

Hemispheric asymmetries in face recognition in health and dysfunction

Marlene Behrmann*

Department of Ophthalmology, University of Pittsburgh School of Medicine, Pittsburgh, PA, United States

*Correspondence to: Marlene Behrmann, PhD, Department of Ophthalmology, University of Pittsburgh School of Medicine, Pittsburgh, PA, 15213, United States. E-mail: mbehrmann@pitt.edu.

Abstract

A defining characteristic of the human brain is that, notwithstanding the clear anatomic similarities, the two cerebral hemispheres have several different functional superiorities. The focus of this chapter is on the hemispheric asymmetry associated with the function of face identity processing, a finely tuned and expert behavior for almost all humans that is acquired incidentally from birth and continues to be refined through early adulthood.

The first section lays out the well-accepted doctrine that face perception is a product of the right hemisphere, a finding based on longstanding behavioral data from healthy adult human observers. Data are then presented from neuropsychological studies conducted with individuals with prosopagnosia, which is either acquired after a lesion to the right hemisphere or is developmental in nature with no obvious lesion. The second section reviews data on the neural correlates of face perception, gathered using a host of imaging methodologies all the way from electroencephalography (EEG) through functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies to transcranial magnetic stimulation and intracranial depth recording. The penultimate section reviews empirical findings that track the emergence of the hemispheric asymmetry for faces, and offers a theoretical proposal that lays out possible origins of the adult asymmetry profile. Lastly, the hemispheric asymmetry associated with the perception of emotional face expression is considered. While considerable progress has been made in understanding the functional organization of the human cerebral cortex and its biases and asymmetries, much remains to be determined and the many inconsistencies remain to be reconciled in future research.

Introduction

One defining characteristic of the human brain is that, despite the anatomic and structural equivalence, the two cerebral hemispheres have different functional superiorities. This hemispheric lateralization of function is thought to be phylogenetically recent given its absence in close relatives of humans such as old-world monkeys, as documented in studies of population-level behavioral, neuroanatomic, and functional asymmetries (Corballis, 1982; Ettlinger, 1988). Consistent with this, no significant differences between face patches of the left hemisphere (LH) and right hemisphere (RH) in macaque monkeys were uncovered in a study using transient pharmacologic inactivation coupled with functional magnetic resonance imaging (fMRI) to explore the circuitry and directional connectivity underlying face processing (Liu et al., 2022). Other studies, however, have uncovered hemispheric differences in nonhuman primates perhaps primarily for the perception of emotional stimuli (Parr and Hopkins, 2000) [for a review, see Hopkins and Cantalupo, 2008 and Hopkins et al., 2015] (Fig. 29.1).

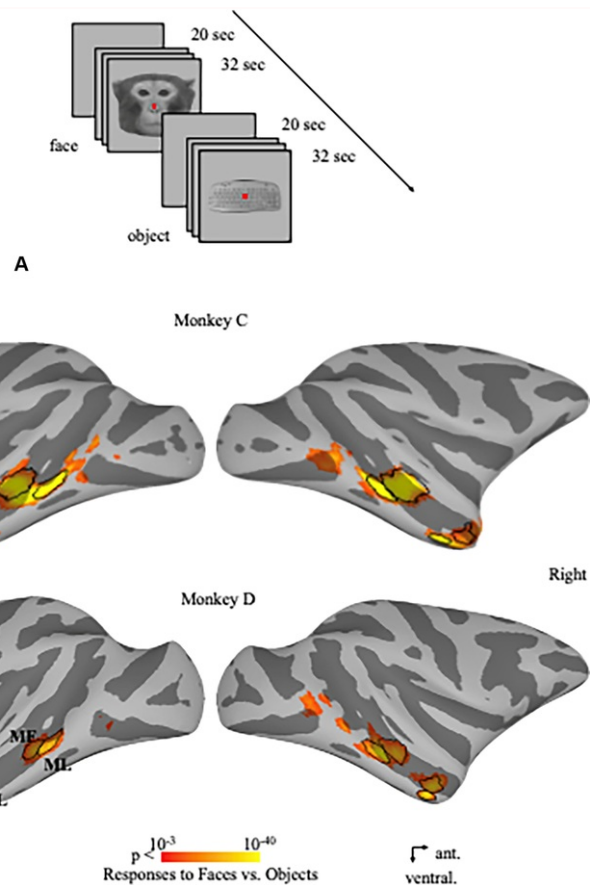


Fig. 29.1 fMRI experiment and face-selective patches in two monkeys, C and D. (A) An illustrative example of a sequence of monkey faces and objects displayed to monkeys while fMRI data were collected. (B), (C) Face-selective (neutral monkey faces vs objects, $P < 0.005$ uncorrected) activation maps shown on lateral views of the inflated cortex in monkeys C and D. The selected voxels in each ROI are encircled by black lines. MF middle fundal face patch, ML middle lateral face patch, AF anterior fundal face patch, and AL anterior lateral face patch.

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The discussion of hemispheric superiorities in humans and the origin and potential malleability of these lateralized differences remains ongoing and continues to motivate hundreds, if not thousands, of investigations of human brain functional organization. As will be evident from this brief review, notwithstanding the massive effort to elucidate the functional arrangement of the cerebral cortices, the exact nature and extent of their lateralization remain unsettled. Here, we focus specifically on the lateralized profile or hemispheric superiority of one particular function, namely face processing, which has long been attributed to the RH in human adults. While some researchers have argued that face perception is solely a function of the RH, others have argued for an RH advantage or a bias that coexists with a more limited left hemisphere (LH) contribution, rather than a purely binary assignment of face processing to the RH [for a review, see [Petunia et al., 2024](#)]. Findings that challenge the RH dominance view of behavior-brain correspondence have demonstrated that laterality may fluctuate and, possibly, even be reversed ([Wu et al., 2022](#)). [Wu et al. \(2022\)](#) used dynamic functional connectivity measures to quantify laterality fluctuations, defined as the standard deviation of the laterality time series, and laterality reversal, defined as the number of zero crossings in the laterality time series. They used dynamic changes of lateralization to map resting state data from the Human Connectome Project (<http://www.humanconnectome.org/data>) and noted that variations in laterality were primarily in lower order brain regions, including in visual and other sensory areas, but not in higher order brain regions. This pattern of fluctuation is conceptually consistent with the fact that lower order regions have shorter intrinsic time scales and, bilaterally, are required to respond to rapidly changing input, which is then integrated to yield a coherent, more stable percept. This variability obviously and directly challenges the central assumption that laterality is a stable trait ([Liu et al., 2009](#); [Gotts et al., 2013](#)) that optimizes neural function ([Rogers and Vallortigara, 2017](#)).

The question to be addressed here then is whether, how, and to what extent, face perception emerges from computations mediated solely by the RH and if so, what mechanisms and pressures drive this lateralized function in humans. First, we describe current

evidence supporting the now-longstanding claim of the RH superiority for face perception, largely drawing on findings from behavioral studies of typical individuals, and we address some possible properties of the RH that predisposes the RH to be well suited for computations underlying face perception. We then provide findings favoring a RH advantage for face processing based on results from neural studies, starting with neuropsychological evidence from individuals with prosopagnosia, either of the acquired variety or of the type that appears lifelong and apparent from birth. We follow this with a presentation of data aggregated from neuroimaging methodologies, including electroencephalography (EEG) and fMRI. We also include results from newer data acquisition methods like transcranial magnetic stimulation and intracranial depth electrodes, and review both spatial as well as latency differences for face perception compared to the perception of other stimulus classes in the two cerebral hemispheres. We then review the literature on the development of face perception over human ontogeny [for a review of face perception over phylogeny, see Behrmann and Avidan, 2022], present an account of the origin of this functional organization, and briefly consider the mechanisms associated with the perception of emotional expression on faces.

Evidence for RH Superiority for Face Perception in Typical Observers

The longstanding claim that the RH has greater involvement than the LH in face perception comes from studies largely conducted in the 1970s and 1980s using the half-field or tachistoscopic procedure. This method entails having an observer seated in front of a screen and while maintaining fixation on the center of the screen; ideally, the observer's eye movements are monitored to ensure maintenance of fixation. A stimulus is presented briefly (too brief to permit a saccade so ideally, for 150 ms or less) to either the left or right visual field and, depending on the task, the participant names the displayed item or makes a decision about it (for example, is the image a face or an object? Is the face smiling or frowning?). Because there is, at least initially, preferential processing of a visual stimulus in the hemisphere contralateral to the field, one can determine whether performance is better for left (RH) or right (LH) visual field stimuli. In this way, one can determine which hemisphere has the advantage for face processing, and the findings consistently point to the RH as having the advantage or superiority for face perception.

Another common paradigm included the use of chimeric stimuli or composite symmetric faces made by, for example, combining the left or right half of a face with its corresponding mirror image (or halves of two different faces). In this latter paradigm, participants fixate the center of the image such that each half of the composite falls in one visual field. Participants indicate which composite (right or left visual field) more closely resembles the original or target face usually displayed prior to the presentation of the chimera. Regardless of the upright or inverted orientation of the image, a preference for the composite half in the left visual field was demonstrated in typical observers, consistent with an RH advantage in face identification (Kolb et al., 1983). These studies also showed that the RH was more engaged for the recognition of previously unfamiliar faces (Levy et al., 1972) and for the recognition of familiar faces, although this latter result is more controversial (Levine and Koch-Weser, 1982). One possible concern with some of these studies, however, is that the RH has other functions that might have supported this advantage: for example, attentional function is generally attributed to the RH (Shulman et al., 2010), and, so, the left field advantage might have been attentional rather than face-selective in nature (a comparison or control from a different stimulus class showing no left visual field advantage was not always tested). These studies also tended to place emphasis and interpret the left visual field/RH advantage in binary terms but there was also, almost always, some selection of the composite face that appeared in the right visual field.

This demonstrable RH face advantage has been well complemented by many recent studies. For example, in a study with a large and heterogeneous sample of 122 participants all of whom completed multiple tasks with unilateral or bilateral stimulus presentation, group-level analyses confirmed the predicted RH lateralization by revealing correlations between performance on faces, global forms, low spatial frequency processing, and spatial attention tasks, and the predicted LH lateralization through correlations between visual word and local feature processing (but not high spatial frequency processing) (Brederoo et al., 2020). These authors attributed the lateralized asymmetries to the causal complementarity principle according to which different processes recruiting similar brain regions come to be lateralized to homolog areas in opposite hemispheres [for related ideas, see the following studies that demonstrate neural competition over development with fine-tuning the LH lateralization for visual word processing during literacy acquisition and its correlation with the RH lateralization for face processing (Dundas et al., 2013)].

For a long time, the RH superiority for face perception was assumed to be a product of the general superiority in visuospatial tasks including configural or holistic processing [but see Gerlach and Poirel, 2020 for critical analysis of divided field measures] but alternative hypotheses have also been proposed. Among these alternative hypotheses is the notion that, whereas the LH processes visual input at a more local or featural level, the RH processes information at a more holistic or global level. For example, compound stimuli (Navon, 1977) made of the letters “H” and “S” whose identities are the same (consistent) or different (inconsistent) at the local and global level (see Fig. 29.2A) have been shown to the right visual field/LH or left visual field/RH of typical observers. In different blocks of trial with appropriate instructions to identify the letter at either the local or global level, participants indicated the letter identity (for example, by pushing either a “H” or “S” button, Fig. 29.2A). Identifying the local letters was faster for stimuli presented in the right visual field/LH than in the left visual field/RH, and the converse was true for the global letter identification trials (Van Kleeck, 1989; Ivry and Robertson, 1998).

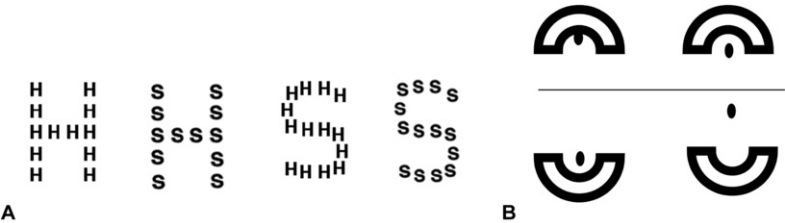


Fig. 29.2 Schematic depiction of stimuli to illustrate experimental conditions. (A) Example of “Navon” or compound letters made of “H” and “S” stimuli, with “consistent” stimuli, i.e., same letter identity at the local and global level (first and fourth examples) and “inconsistent” stimuli, i.e., different lette

identities at the global and local level (the second and third examples). (B) Two kinds of judgments were made on stimuli such as these: (left column) is the dot on or off the contour of a line drawing of a blob (the on/off task; categorical) or (right column) is the dot within 2 mm of the contour (the distance task; coordinate).

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According to [Sergent \(1982\)](#), this local–global hemispheric asymmetry may be a manifestation of a more fundamental spatial frequency sensitivity, with the LH biased toward high spatial frequencies and, hence, responding better to the local elements, and the RH evincing a bias to processing low spatial frequency information and, hence, the global identity ([Sergent, 1982](#); [Ivry and Robertson, 1998](#); [Robertson and Ivry, 2000](#)). Proposals such as these dovetail well with the [Brederoo et al. \(2020\)](#) report mentioned earlier that documented the laterality-specific correlations between spatial frequency, global vs local processing, and word vs face perception.

The specific link to face perception comes from the claim that the LH high spatial frequency superiority permits the processing of local face features while the low spatial frequency RH advantage exists for and enables processing a face as a global whole. Indeed, in a study using positron emission tomography (PET) scanning ([Rossion et al., 2000](#)), the right middle fusiform gyrus was more activated when participants matched whole faces than parts of faces and the left homologous region was more activated for the part than for the whole condition. This held only for faces but not for a control condition of houses and led to the conclusion of lateralized localization of mechanisms supporting face processing. In a related fMRI study, the right fusiform gyrus signal profile was correlated with categorical face vs non-face judgments (Is this a “face”?) ([Meng et al., 2012](#)). The left fusiform gyrus activation, however, was correlated with image-level face-semblance, implicating processing of face resemblance through a more featural process, which, then, provides this earlier emerging signal to deeper, categorical analyses by the RH.

Over time, other claims regarding fundamental but general differences between the hemispheres have also been offered to account for the RH face advantage, although these other proposals are not necessarily mutually exclusive with the hypotheses about spatial frequency and feature or part/whole distinctions. One example hypothesis is that there are two kinds of spatial relations, one tuned more for categorical relations and one for specific coordinate representations. When human participants had to decide whether the dot was on or off (categorical judgment) the object shape (see [Fig. 29.2B](#)), performance was better for stimuli presented to the right visual field/LH than left visual field/RH. When the decision required was the coordinate or metric distance (e.g., the dot within 2 mm of the shape boundary), responses were faster for stimuli presented to the left visual field/RH than the right visual field/LH ([Kosslyn et al., 1989](#)).

Another related account explains the hemispheric differences as a result of the extent to which there is coarse vs fine encoding of the input. The claim is that neurons in the RH and LH have differently sized receptive fields, with larger fields in the RH than LH (although this account was formulated primarily for parietal cortex differences in the two hemispheres) ([Monaghan and Shillcock, 2004](#)). Unsurprisingly, if this were the case, more coarse larger-scale processing would be a property of the RH and smaller, finer-grain processing would be a property of the LH.

A last, different perspective comes from the claim that hemispheric asymmetries operate at an encoding stage beyond the sensory level. The proposal is that the asymmetries arise as a result of differences in within-hemisphere anatomic connections with more distal connection structure between columns in language areas of the LH and more local connection structure between columns in the RH homotopic region ([Hsiao et al., 2013](#)). To explore the implications of this proposal, Hsiao et al. (2013), in a series of neurocomputational simulations, demonstrated the emergence of both processing differences and differential frequency filtering, thereby replicating a host of empirical findings reviewed above. These simulations led to the suggestion that it is not frequency tuning per se that drives the hemispheric asymmetries but, rather, the anatomic differences in connection structure are key [see also [Gomez et al., 2019](#) for changes in receptive field size over development in the two hemispheres].

Neural Evidence for the Role of the RH in Face Perception

Neuropsychological investigations

Studies of typical observers who have delineated behavioral asymmetries, while intriguing and highly suggestive, do not provide a causal link between face perception and the RH [see the transient “lesion model” in [Liu et al., 2022](#) at the beginning of this chapter]. This link in humans has long been inferred on the basis of neuropsychological studies of individuals with a deficit in recognizing faces termed “prosopagnosia” [from the Greek prosopon (face) and gnosis (knowledge)]. Prosopagnosia in premorbidly normal face recognizers can occur following brain injury from stroke, trauma, or tumor. A second type of prosopagnosia, termed “congenital” (CP) or “developmental” prosopagnosia, assessed over the past few decades, can manifest in individuals with a clearly disproportionate difficulty in recognizing faces but in the absence of neurologic damage and after ample exposure to face stimuli. We first describe similarities and differences in the two forms of prosopagnosia and then consider their underlying etiologies.

In both instances of prosopagnosia, with the former being more rare than the latter, the deficit cannot be accounted for by a loss in sensory vision or abnormal low-level visual perception nor by a deficit such as anomia or a semantic impairment. Individuals with prosopagnosia are impaired at identifying individual people by face, even close family members, and are often, but perhaps not always, also impaired at discriminating between individuals ([Behrmann and Avidan, 2005](#); [Behrmann et al., 2005a](#)). In prosopagnosia, recognition is usually accomplished using other visual cues such as gait and body posture [but see [Biotti et al., 2017](#)] or salient clues about hairstyle or clothing and nonvisual cues, predominantly voice. Several studies have noted the specificity of the face perception impairment and have demonstrated that other facial information, such as facial expression and emotions, may be spared ([Lahiri, 2020](#); [Bell et al., 2023](#); [Bennetts et al., 2024](#)) (see section on Facial expression recognition/perception in the following).

Whether the recognition of other objects is also affected remains highly controversial. Whereas some have argued that more complex high-level regions of the visual cortex participate in processing multiple object types and is not domain-specific ([Behrmann and Plaut, 2015](#)), others have proposed that regions associated with face recognition are domain-specific, more modular in nature, and dedicated to processing only one object type, namely the face ([McKone and Kanwisher, 2005](#)). In one study that examines the generality of the

visual recognition deficits in prosopagnosia, individuals with developmental prosopagnosia showed deficits in the recognition of both human and animal faces, and, close inspection at the single case level revealed that of the 60% of cases in whom face recognition was impaired, there was a concurrent deficit in the recognition of animal faces (Epihova et al., 2023). A similar conclusion was reached in a review paper that examined published papers on CP cases from 1976 to 2016. Of the 238 CP cases whose data permitted a satisfactory evaluation of the face vs non-face comparison, 80.3% of the individuals were impaired at face and object recognition, and only 19.7% were impaired at face perception alone (Geskin and Behrmann, 2018). Other studies have also pointed out that this congenital form of prosopagnosia is often accompanied by other developmental comorbidities such as an impairment in memory or ADHD or dyslexia (Svart and Starfelt, 2022) although some dissociations are also present (Kuhn et al., 2020) and some findings are more mixed (Bate et al., 2019; Gray et al., 2019).

Acquired prosopagnosia

Acquired prosopagnosia is one consequence of a lesion to the RH occipitotemporal lobe or middle fusiform gyrus cortex. A lesion on the left side may also result in prosopagnosia (Meadows, 1974; Grüsser and Landis, 1991), albeit less often and less severely (Barton, 2008; Behrmann and Plaut, 2014). For an historical overview of prosopagnosia and its relationship to the lesion site, see Gainotti and Marra (2011) and Gainotti (2023) and for a recent review of the unilateral right and left and bilateral lesions in those with prosopagnosia, see Barton (2022). One recent interesting source of neuropsychological data comes from the Back-of-the-Brain project, a detailed neuroimaging and neuropsychologic examination of 64 patients with unilateral Posterior Cerebral Artery stroke (Rice et al., 2021; Robotham et al., 2023). Of the patients, 32 had a LH lesion, 23 had a RH lesion and 9 had bilateral lesions. The results are of particular interest in that very few patients (6 out of 64) showed a selective deficit in only one domain, and this was in the domain of word processing. About one-third of the patients showed a significant impairment across domains, irrespective of side of unilateral lesion or bilateral lesions and, surprisingly, a further third of the patients showed no deficits whatsoever. While total lesion volume had the strongest relationship with behavioral performance, face recognition impairment was not related to lesion laterality per se but, rather, in a more equipotential way, was related to lesion volume across both hemispheres. These findings offer clear evidence that both hemispheres are involved in higher order processing of faces (and of words too) and deficits can be observed after damage to these extrastriate regions in either hemisphere even in adulthood; see also Behrmann and Plaut (2014). [For a review of hemispheric variability in EEG studies, see Petunia et al., 2024].

In addition to the debate on lateralization, there is ongoing discussion regarding the lesion site, whether more posterior or more anterior just within the RH (Cohen et al., 2019; Barton, 2022). Notably, some individuals who have more anterior temporal lesions (Evans et al., 1995; Barton, 2003) present with a concurrent deficit in voice recognition (Gainotti, 2013, 2023). As illustrated in Fig. 29.1, just as there are multiple face-selective or face “patches” in monkeys, multiple face-selective regions are evident in humans too in both hemispheres albeit to a greater degree in the right hemisphere (Gobbini and Haxby, 2007). Although there may not be direct homology between humans and nonhuman primates (Rossion and Taubert, 2019), the host of face-selective regions in both species indicates that face perception likely requires the joint activity of multiple brain regions distributed throughout the “core” occipital and temporal lobes (and “extended” regions as well), typically with an RH advantage, and some patches/regions contributing slight different computations [e.g., whether patch has viewpoint invariance or not (Dubois et al., 2015)]. Some theories consider this face network a processing hierarchy beginning with the inferior occipital gyrus and fusiform gyrus and projecting to more anterior temporal and even frontal lobe regions while others have suggested a multiple-route network with nonhierarchical components and no strict posterior to anterior directionality. For example, a well-studied prosopagnosic patient, PS, who has a right inferior occipital gyrus lesion, still showed typical face-selectivity more anteriorly in the right fusiform gyrus, implicating direct connectivity from the early visual cortex and the fusiform area and circumventing the proposed intermediate occipital face area (Rossion, 2022).

Congenital or developmental prosopagnosia

Having reviewed the neural characteristics of acquired prosopagnosia, we now consider the neural basis of the congenital (CP) or developmental form of the deficit. CP is not accounted for by any obvious neurologic concomitant and no disease is readily identifiable on conventional MRI neuroimaging. However, multiple, differing hypotheses regarding the etiology have been postulated. One early study of the morphometry and volume of the occipitotemporal cortex in a small group of individuals with CP and matched controls revealed no significant group differences in the depth or deviation from the midline of the occipitotemporal lobe or collateral sulci. In contrast, a larger anterior and posterior middle temporal gyrus and a significantly smaller anterior fusiform (aF) gyrus in the RH was revealed in the CP individuals, and this anatomic change was correlated with the extent of the face recognition deficit (Behrmann et al., 2007). Of course, the question, then, is what gives rise to this particular anatomic alteration. Subsequent research using diffusion tensor imaging offered a possible explanation. In a group of individuals with CP, a relationship was observed between the structural integrity of the tracts that project through the ventral temporal occipital cortex, especially in the RH, and the severity of the face recognition deficit (Thomas et al., 2009; Zemmoura et al., 2021) [and see Lohse et al., 2016]. Specifically, the data revealed that the white-matter fibers of the inferior longitudinal fasciculus and inferior fronto-occipital fasciculus showed a reduction in microstructural integrity (fractional anisotropy measure). No group differences, either macro- or microstructural, were evident when other tracts such as the forceps major and forceps minor were quantified [for similar results, see Zhao et al., 2022].

Note that some of these structural MRI results have not been replicated; whether different criteria are used for participant inclusion, whether there is substantial variability in the population itself, or whether the variability is a product of different methodological approaches is not yet clear. For example, in one study of CP and age-matched control participants, the group differences emerged not in long-range microstructural differences as noted above but, rather, in the differences in local structural changes to face-specific regions of interest, and these changes were correlated with face perception success (Song et al., 2015) [see also Zhang et al., 2015].

Findings from fMRI have also shown differences between CP individuals and controls. Consistent with the structural MRI above, the interruption of signal propagation in the RH from more posterior to more anterior regions is evident in the reduction of functional connectivity during the resting state between more posterior sites and more anterior temporal lobe regions (Avidan et al., 2014). Also, whereas the RH anterior temporal lobe typically serves as the major network hub for face processing in controls, the CPs evinced hyperconnectivity in the posterior regions of the visual cortex, mostly associated with the lateral occipital and the inferior temporal cortices and not with the anterior temporal lobe (Rosenthal et al., 2017) [also see a theoretical framework for explaining eye movement differences,

population receptive fields (pRFs), and connectivity (Avidan and Behrmann, 2021)]. In a study using multi-voxel pattern analysis showing the wide extent of the cortical perturbations, relative to controls, reduced discriminability between faces and objects was identified in the CP individuals, in both the core (occipital and temporal face areas) as well as in the extended region (anterior temporal lobe) (Rivolta et al., 2014).

Although still in its relative infancy, there have been multiple attempts to develop rehabilitation strategies, especially for those with developmental prosopagnosia. Hypothetically, such studies might also contribute to a further understanding of hemispheric differences. The findings to date, however, mostly indicate that compensation for the deficit is not easily achievable [for a review, see DeGutis et al., 2014]. Left to their own devices, patients typically rely on cues such as voice, haircut, or clothing of other individuals but these cues are not foolproof and do not always suffice. Attempts at intervention have included training holistic processing with non-face stimuli (Behrmann et al., 2005b), enhancing sensitivity to spatial distances between features for faces, for example, increasing sensitivity to the between-eye or eye-nose distances or even non-face stimuli, or relying on developing mnemonic cues for faces (Bate and Bennetts, 2014; Davies-Thompson et al., 2017); but, none has yielded extraordinary results. Techniques used to train novice observers with emphasis on featural arrangement (Towler et al., 2021), on eye movement strategies (Bobak et al., 2016), or even with external intervention with oxytocin (Bate et al., 2014) and simultaneous stimulation [for an example of approach, see Willis et al., 2019] might also be a possible avenue to explore in future, and the hemispheric impact of these strategies will be of interest, as well.

More General Review of Neuroimaging Studies

Decades of studies have used EEG with measurement of responses to faces evoked by the presence of visual input (evoked response potentials, ERP) (Petunia et al., 2024). Seminal findings by many investigators have used a target detection task for examining the scalp EEG waveform potentials. One such study involved noting how many butterflies were embedded in a stream of unfamiliar human faces or among isolated face components, or even among inverted faces or other nonface stimuli. The major finding was the appearance of a negative potential at around 170 ms, which was the largest over the posterior temporal scalp and greater over the RH than LH (Bentin et al., 1996). This EEG approach has now been employed extensively in the mapping of face processing and has also demonstrated that a later negative potential around 250 ms can differentiate learned target faces from objects and from other faces, and that one's own face and one's own objects can elicit this potential too, even when not identified a priori as targets (Pierce et al., 2011). Much traction has been leveraged recently from coupling EEG measurement with a novel and implicit visual discrimination paradigm (FPVS: fast periodic visual stimulation) with high signal-to-noise ratio. In this approach, images (e.g., of faces) are displayed at a periodic frequency rate between, for example, 3 and 9 Hz. For faces, the largest response is observed over the right occipitotemporal cortex with a 6-Hz stimulation rate (corresponding to ~170 ms cycle duration) (Rossion, 2014) [see also Yan et al., 2019].

Consistent with the neuropsychological data, the ascription of face perception to the RH found strong support following the advent of human neuroimaging. From the seminal papers of Sergent and colleagues using PET (Sergent et al., 1992; Sergent and Signoret, 1992) and of Kanwisher and colleagues using functional magnetic resonance (Kanwisher et al., 1997), the greater activation of the RH in response to faces in the “fusiform face area” or “FFA” was robustly confirmed and documented. Further support for the RH face perception advantage was also provided by correlational evidence that the strength of the left visual field bias during face perception, as measured using fMRI data, covaried with lateralization indices of the FFA (Yovel et al., 2008). Hundreds of fMRI studies have now replicated these findings but, interestingly, with close scrutiny of the data, many studies uncover activation in response to faces in homologous regions in the LH as well (e.g., Hasson et al., 2002; Wang et al., 2019). There are now several reviews offering a broad perspective of studies using fMRI to characterize the neural basis of face processing, and the interested reader may consult them for further details (e.g., Rossion et al., 2018; Rossion and Lochy, 2022).

New Approaches for Examining Right-Hemisphere Face Superiority

A growing approach that has generated increasing interest is one in which face selectivity can be directly assayed from intracerebral electrophysiologic signals measured in individuals, who are being clinically evaluated for surgery for the treatment of drug-resistant epilepsy. In the early 1990s, Allison and colleagues (Allison et al., 1994a,b; McCarthy et al., 1999) reported findings of responses to face stimuli from strips of electrodes placed over ventral temporal cortex for the localization of seizure activity. Across many studies (Puce et al., 1999), they replicated the finding that a discrete region of the occipitotemporal cortex was activated in response to faces. More recently, but along similar lines, recordings from intracranial depth electrodes, as depicted in Fig. 29.3A, have indicated widespread neural activity in response to faces (using FPVS in some cases), extending broadly even as far as the anterior regions of the ventral occipitotemporal cortex (Rossion et al., 2023). There is, however, clustering of the contacts with greater amplitude of face selectivity to the RH in the vicinity of the middle section of the lateral fusiform gyrus, consistent with much of the existing neuroimaging data.

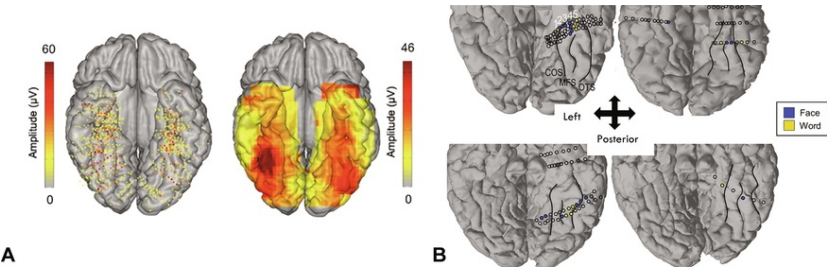


Fig. 29.3 (A) Quantification of face selectivity from intracranial depth electrodes at the group level in a common space. Significant contacts across 84 subjects were color-coded according to their relative face-selective amplitude and displayed in the Talairach space (left panel). Amplitude across contacts are smoothed and projected on the cortical surface by plotting the mean face-selective amplitude within 15 mm × 15 mm voxels (right panel). (B) Multiple adjoining word- and face-selective patches in four individual participants. See alternating bands of word- and face-selectivity along the

left fusiform gyrus. Major VTC sulci (collateral sulcus [COS], midfusiform sulcus [MFS], and occipitotemporal sulcus [OTS]) have been outlined for clarity. Shaded electrodes are those selective to words (yellow) and faces (blue). Open circles represent ventral temporal electrodes that did not reach the selectivity criterion for either of these categories.

Panel (A) adapted from Rossion B, Jacques C, Jonas J (2023). Intracerebral electrophysiological recordings to understand the neural basis of human face recognition. Brain Sci 13, with the author's permission. Panel (B) adapted with the author's permission from Boring MJ, Silson EH, Ward MJ, et al. (2021). Multiple adjoining word- and face-selective regions in ventral temporal cortex exhibit distinct dynamics. J Neurosci 41: 6314–6327.

alt-text: Fig. 29.3

Intracranial data has also permitted examination of the medial to lateral loci of activation for faces relative to other stimuli such as words in adjoining cortical regions (see Fig. 29.3B) and, for the first time, has enabled researchers to uncover the relative temporal dynamics and location of regions that respond to centrally presented faces (and words), as is common in daily life to ensure high-resolution foveal input. Face-selective responses were initially evident bilaterally in posterior fusiform regions bilaterally, and then were propagated to more anterior regions. Studies such as these begin to offer glimpses into the complex and dynamic bihemispheric, albeit RH weighted, distributed circuits involved in face processing.

Last, transcranial magnetic stimulation (TMS), a method that creates a refractory period or temporal loss of function has been used as has the more recent variant, transcranial direct current stimulation (tDCS). Studies have, for example, uncovered evidence that same-different judgments or part-whole matching of faces, but not houses, can be disrupted by TMS to the right occipital face area (OFA), which is close to the lateral surface and more accessible from the scalp than the FFA (Pitcher et al., 2007; Bona and Silvano, 2014; Bona et al., 2018). Likewise, when a sham version of tDCS was applied to the locus of electrode P08 in the RH (where face inversion effects are typically found using EEG), in participants viewing upright vs inverted faces of the same or different race from the participant, a large face inversion was observed especially for own-race faces, as would be expected. However, when anodal-tDCS was applied at this same location, this large own race inversion was reduced as performance for upright faces was adversely affected, offering insight into face perception in the RH (Civile et al., 2021; Civile and McLaren, 2022).

The Emergence of Lateralized Superiority for Faces and Hemispheric Plasticity

Thus far, the focus of this review has been almost exclusively on the mature face recognition system, its neural bases and ways in which hemispheric asymmetry has been demonstrated. Of course, one might ask how this mature system and its remarkably replicable topography arises across individuals. Although face processing is clearly superior over the RH in adults, this does not seem to be the case for younger individuals. Provocatively, in individuals aged 5–17 years, a posterior injury (pre-, peri-, or post-natal) involving the temporal regions of either hemisphere resulted in a face processing deficit (Mancini et al., 1994; de Schonen et al., 2005).

Relatedly, a recent study in a relatively large group of 39 individuals (median age 16.7 years at testing, median age at surgery 5.5–6 years) all of whom had hemispherectomy during childhood for the treatment of pharmacologically intractable epilepsy (Granovetter et al., 2022) also showed bilateral hemispheric competence for face perception. Of the patients, 15 had a preserved LH and 24 had a preserved RH, and age- and gender-matched controls were tested too. In two experiments, participants made the same/different judgments to a pair of faces or pair of words presented sequentially (see Fig. 29.4 on left for the experimental procedure). In the first experiment, all participants viewed stimuli in central vision (permitting the contrast between having two hemispheres versus a single hemisphere) and, in the second experiment, the first item in the pair was shown in central vision and the second item was shown in the periphery (the intact visual field for the hemianopic patients), permitting the contrast between just a single hemisphere in the patients versus controls. The results from the two studies did not differ and, surprisingly, independent of central or peripheral presentation, both the left and right resection patients averaged approximately 85% accuracy (see Fig. 29.4 on right). It is especially interesting that the preservation of just the LH or just the RH yielded equivalent results and that this held for both the face and word conditions. While the patients performed statistically more poorly than controls (with accuracies around 95%), the patients' performance was still impressive given the extent of the cortical resection (hemispherectomy or hemispherotomy). These findings suggest that, perhaps earlier in development, either hemisphere may be sufficient to assume representation of both stimulus classes, which then become increasingly lateralized over the course of typical development. With age, then, the lateralization of functions (although not totally dichotomous) becomes more apparent. But, the finding that the mean accuracy of the patients does not reach normal performance still demands explanation. One possibility is that the relative accuracy decrement in the patients may result from increased competition or “neural crowding” in a limited neural space (Lidzba et al., 2006; Kragehlo-Mann et al., 2017; Danguécan and Smith, 2019). Thus, cortical territory cannot fully accommodate both face- and word-processing functions in a single hemisphere, in contrast with controls, who have somewhat lateralized functions distributed over the two hemispheres.

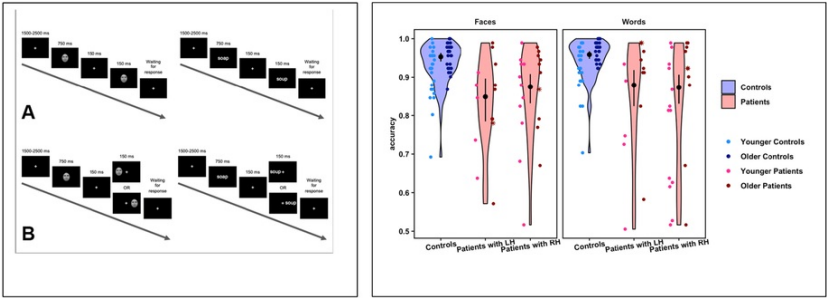


Fig. 29.4 Left: (top row) Sequential matching paradigm for faces and words with both pairs of the single trial shown in central vision. (bottom row) Sequential matching paradigm for pairs of faces and words with the “target” shown centrally first followed by the second stimulus shown in either the le

or right visual field (to accommodate the hemianopia in the resected patients). (This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Adapted and reprinted from Granovetter MC, Robert S, Ettensohn L, et al. (2022). With childhood hemispherectomy, one hemisphere can support-but is suboptimal for-word and face recognition. Proc Natl Acad Sci U S A 119: e2212936119.

alt-text: Fig. 29.4

Despite the consensus on mechanisms such as “neural crowding,” little direct evidence for the competition between functions during the process of reorganization exists. Because longitudinal neuroimaging and behavioral data must be tracked to uncover the microgenesis of reorganization, there has not been much attention to this question. One study, which has addressed this dynamic process, acquired fMRI data from a single child, UD, who had his right occipitotemporal region resected at age 6 years 9 months to manage drug-resistant epilepsy resulting from a low-grade, slow-growing, dysembryoplastic neuroepithelial brain tumor (Liu et al., 2018). UD showed normal performance on face and word experiments (like those shown in Fig. 29.4 left). Data from functional MRI acquired over four time points postsurgically (see stimuli employed in Fig. 29.5A), roughly 6 months apart, confirmed the presence of an immutable left visual field hemianopia. In extrastriate cortex, however, even at the first postsurgical scan, object- and scene-selective responses were observed in the typical category selective Lateral Occipital Cortex and Parahippocampal Place Area, and the topography, extent, and selectivity of these regions fell within the normal distribution and did not change longitudinally as seen in Fig. 29.5 compared to the matched control participants. In contrast, activation for faces and for words showed significant change in location as well as in magnitude of activation over a session, with the location of the word-selective “Visual Word Form Area” shifting more laterally over sessions and the extent of the left FFA expanding and abutting it but more medially located (see Fig. 29.5).

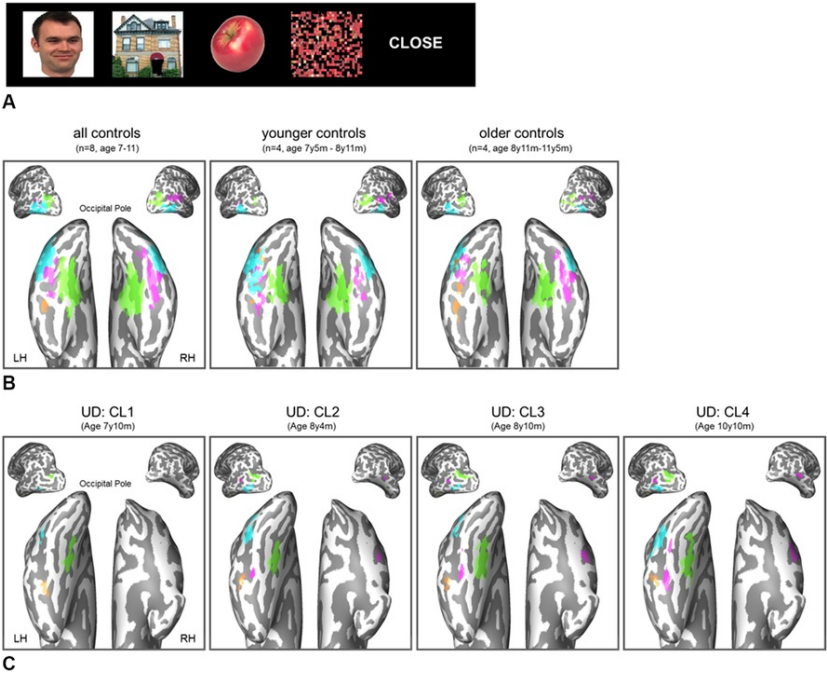
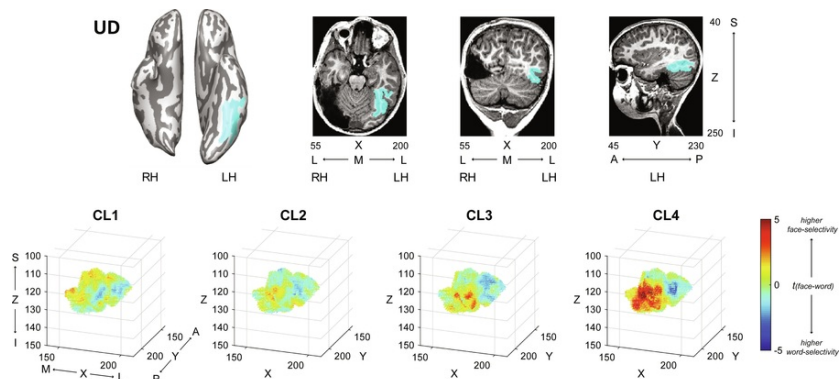


Fig. 29.5 Category-selective activations in controls and UD. (A) Examples of stimuli used in the fMRI experiments of category localizer (CL). (B) Category-selective activations for all eight controls, four younger controls, and four older controls. (This 8 year 11 month child is different from the other 8 year 11 month child in the young controls. One was slightly older than the other and they fell on different sides of the median split.) (C) Category-selective activations visualized in UD from CL1 to CL4 (left to right). Blue: object-selective activation (LOC); green: scene-selective activation (PPA and TOS); pink: face-selective activation (FFA and STS); orange: word-selective activation (VWFA).

Adapted from Liu TT, Nestor A, Vida MD, et al. (2018). Successful reorganization of category-selective visual cortex following Occipito-temporal lobectomy in childhood. Cell Rep 24: 1113, (Fig. 2). This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

alt-text: Fig. 29.5

Specifically, tracking the voxels located in a 3D volume superimposed over the Fusiform Gyrus and occipitotemporal sulcus revealed the shift in category selectivity from a response that, initially, was only mildly selective for one of the two categories, and then gradually becoming more selective for either faces or words. These longitudinal findings reveal the dynamics by which plasticity may come about in the human visual system and implicate processes of cooperation (between voxels with similar selectivities) and competition (between voxels with differing selectivities) in the process of neural crowding and reorganization (Fig. 29.6).



Reproduced from Liu et al. (2018)

Fig. 29.6 (A) Fusiform Gyrus (FG) and OccipitoTemporal Sulcus (OTS) hand-drawn in the surface space. (B) FG and OTS in the corresponding volume space (coordinates in native space). (C) Change over time in each voxel's response to faces over words within the FG/OTS region, where the XYZ coordinates and the t score $[t_{\text{face-word}}]$ are plotted for each voxel. Color: darker in red denotes higher sensitivity to faces and darker in blue denotes higher sensitivity to words.

Adapted from Liu TT, Nestor A, Vida MD, et al. (2018). Successful reorganization of category-selective visual cortex following Occipito-temporal lobectomy in childhood. *Cell Rep* 24: 1113, (Fig. 4). This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

alt-text: Fig. 29.6

Inspired by findings of initial hemispheric equivalence for faces and then, over development subsequent fine-tuning in the RH, Behrmann and Plaut (Plaut and Behrmann, 2011; Behrmann and Plaut, 2020) proposed a theoretical account in which the principles of cooperation and competition in the cortex serve to craft or configure the hemispheric asymmetries, which are robustly and replicably noted in adulthood. The hypothesis is that, prior to the acquisition of literacy, both hemispheres are engaged in the process of face recognition [and hence a lesion to either early in life can result in a deficit in face perception (de Schonen et al., 2005)]. With the acquisition of orthographic competence and literacy, the optimization of the LH becomes tuned for the perception of words (and reading, more generally). This LH engagement in the representation of words comes about by virtue of the pressure to retain a close coupling between extrastriate visual areas and language regions in the dominant LH (in the modal right-hander). The pressure to keep the connection length short was inspired by the implementation of neural networks in which error-driven learning was augmented with a spatial loss function penalizing large weights on longer vs shorter connections to a greater degree (Jacobs and Jordan, 1992). It is this connectivity constraint, which results in the tweaking of the LH to have superiority for word over face perception and, by competition, leads to the increased superiority of face over word (and other classes too) recognition in the RH (Behrmann and Plaut, 2013, 2020). Both half-field behavioral testing of face and word discrimination and EEG data acquired from right-handed children, adolescents, and adults (Dundas et al., 2013, 2014, 2015) supported the emergence of LH word recognition in the right visual field/LH and its correlation with the lateralization of face recognition in the RH [and for computational implementation and simulations of this hypothesis, see Blauch et al., 2022]. This initial more bilateral organization for faces, which evolves into more lateralized function over age appears to be true across other functions too—see findings showing bilateral language functions in early childhood with a slight LH bias, which is enhanced with age and a “weak shadow” of language function in the RH (Olulade et al., 2020; Martin et al., 2022).

There are ongoing debates about the exact nature of the competition and continued discussion about the exact nature of the lateralized competition or neural recycling (Dehaene and Cohen, 2007; Dehaene et al., 2015; Dehaene-Lambertz et al., 2018) for faces vs words or for words vs other categories like limbs (Nordt et al., 2021). Also, one study reported that the word-selective cortex did not recycle the previously face-selective cortex (Dehaene-Lambertz et al., 2018). Rather, word-selective voxels appeared to show weak selectivity before the onset of reading, some showing mild preferences for tools, but not for faces.

Further challenges to the view that the RH face advantage is a consequence of the acquisition of word recognition in the LH comes from findings showing a left visual field gaze (but not necessarily perceptual processing) bias in 6-month-old children (Donati et al., 2020) and even in some nonhuman species (Guo et al., 2009). These findings contest the claim that literacy per se is the trigger for hemispheric differentiation for faces and for words (Lochy et al., 2020; Rossion and Lochy, 2022). Evidently, much remains to be learned about the inherent biases of the two hemispheres and the nonlinearities in hemispheric asymmetry, which seem to be present as well—for example, whereas 4–6 month-old infants evinced a RH lateralization for faces in an EEG fast period visual stimulation study (de Heering and Rossion, 2015), 5-year-old children exhibited a bilateral response under the exact same conditions (Lochy et al., 2017). Obviously, understanding the process by which the mature pattern of hemispheric lateralization emerges requires further investigation and consideration [see also Davies-Thompson et al., 2016].

Facial Expression Perception

This chapter, thus far, has focused on mechanisms that support face identification and its hemispheric underpinnings. Although there has been less research into the hemispheric differences in the perception of facial expression, there is, nevertheless, interesting work that warrants consideration. There is a general consensus that emotional facial expression is better perceived when the face is viewed in the observer's left visual field than the right, supporting the claim that facial expression is computed superiorly in the right

hemisphere (Bourne, 2010; Blom et al., 2020). Consistently, the left of a chimeric face is considered to be more expressive than the right hemiface of the chimeric (Sackeim et al., 1978; Sackeim and Gur, 1980). Last, neuropsychological data have shown that RH brain damage results in difficulties in the perception and processing of emotional expressions of faces (Kucharska-Pietura et al., 2003; Kucharska-Pietura and David, 2003).

As noted in the introduction, studies of emotional face perception in nonhuman primates have been fairly extensive. In one of the key papers examining the neural underpinning of this behavior in nonhuman primates, monkeys viewed images of neutral faces or faces showing aggression, fear, or submission expressions. Both the amygdala and the inferior temporal were modulated by facial expressions, especially in response to fear and the regions of activation were essentially independent of maps of facial identity perception (Hadj-Bouziane et al., 2008). No obvious hemispheric differences were apparent as is typical for studies like this [for a reviews, see Hopkins and Cantalupo, 2008, Leopold and Rhodes, 2010 and Hopkins et al., 2015].

The central claim that, in humans, all emotions, independent of valence, are processed in the RH has come to be called the RH dominance account. This can be contrasted with the valence lateralization view in which positive emotions are processed in the LH and negative emotions in the RH. Neither hypothesis has iron-clad evidence (Fridlund et al., 1985; Fridlund, 1988). In light of this latter, a more nuanced approach, in which emotion expression is mediated by a host of interrelated networks in a more flexible fashion has been proposed (Palomero-Gallagher and Amunts, 2022). An example of such networks and their differential engagement is reported by Prete et al. (2022) who, using EEG, monitored the distribution of signals associated with the perception of emotional expression. Networks include temporal regions of the RH and, to a lesser degree, the LH, as well as temporoparietal areas bilaterally and, last, right frontal cortex. Recent studies using neuroimaging and meta-analysis have also shown bilateral engagement, primarily in the processing of images showing disgust; but, a right-lateralized superior temporal-frontal network was found to be more involved in social disgust and social cognition (Gan et al., 2022).

Clearly, the jury is still out (and the jurors do not seem ready to appear any time soon) and much research is needed. Perhaps the most intriguing mission to interested researchers at present is to consider the recent findings of networks and distributed functions with multiple regions involved in emotion processing. Attention to the amygdala and its role in emotional face expression, especially fear, is also important (Wang et al., 2023). The move toward using big data to uncover the full complement of neural tissues that underlie complex social and emotional processing is noteworthy, and several relevant atlases and big data analyses are helpful in this regard (Fusar-Poli et al., 2009a,b).

Conclusion

As is apparent from even this brief review, face identity and emotion perception and their underlying neural correlates have been the foci of probably thousands of studies by now. And still, notwithstanding the plethora of studies, which have yielded progress, there are still no definitive conclusions. While there is growing recognition that there are likely complex networks in each hemisphere and multiple regions whose joint activity determine the behavioral outcome, there is much that we still do not know. The increasingly refined methodological approaches as well as the novel cutting-edge analytic techniques will surely advance our understanding, and perhaps a less hemisphere-specific and more interactive and dynamic neural mechanism will, in time, be revealed and confirmed.

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Dedication

Over the years, Michael Corballis inspired my interest in hemispheric asymmetries with his elegant and creative observations and studies. This chapter is dedicated to his memory.

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Keywords: Face perception; Hemispheres; Lateralization; Asymmetry; Behavior; Neuroimaging; Development

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Query:

Pleas provide appropriate section citation in place of "Facial expression recognition" in this occurrence.

Answer: FACIAL EXPRESSION PERCEPTION

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Answer: facial expression is computed superiorly

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Please check whether the inserted volume number and also the modified page numbers are appropriate for the reference "Bobak et al. (2016)" and correct if necessary.

Answer: This is correct in text. Here it is again

Bobak, A. K., Parris, B. A., Gregory, N. J., Bennetts, R. J., & Bate, S. (2016). Eye-movement strategies in developmental prosopagnosia and "super" face recognition. *Q J Exp Psychol (Hove)*, 1-17.

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Answer: yes, correct.

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Nordt, M., Gomez, J., Natu, V. S., Rezai, A. A., Finzi, D., Kular, H., & Grill-Spector, K. (2021). Cortical recycling in high-level visual cortex during childhood development. *Nat Hum Behav*, 5(12), 1686-1697. doi:10.1038/s41562-021-01141-5

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