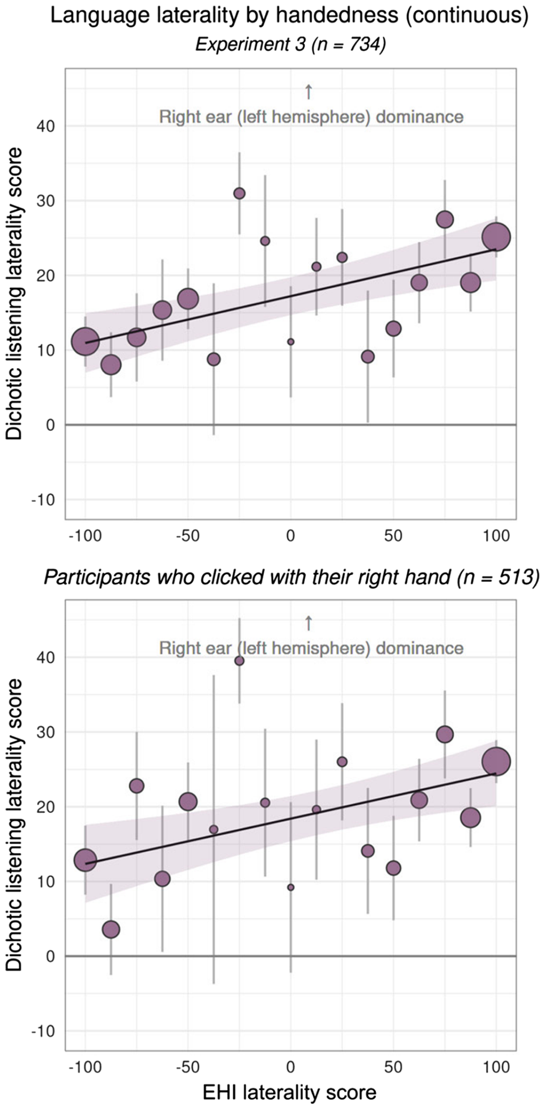
With click hand included in the model, the effect of handedness on language laterality persisted, with a slightly smaller effect size, slope = 0.047 dichotic listening score units per EHI unit (95% CI [0.014, 0.082]), $\rho(732) = .10$ (95% CI [.03, .17], $p = .006$). The effect of click hand on language laterality was significant, in the direction predicted by a response-hand congruence effect, slope = .044 dichotic listening score units per click hand EHI unit (95% CI [.005, .083]), $F(1, 732) = 4.89$, $p = .027$. Because of this effect of click hand on language laterality, click hand was included in subsequent analyses involving the relationship between handedness and language laterality.

The effect of handedness on language laterality also persisted when limiting analysis to participants who always clicked with their right hand, slope = 0.061 dichotic listening score units per EHI unit (95% CI [0.023, 0.098]), $\rho(511) = .14$, $p = .002$; see Figure 7.

Does Handedness (Categorical) Predict Language Laterality? Treating handedness categorically, right handers were significantly more left hemisphere dominant than left handers, difference in mean laterality score = 9.98 (95% CI [4.48, 15.48]), $t(633) = 3.57$, $p = .0004$; see Figure 8. This difference persisted when click hand was included in the model, difference = 7.64 (95% CI [1.71, 13.57]), $t(632) = 2.53$, $p = .012$. Both handedness groups showed left-hemisphere dominance: Right handers' mean laterality score was 21.06 (95% CI [16.85, 25.62]), $t(632) = 9.83$, $p < .0001$; left handers, 13.42 (95% CI [9.56, 17.29]), $t(632) = 6.81$, $p < .0001$. The difference between right and left handers also persisted when limiting analysis to participants who clicked only with their right hand, difference in mean laterality score = 9.65 (95% CI [3.17, 16.13]), $t(450) = 2.92$, $p = .004$; see Figure 8.

Figure 7

Language Laterality by Handedness (Continuous), With and Without Correcting for Response Hand



Note. Language laterality (measured by dichotic listening ear preference, continuous) by handedness (continuous), in all Experiment 3 participants meeting inclusion criteria (top panel), and within participants who reported responding only with their right hand (bottom panel). Dots and vertical error lines show subject-level means and standard error of the mean. The shaded area shows 95% confidence interval around the model-estimated line of best fit. See the online article for the color version of this figure.

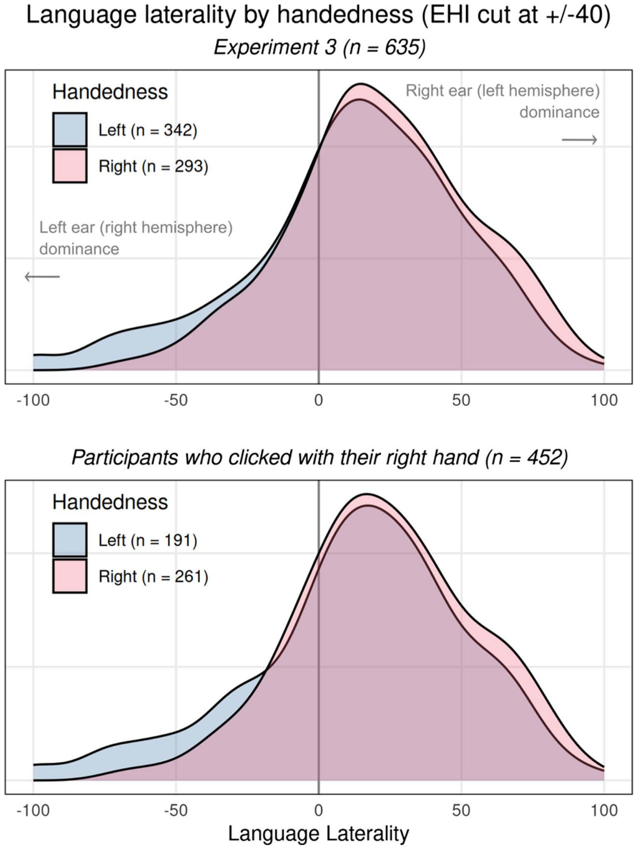
Binning participants as left hemisphere dominant (dichotic listening laterality score > +10) or right hemisphere dominant (dichotic listening laterality score < −10), 64.16% of right handers and 58.19% of left handers showed left-hemisphere dominance.

Exploratory Analyses

Does Handedness (Continuous) Predict Frequency Specialization, When Controlling for Language Laterality? The effect

Figure 8

Language Laterality by Handedness (Categorical), With and Without Correcting for Response Hand



Note. Distribution of language laterality (measured by dichotic listening ear preference, continuous) by handedness (categorical), in all Experiment 3 participants meeting inclusion criteria (top panel), and within participants who reported responding only with their right hand (bottom panel). EHI = Edinburgh Handedness Inventory. See the online article for the color version of this figure.

of handedness (continuous) on frequency specialization persisted when language laterality was included in the model (0.134 ms per EHI unit, 95% CI [0.053, 0.216]), $t(87, 058.21) = 3.23$, $p = .001$; because of the effect of click hand on dichotic listening laterality, click hand was modeled as well, so that this model included the interaction of Field by Level × Handedness × Language Laterality × Click Hand. Within the local level, left handedness predicted reduced RVF bias (0.135 ms per EHI unit, 95% CI [0.077, 0.193]), $t(87, 058.8) = 4.54$, $p \leq .0001$.

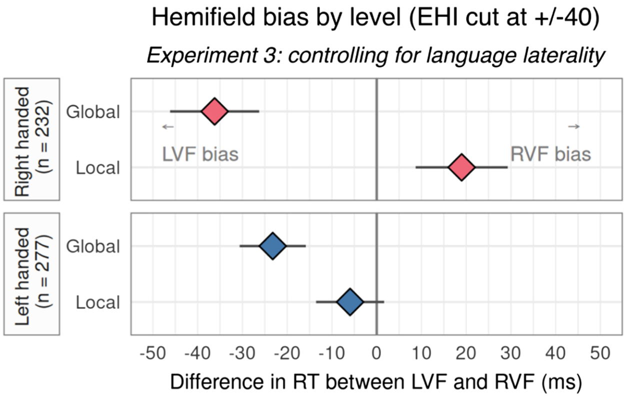
If language laterality were responsible for the correlation between handedness and frequency specialization, the effect should be driven by the small number of left handers with reversed (right hemisphere) language dominance. Accordingly, if handedness predicts frequency specialization within participants who have typical, left-hemisphere language dominance, this effect of handedness on frequency specialization could not be explained away by differences in language laterality. Limiting analysis to participants with left-hemisphere language dominance (dichotic listening laterality score ≥10), the effect of handedness on frequency specialization persisted (0.105 ms per EHI unit, 95% CI [0.017, 0.193]), $t(53, 742.1) = 2.34$, $p = .019$. Within the local level, left handedness continued to predict reduced RVF bias (0.134 ms per EHI unit, 95% CI [0.052, 0.217]), $t(53, 742.5) = 4.18$, $p = .0002$.

Does Handedness (Categorical) Predict Frequency Specialization, When Controlling for Language Laterality? With language laterality included in the model, RVF local > global bias was still significantly reduced in left handers ($n = 277$, EHI ≤ -40) compared to right handers ($n = 232$, EHI $\geq +40$); difference between groups = 37.91 ms (95% CI [20.10, 55.72]), $t(60, 263.63) = 4.17$, $p < .0001$. Both groups showed significant RVF local > global bias: For right handers, the effect size was 55.19 ms (95% CI [40.88, 69.50]), $t(60, 263.9) = 7.56$, $p \leq .0001$; for left handers, 17.29 ms (95% CI [6.69, 27.89]), $t(60, 263.2) = 3.20$, $p = .001$. Within the local level, left handers showed extinguished hemifield bias: Right handers responded faster to local targets in the RVF than LVF by 18.99 ms (95% CI [8.71, 29.27]), $t(60, 265.0) = 3.62$, $p = .0003$, whereas left handers showed no significant difference between responses to local targets in the LVF and RVF, 5.94 ms faster in the LVF (95% CI [−1.66, 13.54]), $t(60, 263.4) = 1.53$, $p = .125$; difference = 24.93 ms (95% CI [12.15, 37,71]), $t(60, 264.4) = 3.82$, $p = .0001$; see Figure 9.

Limiting analysis to participants with left-hemisphere language dominance (DL score ≥ 10), the effect of handedness on RVF local > global bias persisted, difference = 16.19 ms (95% CI [1.21, 31.18]), $t(45, 905.0) = 2.12$, $p = .034$. Both groups showed significant RVF local > global bias: For right handers ($n = 188$), the effect size was 45.95 ms (95% CI [35.19, 56.71]), $t(45, 905.0) = 8.37$, $p \leq .0001$; for left handers ($n = 199$), 29.76 ms (95% CI [19.33, 40.19]), $t(45, 905.0) = 5.59$, $p < .0001$. Within the local level, left handers showed extinguished hemifield bias: Right handers responded faster to local targets in the RVF than LVF by 21.52 ms (95% CI

Figure 9

Hemifield Frequency Bias by Handedness (Categorical), Controlling for Language Laterality



Note. Hemifield frequency bias by level by handedness (categorical), estimated with a model including the interaction of Field by Level × Handedness × Language Laterality × Click Hand, and all component terms, with item (square vs. rectangle) and subject as random intercepts. Diamonds show mixed-effects model point estimates, with 95% confidence interval. EHI = Edinburgh Handedness Inventory; RT = reaction time; RVF = right visual field; LVF = left visual field. See the online article for the color version of this figure.

[13.78, 29.26]), *t*(45, 905.5) = 5.45, $p < .0001$, whereas left handers showed no significant difference between responses to local targets in the LVF and RVF, 1.60 ms faster in the RVF (95% CI [−5.85, 9.04]), *t*(45, 905.4) = 0.42, $p = .68$; difference = 19.92 ms (95% CI [9.18, 30.66]), *t*(45, 905.4) = 3.63, $p = .0003$.

Does Language Laterality Predict Frequency Specialization? Controlling for handedness, language laterality did not significantly influence the interaction of field by level, whether laterality was measured continuously, slope = 0.16 ms per dichotic listening score unit (95% CI [−0.03, 0.35]), *t*(87, 058.18) = 1.69, $p = .09$, or categorically, difference = 11.24 ms greater RVF local > global bias for those with left-hemisphere dominance (95% CI [−6.57, 29.05]), *t*(60, 263.6) = 1.24, $p = .216$.

However, within the local level, degree of right ear preference (i.e., left-hemisphere language dominance) predicted rightward visual field bias, slope = 0.21 ms per dichotic listening score unit (95% CI [0.08, 0.35]), *t*(87, 059.4) = 3.12, $p = .002$. Participants with left-hemisphere dominance (dichotic listening score >10) showed RVF bias of 12.99 ms (95% CI [6.30, 19.69]), *t*(60, 264.1) = 3.80, $p = .0001$, whereas participants with right hemisphere language dominance showed RVF bias of 0.06 ms (95% CI [−10.83, 10.95]), *t*(60, 264.61) = 0.01, $p = .99$; difference = 12.93 ms (95% CI [0.15, 25.72]), *t*(60, 264.46) = 1.98, $p = .047$.

Discussion

Experiment 3 replicated the weak relationship between handedness and language laterality observed in previous studies. Of primary interest here, it also confirmed that the effect of handedness on frequency specialization cannot be explained away by language laterality. The effect of handedness persisted when language laterality was modeled as a covariate and when analysis was limited to participants with typical, left-hemisphere language laterality. In contrast, language laterality did not significantly predict frequency specialization when controlling for handedness, although language laterality did predict hemifield bias within the local level. This pattern of results suggests that the correlation between handedness and frequency specialization is not driven by the slightly higher incidence of atypical language laterality among left handers.

General Discussion

Hemispheric specialization for spatial frequency in vision differed significantly between left and right handers. Across two experiments, left handers showed an extinguished interaction of Visual Hemifield × Level of the Hierarchical Visual Stimuli (global vs. local) and a *reversed* hemifield bias for high-spatial-frequency information. A third experiment confirmed that the effect of handedness cannot be explained by a difference in language laterality. These results challenge the FAH and the LAH, neither of which predicts that frequency specialization should depend on handedness, and they provide initial support for the AAH: Frequency asymmetries in vision may be explained by frequency asymmetries in hand action.

The AAH is an offshoot of the body-specificity hypothesis (Casasanto, 2011). Because the hands are an important point of interface between the mind and the world, patterns of hand use have been found to influence the cognitive and neural organization of emotional valence (Casasanto, 2009), affective motivation (Brookshire & Casasanto, 2012), action verb semantics (Willems et al., 2010), and object affordances (Chrysikou et al., 2017). The present study adds a new relationship between patterns of bodily action and brain organization: Systematic differences in how people use their hands may lead to systematic differences in the neural basis of frequency specialization.

Two mechanisms could explain how hand action shapes spatial-frequency specialization in vision. First, visual areas might develop specialization for the kind of input that supports motor action controlled by the ipsilateral hemisphere. Such ipsilateral connectivity could facilitate efficient coordination between perception and action. Second, visual areas might specialize based on exposure to asymmetrical visual input from asymmetric motor actions. If people are more likely to perform high-frequency actions in their dominant-side hemispace, then they should see more high-frequency information in their dominant-side visual hemifield. The results of the present study would be consistent with either or both of these mechanisms connecting asymmetries in action to asymmetries in vision.

In principle, both proposed mechanisms could explain an influence of hand action on specialization for both spatial and temporal frequency, across both vision and audition. Stabilizing and manipulating hand actions involve asymmetry in both spatial and temporal frequency: For example, in writing with a pen, the dominant hand makes movements that are fast and fine-grained across both time and space. These dominant-side movements, with relatively high-spatial and temporal frequency, are controlled by the contralateral hemisphere, satisfying the conditions of the “ipsilateral connectivity” mechanism. Assuming these dominant-side movements produce high-temporal frequency sounds in right hemispace that are preferentially processed in contralateral auditory cortex, input asymmetry could lead to temporal frequency specialization in audition as well as vision. However, whether hand action can explain temporal frequency specialization across sensory modalities has yet to be confirmed empirically. Additionally, future research could test the motivating assumption of the “input asymmetry” mechanism proposed here by using ecological video and audio recordings to compare how often right and left handers experience high- versus low-frequency visual and auditory input in their dominant and nondominant hemispace. Analysis of gaze position could confirm whether people experience asymmetries in their visual hemispace, relative to where they fixate during skilled actions.

AAH proposes that frequency specialization is due to asymmetries in bimanual actions that, in the strongest cases, may reverse completely between right and left handers (e.g., using the left hand to hold a page steady and the right hand to write with a pen, or vice versa); on the basis of such actions, AAH appears to predict a reversed direction of frequency specialization between strong left and right handers, for both high-frequency and low-frequency stimuli. Yet, we found this reversal for high-frequency stimuli but not low-frequency stimuli. 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, overall. Furthermore, the reversal in frequency specialization may be more clearly predicted for high-frequency than for low-frequency action: The dominant hand is important for high-frequency manipulation actions, whereas either hand can be used for low-frequency stabilizing actions, consistent with our pattern of results.

Could LAH explain left handers' frequency specialization? The rate of atypical language laterality was slightly higher in our left handers than our right handers, consistent with previous dichotic listening studies (e.g., Karlsson et al., 2023; Packheiser et al., 2020). In principle, this difference could explain a *reduction* in left handers' frequency specialization. However, given that language laterality does not *reverse* between right and left handers (in our Experiment 3 or in previous studies, e.g., Karlsson et al., 2023; Packheiser et al., 2020), language laterality cannot explain the hemispheric reversal we found for high-frequency stimuli. Furthermore, Experiment 3 confirmed that the effect of handedness on frequency specialization holds even when statistically controlling for language laterality and when limiting analysis to participants with typical language dominance.

In Experiment 3, language laterality predicted hemifield bias for local targets, in the direction predicted by LAH: Left-hemisphere-dominant participants showed right visual field bias, whereas right-hemisphere-dominant participants showed no significant hemifield bias. This result is consistent with the possibility that both handedness and language laterality contribute to frequency specialization. However, causality could run the other direction: In principle, the laterality effect commonly found in dichotic listening could depend on hemispheric specialization for frequency. To distinguish the syllables present in the consonant–vowel dichotic listening paradigm, participants need to make use of relatively high-temporal-frequency information (compared to the frequency information in other components of language, such as prosody). As such, rather than reflecting a general specialization for language, dichotic listening laterality could emerge from hemispheric specialization for information in different frequency ranges (Poeppel, 2003). Perhaps other effects typically ascribed to language dominance, such as left-hemisphere dominance for word generation (e.g., Jansen et al., 2006), could emerge from hemispheric specialization for frequency, when the content of perception happens to be linguistic. Future research could aim to disentangle the relationship between language and frequency specialization by using linguistic tasks that control the spatial and temporal frequency of the stimuli.

Could the correlation between hand action and hemispheric specialization for frequency observed here be explained by causation in the opposite direction? In principle, if specialization for frequency in perception is set early in development, humans could develop patterns of hand use that fit their perceptual specialization. Alternatively, a common cause could lead to both hemispheric specialization for perception and handedness. However, there is a clear functional explanation for the development of frequency specialization in manual actions: It is adaptive for an organism that uses tools to have a manipulating and stabilizing hand. Hemispheric specialization for frequency in perception does not have an obvious functional explanation, independent of action asymmetries that it may support. Furthermore, there is evidence that hand action asymmetries begin as early in utero (Hepper, 2013) presumably before visual asymmetries begin to develop. Future causal experiments could directly test whether manipulating the spatiotemporal frequencies of action (e.g., by training participants to use their nondominant hand for high-frequency actions) can influence frequency asymmetries in vision and audition.

Constraints on Generality

We found that handedness predicted frequency specialization in an online sample of English speakers from the United States and United Kingdom, between the ages of 18 and 40. Although global precedence may differ between cultures (Davidoff et al., 2008; McKone et al., 2010), we are not aware of any theoretical reason why the effect of field by level would fail to generalize to populations from other places and who speak other languages, given that the proposed mechanism by which frequency specialization emerges depends on hand-action asymmetries that should be found throughout adult populations worldwide (Kushner, 2017; Papadatou-Pastou et al., 2020). However, the effect we report here has not been tested in other countries or cultures, beyond the United States and United Kingdom. We chose national samples of people in the United States and United Kingdom so that we could ensure a large number of native English speakers who could interpret the instructions and respond sensibly to the demographic questions we asked. We used an online sample in order to recruit a large number of left handers (over 800 left handers recruited): A larger sample than it would be practical to recruit in person. Compared to general populations, participants from Prolific's research pool were highly educated, and all were computer literate, but we do not have reason to believe that relevant effects depend on these characteristics. The effect of handedness on frequency specialization held across male and female participants and should theoretically hold in any human population that shows frequency specialization and heterogeneous handedness, though this speculation remains to be confirmed empirically.

The effect of handedness on frequency specialization (and the magnitude of frequency specialization) may depend on participants' age. If the effect emerges from experience interacting with the world using one's hands, children may show weaker effects than the participants in our sample. Indeed, testing whether the effect holds in infants, who do not yet have substantial experience with asymmetric hand actions, would be a useful way to distinguish whether the effect emerges over developmental or evolutionary time. In older participants, age-related decline in high-spatial-frequency vision could decrease frequency asymmetry effects, but alternatively a longer history of hand use could plausibly heighten the effect of handedness on frequency specialization (if the effect emerges over a lifetime of hand action).

In principle, the effect of handedness on frequency specialization could hold in nonhuman animals that show manual asymmetry for stabilization and manipulation. While no study has directly tested the relationship between handedness and frequency specialization in nonhuman animals, baboons (Deruelle & Fagot, 1997; Fagot & Deruelle, 1997) and chimpanzees (Hopkins, 1997) show hemispheric specialization for spatial frequencies in the same direction as right-handed humans. Because baboons (Molesti et al., 2016; Vauclair et al., 2005) and chimpanzees (Meguerditchian et al., 2013) tend to show right-hand bias at the population level, these findings are consistent with the possibility that action asymmetry influences frequency specialization across the animal kingdom. Future research could test whether motor asymmetry predicts frequency specialization within these nonhuman species.

We used hierarchical shape stimuli to assess hemispheric specialization for spatial frequencies in vision. If AAH is correct, handedness should influence any sensitive measure of lateralization for spatial frequency, such as hierarchical letter stimuli, spatial-frequency gratings, or frequency-filtered natural scenes. While AAH predicts that hand action should shape perception of ecologically relevant spatial frequencies, such as those present during natural interactions with the environment, this possibility has not yet been tested.

Conclusions

Across three experiments, we found that hemispheric specialization for spatial frequency in vision can be explained by asymmetries in hand action and cannot be explained by asymmetries in language laterality or in fetal brain development. Our proposed mechanisms suggest that hand action may contribute to specialization for spatial and temporal frequency in both vision and audition. To the extent that these perceptual frequency asymmetries may underlie asymmetries in higher order functions in language and numerical cognition, the AAH gives a functional explanation for a broad principle of brain organization. These findings expand the scope of evidence for the body-specificity hypothesis (Casasanto, 2011): People with different kinds of bodies, who use their hands to interact with the environment in different ways, show corresponding differences in the neural organization of visual perception.

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Appendix

Exploratory Analyses of Accuracy, Response-Hand Congruence, and Task Order

Exploratory Analyses: Accuracy

Experiment 1

Does Handedness (Continuous) Predict Frequency Specialization?

With handedness treated as continuous, left handedness did not significantly predict degree of RVF local > global bias, accuracy; $\beta = .0002$ log(odds) units per EHI unit (95% CI [−0.001, 0.002], $p = .80$).

Does Handedness (Categorical) Predict Frequency Specialization?

We observed no significant interaction of Field by Level × Handedness on accuracy ($OR = 1.11$, 95% CI [0.86, 1.44]), $\chi^2(1) = 0.65$, $p = .42$. Both groups showed RVF local > global bias, indicated by odds ratios greater than one: The relative odds of correct/incorrect responses for local/global, RVF/LVF stimuli for right handers was 1.76 (95% CI [1.49, 2.09], $z = 6.48$, $p < .0001$); for left handers, 1.96 (95% CI [1.63, 2.37], $p < .0001$).

Within the local level, left handers' hemifield bias did not differ significantly from right handers' ($OR = 1.04$, 95% CI [0.89, 1.21], $z = 0.44$, $p = .66$). Right handers showed significant RVF bias ($OR = 1.16$, 95% CI [1.04, 1.29], $z = 2.66$, $p = .008$), and left handers showed marginal RVF bias ($OR = 1.12$, 95% CI [1.00, 1.25], $z = 1.96$, $p = .050$).

Experiment 2

Does Handedness (Continuous) Predict Frequency Specialization?

With handedness treated as continuous, the model testing the interaction of field by level by handedness, with subject as a random slope, did not converge.

Does Handedness (Categorical) Predict Frequency Specialization?

We observed a significant interaction of Field by Level × Handedness on accuracy, with left handers showing reduced RVF local > global bias ($OR = 0.68$, 95% CI [0.56, 0.82]), $\chi^2(1) = 14.62$, $p = .0001$. Both groups showed RVF local > global bias, indicated by odds ratios greater than one: The odds ratio of correct/incorrect responses for local/global, RVF/LVF stimuli for right handers was 2.56 (95% CI [2.21, 2.97], $z = 12.46$, $p < .0001$); for left handers, 1.73 (95% CI [1.52, 1.97], $z = 8.17$, $p < .0001$).

Within the local level, left handers showed significantly reduced right hemifield bias compared to right handers ($OR = 1.48$, 95% CI [1.32, 1.66], $z = 6.73$, $p < .0001$). Right handers showed significant RVF bias ($OR = 1.58$, 95% CI [1.45, 1.72], $z = 10.60$, $p < .0001$), and left handers showed marginal RVF bias ($OR = 1.07$, 95% CI [1.00, 1.16], $z = 1.73$, $p = .083$).

(*Appendix continues*)

Exploratory Analyses: Response-Hand Congruence

Because participants responded with either their left or right hand in each block, approximately half of their responses were "response-hand congruent": for example, responding to a target in the right visual hemifield with a right-hand button press. In principle, response-hand congruence could speed reaction times for both right and left handers, and modeling this potential effect could make analyses of effects of interest more sensitive.

Experiment 1

Response-hand congruence facilitated reaction times by 10.28 ms (95% CI [7.53, 13.03]), *t*(85,497.8) = 7.33, $p < .0001$. Including response-hand congruence as a covariate, the effect of handedness on the interaction of field by level was virtually unchanged (11.65 ms, 95% CI [0.64, 22.67]), *t*(85, 498.3) = 2.07, $p = .038$.

Experiment 2

Response-hand congruence facilitated reaction times by 9.83 ms (95% CI [7.33, 12.32]), *t*(111, 141.5) = 7.33, $p > .0001$. Including response-hand congruence as a covariate, the effect of handedness on the interaction of field by level was virtually unchanged (20.41 ms, 95% CI [10.35, 30.46]), *t*(111, 143.37) = 3.98, $p < .0001$.

Experiments 1 and 2 (Combined)

Response-hand congruence facilitated reaction times by 10.03 ms (95% CI [8.18, 11.88]), *t*(196, 646.2) = 10.64, $p < .0001$. Including response-hand congruence as a covariate, the effect of handedness on the interaction of field by level was virtually unchanged (15.34 ms, 95% CI [7.94, 22.74 ms]), *t*(196, 648.5) = 4.06, $p < .0001$.

Exploratory Analyses: Task Order

The participants of Experiments 2 and 3 completed both a Navon task and a dichotic listening task, with task order pseudorandomized. Here, we explore whether task order influenced reaction time or any effects of interest.

Experiment 2

Task order showed no significant effect on reaction time, difference = 10.32 ms in the direction of faster RT for participants who completed the dichotic listening task first (95% CI [−11.77, 32.41]), *t*(938.5) = 0.92, $p = .36$, or on the interaction of Field by Level × Handedness, difference = 6.93 ms in the direction of a greater effect for those who completed the dichotic listening task first (95% CI [−13.19, 27.05]), *t*(111, 138.4) = 0.68, $p = .50$.

Experiment 3

Task order showed no significant effect on Navon task reaction time, difference = 9.93 ms in the direction of faster RT for participants who completed the dichotic listening task first (95% CI [12.18, 32.04]), *t*(936.5) = 0.88, $p = .38$, or on the interaction of Field by Level × Handedness, difference = 9.00 ms in the direction of a greater effect for those who completed the dichotic listening task first (95% CI [−11.32, 29.33]), *t*(111, 126.4) = 0.87, $p = .39$. Task order also showed no significant effect on language laterality, difference = 0.92 dichotic listening score units (95% CI [−4.57, 6.41]), *t*(632) = 0.33, $p = .74$, and no effect on the relation between handedness and language laterality, difference = 9.15 dichotic listening laterality units, in the direction of a stronger relationship for participants who completed the Navon task first (95% CI [−1.85, 20.16]), *t*(631) = 1.63, $p = .10$.

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