Hemispheric Asymmetries: Attention to Visual and Auditory Primitives

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Abstract

A computational theory of hemispheric asymmetries in perception (double filtering by frequency) is described. Its central tenet is that the cerebral hemispheres first perform symmetric filtering of visual and auditory information. Functional hemispheric asymmetry arises from a second filtering stage (containing filters skewed in different directions in the two hemispheres). The first stage selects a range of task-relevant spatial or auditory frequencies from the absolute values. This range is passed to the asymmetric filters. In this way, the hemispheric difference becomes one of relative rather than absolute information. Behavioral deficits due to unilateral lesions in neurological patients and neuroimaging and electrophysiological measures in normal subjects implicate posterior cortex in these hemispheric differences.

Keywords

cognitive neuroscience; hemispheric specialization; neuropsychology; perception; attention

Despite the superficial similarity of the two cerebral hemispheres of the human brain, there exist significant asymmetries in their functions. For the vast majority of people, the left hemisphere (LH) plays a primary role in the production and perception of language. The LH's role is most clearly demonstrated by language and speech deficits that frequently accompany damage to this side of the brain. Similarly, perceptual and attentional deficits are generally more striking after right-hemisphere (RH) damage.

PROCESS-BASED HYPOTHESES OF HEMISPHERIC SPECIALIZATION

The obvious clinical differences following LH and RH damage have inspired extensive debate concerning the best way to characterize functional hemispheric specialization. Initial theories tended to focus on task domains, emphasizing that the LH and RH were specialized for processing linguistic and spatial information, respectively. With more careful study, it became obvious that such simple dichotomies failed to capture the complexity of brain function. Aspects of language such as prosody are more often disrupted following RH than LH damage, and visuospatial deficits can be observed following LH damage (Fig. 1). With the rise of cognitive psychology, task-based dichotomies have been supplanted by theories that emphasize asymmetries in terms of how information is represented and processed in the two cerebral hemispheres (e.g., analytic vs. holistic processes).

These process-oriented dichotomies represented a major conceptual advance but were, for the most part, descriptions of the observed phenomenon. Still missing were computational hypotheses of such asymmetries. A major step in this direction was provided by a study by Sergent (1982) in which subjects viewed hierarchically structured letters (e.g., Fig. 1, left column) that were presented to the left or right of fixation, that is, in the left visual field (LVF) or right visual field (RVF), respectively. Stimuli presented in the LVF are projected directly to the RH, and stimuli presented in the RVF are projected directly to the LH. Neurologically normal young participants exhibited an RVF (LH) advantage in response time when the target they were asked to identify was defined by the component, or local, shape, and they showed an LVF (RH) advantage when the target was defined by the overall, or global, shape. Sergent hypothesized that this local-global asymmetry indicates that the two hemispheres differ in sensitivity to different visual information in the stimulus. Building on neurophysiological studies in animals (DeValois & DeValois, 1990), she argued that the RH responded more efficiently to low-spatial-frequency information and the LH to high-spatial-frequency information (Fig. 2).

Studies (such as Sergent's) in which information is presented separately to the two visual fields are based on the assumption that the hemisphere contralateral to the stimulus dominates processing. This assumption has a long and checkered history in psychology (Efron, 1990). However, studies with neurological patients provide converging support for the hypothesis that these global-local asymmetries reflect functional differences between the two cerebral hemispheres, thus supporting the evidence from normal subjects. For instance, in several studies examining the representation of hierarchi-

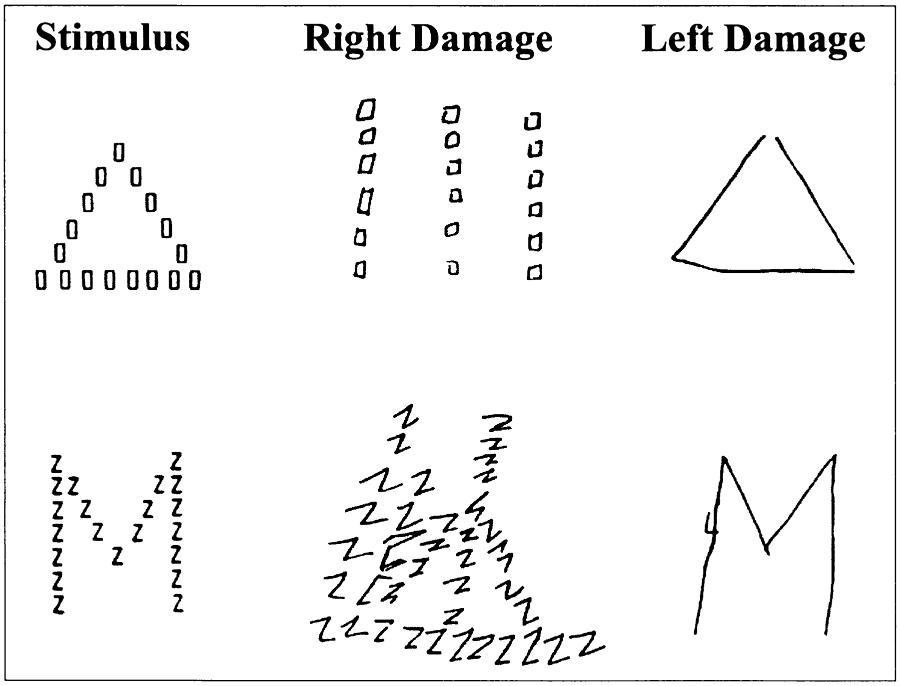

Fig. 1. Examples of hierarchical stimuli (a global triangle created from local rectangles and a letter *M* created from Zs) and how they were copied by patients with right- or left-hemisphere brain damage. (Adapted from Ivry & Robertson, 1998.)

cal stimuli following unilateral brain damage, patients with unilateral RH damage not only were impaired in drawing global objects but also exhibited perceptual and memory deficits for global information. Conversely, patients with unilateral LH damage exhibited similarly poor performance, but for local objects (reviewed in Ivry & Robertson, 1998).

Subsequent research with both normal and neurologically impaired populations has led to an important qualification of the local-global hypothesis. Casual observation makes obvious that the terms global and local refer to relative spatial relationships rather than absolute differences in size. A local component in one context may be global in another. For example, a global shape of a tree is defined by the configuration of its trunk, branches, and leaves. This same tree can serve as a local form within the overall landscape. In addition, the absolute size of a stimulus will vary with viewing distance, but the size ratio between local and global is maintained. Differences in local and global processing by patients with unilateral RH or LH damage are relatively independent of the range of absolute sizes in the stimulus (i.e., visual angle).

Consideration of this scaling property raises questions concerning the level at which local-global hemispheric asymmetries arise. One cannot simply argue that cells in visual cortex that initially receive information (i.e., visual striate cortex) are more sensitive to higher spatial frequencies in the LH than in the RH. Moreover, there is scant physiological evidence in support of such a hypothesis. Laterality effects occur later in visual processing and are a function of relative size.

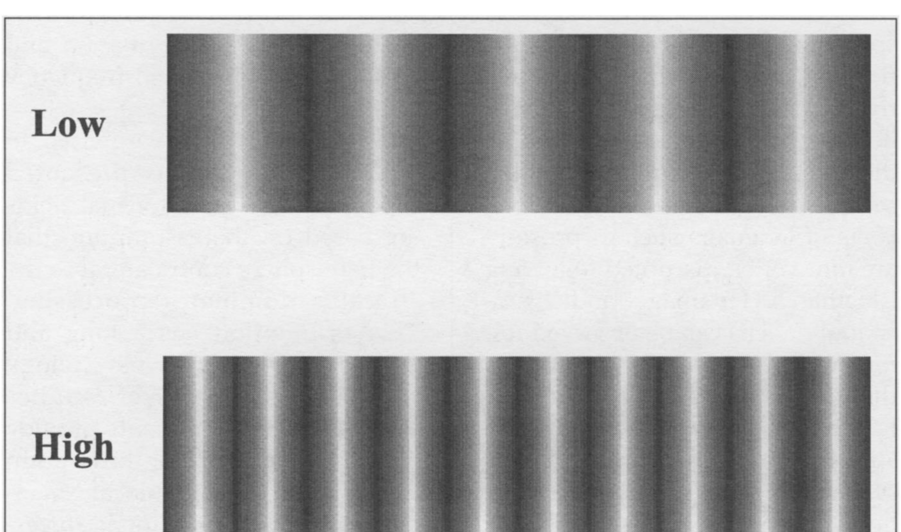

Fig. 2. Examples of gratings with low and high spatial frequency. Spatial frequency is measured in terms of number of light and dark luminance cycles over a unit of space, typically the number of cycles per degree of visual angle (measured with reference to the distance spanned by the stimulus over the globe of the eye). High-frequency gratings have more cycles per degree than low-frequency gratings.

HEMISPHERIC ASYMMETRIES IN THE REPRESENTATION OF RELATIVE SPATIAL FREQUENCY

Motivated by Sergent's proposal relating hemispheric differences to spatial frequencies, Hellige (1993) reported several experiments using sinusoidal gratings to test the theory. When gratings with low or high spatial frequencies were presented in either the LVF or RVF, the ability to detect the gratings was equal for the two fields. However, when the participants were asked to identify whether each stimulus was composed of "thick bars" (low frequency) or "thin bars" (high frequency), the thick bars were identified more rapidly in the LVF (RH), and the thin bars were identified more rapidly in the RVF (LH). Interestingly, the field-by-frequency differences were obtained when sinusoidal gratings of 1 and 3 cycles/deg formed the stimuli for the thick and thin bars and when the grating pairs were 3 and 9 cycles/deg (Fig. 2). Thus, the response pattern to the 3 cycles/deg stimulus reversed depending on whether it was the relatively high or relatively low member of the stimulus set. In another study, participants were required to discriminate whether a stimulus comprised two or three sinusoids. The third component in the three-sinusoid stimulus was always 2 cycles/deg. In one block of trials, this component was paired with two sinusoids of lower spatial frequency, and in another block it was paired with two sinusoids of higher spatial frequency. When the 2 cycles/deg component was the highest frequency, responses were faster to stimuli presented in the RVF (LH), and when this component was the lowest frequency, responses were faster to stimuli presented in the LVF (RH).

Spatial frequency analysis has been directly linked to global and local information in hierarchical stimuli. Shulman and Wilson (1987) had participants make local/global judgments of hierarchical stimuli while also performing a secondary task involving detecting low-contrast sinusoidal gratings of varying spatial frequency. Attending to the global level on the primary task influenced detection of low-frequency gratings more than high-frequency gratings, and attending to local properties influenced detection of high-frequency gratings more than low-frequency gratings.

Finally, clinical data collected using more naturalistic scenes are consistent with relative processing. Neurological patients with damage to the RH exhibit deficits in globally processing whole scenes, whereas those with damage to the LH exhibit deficits in processing local parts of scenes.

DOUBLE FILTERING BY FREQUENCY (DFF)

The preceding overview indicates that a computational theory of hemispheric specialization in visual perception must account for at least two critical observations. First, the two hemispheres differ in their sensitivity to spatial frequency information contained in complex visual patterns, with the RH biased toward lower-frequency information and the LH toward higher-frequency information. Second, this asymmetry is relative rather than absolute. In the DFF theory, we have proposed two successive filtering stages based on visual-processing mechanisms tuned to spatial frequency (Fig. 3). First, there is selection of the range of spatial frequencies that are relevant for the task at hand. We assume this stage is performed symmetrically by the two hemispheres. The output of this stage serves as input for the second processing stage. It is at this stage that hemispheric asymmetries appear. Each hemisphere operates as a filter on the selected input from the first processing stage: The RH operates as a low-pass filter (it allows more low-frequency information to pass on for further processing), and the LH operates as a high-pass filter (it allows more high-frequency information to pass).

According to the DFF theory, both hemispheres have access to the task-relevant information, but asymmetric filtering of the initially selected information will yield nonidentical representations. The representation associated with LH processing will be more efficient for certain types of tasks, whereas the representation associated with RH processing will be more efficient for other types of tasks. The two hemispheres are not simply performing redundant analyses.

Consider a task in which participants look at a hierarchical stimulus to see if a target letter is present but do not know before the trial begins if that letter will be defined at the local or global level. The LH representation resulting from high-pass filtering should be more efficient for identifying the target if it is relatively local. In contrast, the RH low-pass representation should be more efficient for identifying the target if it is relatively global. Note that, according to DFF, both hemispheres are capable of performing the task. They will simply differ in the fidelity with which they represent information required to make local or global judgments. Laterality effects do not emerge because one hemisphere or the other is required to perform a particular task, but rather because the hemispheres differ in the efficiency with which they represent different kinds of information and because the information that is most useful varies from task to task.

An appealing aspect of the DFF theory is that similar computational principles may underlie laterality effects observed in other perceptual domains. Auditory stimuli can be described in terms of their frequency spectra, although in this case frequency refers to periodic changes in sound pressure rather than luminance variation across space. Various phenomena in pitch perception and music perception are consistent with the hypothesis that the RH and LH are biased to represent lower- and higher-frequency information, respectively. Again, these asymme-

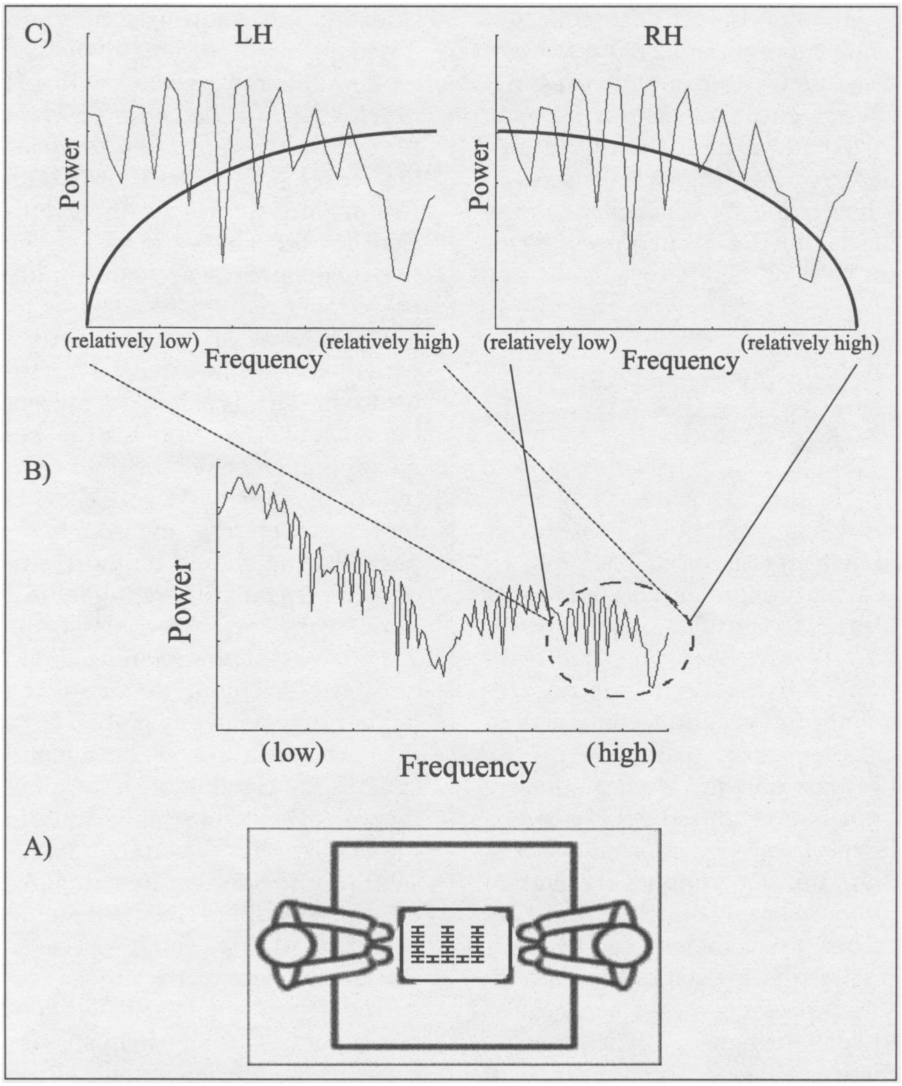

Fig. 3. Schematic example of the double-filter-by-frequency theory. An experimenter and participant attending to a hierarchical stimulus are shown in (a). For simplicity, (b) shows a one-dimensional representation of absolute spatial frequencies plotted through the middle horizontal axis of (a). The dashed circle indicates the region of the power spectrum that is selected by the attentional filtering stage for further analysis in both hemispheres. The selected spectral information is processed asymmetrically in the two cerebral hemispheres, as shown in (c). The black curves in this panel represent the filtering operations of the hemispheres; information above each curve is filtered out. The left hemisphere (LH) performs a high-pass filtering operation, amplifying the higher-spatial-frequency information in the selected region. The right hemisphere (RH) performs a low-pass filtering operation, amplifying the lower-spatial-frequency information in the selected region. (See the text for further explanation.) This second filtering stage results in asymmetric representations.

tries are observed in terms of relative differences in frequency rather than absolute differences.

This hypothesis also provides a novel, provocative perspective on how the two hemispheres may contribute to speech perception. Phonetic information that contributes to discrimination of one syllable from another (e.g., "ba" vs. "da") is primarily carried in the higher frequencies of the speech spectrum, and the LH is better than the RH at making these discriminations. There is also important paralinguistic information that is conveyed by the lower frequencies. For example, prosodic cues and perhaps voice recognition are dependent on variation in the lower frequencies of the speech signal. Neuropsychological studies have convincingly shown that the RH is more critical than the LH for analyzing these aspects of speech. As in visual perception, the DFF theory posits that laterality effects do not arise because one hemisphere has evolved a specialization to solve a certain type of task (e.g., language vs. space). Rather, the differences result from the asymmetric filtering operations performed by the two hemispheres on task-relevant information.

FUNCTIONAL NEUROANATOMY AND PERCEPTUAL ASYMMETRIES

Neuropsychological studies of patients with limited unilateral brain damage have shown that deficits in local and global processing are associated with damage in the posterior areas of the cortex. In particular, the border of the temporal and parietal lobes appears critical for the normal asymmetric filtering stage posited by the DFF theory. Patients with lesions in this area in the RH or LH are impaired in making global and local judgments, respectively. These deficits are apparent across a wide range of stimulus sizes. In contrast, other patient groups (e.g., patients with lesions centered in more superior areas of the parietal lobe or patients with frontal lobe damage) perform comparably to control subjects on these tasks.

Electrophysiological and brain-imaging techniques have provided additional confirmation that the processing asymmetries have a posterior cortical focus. There is some debate about the precise critical area in the posterior cortex. Nonetheless, as predicted by the DFF theory, asymmetries appear to arise at a relatively early processing stage within the visual system, but beyond primary visual cortex (Fink et al., 1996; Heinze, Johannes, Munte, & Mangun, 1994).

WHAT NEEDS TO BE DONE NEXT?

The DFF theory offers an integrated, computational model to account for a large set of findings in the laterality literature. The theory builds on relatively simple ideas regarding how information is transformed during the initial stages of perceptual analysis. Unlike many alternative theories, DFF does not focus on particular task domains, nor does it entail a strong dichotomy between LH and RH function. The theory offers an explicit account of successive processing stages that could underlie marked functional asymmetries. It remains to be seen if spatial and sound frequencies are the correct primitives from which laterality effects emerge.

More research is clearly needed to directly test the generalizability of the DFF theory. In the auditory domain, one could evaluate laterality effects for different speech contrasts because they vary in the importance of high and low spectral information. The theory might also apply to asymmetries concerning how the two hemispheres respond to temporal changes in information (see Tallal, Miller, & Fitch, 1993). The link between the spatial and auditory domains also needs examination. Why might similar asymmetries emerge in how the brain processes spatial and sound frequencies?

Finally, it is worth considering whether the proposed DFF computations could be useful in accounting for other task domains in which laterality effects are marked. For example, the nondominant hand is generally used in the contextual aspects of bimanual tool manipulation, whereas the dominant hand is used for more local, precise movements (Guiard, 1987). (For instance, right-handers will hold a fishing pole with their left hand while reeling in with their right hand.) The representation of semantics within the two hemispheres has also been characterized in terms of local and global representations. It remains to be seen if there is a causal link between these different task domains, or if the apparent parallels result from the limited set of descriptive terms used to account for differences in processing between the left and right hemispheres.

Recommended Reading

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Note

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