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Hemispheric specialization in face recognition: from spatial frequencies to holistic/analytic cognitive processing

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Abstract

We present clinical and neurophysiological studies that show brain areas that are involved in face perception and how the right and left hemispheres perform holistic and analytic processing, depending on spatial frequency information. The hemispheric specialization of spatial frequency in face recognition is then reviewed and discussed. The limitations of previous work and suggestions for further investigations are discussed. Our conclusion is that functional sensorial asymmetries may be the basis for high-level cognitive asymmetries. **Keywords:** face recognition, hemispheric specialization, holistic and analytic processing, spatial frequency.

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Introduction

There is multidisciplinary interest in the study of the human face because of its evolutionary and social relevance. Research on face recognition focuses on complex cognitive processes, practical applications, clinical studies, and even computational simulations and biometric models. Understanding basic sensorial and perceptual operations that are performed by the human visual system to process and recognize faces is important. In this paper, we review the literature on how lateralized high-level cognitive strategies are supported by the processing of elementary sensorial information. In particular, we seek to clarify holistic and analytic processing in face recognition based on spatial frequency information and how the brain hemispheres process different bandwidths of spatial frequency.

We first review basic information about face recognition. We then present clinical and neuroimaging studies that show the brain areas that are involved in face perception and how the right and left hemispheres perform different kinds of processing. The relationship between holistic/analytic processing and low/high spatial frequency information is established, and the hemispheric specialization of spatial frequency in face recognition is reviewed and discussed.

Face recognition

Humans are experts in face recognition. We can recognize minimal variations in facial features, even at a distance and under low light conditions, different haircuts, and different angles. Recognition happens automatically in less than 1 s, without posing cognitive load (Maurer et al., 2007). Face recognition is fast and accurate. Adults are capable of recognizing familiar faces with an accuracy greater than 90%, even if some faces have not been seen for 50 years (Carbon, 2003).

The human face is an important source of information and communication and has several aspects including ethnicity, age, gender, attractiveness, emotion and health condition. Thus, the face is the most expressive part of the body (Chellappa, Wilson, & Sirohey, 1995). Faces provide several social features that can be detected by other individuals and are essential for interpersonal relationships. To a large extent, social interaction is facilitated by the rapid processing of face recognition, which is linked to our biological necessity of identifying who is approaching and what kind of greetings or emotional signs an individual presents.

During the evolutionary process, primates that had a cortical area and specific processing devoted to face perception were better adapted and favored by natural selection (Carmel & Bentin, 2002; Chellappa et al., 1995). Details about this perceptual process, however, remain unclear. There are two theories on the origin of face recognition.

The expertise hypothesis supports the view that face recognition is a generic ability that is similar to the processing of other classes of stimuli, and faces represent a special case because of experience and the

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need to discriminate at the individual level. This implies that the same processing mechanism may apply to any kind of visual object (Gauthier & Tarr, 1997; Meadows, 1974). The domain-specific hypothesis states that face recognition is a specific process that is devoted only to this type of stimulus. The origin of this processing mechanism remains unclear, but it possibly has innate factors or requires experience during a critical developmental period (Robbins & McKone, 2007; Yovel & Kanwisher, 2004).

Apart from the uncertainty of the origin of facial processing, the idea that faces involve holistic processing is consolidated in the literature. Faces have a peculiar organization, and their elements are organized to allow global perception as a gestalt combination between specific features. Even slight changes in these elements allow distinguishing between individuals. Converging evidence shows that facial patterns are processed holistically, which is different from other types of stimuli (Cheung, Richler, Palmeri, & Gauthier, 2008). This would be related to the processing style of the right hemisphere (Ellis, 1983; Springer & Deutsch, 1993). This hypothesis has been supported by research on hemispheric dominance and brain asymmetry in face perception and the processing modality observed in each hemisphere.

Hemispheric specialization and the neural substrates of analytic and holistic face processing

In the 1960s, research on patients with brain injury showed that the majority of individuals with prosopagnosia had lesions in the right hemisphere. In the following years, Levy, Trevarthen, and Sperry (1972) reported similar results in patients who had undergone commissurotomy: a strong asymmetry in facial recognition in favor of the right hemisphere, whereas the left hemisphere was capable of recognizing familiar faces but had serious difficulties processing unfamiliar faces as a whole. Moreover, other advantages of the right hemisphere over the left hemisphere were observed, especially in processing speed, accuracy in identifying faces, access to long-term memory, and the reception and storage of facial information (Chellappa et al., 1995; Curyto, 2000; Gazzaniga, 2000).

The superior performance of the right hemisphere in face recognition stems from its expertise in coding and processing synthetic and holistic visuospatial stimuli and configural information[1] (Rhodes, 1993; Springer & Deutsch, 1993). In particular, it processes non-verbal, simultaneous, analogical, gestalt, synthetic, and intuitive information. Conversely, the left hemisphere has processing mechanisms that are suitable for verbal, sequential, temporal, digital, logical, analytical, and rational information (Springer & Deutsch, 1993).

Human faces activate specific regions of the human brain, which has been consistently reported in electroencephalography and neuroimaging studies and case reports on patients with prosopagnosia (Goffaux, Peters, Haubrechts, Schiltz, Jansma, & Goebel, 2011; Rossion et al., 2000). Many studies that compared face and object discrimination showed that faces produced bilateral activation in medial portions of the fusiform gyrus, with more activity in the right hemisphere. These results are consistent with cases of prosopagnosia caused by bilateral lesions in the occipitotemporal cortex and unilateral lesions in the right fusiform gyrus (Rossion et al., 2000).

The region associated with face recognition comprises the ventromedial surface of the temporal and occipital lobes in the mediolateral fusiform gyrus, known as the Fusiform Face Area (FFA). Activity in this area varies according to the attention directed toward the stimuli, showing that it is not exclusively triggered by the face itself (Sergent, Ohta, & MacDonald, 1992; Kanwisher, McDermott, & Chun, 1997).

The middle fusiform gyrus is activated in both hemispheres, with higher activation on the right side. The posterior fusiform gyrus is activated only in the right hemisphere when attention is focused on facial patterns. The brain area located in the inferior temporal gyrus, known as the Facial Occipital Area, is more activated by faces than by objects, again with more activation on the right side (Rossion, Caldara, Seghier, Schuller, Lazeyras, & Mayer, 2003). Additionally, selective activity in the superior temporal sulcus and inferior occipital gyrus was reported, but these observations are not consistent (Haxby, Ungerleider, Clark, Schouten, Hoffman, & Martin, 1999; Rossion et al., 2000, 2003).

The involvement of the left hemisphere in face recognition is still a matter of debate. Some researchers argue that the fusiform area of the right hemisphere is responsible for face recognition, whereas the equivalent area of the left hemisphere performs general object recognition. However, the total disruption of face processing has been suggested to be caused by bilateral lesions, whereas unilateral damage causes only selective impairments (Boeri & Salmaggi, 1994). Furthermore, considerable evidence indicates that both hemispheres are involved in the recognition of facial patterns, but they perform different roles. According to this point of view, the right hemisphere processes faces in an integrative and comprehensive manner, whereas the left hemisphere is responsible for facial features.

The idea of hemispheric specialization that associates the right hemisphere with holistic processing and the left hemisphere with analytical processing is

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[1] The term *configural* has been applied to describe phenomena that involve the perception of relations between facial features. Configural processing may be divided into three types: (1) first-order relations regarding the facial pattern with two eyes, one mouth, and one nose, (2) holistic processing, which is the perception of the face as a gestalt, and (3) second-order relations in the perception of distances between features. However, no consensus on this term has been reached. Some researchers adopt the three types, and others adopt only one (Maurer, Le Grand, & Mondloch, 2002). In this review, the terms configural, holistic, and global are synonymous.

supported by some studies. Faces that are presented upright or with differing spaces among facial elements favor configural processing in the left visual field (projecting to the right hemisphere; see the divided visual field method in Bourne, 2006) and are perceived more quickly and accurately than when presented in the right visual field (projecting to the left hemisphere; Cattaneo, Renzi, Bona, Merabet, Carbon, & Vecchi, 2014; Ramon & Rossion, 2012; Rhodes, 1993). When faces are presented inverted (upside-down) or modified, inducing the processing of individual features in a divided visual field, the advantage of the right hemisphere is eliminated or reduced because of the interruption of holistic coding (Hillger & Koenig, 1991; Leehey, Carey, Diamond, & Cahn, 1978; Rhodes, 1993). The lateralized repetition-priming paradigm was tested by Bourne, Vladeaunu, and Hole (2009) using blurred faces and displaced facial features. The results supported the role of both hemispheres. Configurally degraded faces produced negative and positive priming in the left and right visual hemifields, respectively, and featurally degraded faces produced the opposite effect. In two event-related potential (ERP) studies, upright and inverted faces activated the right and left hemispheres with more intensity, respectively (McCarthy, Puce, Belger, & Allison, 1999; Rossion et al., 1999). In another ERP study, faces were altered by either moving or replacing facial features, inducing configural and featural processing, and the same results were obtained (Scott & Nelson, 2006). A positron emission tomography study also supported the involvement of both hemispheres in face processing. Rossion et al. (2000) observed a decrease in face-specific activity in the FFA of the right hemisphere when attention was focused on facial components. In contrast, activity increased in the equivalent area of the left hemisphere. However, evidence argues against differential holistic/analytic processing in the FFA (Yovel & Kanwisher, 2004). Additionally, other cortical areas are necessary and recruited for facial identification (Avidan, Hasson, Malach, & Bermann, 2005; Haxby, Ungerleider, Clark, Schouten, Hoffman, & Martin, 2001). Functional magnetic resonance imaging (fMRI) allowed the mapping of non-overlapping neural areas and networks for configural and featural processing when participants judged spaced-feature faces and altered-feature faces (Maurer et al., 2007). The results showed no differences between featural and configural processing in the FFA, supporting the findings of Yovel and Kanwisher (2004). The spacing condition more robustly activated an area of the fusiform gyrus adjacent to the FFA (slightly superior and posterior to it) and areas of the frontal and inferior parietal cortices in the right hemisphere, whereas the featural condition activated the middle prefrontal areas of the left hemisphere. However, ERP and fMRI data only correlate alterations in brain activation caused by visual stimulus manipulation. Renzi et al. (2013) performed a transcranial magnetic stimulation (TMS) study. This technique allows the modulation of brain activity in a controlled task and establishes cause-effect relationships. The TMS was delivered in cortical areas based on the study by Maurer et al. (2007). The results showed that TMS disrupted holistic and analytic processing over the right inferior and left middle frontal gyri, respectively. These summarized behavioral and neurophysiological studies provide strong evidence of a dissociation between holistic and analytic processes in face perception mediated by separate and lateralized networks in the human cortex.

In the facial processing literature, the holistic/global model has received much attention in the last three decades (Goffaux & Rossion, 2006). The majority of the results regarding the activation, reaction time, and hit rate advantage of global processing and the right hemisphere may be attributable to its mode of operation. Lux et al. (2004) suggested that global processing is the automatic default setting of visual attention and requires less activation than local processing, which requires attentional control. The local analysis of stimuli is not natural because of two conflicts that occur: (1) the default processing of global information and (2) the tendency to focus on items of interest. Thus, the global system is more frequently used, but both types of processing are fundamental to this task (Casey & Newell, 2007).

In short, the perception and recognition of faces have two different processing systems. The global/holistic system utilizes a type of processing that is mainly performed by the right hemisphere in which features interact in an integrated fashion. The local/analytical system, in contrast, specializes in feature processing and is mainly performed by the left hemisphere. Behavioral and neurophysiological evidence suggests that human face processing requires both featural and configural processing (Goffaux, Hault, Michel, Vuong, & Rossion, 2005).

Hemispheric specialization of spatial frequencies in face recognition

Configural, global, or holistic perception, as opposed to featural, local, or analytical perception, involves high-level cognitive operations that depend on low-level perceptual processing (Hills & Lewis, 2009)2002. The analysis of spatial frequencies (i.e., variations in luminance across space) is one of the first processes that occur during the encoding of visual information. This may play an important role in hemispheric asymmetry (Yamaguchi, Yamagata, & Kobayashi, 2000) and face perception (Goffaux et al., 2005).

Accumulating evidence indicates that the visual system has specific filters for different bandwidths of spatial frequency (Campbell & Robson, 1968). These filters decompose the visual scene in the retina, initiating highly complex perceptual and cognitive functions. Cells of the visual system that are sensitive to high spatial frequencies process sharp borders with high variations in luminance. Thus, discrete and detailed facial features are perceived, which is the basis of analytical operations. Cells that are sensitive to low spatial frequencies process coarse signals in regions of low variations in luminance, forming the basis of holistic operations (Goffaux et al., 2005; Livingstone & Hubel, 1988). Therefore, different bandwidths of spatial frequency encode different aspects of visual objects. With regard to the face, a given bandwidth of the spectrum can affect its perception and recognition, given that face perception relies on both configural and featural processing (Goffaux et al., 2005; Sergent, 1996). Additionally, behavioral and neuroimaging data indicate that face processing is more sensitive to spatial frequency information than to other visual stimuli (Collin, Liu, Troje, McMullen, & Chaudhuri, 2004; Yue, Tjan, & Biederman, 2006).

According to the idea that low spatial frequencies underlie holistic operations and that high spatial frequencies underlie analytical operations and considering that holistic and analytical operations are better performed by the right and left hemispheres, respectively, Sergent (1982) postulated the hypothesis of the hemispheric specialization of spatial frequencies. This hypothesis states that the left hemisphere is more sensitive to high spatial frequencies, whereas the right hemisphere is more sensitive to low spatial frequencies. The hemispheric specialization of cognitive functions is suggested to derive from differences in low-level resolution capacity between the brain hemispheres. Thus, the competence of each hemisphere in visual tasks depends on its sensorial resolution in information processing. This hypothesis was further supported by psychophysical (Kitterle, Christman, & Conesa, 1993), electrophysiological (Reinvang, Magnussen, & Greenlee, 2002) clinical (dos Santos, Andrade, & Fernández-Calvo, 2013), and neuroimaging (Peyrin, Baciu, Segebarth, & Marendaz, 2004) studies using basic stimuli such as sinusoidal gratings (Proverbio, Zani, & Avella, 1997) or stimuli with ecological value such as landscapes (Peyrin, Chauvin, Chokron, & Marendaz, 2003).

Considering that the brain has a specialized system for face recognition, remaining unclear is whether faces are differentially encoded in the brain hemispheres based on spatial frequency. Some studies were conducted to explore this issue (Table 1). According to our bibliographic search, the first attempt to address this issue was made by Keegan, Whitman, and Tanenhaus (1981; as cited in Keenan, Whitman, & Pepe, 1989, and Whitman & Keegan, 1991). This paper was presented to the International Neuropsychological Society and describes a task of matching faces in high and low spatial frequencies in a divided visual field. The results revealed that performance was better for faces with a low spatial frequency in the left visual hemifield.

In a subsequent study, Moscovitch and Radzins (1987) investigated the effects of different types of backward masking in the recognition of previously memorized lateralized faces. They analyzed the interstimulus interval, which is the critical time gap between the mask and the target to achieve a given criterion of performance in target recognition. In Experiment 2 in their study, the masking comprised dot clusters in different spatial frequencies. This was an indirect method of investigation that was supported by empirical evidence (Legge, 1978), based on the assumption that the target stimulus is strictly masked by the spatial frequencies that are present in the mask. The results did not support the hypothesis of the hemispheric specialization of spatial frequencies. According to the authors, the results could have reflected two biases: (1) the narrow band of spatial frequency covered by the masks (.5, 3, 8, and 24 cycles per degree [cpd] of visual angle) and (2) the masks' higher intensity compared with the target stimuli.

Taking these factors into consideration, Keenan et al. (1989) also proposed a face recognition task with spatial frequency masking and a divided visual field. They used a tachistoscope to present faces for 10 ms that were masked by square-wave gratings of 1, 24, and 48 cpd. The subjects were asked to choose which of five stimuli was the target. As a measure of performance, however, they used the percentage of judgment errors, and the results supported the hypothesis of hemispheric specialization.

At the time that these studies were conducted, the technology could not handle the spatial frequency spectrum in a simple manner, and the early studies had methodological difficulties and employed indirect techniques. Sergent was the first researcher to use Fourier transform for the digital filtering of images (Sergent, 1985, 1987). In Experiment 1, Sergent (1985) found lower response times when faces were presented in high resolution (high luminance variation) for 100 ms in the right visual field in a verbal identification and manual categorization task that used members of the subject's department as the facial stimuli. In Experiment 2, the same faces were presented using two types of band-pass filters. When the high-pass filter (0-32 cpd) was used, the faces were better recognized by the right visual field, as in Experiment 1. When the low-pass filter (0-2 cpd) was used, the results were reversed in both tasks, in addition to a manual male/female categorization task. These results support the hypothesis of the hemispheric specialization of spatial frequency.

In a subsequent study, Sergent (1987) presented lateralized faces for 40 or 180 ms in a male/female categorization task using band-pass (0-32 cpd), low-pass (0-2 cpd), and coarsely quantized (4 blocks per cpd) filters. Regardless of the filter, the response latency was shorter for faces that were presented in the left visual field in the faster-presentation condition (40 ms). However, in the longer-presentation condition, band-pass faces were better processed when presented in the right visual field, and no performance differences between visual hemifields were observed for low-pass faces. Later studies showed that broad band-pass filtering, such as the 0-32 cpd filter used by Sergent, is not an appropriate technique to investigate sensitivity to high spatial frequencies and featural processing performed in facial recognition. The optimal range for face recognition is 8-16 cycles per face [cpf]. The filter comprises the best band for face recognition, consisting of both coarse and fine visual cues (Morrison & Schyns, 2001; Parker & Costen, 1999). Therefore, the psychophysical studies show that the visual system processes faces more quickly with the full spectrum of spatial frequency or 8-16 cpf compared with high-pass or low-pass filters outside this range (Goffaux et al., 2011; Perílla-Rodríguez, de Moraes Júnior, & Fukusima, 2013). The band-pass filter that Sergent (1987) used may have indicated the general ability to recognize faces in each hemisphere. By increasing the exposure time, the analytical process that is best performed by the left hemisphere was improved, which had an advantage in the condition with the higher exposure time (i.e., 180 ms). Global processing in the right hemisphere is stronger in early stages of perception (Ramon & Rossion, 2012).

Whitman and Keegan (1991) also conducted a study that was not based on indirect methods. Additionally, low spatial frequencies were extracted from the original set of images to achieve high-pass-filtered faces. Pairs of faces were filtered to preserve low or high spatial frequencies, and the faces were presented for 200 ms in the left or right visual hemifields. The participants were required to perform same-different judgments. The results partially supported the hypothesis of the hemispheric specialization of spatial frequency. Presentation in the right hemifield produced more errors, and this difference was greater for faces in a low spatial frequency. In the left hemifield, faster response times and lower error rates were observed for faces presented in a low spatial frequency.

Our literature review only found psychophysical studies that investigated the relationship between hemispheric specialization and spatial frequency using faces as stimuli. In a neuroimaging study, Goffaux et al. (2011) observed the activation of brain areas that are sensitive to facial patterns. The participants performed a behavioral task to categorize the phase of the stimuli (i.e., intact vs. scrambled), in which high, intermediate, or low spatial frequencies were presented for 75, 150 or 300 ms and masked. In both hemispheres, the FFA showed a coarse-to-fine pattern of activation for spatial frequency but in different time intervals. No evidence of hemispheric asymmetry was observed, as proposed by Sergent (1982). However, this work supported the idea that spatial frequency processing is dynamic and time-dependent, and the results showed that only around 300 ms low and high spatial frequencies are equally processed in both the right and left FFA.

Taking this into account, Perilla-Rodríguez et al. (2013) conducted a study of face recognition in high and low spatial frequencies of unfiltered faces previously memorized. The faces were presented lateralized for 300 ms using an adaptation of the divided visual field method. The data were analyzed by the confidence rating method of Signal Detection Theory. Similar to other previous studies, the hypothesis of the hemispheric specialization of spatial frequency was partially supported. Low spatial frequency-filtered faces were better recognized than the high-pass faces when presented in the left visual hemifield. Significant differences between brain hemispheres were found only for high spatial frequencies. Again, the higher exposure time may likely be involved in the high frequencies advantage of face recognition in the right visual field.

In short, the first studies performed in the 1980s had limitations because they used indirect methods (Keenan et al., 1987; Moscovitch & Radizins, 1987) or performed inadequate digital filtering that did not maximize the difference between high and low spatial frequencies (Sergent, 1985, 1987; Whitman & Keegan, 1991). This scenario was improved with the computer revolution and the popularization of algorithms, such as fast Fourier transform, that were incorporated in new studies (Perilla-Rodríguez et al., 2013; Whitman & Keegan, 1991). Processing time was suggested to play a key role in the occurrence of this perceptual phenomenon. Therefore, the question that best addresses this issue is not whether there is hemispheric specialization for spatial frequency in face perception. Instead, we should ask what are the temporal and spatial dynamics in the brain hemispheres. This point of view is consistent with trends in cognitive neuroscience that focus on spatial-temporal relations of distributed networks in the cortex (Nicolelis, 2010). A recent fMRI study contributed to this topic (Goffaux et al., 2011). This technique has spatial precision but does not have good temporal resolution. Thus, electrophysiological as well as optical imaging investigations would be interesting for such a topic (for a review of human electrophysiology in face perception, see Rossion, 2014).

Final considerations

Face perception and recognition have been widely studied in the past decades. The present article is important because we review the basic operations of the human visual system in the processing of facial patterns and how the brain hemispheres differentially contribute to this process. The models of hemispheric specialization of the sensorial system may be a basis for broader cognitive models (or models of cognition) and may help better understand the basis of mental functioning (Christman, 1997). We conclude that functional asymmetries are not restricted to high-level processes.

Notably, however, the brain hemispheres may differ in the modality and efficiency of certain operations, but the differences are restricted to controlled conditions in laboratory studies. In activities in everyday life, the brain hemispheres constantly interact via the corpus callosum as a harmonic behavioral unity (Hellige, 1993; Sergent, 1995).

We report a functional asymmetry in the processing of spatial frequency information in face recognition

Table 1. Studies on the hemispheric specialization of spatial frequency in facial perception tasks.

Reference	Type of study*	Task	Dependent variable	Results
Keegan et al. (1981)	Behavioral	Matching task of faces in high and low spatial frequencies	**	• Partially supported the hypothesis of hemispheric specialization • Performance was better for faces in low spatial frequency in the left visual hemifield
Moscovitch and Radzins (1987)	Behavioral	Backward masking of dot clusters in different spatial frequencies (Experiment 2)	Interstimulus interval	• Did not support the hypothesis of hemispheric specialization
Keenan et al. (1989)	Behavioral	Backward masking of square-wave gratings.	Error percentage	• Supported the hypothesis of hemispheric specialization
Sergent (1985)	Behavioral	Verbal identification and manual categorization (male/female and members of the subject's department) of low-pass-filtered and band-pass-filtered faces	Response time and error percentage	• Supported the hypothesis of hemispheric specialization
Sergent (1987)	Behavioral	Male/female categorization task of band-pass-filtered, low-pass-filtered, and coarsely quantized faces	Response time and error percentage	• Partially supported the hypothesis of hemispheric specialization • Band-pass-filtered faces were better processed when presented in the right visual field in the longer-presentation condition
Whitman & Keegan (1991)	Behavioral	Same-different judgments of pairs of spatial frequency-filtered faces presented in the same hemifield	Response time and error percentage	• Partially supported the hypothesis of hemispheric specialization • Presentation in the right hemifield produced more errors that were greater for faces in low spatial frequency • In the left hemifield, faster response times and lower error rates were observed for faces presented in low spatial frequency
Goffaux et al. (2011)	Neuroimaging (fMRI)	Phase categorization (intact *vs*. scrambled) of high, intermediate, or low spatial frequencies	FFA activation, response time and d'	• Did not support the hypothesis of hemispheric specialization
Perílla-Rodríguez et al. (2013)	Behavioral	Learning phase of unfiltered faces followed by a recognition test of unfiltered and spatially filtered faces	Response time and SDT indexes extracted from receiver operating characteristic curves	• Partially supported the hypothesis of hemispheric specialization • Performance was better when high spatial frequency-filtered faces were presented in the right visual field, whereas low spatial frequency-filtered faces were better recognized than high-pass-filtered faces when presented in the left visual hemifield

* All of the behavioral experiments listed above implemented the divided visual field technique to investigate hemispheric specialization.

** Information not available because we did not have access to the original study.

tasks. Some of the studies reviewed herein, however, did not support the hypothesis of hemispheric specialization (for review, see Grabowska & Nowicka, 1996). Behavioral experiments may be more influenced by methodological procedures than by hemispheric specialization *per se* (Sergent & Bindra, 1981; Sergent, 1985, 1987, 1995). Similarly, many variables are at stake in the lateralization of specific processes, such as stimulus exposure time, eccentricity in the visual field, experiment duration, and hormonal variations (Bourne, 2006; Hausmann, Becker, Gather, & Güntürkün, 2002; Sergent, 1987). The task's demands and experimental design might influence such variables, thus producing conflicting results.

Also worth noting is the interchannel inhibition of spatial frequencies. Given the relative frequency between the components of a complex stimulus, low frequencies may inhibit the high frequencies and *vice versa* (Gilbert & Wiesel, 1990). Thus, when one component of spatial frequency is isolated in a single-component stimulus (e.g., sinusoidal gratings), it may be processed differently than a compound stimulus (e.g., faces; Christman, 1997).

Two studies that used basic stimuli argue that the sensitivity to different bandwidths is retinotopically mapped in the visual cortex and do not support the hemispheric specialization hypothesis. In an ERP study (Boeschoten, Kemner, Kenemans, & Engeland, 2005) and visual evoked potential study (Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000), the processing of spatial frequency occurred medially for local and high spatial frequency information and laterally for global and low spatial frequency information. In a similar study, Sasaki et al. (2001) mapped sensitivity attention areas for local and global characteristics and spatial frequency in the occipital cortex using fMRI. The attention to local features activated the foveal representation in the cortex where the sensitivity was higher for high spatial frequencies. When global attention was required, an increase in low spatial frequency sensitivity occurred in more peripheral areas. Maps of attention and spatial frequency were symmetrical, bilateral, and retinotopically marked. As another conflicting result, the right hemisphere was suggested to be more sensitive than the left hemisphere to process any spatial frequency (Rebaï, Bernard, Lannou, & Jouen, 1998; Rebaï, Bagot, & Viggiano, 1993). In a recent fMRI study that performed a different data analysis, participants performed a categorization of spatially filtered natural scenes, and spatial frequency processing in the occipital cortex was mapped retinotopically and lateralized (Musel et al., 2013).

Two studies do not corroborate the hypothesis proposed by Sergent (1982) in our review of studies that investigated the hemispheric specialization of spatial frequencies in face perception tasks. The first study, Moscovitch and Radzins (1987), reported problems with the intensity and bands of the masks. These issues were addressed in a later study that corroborated the hypothesis of hemispheric specialization (Keenan et al., 1989). The second study, Goffaux et al. (2011), had no direct purpose of investigating hemispheric differences, and only the FFA was mapped. The low temporal resolution of fMRI may not have been sufficiently sensitive to capture asymmetries that occur more intensely under conditions of high temporal constraints (Blanca, Zalabardo, Gari-Criado, & Siles, 1994; Peyrin, Mermillod, Chokron, & Marendaz, 2006). Another explanation is that asymmetry may occur in other cortical areas that were not scanned (Maurer et al., 2007; Renzi, Schiavi, Carbon, Vecchi, Silvanto, & Cattaneo, 2013).

Finally, we did not perform a systematic review. Thus, the article selection and discussion of the studies herein may be biased, albeit unintentionally. Future systematic reviews on face recognition should address issues not discussed in this paper. The facial expressions of emotions, for example, influence both the sensitivity of spatial frequencies (Comfort, Wang, Benton, & Zana, 2013) and hemispheric specialization (Torro-Alves, Fukusima, & Aznar-Casanova, 2008). Additionally, the perception of facial expressions recruits different processing that involves other structures and networks than those used for facial recognition (Vuilleumier, Armony, Driver, & Dolan, 2003). Because of the complexity of this issue and given that it was beyond the scope of this article, facial expressions were not addressed and would require another extensive review. Processing time is also another factor that influences both spatial frequency (Goffaux et al., 2011) and hemispheric specialization (Sergent, 1987). In our literature review, only behavioral studies were found, revealing the need to address the issue of specialization using other clinical, neuroimaging, and electrophysiological techniques. Moreover, the importance of spatial-temporal relations of distributed networks in the cortex was addressed instead of functional asymmetries *per se* that are highly dependent on input factors. We expect that future studies might provide a better understanding of this issue.

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Correction to Moraes Júnior, Sousa, and Fukusima (2014)

In the article "Hemispheric Specialization in Face Recognition: From Spatial Frequencies to Holistic/Analytic Cognitive Processing," by Rui de Moraes Júnior, Bruno Marinho de Sousa, and Sérgio Fukusima (*Psychology & Neuroscience*, 2014, Vol. 7, No. 4, pp. 503–511, http://dx.doi.org/10.3922/j.psns.2014.4.09), the second full paragraph on page 507, after the first sentence, was revised to read as follows:

> In a neuroimaging study, Goffaux et al. (2011) observed the activation of brain areas that are sensitive to facial patterns. The participants performed a behavioral task to categorize the phase of the stimuli (i.e., intact vs. scrambled), in which high, intermediate, or low spatial frequencies were presented for 75, 150 or 300 ms and masked. In both hemispheres, the FFA showed a coarse-to-fine pattern of activation for spatial frequency but in different time intervals. No evidence of hemispheric asymmetry was observed, as proposed by Sergent (1982). However, this work supported the idea that spatial frequency processing is dynamic and time-dependent, and the results showed that only around 300 ms low and high spatial frequencies are equally processed in both the right and left FFA.

All versions of this article have been corrected.

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