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RUI DE MORAES JR.

Laterality and processing time-course of spatial frequencies on face encoding

Ribeirão Preto
2016

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Tese apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Doutor.

Área de concentração: Psicobiologia

Orientador: prof. Dr. Sérgio Sheiji Fukusima

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Rui de Moraes Jr.
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Aos meus pais, Ana e Rui

À minha companheira, Sarah

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RESUMO

de Moraes, R., Jr. (2016). *Lateralidade e curso temporal do processamento de frequências espaciais na codificação de faces*. Tese de Doutorado, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto.

O sinal de entrada na retina é decomposto em termos de frequência espacial (FE), variações periódicas de luminância ao longo do espaço. Existe vasta literatura sobre o processamento de FE no córtex visual primário. No entanto, não se sabe ao certo como esta informação sensorial básica é processada e integrada numa visão de alto nível. Esta tese aborda este tema ao investigar lateralidade cerebral, tempo de processamento e contexto cognitivo em três diferentes seções com objetivos específicos. Estas seções investigaram comportamentalmente visão de alto nível tendo a face humana como estímulo, dado sua relevância biológica e social. Na primeira seção (*Theoretical Review*), uma revisão apresenta estudos clínicos e neuropsicológicos que mostram áreas cerebrais envolvidas na percepção de faces e como os hemisférios esquerdo e direito realizam um processamento holístico e analítico baseado em informações de FEs. A especialização hemisférica de FE no reconhecimento de faces é então revisada e discutida. Concluiu-se que assimetrias sensoriais podem ser a base para assimetrias cognitivas de alta ordem. Ademais, foi destacado a influência do tempo de processamento. Na segunda seção (*Study 1*), foi investigado por método psicofísico a lateralidade de baixas e altas FEs no reconhecimento de faces em diferentes tempos de exposição. Faces com filtragem de FE foram apresentadas em campo visual dividido em alta e baixa restrição temporal em duas tarefas: reconhecimento facial (Experimento 1) e reconhecimento do sexo facial (Experimento 2). No Experimento 1, informações faciais de baixas e altas FEs foram mais eficientemente processadas no hemisfério direito e esquerdo, respectivamente, sem efeito do tempo de exposição das faces. Os resultados do Experimento 2 mostraram uma assimetria do hemisfério direito para baixas FEs em baixa restrição temporal. Conclui-se que o processamento de altas e baixas FEs é lateralizado nos hemisférios cerebrais no reconhecimento de faces. No entanto, a contribuição de altas e baixas FEs é dependente da tarefa e do tempo de exposição. Na terceira seção (*Study 2*) foi investigado qual estratégia temporal, *coarse-to-fine* (de baixas para altas FEs) ou *fine-to-coarse*, cada hemisfério cerebral utiliza para integrar informação de FE de faces humanas numa tarefa de categorização facial homem-mulher. Sequências dinâmicas breves *coarse-to-fine* e *fine-to-coarse* de faces foram apresentadas no campo visual esquerdo, direito e central. Os resultados do tempo de resposta e do *score* de eficiência invertida mostraram uma prevalência geral de um processamento *coarse-to-fine*, independente do campo visual de apresentação. Ainda, os dados da taxa de erro ressaltam o processamento *coarse-to-fine* realizado pelo hemisfério direito. No geral, esta tese fornece *insights* sobre assimetria cerebral funcional, integração de alto nível e curso temporal do processamento de FEs, principalmente para aqueles interessados na percepção de faces. Também foi mostrado que operações lateralizadas, tarefa-dependente e *coarse-to-fine* podem coexistir e interagir no cérebro para processar informação de FE.

Palavras-chave: Percepção de faces. Frequência espacial. Especialização hemisférica. *Coarse-to-fine*.

ABSTRACT

de Moraes, R., Jr. (2016). *Laterality and processing time-course of spatial frequencies on face encoding*. Tese de Doutorado, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto.

Retinal input is decomposed in terms of spatial frequency (SF), i.e., periodic variations of luminance through space. There is extensive literature on the processing of SF in the primary visual cortex. However, it is still unclear how SF information is processed and integrated in high-level vision. This thesis addressed this issue in terms of laterality effects, processing time-course, and the cognitive context in three different sections with specific purposes. These sections behaviorally tackle high-level vision using human faces as stimuli due to their biological and social relevance. In the first section (Theoretical Review) a literature review presented 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 SF information. The SF hemispheric specialization in face recognition is then reviewed and discussed. Our conclusion is that functional sensorial asymmetries may be the basis for high-level cognitive asymmetries. In addition, we highlighted the role of the processing time. In the second section (Study 1), we psychophysically investigated laterality of low and high SF in face recognition at different exposure times. The SF filtered faces were presented in a divided visual field at high and low temporal constraint in two tasks: face recognition (Experiment 1) and face gender recognition (Experiment 2). In Experiment 1, low and high SF facial information were more efficiently processed in the right and in the left hemisphere, respectively, with no effect of exposure time. In Experiment 2, results showed a right hemisphere asymmetry for low SF faces at low temporal constraint. We concluded that the processing of low and high SF is lateralized in the brain hemispheres for face recognition. However, low and high SF contribution is dependent on the task and the exposure time. In the third section (Study 2), we aimed to investigate which temporal strategy, i.e., coarse-to-fine (from low to high SF) or fine-to-course, each brain hemisphere performs to integrate SF information of human faces in a male-female categorization task. Coarse-to-fine and fine-to-course brief dynamic sequences of faces were presented in the left, right and central visual field. Results of the correct response time and the inverse efficiency score showed an overall advantage of coarse-to-fine processing, irrespective of the visual field of presentation. Data of the error rate also highlights the role of the right hemisphere in the coarse-to-fine processing. All in all, this thesis provided some insights on functional brain asymmetry, high-level integration, and processing time-course of SF information, mainly for those interested in face perception. It was also shown that lateralized, diagnostic-oriented, and coarse-to-fine operations may coexist and interact in the human brain to process SF information.

Keywords: Face perception. Spatial frequency. Hemispheric specialization. Coarse-to-fine.

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LIST OF ABBREVIATIONS

ANOVA. analysis of variance

BSF. broadband spatial frequencies

cpd. cycles per degree (of visual angle)

cpf. cycles per face (width)

cpi. cycles per image (width)

CRT. cathode ray tube (computer monitor)

CtF. coarse-to-fine

CVF. central visual field

ER. error rate (%)

ERP. event-related potential

FFA. fusiform face area

fMRI. functional magnetic resonance imaging

HSF. high spatial frequencies

Hz. hertz (cycles per second)

IES. inverse efficiency score

LED. light-emitting diode (computer monitor)

LH. left hemisphere

LSF. low spatial frequencies

LVF. left visual field

ms. millisecond

OFA. occipital face area

RH. right hemisphere

RT. response time

RVF. right visual field

SD. standard deviation (of the mean)

SE. standard error (of the mean)

SF. spatial frequency

TMS. transcranial magnetic stimulation

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1. Introduction

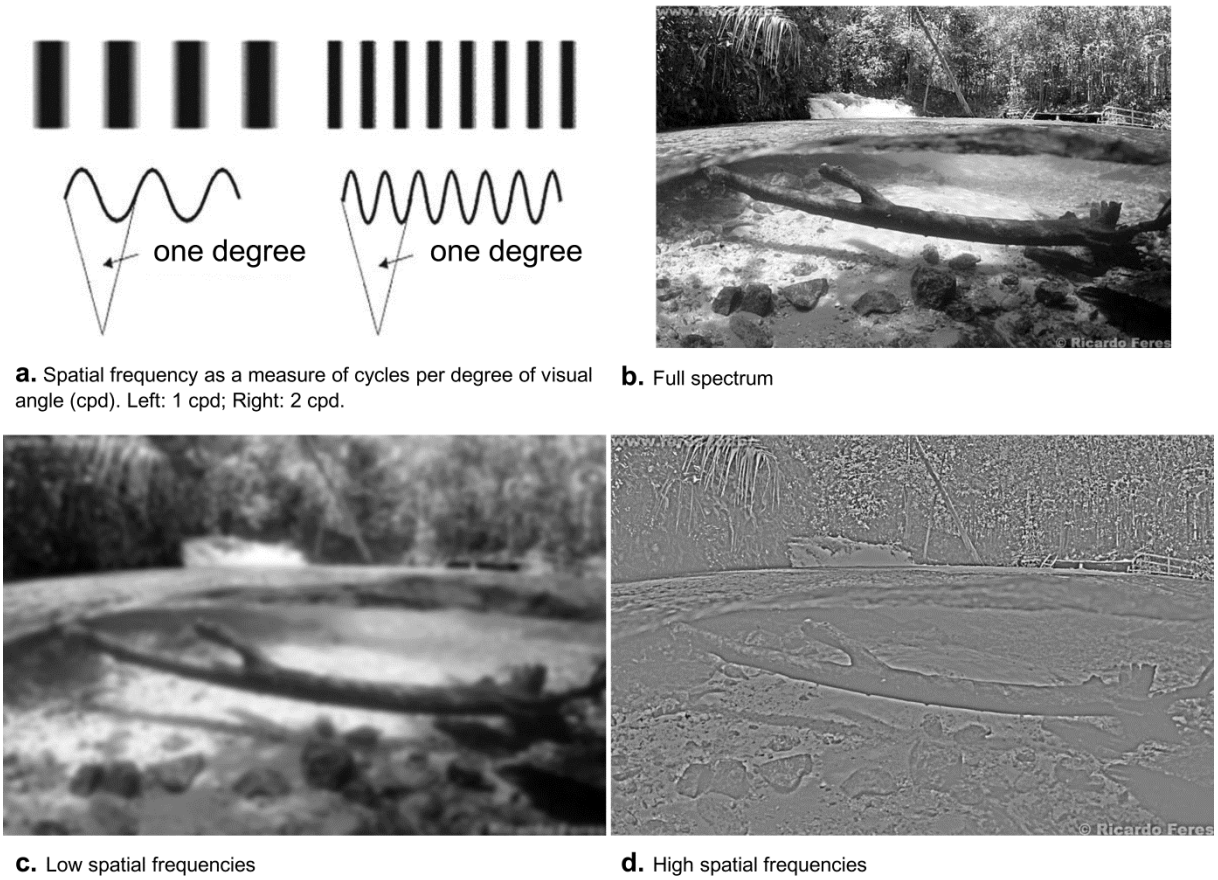
In my biased standpoint as a young experimental psychologist, the visual system is one of the most impressive gadgets forged during the history of human evolution. Consider (in case you have not yet done so): just a small range of the electromagnetic spectrum is coded by the human eye, i.e., visible light. Depending on the light intensity, our eye's colored ring called the iris modulates the pupil size. Light enters through this aperture and reaches the retina. The small image reflected on this two-dimensional plan is upside down and partially occluded by a blind spot. Retinal specialized cells analyze and transform electromagnetic energy waves into discrete on-off electrochemical energy. The signal travels through different neural routes at different speeds and only after sequential complex computations the visual information is integrated in cortical association areas. Almost instantaneously and with no awareness of this process, the output is the perception of an organized world in depth, color, contrast, and movement!

Visual perception seems complex, and it is indeed. For centuries scientists from different fields have been exploring the visual system. One way they try to reveal the complexity of vision is by exploring the fundamentals and basic aspects. It is known that in the first stages of vision the retinal input is decomposed into two main dimensions: orientation and spatial frequency. This thesis followed this path and investigated the latter: spatial frequency processing.

Spatial frequency is defined as periodic variations of luminance through space. It is measured in cycles of alternating light and dark areas in a given unit of distance. A cycle consists of one dark and one light area adjacent in space. In visual perception it is measured in cycles per degree of visual angle. The greater the amount of luminance alternation in a given space, the more detailed the perception is (Figure 1a). Therefore, high spatial frequencies convey information of small details and sharp edges of the visual scene. Conversely, low spatial frequencies convey coarse information of the visual scene (see Figure 1b, 1c and 1d). There is extensive literature specifying the role of specialized cells in the primary visual cortex that respond to different spatial frequency bandwidths (De Valois, Albrecht, & Thorell, 1982; Hubel & Wiesel, 1968; Poggio, 1972). However, it is still unclear how spatial frequency information is processed and integrated in high-level vision.

This thesis addressed high-level vision in one of the most important visual stimuli: the human face. The human face is a ubiquitous visual stimulus for everyone throughout the whole lifespan. It is the most expressive part of the human body, being essential for interpersonal relations and to express biological signals. As a result, we have developed extremely efficient strategies to extract and encode facial information. In addition and more

related to the thesis purpose, previous works suggest that face perception is more sensitive to spatial frequency information than other types of complex stimuli (Collin, Liu, Troje, McMullen, & Chaudhuri, 2004; Goffaux, Gauthier, & Rossion, 2003; Yue, Tjan, & Biederman, 2006).



a. Spatial frequency as a measure of cycles per degree of visual angle (cpd). Left: 1 cpd; Right: 2 cpd.

b. Full spectrum

c. Low spatial frequencies

d. High spatial frequencies

Figure 1.1: The upper left image (a) illustrates the idea of spatial frequency; adapted from: webvision.med.utah.edu. The upper right image (b) shows a complex visual scene that was filtered to preserve low (c) and high spatial frequencies (d); original photo: Ricardo Feres (Jalapão State Park, TO, Brazil).

Influential theoretical frameworks and assumptions on the processing of spatial frequency information based the questions in this thesis to investigate face encoding. Two of them were markedly important: hemispheric specialization of spatial frequencies and coarse-to-fine hypotheses. The first states that the right hemisphere is more efficient in processing low spatial frequencies and the left hemisphere is more efficient in processing high spatial frequencies (Sergent, 1982). The latter assumes that there is a precedence of low over high spatial frequencies in the processing time-course of the visual input (Hegdé, 2008; Schyns & Oliva, 1994). Although both of them are supported by many investigations, it is unclear how they relate.

This central gap guided the course of this thesis and provoked some questions. In the Theoretical Review section, I explored the literature to investigate if there is a relation between lateralized holistic/analitic processing and low/high spatial frequencies on face processing. Could cognitive brain asymmetries be an extension of sensorial lower-level brain asymmetries? And what is the role of the processing time? In Study 1, I wondered if there are hemispheric differences in the perception of low and high spatial frequency facial information at high and low temporal constraint. Could a right-hemisphere asymmetry for low spatial frequencies at high temporal constraint and a left-hemisphere asymmetry for high spatial frequencies at low temporal constraint conciliate the coarse-to-fine and the hemispheric specialization hypotheses? Moreover, could the cognitive context interfere in this process? In Study 2, I wondered if the left hemisphere could reverse the default coarse-to-fine processing. Since the left hemisphere is assumed to be more efficient in processing high spatial frequencies, could spatial frequencies be integrated in a fine-to-coarse fashion?

In spite of a central topic of investigation, the sections of this thesis are independent studies. Each one raised specific questions, literature, method, and highlighted different aspects of the problem. Besides facilitating the publication in scientific journals, this thesis format provides more flexibility than the more traditional formats with restrictive scope. In addition, this format also enables a straight-to-the-point reading for those pursuing specific information. A concluding section summarizes the main findings and contribution of this thesis and shows how the sections are connected and how they were conceived.

2. Theoretical review

Hemispheric specialization in face recognition: From spatial frequencies to holistic/analytic cognitive processing[1]

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.

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2.1 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.

2.2 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 second, 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 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.

2.3 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[2] (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 in 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 in 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; Rossion et al., 2003).

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[2] 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.

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 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).

2.4 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). 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, 1985a, 1987). In Experiment 1, Sergent (1985a) 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, & 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).

Table 2.1. 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 (1985a)	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.

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. 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, 1985a, 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).

2.5 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 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, 1985a, 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. 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, 2006b). 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.

3. Study 1

Task and exposure time modulate laterality of spatial frequency for faces[3]

The current paper psychophysically investigated laterality of low (LSF) and high spatial frequencies (HSF) in face recognition at different exposure times. Spatial frequency filtered faces were presented in a divided visual field at high and low temporal constraint in two tasks: face recognition (Experiment 1) and face gender recognition (Experiment 2). Both experiments showed a general primacy in the recognition of LSF over HSF faces. In Experiment 1, LSF and HSF facial information were more efficiently processed in the right and in the left hemisphere, respectively, and exposure time had no effect. In Experiment 2, results showed a right hemisphere asymmetry for LSF faces at low temporal constraint. We concluded that the spatial frequency processing is lateralized in the brain hemispheres for face recognition. However, LSF and HSF contribution is dependent on the task and exposure time.

[3] Part of this section was presented as poster at the Vision Sciences Society Meeting (Saint Pete Beach, FL, USA) and the abstract was published in the Journal of Vision (September 2015, Vol.15, 682. doi:10.1167/15.12.682).

3.1 Introduction

The human face provides much biological and social information and it is the most expressive part of the body. We are experts, being fast and accurate in recognizing faces because of their social and evolutionary relevance. Therefore, there is an effort to understand the basis of human face perception. Studies have been exploring the role of low-level visual information of faces, especially the spatial frequency (SF) content, i.e., periodic variations of luminance through space. Different SF ranges convey different types of facial information. Low spatial frequencies (LSF) represent large-scale variations of luminance change and convey coarse facial information, such as the metric distance between the eyes. High spatial frequencies (HSF) represent narrow-scale variations of luminance change and convey fine facial information, such as the shape of the mouth.

Some factors influence the extraction of SF in visual perception. Many studies have shown that the processing of SF is time- and hemisphere-dependent. Regarding the processing time-course, the visual system does not extract the spectrum of SF at once. Instead, visual perception is dynamic and progressively integrates different SF ranges. The LSF conveyed by fast magnocellular pathways are extracted in the early stages of visual processing, initiating the visual scene analysis. This low-pass scenario is then detailed by local information of HSF conveyed by slower parvocellular pathways (Bullier, 2001; Hegdé, 2008). Neurological and behavioral evidence of such coarse-to-fine processing has been found in a wide variety of visual stimuli: sinusoidal gratings (Breitmeyer, 1975), hierarchical forms (Navon, 1977), hybrid images (Schyns & Oliva, 1994), natural scenes (Peyrin et al., 2010) and human faces (Goffaux et al., 2011). In addition to the evidence that the processing of SF changes over time, studies show that SF bands are processed differently in the brain hemispheres. Sergent (1982) postulated the hypothesis of SF hemispheric specialization, which states that the right hemisphere (RH) is predominantly involved in LSF processing, while the left hemisphere (LH) would be more sensitive to HSF processing. This hypothesis was also supported by studies using different types of stimuli: sinusoidal gratings (Proverbio, Zani, & Avella, 1997), natural scenes (Peyrin, Chauvin, Chokron, & Marendaz, 2003) and human faces (Keenan, Whitman, & Pepe, 1989). Additionally, the cognitive context also modulates the extraction of SF in visual perception. Even considering conditions of same visual stimulation, the visual system tunes to the input information that carries the most useful cues, associated with a particular SF range, in a given cognitive task (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003; Schyns & Oliva, 1999).

Despite literature support on coarse-to-fine and hemispheric specialization hypotheses, it is unclear how they relate and, to our knowledge, no psychophysical study considered both issues to assay the role of LSF and HSF in face recognition. One way to investigate stimulus processing time, and hence the coarse-to-fine assumption, is by manipulating its exposure duration. The observer's performance when perceiving a stimulus in a given exposure duration is related to the stimulus processing time, especially if backward masked (Enns & Di Lollo, 2000; Keysers & Perrett, 2002). This method has been used in SF sensitivity and face perception research (e.g., Goffaux et al., 2011; Schyns & Oliva, 1994). Regarding hemispheric specialization, a classical technique to behaviorally access laterality effects is the divided visual field method (Bourne, 2006). The anatomical structure of the visual system validates this method, since the RH initially processes a stimulus presented in the left visual field (LVF), and the LH initially processes a stimulus presented in the right visual field (RVF). Many investigations on SF processing and face recognition also implemented this method (e.g., Cattaneo et al., 2014; Peyrin et al., 2006a).

The main purpose of the current paper was to examine hemispheric differences in the perception of LSF and HSF facial information by manipulating the stimulus presentation time. Faces containing LSF, HSF, and broadband spatial frequencies (BSF) were presented in the LH/RVF and RH/LVF at high and low temporal constraint. As a general assumption based on coarse-to-fine and SF hemispheric specialization framework, we expected that at high temporal constraint the coarse LSF information would be more efficiently processed when presented in the RH/LVF, and at low temporal constraint the detailing from HSF would favor recognition in the LH/RVF. Since the cognitive context is another factor that modulates SF extraction from the visual input, we addressed this issue in two tasks: face recognition (Experiment 1) and face gender recognition (Experiment 2). Our results indicated that the task and exposure time can influence the laterality of SF in the visual processing of human faces.

3.2 Experiment 1

In Experiment 1 participants performed a matching task of SF filtered faces presented in a divided visual field at high and low temporal constraints. We investigated if the stimulus presentation time affects SF sensitivity in the brain hemispheres in face recognition.

3.2.1 Method

Participants. Thirty students (15 females) from the University of São Paulo participated in the study (mean age = 25 years, SD = 4.4 years). The selected volunteers were: (a) over 18 years old; (b) with normal or corrected-to-normal visual acuity, as assessed by a Snellen chart, and free from ocular diseases; (c) without neurological disease history; and (d) right-handed evaluated by the Edinburgh Inventory (Oldfield, 1971; mean score = 82.7, SD = 20.3). All participants read and signed the Statement of Consent approved by the local Research Ethics Committee.

Stimuli. Fifty-two frontal images of Caucasian and pardo faces (26 female) with neutral expression of emotion were extracted from the face database of Mendes, Arrais, & Fukusima (2008). Using Photoshop 7.0 (Adobe), striking facial attributes (wrinkles, blemishes, pimples, beard) were attenuated and external features (hair, ears, neck) were removed using an oval surrounding frame. The oval frame surround within the quadrant in which the stimulus was inserted (256 x 256 pixels, the equivalent of 5.8 × 5.8 degrees of visual angle) was filled with uniform medium gray. The faces were observed at 4 × 5.8 degrees of visual angle from the observer on a screen also filled with uniform medium gray on a 19" CRT monitor.

The filtering process was performed using MATLAB 7.9.0 (MathWorks) as implemented by Goffaux et al. (2011). The quadrants were multiplied by Gaussian bandpass filters in the frequency domain. One filter preserved a wide range of the visual spectrum, which generated BSF faces [0-130 cycles per image (cpi), the equivalent of 0 to 22.34 cycles per degree of visual angle (cpd)]. Another filter preserved only LSF (0-10 cpi; 0-1.68 cpd), and the last just HSF (30-130 cpi; 5.06-22.34 cpd). Before and after spatial filtering the luminance of the image set was normalized to global luminance equal to zero and the root mean square SD of the contrast equal to one. The optimal bandwidth for face recognition did not overlap with the bandwidths containing LSF and HSF used in our study, so we could maximize the differences between them (Gao & Maurer, 2011). In addition, the SF bands that were preserved in the filters used in this experiment were based on the configural processing dependent on LSF, as well as the featural processing dependent on HSF for face perception (Goffaux, Hault, Michel, Vuong, & Rossion, 2005). Figure 3.1 (bottom half) shows examples of the stimuli used.

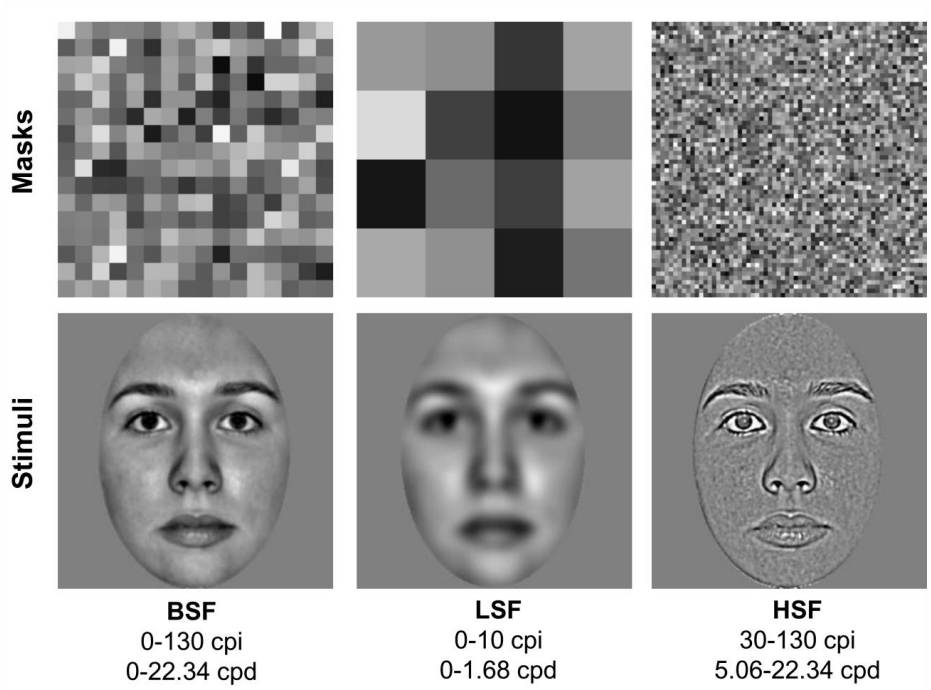

Figure 3.1. Examples of stimuli used in the experiment along with their respective masks and spatial frequency cutoffs in cycles per image (cpi) and cycles per degree of visual angle (cpd). Legend: BSF - broadband spatial frequencies; LSF - low spatial frequencies; HSF - high spatial frequencies.

Procedure and experimental design. The experimental procedure was performed in an individual and single session, in a dark and adapted room, in front of the computer using a chin and forehead rest. Instructions were given by the researcher and the computer screen and emphasized the importance of fixating at the central fixation point during the stimulus presentation.

Each trial began with an initial screen to ensure that the participant was prepared for the trial. The next screen was displayed only after a white key was pressed (variable inter-trial interval in self-paced trials). Then a BSF target face was presented centralized for 1200 ms. It was followed by a fixation point presented in the center of the screen for 500 ms, that in the last 150 ms changed its color and shape to direct the participant's attention to it and to warn that the probe face was about to be presented (warning cue). The probe face was presented lateralized in the RVF or LVF, with the face's inner edge at 2.5 degrees of visual angle from the fixation point, according to the divided visual field technique (Bourne, 2006). Furthermore, it was presented in BSF, HSF or LSF for 6 or 13 frames, approximately 71 and 153 ms, respectively (refresh rate set at 85 Hz). The exposure times were based on a previous study that found a coarse-to-fine pattern for faces (Goffaux et al., 2011). The opposite hemifield was filled by a Gaussian noise mask at the same size and eccentricity as the stimulus and presented during the same time as the probe. This procedure improves fixation

control over trials by avoiding that attention driven to a unilaterally presented stimulus initiates a saccade toward it (Carpenter, 1988). Immediately subsequent, the same Gaussian noise was applied in both hemifields for 200 ms to eliminate any persisting retinal image of the stimulus and to limit processing time (Enns & Di Lollo, 2000; Keysers & Perrett, 2002). To maximize this effect we built a noise mask adjusted for intermediate frequencies for each SF filter by varying the pixel cluster size: LSF mask (64 × 64 pixels, i.e., 4 cpi in a 256 × 256 pixel image), BSF mask (16 × 16 pixels; i.e., 16 cpi) and HSF mask (4 × 4 pixels; i.e., 64 cpi). In every trial the experiment computed a new mask with rearranged clusters (see the top half of Figure 3.1 for examples of the masks). At the mask offset, participants must respond if target and probe faces were from the same person. The answer was given by pressing a "yes" green button or a "no" red button. When the response was given, the initial rest screen was presented again, starting the subsequent trial. Figure 3.2 (top half) illustrates a trial.

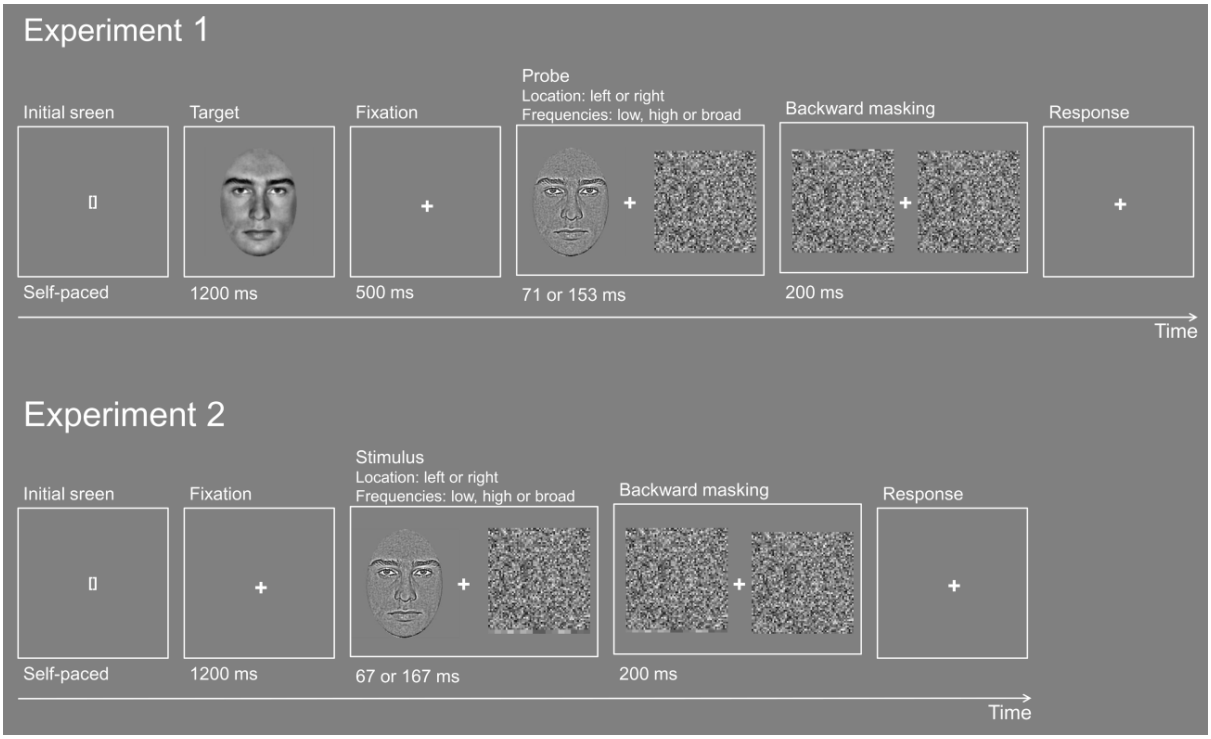

Figure 3.2. Illustration of one trial in Experiment 1 and 2. Each trial began after a key was pressed. In Experiment 1 this triggered the target face presentation. A fixation screen followed the target. Subsequently, the probe face was presented and immediately backward masked. At the mask offset, participants must respond if target and probe faces were from the same person. In Experiment 2 the initial screen was followed by a fixation screen. Then, the experiment displayed the stimulus, which was backward masked. At the mask offset, participants must respond if the face was male. In both experiments the response was given by pressing yes/no buttons. The stimulus in Experiment 2 and the probe face in Experiment 1 were presented: (a) in the right or left visual hemifield; (b) in high, low or broad spatial frequencies; (c) at high or low temporal constraint.

The design "2 Exposure Duration × 2 Visual Field of Presentation × 3 SF Content" had 52 trials per experimental condition, 26 same-face trials and 26 different-face trials. The

same face pairs were presented in each condition. The experiment had 624 trials randomly presented within and among conditions, plus 12 training trials at the beginning of the experiment. Each condition had the same number of male and female face trials for both same-face and different-face trial conditions. The entire experiment lasted approximately 45 minutes. Three predetermined rest intervals were taken during the experiment. Psychtoolbox 3 in MATLAB was used to Gamma-correct, display the images, and to collect data (Kleiner, Brainard, & Pelli, 2007).

3.2.2 Results

Z-scores from hit and false alarm rates of each participant were used to calculate the sensitivity parameter d'. A three-way repeated-measures ANOVA (α = .05) was performed with Exposure Duration (71 and 153 ms), SF Content (BSF, LSF and HSF), and Visual Field of Presentation (LH/RVF and RH/LVF) as within-participant factors. We used the Bonferroni adjustment for multiple comparisons and the Greenhouse-Geisser correction (ε_{GG}) when the sphericity criteria was violated. We conducted the statistical analyses with SPSS PASW 18 (IBM).

Figure 3.3 (top half) shows the mean d' and the standard error of the mean for each experimental condition. The ANOVA revealed a significant main effect of Exposure Duration, F(1,29) = 52.43, p < .001, η_p^2 = .64, reflecting a better recognition of faces presented for 153 ms (d' = 1.52) than when presented for 71 ms (d' = 0.97). There was also a significant main effect of SF Content, F(2,58) = 44.04, p < .001, η_p^2 = .60, showing that BSF faces (d' = 1.63) were better recognized than LSF (d' = 1.24) and HSF faces (d' = 0.87), which in turn had a significant mean difference between them (all pairwise comparisons with p < .001). There was no main effect of the factor Visual Field of Presentation, F(1,29) = 0.34, p = .563, η_p^2 = .01, and no significant effects in the following double interactions: Exposure Duration × Visual Field of Presentation, F(1,29) = 0.17, p = .680, η_p^2 = .01, and Exposure Duration × SF Content, F(2,58) = 2.01, p = .143, η_p^2 = .07. There was also no significant effect of the triple interaction Exposure Duration × SF Content × Visual Field of Presentation, F(2,58) = 0.45, p = .588, η_p^2 = .02, ε_{GG} = .77. However, there was a significant interaction between Visual Field of Presentation and SF Content, F(2,47) = 5.93, p = .008, η_p^2 = .17, ε_{GG} = .81.

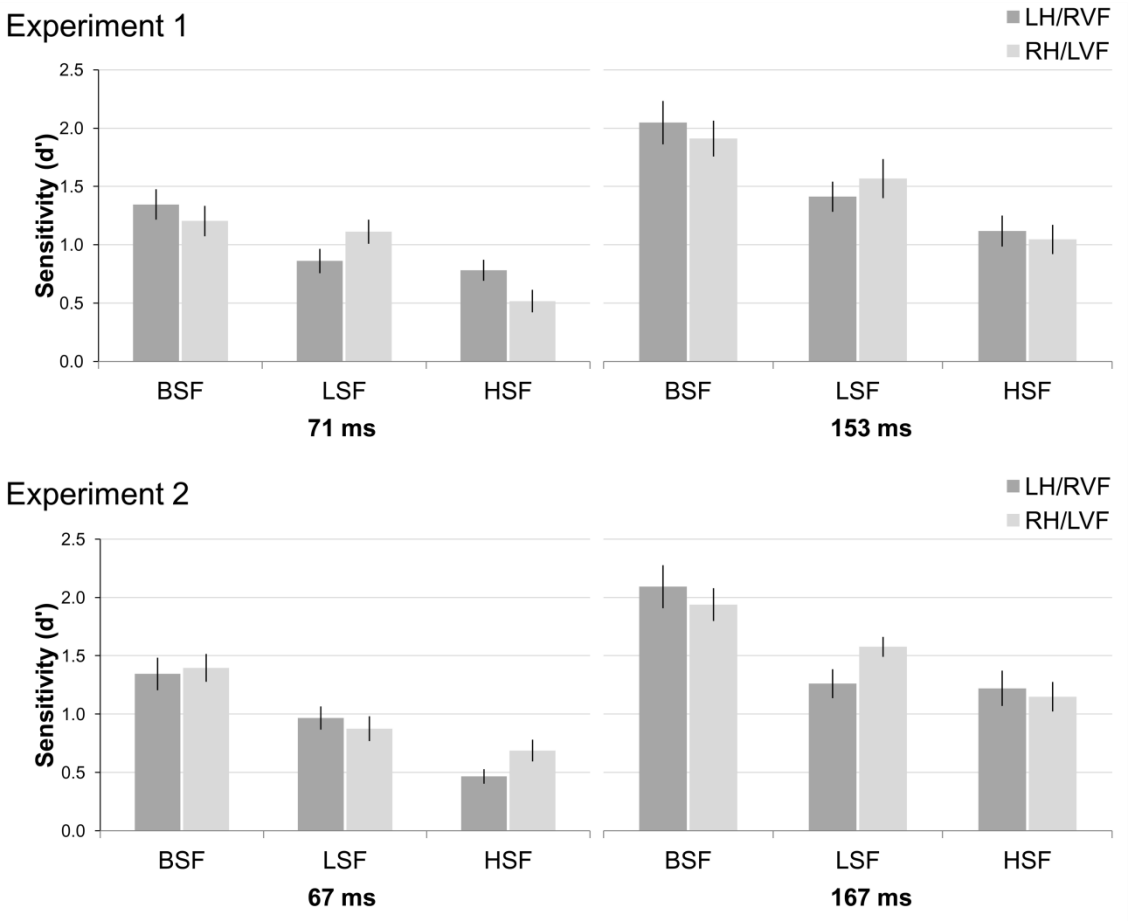

Figure 3.3. Average d' for faces presented in broadband (BSF), high (HSF) and low spatial frequencies (LSF) in the left hemisphere/right visual field (LH/RVF) and in the right hemisphere/left visual field (RH/LVF). The faces were presented at high (left half) and low temporal constraint (right half) in Experiment 1 (top half) and Experiment 2 (bottom half). Error bars indicate the standard error of the mean.

In order to reveal the source of such interaction, we carried out Bonferroni's *post hoc* tests to analyze differences among SF conditions in the LH/RVF and in the RH/LVF when the Exposure Duration factor was not taken into account. In the LH/RVF, observers had a better performance in recognizing BSF faces (d' = 1.70) than LSF (d' = 1.38; $p < .001$) and HSF faces (d' = 0.95; $p < .001$), and LSF and HSF d' means also had a significant difference ($p = .049$). These results regarding the LH/RVF follow the same pattern of those shown in the main effect of the SF Content factor. However, when presentation occurred in the RH/LVF, BSF (d' = 1.56) and LSF faces (d' = 1.34) were recognized with similar efficiency by the visual system ($p = .111$), and more efficiently than HSF faces (d' = 0.78; both comparisons with $p < .001$). We also carried out *post hoc* tests (Bonferroni) to analyze differences between the visual hemifields for each SF condition. No difference was observed between the RH/LVF and the LH/RVF in recognizing BSF faces ($p = .160$). Notably, there was a difference at the limit of significance for LSF faces, favoring the recognition in the RH/LVF when compared

to the LH/RVF (p = .050). The recognition of HSF faces also supports a functional asymmetry of SF: participants were more efficient at recognizing faces in HSF presented in the LH/RVF than in the RH/LVF (p = .035).

3.2.3 Discussion

We aimed to investigate how the brain hemispheres use LSF and HSF information over time at early stages of visual processing in a face recognition task. Thus, we ran a matching task of SF filtered faces in a divided visual field at high and low temporal constraint. The exposure time had no effect on the results of this first experiment, which did not confirm our initial hypothesis where we had stated a LSF-RH asymmetry at high temporal constraint and a HSF-LH asymmetry at low temporal constraint. However, our results support the literature on face perception and functional asymmetry of SF. The analysis of d' suggests that LSF information was more important in recognizing faces when the hemifield of presentation is not considered. In addition, LSF and HSF facial information were more efficiently processed in the RH and in the LH, respectively.

Considering the general advantage of LSF over HSF, studies indicate that LSF are more important than HSF for face perception. In a previous event-related potential (ERP) study, participants were asked to categorize the orientation (upright or inverted) of faces and cars in BSF, LSF and HSF. Results showed that the face-specific N170 marker to LSF faces was larger than to LSF cars, and the inversion delayed its latency for LSF faces, but not for LSF cars. No amplitude difference was observed between HSF faces and cars, nor latency delay in the inverted HSF faces (Goffaux, Gauthier, & Rossion, 2003). More directly related to our task, some evidence supports that LSF are more important to face recognition than HSF. The study of Deruelle and Fagot (2005) performed a matching task in which a target face was followed by two probe faces (Experiment 1). There were two types of trials. In the high-pass or low-pass trials, the SF filtered target face was derived from one of the two unfiltered probe faces. In the hybrid trials, the two probe faces produced the hybrid target face. The analyses of error rates in the high- and low-pass trials and analyses of response choices in the hybrid trials showed that participants relied primarily on LSF. In addition, our results also showed that participants were more efficient in recognizing BSF faces than HSF and LSF faces. The BSF filter we used contains intermediate SF that comprises the optimum range for face recognition, which convey coarse and fine facial information cues (Morrison & Schyns, 2001; Parker & Costen, 1999).

Regarding hemispheric differences, our results showed that the sensitivity to SF bands is hemispheric-dependent. LSF facial information is better processed in the RH and HSF information is better processed in the LH. Previous works using spatial filtered stimuli support the SF hemispheric specialization hypothesis (Coubard et al., 2011; Peyrin, Baciu, Segebarth, & Marendaz, 2004; Peyrin et al., 2003). When it comes to face perception, a previous study performed three tasks: identification, categorization of gender, and categorization of membership of the subject's department (Sergent, 1985b). The faces were broad-pass and low-pass filtered and presented lateralized for 100 ms (Experiment 2). The face identification and member categorization tasks yielded a LH-asymmetry for broad-pass faces, and the three tasks yielded a RH-asymmetry for LSF. The broad-pass filter containing high luminance variation (0-32 cpd) was used to access a HSF preference. However, even considering the technological difficulties to process the stimuli at the time the study was carried out, we must report that the broad-pass filter used comprises both coarse and fine cues for face recognition. The unidirectional RH asymmetry for LSF found in the male-female categorization is in line with our second experiment, and we will discuss this point later. Another behavioral study also supports a differential processing of SF between the brain hemispheres. Perilla-Rodríguez, de Moraes and Fukusima (2013) presented memorized and distractor faces in a divided visual field in LSF, HSF, and unfiltered versions. Signal detection parameters showed that LSF faces were better recognized than HSF faces in the RH/LVF, and that HSF faces were better recognized by the LH/RVF.

Based on our results we can assume that LSF carry more diagnostic cues important for face recognition than HSF. Furthermore, fine gradients of luminance variation of the facial pattern are more efficiently analyzed in the LH, while a coarse resolution analysis is more efficiently performed by the RH.

3.3 Experiment 2

Studies show that that the processing of facial SF information is modulated by the task. In Experiment 2 we investigated if SF asymmetry effects and its timing are affected by the task. The same type of stimuli (i.e., neutral faces) and response modality (i.e., yes-no) of Experiment 1 were used in a face gender recognition task. In addition, we increased the experimental control by monitoring the participant's gaze location using an eye tracker.

3.3.1 Method

Participants. Thirty students (18 females) from the University of Montreal participated in the study (mean age = 26 years, SD = 5.2 years). Laterality was assessed by the Edinburgh Inventory (mean score = 81.3, SD = 22.4). We followed the same ethical and methodological criteria of Experiment 1.

Stimuli and apparatus. Fifty-two frontal images of Caucasian faces (26 female) with neutral expression of emotion extracted from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998) were used in Experiment 2, since this set is more suitable for the Canadian sample. The image treatment and spatial filtering was carried out just as in Experiment 1, as well as the presentation, in which faces were observed at 4 × 5.8 degrees of visual angle from the observer on a 23" LED monitor.

FaceLAB 5 (Seeing Machines) monitored the fixation locations at a sampling rate of 60 Hz with an accuracy error ranging from 0.5 to 1 degree of visual angle. The eye-tracking device comprises two infrared cameras, one infrared light and EyeWorks software (Eye Tracking Inc.). In-house code written in MATLAB registered temporal markers to analyze the gaze location between stimuli onset and offset.

Procedure and experimental design. The experimental procedure was performed in an individual and single session in a dark room, in front of the computer using a chin and forehead rest. The eye tracker was calibrated for each participant using a standard 9-point grid. Instructions were given by the researcher and the computer screen and emphasized the importance of fixating at the central fixation point during the stimulus presentation.

Each trial started with a press on a white key on the initial screen and triggered a 1200 ms presentation of the fixation point, which changed its color and shape in the last 250 ms. Then, a face was presented in the LVF or RVF, with the face’s inner edge at 3 degrees of visual angle from the fixation point. The face was presented in BSF, LSF or HSF during 4 or 10 frames, approximately 67 and 167 ms, respectively (refresh rate set at 60 Hz). The opposite hemifield was filled by a Gaussian noise mask at the same size and exposure duration of the stimulus. We varied the size of the mask's pixel cluster for each SF condition as in Experiment 1. Subsequently, the same Gaussian noise was applied for 200 ms as backward masking in both hemifields. At the mask offset, participants must respond if the face was male. The answer was given by pressing a "yes" green button or a "no" red button.

When the response was given, the initial rest screen was presented again, starting the subsequent trial. Figure 3.2 (bottom half) illustrates a trial. The choice of male faces as "signal" and female faces as "noise" was arbitrary, and we did not counterbalance the female faces as signal across participants to avoid differences in sensitivity and response criteria. We also preferred a yes-no signal detection task rather than a categorization task, the latter being more common in the literature. The use of d' as performance parameter could allow us a better comparison with the results of Experiment 1 and avoid any possible bias resulting from the response modality.

All the stimuli set were presented in each condition. Thus, the design "2 Exposure Duration × 2 Visual Field of Presentation × 3 SF Content" had 52 trials per experimental condition, totaling 624 trials, randomly presented within and among conditions, plus 12 training trials at the beginning of the experiment. The entire experiment lasted approximately 45 minutes and three predetermined rest intervals were taken. Psychtoolbox 3 in MATLAB displayed the images and collected the data.

3.3.2 Results

An offline analysis eliminated trials in which the participants switch the gaze to the left or to the right 1.5 degrees of visual angle away from the central fixation point during stimulus presentation. One participant had more than 30% of the trials invalidated and was excluded from the sample. Altogether, 8.38% of the trials were excluded for inaccurate gaze. Likewise in Experiment 1, we calculated the sensitivity parameter d'. Two cases were excluded because they were outside the boundaries of 3.5 SD units within their experimental condition and because each isolated case was responsible for significant effects. Both cases were replaced by the mean of the condition. Statistical analyses were performed exactly as in Experiment 1.

Figure 3.3 (bottom half) shows the mean d' and the standard error of the mean for each experimental condition. The ANOVA revealed a significant main effect of Exposure Duration, $F(1,28) = 133.81$, $p < .001$, $\eta_p^2 = .83$, which showed that increasing the exposure time from 67 ms (d' = 0.96) to 167 ms (d' = 1.54) resulted in greater d'. There was also a significant main effect of SF Content, $F(2,56) = 53.95$, $p < .001$, $\eta_p^2 = .66$. As in Experiment 1, BSF (d' = 1.69) faces were better recognized than LSF (d' = 1.17) and HSF faces (d' = 0.88), which in turn had a significant mean difference between them (all pairwise comparisons with $p \leq .001$). There was no main effect of the factor Visual Field of

Presentation, F(1,28) = 0.66, p = .425, η_p^2 = .02. All double interactions were also non-significant: Exposure Duration × Visual Field of Presentation, F(1,28) = 0.09, p = .766, η_p^2 < .01; Exposure Duration × SF Content: F(2,56) = 0.58, p = .563, η_p^2 = .02; Visual Field of Presentation × SF Content: F(2,56) = 1.11, p = .338, η_p^2 = .04. However, there was a significant triple interaction: Exposure Duration × Visual Field of Presentation × SF Content, F(2,56) = 5.74, p = .005, η_p^2 = .17.

In order to specify the dynamics of hemispheric differences as function of exposure duration, we divided the ANOVA in the two Exposure Duration conditions. Results showed a significant Visual Field of Presentation × SF Content interaction for the 167 ms condition, F(2,56) = 5.01, p = .010, η_p^2 = .15, but not for the 67 ms condition, F(2,56) = 1.85, p = .167, η_p^2 = .06. Subsequently, we examined differences among SF conditions in the LH/RVF and in the RH/LVF for the 167 ms condition. Pairwise comparisons (Bonferroni corrected) showed that observers were more efficient at recognizing BSF (d' = 2.09) than LSF (d' = 1.26; p < .001) and HSF (d' = 1.22; p < .001) in the LH/RVF. Likewise, they were also more efficient at recognizing BSF (d' = 1.94) than LSF (d' = 1.58; p = .043) and HSF (d' = 1.15; p < .001) in the RH/LVF. On the other hand, LSF faces were more efficiently recognized than HSF faces in the RH/LVF (p = .013), but not in the LH/RVF (p > .999), revealing a RH-LSF asymmetry. We also performed Bonferroni's *post hoc* tests to analyze differences between the visual hemifields for each SF condition. There was no difference between the RH/LVF and the LH/RVF when recognizing BSF (p = .280) and HSF faces (p = .419). However, the recognition of faces in LSF was more efficient in the RH/LVF than when presented in the LH/RVF (p = .021), supporting the RH-LSF asymmetry for faces in the 167 ms condition.

3.3.3 Discussion

In Experiment 2 we aimed to investigate how the brain hemispheres use SF information over time at early stages of visual processing in a male-female facial recognition task. We used similar stimuli and response modality of Experiment 1 to investigate if the task can modulate laterality and temporal processing of SF in face encoding. Our results showed a better general sensitivity for LSF, a RH asymmetry for LSF faces at low temporal constraint, and no HSF preferences. Results suggest that gender facial information is more efficiently driven by LSF in the RH.

Previous experiments support the notion that gender facial information is mostly conveyed by LSF cues. A behavioral study investigated perception of identity, gender and

emotion in adults and children using LSF-HSF hybrid faces. In one session of Experiment 2, the participants were asked to categorize the gender of the face displayed in the center of the screen for 400 ms (for children) or 100 ms (for adults). The number of low-pass choices showed a LSF bias for children and adults (Deruelle & Fagot, 2005). However no bias for SF was found in the task of gender categorization using hybrid faces conducted by Schyns and Oliva (1999). More behavioral evidence comes from a study with SF filtered faces, rather than hybrids. The faces were displayed until response or up to 2000 ms. In the gender categorization task of expressive faces (Experiment 1) and neutral faces (Experiment 3), HSF faces had a greater error rate than LSF faces, although the response latencies to LSF faces were slower than HSF faces (Aguado, Serrano-Pedraza, Rodríguez, & Román, 2010). In an ERP study, participants performed a gender and a familiarity task by responding male/female and familiar/unfamiliar after a training phase. The N170 face-sensitive ERP showed larger amplitude in the gender task compared to the familiarity task for LSF faces only. The gender task showed difference of amplitude between LSF and HSF faces. In addition, the behavioral data showed less accurate and slower responses for HSF than LSF faces in the gender categorization task (Goffaux et al., 2003).

Besides showing a LSF primacy for processing gender information of the face, Experiment 2 also highlights the role of the RH supporting a RH asymmetry for LSF, as was expected when considering the hypothesis of SF hemispheric specialization (Sergent, 1982). Our results are in accordance with a previous work. This study presented lateralized broad-pass and low-pass filtered faces for 100 ms in three tasks: identification, membership (of the subject's department) categorization, and male-female categorization. Unlike identification and membership categorization, which yielded double asymmetry for SF as described in the discussion section of Experiment 1, the gender categorization only showed a RH asymmetry for LSF (Sergent, 1985b). This may reflect an absence of an HSF lateralized process for gender recognition, since HSF do not seem to contain the most diagnostic cues for such a task.

We were expecting to observe this RH-LSF asymmetry in the high temporal constraint condition, since coarse information is conveyed faster than fine information. In the study of Aguado et al. (2010) reported above, responses to LSF faces had longer latencies in the male-female categorization tasks, although LSF faces yielded less errors. The authors proposed an interpretation based on speed-accuracy trade-off. In short, an efficiency in processing LSF faces was not followed by: (a) faster processing reflected by the response time, in Aguado et al. (2010); and (b) better sensitivity in the RH in the experimental condition of high temporal

constraint, in our Experiment 2. Here we propose an alternative interpretation for this issue other than speed accuracy trade-off. New evidence suggests that the initial LSF input rapidly reaches high-order areas which send feedback to low-level areas to modulate visual processing (see Kauffmann, Ramanoël, & Peyrin, 2014). It is possible that task demands may modulate this rapid top-down analysis of LSF and influence the subsequent SF processing. We will return to and explore this hypothesis in the general discussion.

Based on our results, we can propose that HSF are not as critical as LSF to recognize the gender of a face. Futhermore, the RH seems to play a major role in this task. Finally, top-down processes may modulate the asymmetrical sensitivity of LSF in the RH and its occurrence in later stages of visual processing.

3.4 General discussion

Here we investigated how the visual system processes LSF and HSF in the brain hemispheres at high and low temporal constraints in a face recognition matching task (Experiment 1) and in a male-female recognition task (Experiment 2). Results of Experiment 1 showed that LSF and HSF facial information are more efficiently processed in the RH and LH, respectively, for face recognition, with no effect of the exposure time. Results of Experiment 2 showed a clear RH asymmetry for recognizing the gender of the face when presented in LSF in the low temporal constraint condition. Our results show that SF bands are processed differently by the brain hemispheres, and that the task and the presentation time influence SF hemispheric specialization.

Behavioral studies show that not only the visual input properties, but also the task modulates LSF and HSF processing of facial information (for examples of task and stimulus modulating SF processing, see: Awasthi, Sowman, Friedman, & Williams, 2013; Rotshtein, Schofield, Funes, & Humphreys, 2010; Schyns & Oliva, 1999). In this paper we go further, addressing the role of the task in the processing time-course and in asymmetry effects. When comparing Experiments 1 and 2, we observed different patterns of functional asymmetry, and in Experiment 2 the stimulus presentation time influenced the emergence of the asymmetry effect. Considering that both experiments used neutral faces and yes-no responses, we attribute different results as a function of the task the participants performed.

Our results provide evidence that visual perception is flexible even for highly expertise stimuli such as faces, adapting its spatial and temporal processing to demands of the cognitive

context. Cognitive top-down factors may modulate the extraction of SF content in face perception, selecting the most important information for a given high-level process. Therefore, our data argue against the cognitive impenetrability hypothesis, which states that there are no cognitive influences over perceptual processes (Pylyshyn, 1999). Our contribution to this issue is showing that not only SF sensitivity is modulated by the cognitive context, but also functional asymmetries and their timing. However, the direction of the functional asymmetry seems to be unidirectional, i.e., when information selection favors LSF, the processing is carried out mostly by the RH, as occurs to the LH when information selection favors HSF.

Recent studies investigated the neural basis of this top-down modulation of SF extraction from visual input. Besides underlying face perception, LSF may play an important and general role in the beginning of visual analysis guiding SF processing. Evidence from primate neurophysiological recordings (Hupé et al., 2001), EEG (Peyrin et al., 2010), neuroimaging (Bar et al., 2006) and dynamic causal modeling (Kveraga, Boshyan, & Bar, 2007) showed that LSF information conveyed by magnocellular pathways rapidly reaches high-order areas: dorsal cortical stream (Bullier, 2001), orbitofrontal cortex (Bar et al., 2006), and frontal and temporo-parietal areas (Peyrin et al., 2010). These areas perform a coarse initial analysis that triggers top-down processes and then send information back to refine HSF analysis. The feedback projection site is a matter of debate: fusiform gyrus in Bar et al. (2006) and occipital cortex in Peyrin et al. (2010). Top-down parsing may influence SF bandwidths precedence and lateralization, and may overcome default cognitive operations, such as coarse-to-fine processing. This model offers an explanation for our experiments, which had different asymmetry effects and timing, in spite of the same visual stimulation.

Although we still have no answers for many questions regarding neural circuits, connectivity, and temporal dynamics of this rapid top-down LSF-based facilitation, efforts are being made to characterize this process in scene perception (see Kauffmann et al., 2014). An equal effort to characterize this process in face perception would be interesting since the human face: (a) is strongly mediated by top-down processes; (b) is strongly dependent on LSF, mainly in the RH; and (c) has delimited face-sensitive cortical areas, which enables to better define the connectivity among related areas. In addition, configural and featural manipulation of faces activate independent networks in the RH and in the LH, respectively, that include frontal and parietal cortical areas, as shown by functional magnetic ressonance (fMRI) and transcranial magnetic stimulation (TMS) investigations (Maurer et al., 2007;

Renzi et al., 2013). Evidence shows that configural and featural high-level cognitive operations are based on LSF and HSF information (we will discuss this point shortly).

Several studies related facial recognition with SF sensitivity, temporal processing, hemispheric specialization or task influence. Nonetheless, to our knowledge, this is the first study that put together all these variables and hence gives better comprehension of the interactions among them. Furthermore, unlike previous behavioral studies that used classical performance indexes such as accuracy and error rate, we used the d' from Signal Detection Theory as the sensitivity parameter. Signal detection measures are uncontaminated by response bias, and therefore variability in measured sensitivity is reduced since there is no variability due to changes in decision criteria (Pastore & Scheirer, 1974; Stanislaw & Todorov, 1999).

Additionally, the present work may be of value for researchers interested in high-level integration of information. Influential models assume that visual perception starts with SF analysis (Bar, 2003; Bullier, 2001; Hegdé, 2008; Schyns & Oliva, 1994). There is extensive literature on the processing of SF from specialized cells in the retina to the primary visual cortex (De Valois, Albrecht, & Thorell, 1982; Livingstone & Hubel, 1988). However, it is not clear how information is integrated in higher-order cognitive representations (Goffaux et al., 2011). Here we offer some insights of how cognitive representations of the human face, a highly expertise and complex stimulus, use SF information in the brain hemispheres depending on factors such as the task and exposure time.

Furthermore, it is possible that the low-level asymmetry we found may be the basis for the high-level cognitive operations carried out in face processing (see de Moraes, Sousa, & Fukusima, 2014). Behavioral (Bourne, Vladeanu, & Hole, 2009), ERP (Scott & Nelson, 2006), fMRI (Maurer et al., 2007) and TMS (Renzi et al., 2013) data provide evidence for configural and featural processing in the RH and LH, respectively. Some studies argue that configural and featural face processing rely on LSF and HSF information, respectively (Collishaw & Hole, 2000; Valérie Goffaux et al., 2005; Maurer et al., 2007; Scott & Nelson, 2006). However, this assumption is not a consensus and the literature reports contradictory results (Boutet, Collin, & Faubert, 2003; Collin, Rainville, Watier, & Boutet, 2014; Watier, Collin, & Boutet, 2010). Collin et al. (2014) argue that inconsistent results might be due to an interdependence of configural and featural strategies, which possibly rely on the same SF range. They also pointed out that if both processes are distinct, previous studies used approaches that did not directly access the problem.

To summarize, in the two experiments we reported in this paper we investigated how the brain hemispheres process LSF and HSF at high and low temporal constraints in a face recognition task (Experiment 1) and in a face gender recognition task (Experiment 2). We initially established a general hypothesis based on coarse-to-fine and hemispheric specialization assumptions: a RH asymmetry for LSF at high temporal constraint and a LH asymmetry for HSF at low temporal constraint. The results did not confirm this initial hypothesis, but interesting interactions emerged from the data. Both experiments showed a general primacy in the recognition of LSF over HSF faces, which indicate that LSF bands convey more diagnostic cues in the tasks we carried out. In Experiment 1, LSF and HSF facial information were more efficiently processed in the RH and in the LH, respectively, although exposure time had no effect. In Experiment 2, the results showed a RH asymmetry for LSF faces at low temporal constraint. We concluded that the LSF and HSF processing are lateralized in the RH and LH, respectively, for face recognition. However, their contribution is dependent on the task and the exposure time.

4. Study 2

Behavioral evidence for a predominant and non-lateralized coarse-to-fine encoding for faces[4]

Influential models on visual perception assume that there is a precedence of low over high spatial frequencies (SF) in the processing time-course of the visual input, i.e., a coarse-to-fine encoding (CtF). Additionally, hemispheric asymmetries for strategies of SF processing have been shown. A CtF processing would be favored in the right hemisphere, whereas the reverse fine-to-coarse (FtC) processing would be favored in the left hemisphere. In the current paper we aimed to behaviorally investigate which temporal strategy, i.e., CtF or FtC, each brain hemisphere performs to integrate SF information of human faces. To address this issue we conducted a male-female categorization task using the divided visual field paradigm; CtF and FtC brief dynamic sequences of faces were presented in the left, right, and central visual field. Results of the correct response time and the inverse efficiency score showed an overall advantage of CtF processing for face categorization, irrespective of the visual field of presentation. Error rate data also highlights the role of the right hemisphere in CtF processing. Here we provide evidence at the behavioral level for a general and non-lateralized precedence of the default CtF strategy, carried out by the visual system to encode faces, a complex stimulus with ecological value.

[4] The experiment of this section was presented in poster format and awarded with an honorable mention at the "X Reunião Anual do Programa de Pós-Graduação em Psicobiologia e VII Reunião Anual do INeC" (Ribeirão Preto, SP, Brazil) in September 2015.

4.1 Introduction

The human face is a special class of visual stimulus due to its biological and social relevance. Evolutionary and environmental pressures pushed the visual system to develop efficient strategies to encode facial information. Thus, there is a whole field devoted to understand how visual information is processed and integrated during face perception. From a neurobiological point of view, neurophysiological data indicate that cells of the primary visual cortex decompose the visual input mainly in terms of spatial frequencies (SF; i.e., periodic variations of luminance through space) and orientations. More and more complex computations are subsequently performed by higher-level areas along the ventral visual stream, until visual information is integrated to yield high-level face representations in inferior temporal cortices (De Valois, Albrecht, & Thorell, 1982; Hubel & Wiesel, 1968; Poggio, 1972). However, it is not clear how exactly sensorial low-level information such as SF is integrated in high-order cognitive representations during face perception.

Influential and recent models of visual perception assume that the visual system integrates SF information following a predominantly coarse-to-fine (CtF) processing strategy (Bar, 2003, 2007; Bar et al., 2006; Bullier, 2001; Hegdé, 2008; Kauffmann, Ramanoël, & Peyrin, 2014; Marr, 1982; Schyns & Oliva, 1994). According to these models, low SF, which convey coarse information about a visual stimulus, are rapidly processed via fast magnocellular pathways enabling a coarse parsing of the visual input. This initial low-pass analysis is subsequently refined by the extraction of detailed information contained in high SF, conveyed more slowly through parvocellular pathways. Evidence of such CtF processing has been found in studies using a wide variety of visual stimuli: sinusoidal gratings (Breitmeyer, 1975), hierarchical forms (Navon, 1977), hybrid images (Schyns & Oliva, 1994), natural scenes (Kauffmann, Chauvin, Guyader, & Peyrin, 2015; Musel, Chauvin, Guyader, Chokron, & Peyrin, 2012) and human faces (Goffaux et al., 2011; Halit, de Haan, Schyns, & Johnson, 2006; Vlamings, Goffaux, & Kemner, 2009). Therefore, the literature supports the CtF strategy as a general and default integration mode performed by the visual system to process SF information.

However, many studies showed that the strategy of SF processing is flexible and that a CtF processing strategy can be reversed in favor of a fine-to-coarse (FtC) strategy, depending on factors such as task constraints (e.g., Schyns & Oliva, 1994; Oliva & Schyns, 1997; Schyns & Oliva, 1999) and also hemispheric specialization. For example, Peyrin et al. (2005) conducted an fMRI study to investigate how the brain hemispheres integrate SF information

during scene perception. Pairs of scene images were presented in succession for 100 ms and separated by a time gap of 400 ms. The pairs of images were presented either in a CtF (a low-pass scene followed by a high-pass scene) or FtC sequence (a high-pass scene followed by a low-pass scene). For fMRI data analysis, the authors used a direct inter-hemispheric comparison method to address hemispheric asymmetries during CtF and FtC scene processing. This method enables the assessment of whether activity in regions of one hemisphere differ from activity in homologous regions of the opposite hemisphere according to the experimental conditions. Results showed that CtF sequences elicited greater activation within the right than left occipito-temporal cortex whereas FtC sequences elicited greater activation in the left than right occipito-temporal cortex. These results thus suggested a right-hemispheric predominance for CtF processing, and a left-hemispheric predominance for FtC processing.

These results are supported by other studies suggesting a functional brain asymmetry to process SF information. Sergent (1982) first proposed that the right hemisphere is more efficient in processing low SF, whereas the left hemisphere is more efficient in processing high SF. A large empirical framework further supported this hypothesis (e.g., dos Santos, Andrade, & Fernandez-Calvo, 2013; Musel et al., 2013; Reinvang, Magnussen, & Greenlee, 2002). Interestingly, past studies also showed SF asymmetry for face processing (de Moraes, Sousa, & Fukusima, 2014; Perilla-Rodríguez, de Moraes, & Fukusima, 2013; Sergent, 1985b). Overall, previous studies on SF processing and hemispheric functional asymmetries led us to wonder about the temporal integration of SF to encode human faces in the brain hemispheres.

Despite the general assumption that SF processing is time-dependent, most of the past studies on SF processing during face perception used long stimuli exposure duration or did not directly address the CtF hypothesis (Eger, Schyns, & Kleinschmidt, 2004; Gauthier, Curby, Skudlarski, & Epstein, 2005; Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Vuilleumier, Armony, Driver, & Dolan, 2003). Some insights about this issue were provided in a recent fMRI study using a slow event-related design conducted by Goffaux et al. (2011). In this study, participants viewed intact- or scrambled-phase versions of filtered faces containing low, middle or high SF presented for 75, 150 or 300 ms and subsequently masked. They performed an intact-scrambled manual categorization task. Face-preferring areas (bilateral Fusiform Face Area - FFA, superior temporal sulci, anterior inferotemporal cortex and right occipital face area) were identified with an independent functional localizer. Data showed that the bilateral FFA, superior temporal sulci and anterior inferotemporal cortex

robustly responded more strongly to low SF at 75 ms. This response to low SF decayed with face exposure duration, mostly at the 150 ms condition. Conversely, at the 150 ms or 300 ms condition (depending on the face-sensitive site) response to high SF increased. These results therefore suggested that a CtF integration of SF information was favored within face-selective cortex. Importantly for our purpose, the results did not reveal any hemispheric asymmetry in the strategy of SF processing for face encoding within these regions. However, these authors did not directly compare activity in homologous face-selective regions of each hemisphere according to the experimental conditions, as performed in the study of Peyrin et al. (2005). It is therefore not guaranteed that both hemispheres process SF information in a predominantly CtF fashion during face processing.

The present study aimed to examine at the behavioral level the strategy of SF processing favored during face categorization, and explicitly considered potential hemispheric asymmetries in this process. A behavioral experiment is interesting since the relatively low temporal resolution (i.e., sampling rate) of fMRI may impair investigations on the processing time-course of rapid sensorial and cognitive operations (Amaro & Barker, 2006). In addition, neurophysiological data not always represents the behavioral output.

In order to investigate strategies of SF processing during face encoding, we used sequences of filtered faces adapted from previous studies on scene perception (Musel et al., 2012; Kauffmann et al., 2015). These sequences mimic the default CtF or the reverse FtC sequence of SF processing, in order to impose either of these two processing strategies, while participants performed a categorization task. In order to address hemispheric asymmetries, these stimuli were presented in a divided visual field. This classic experimental paradigm enables behavioral investigations on functional brain asymmetry. It consists of brief lateralized presentations of the stimulus. The anatomical structure of the visual system validates the approach, since the right hemisphere initially processes a stimulus projected in the left visual field (LVF), and the left hemisphere initially processes a stimulus projected in the right visual field (RVF) (see Bourne, 2006).

We used the divided visual field method to present SF filtered faces in CtF and FtC brief sequences in the LVF, RVF and central visual field (CVF). The participants performed a male-female categorization task while response latency and accuracy were recorded. Our task aimed to behaviorally tackle high-level vision. The male-female categorization is a real-world-based task with ecological value and it is more complex than the "intact vs. scrambled" task in Goffaux et al. (2011; although it was well-suited for the fMRI design). The displayed

sequences, besides simulating the visual system operation, samples more SF than most studies, which generally use a single filter for each extreme in the SF domain.

Based on previous data suggesting a predominant CtF processing strategy for face perception (Goffaux et al., 2011), we expected that stimuli depicting a CtF sequence would be categorized faster overall than those depicting a FtC sequence in a face categorization task. Furthermore, if the strategy of SF processing for face encoding varies according to the brain hemisphere predominantly involved to perform the task, we would expect better performances to categorize CtF and FtC sequences presented in the LVF and in the RVF, respectively.

4.2 Method

Participants

Thirty-two right-handed students with normal or corrected-to-normal vision were recruited at the University of São Paulo. Two students failed the acuity test as assessed by a Snellen chart (visual acuity below 6/7.5) and another was considered ambidextrous when evaluated by the Edinburgh Inventory (Oldfield, 1971). Thus, 29 subjects (16 females) took part in the study (mean age: 22.9, SD = 4.6; mean score in Edinburg Inventory: 84.7, SD = 18.8). None of them had neurological or ocular disorders. All participants read and signed the Statement of Consent approved by the local Research Ethics Committee.

Stimuli

Forty images of faces (half females) posing in frontal view and with neutral expression were extracted from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998). Striking facial attributes (e.g., wrinkles, blemishes, pimples, beard) were attenuated using Photoshop 7.0 (Adobe). The faces were gray-scale transformed and inserted into a 256 × 256 pixel-size quadrant. Viewed at 85 cm, the images subtended a visual angle of 5.8 × 5.8 degrees and the faces themselves encompassed about 4.0 degrees of visual angle. An egg-shaped mask in uniform medium gray superimposed external features (e.g., hair, ears, neck).

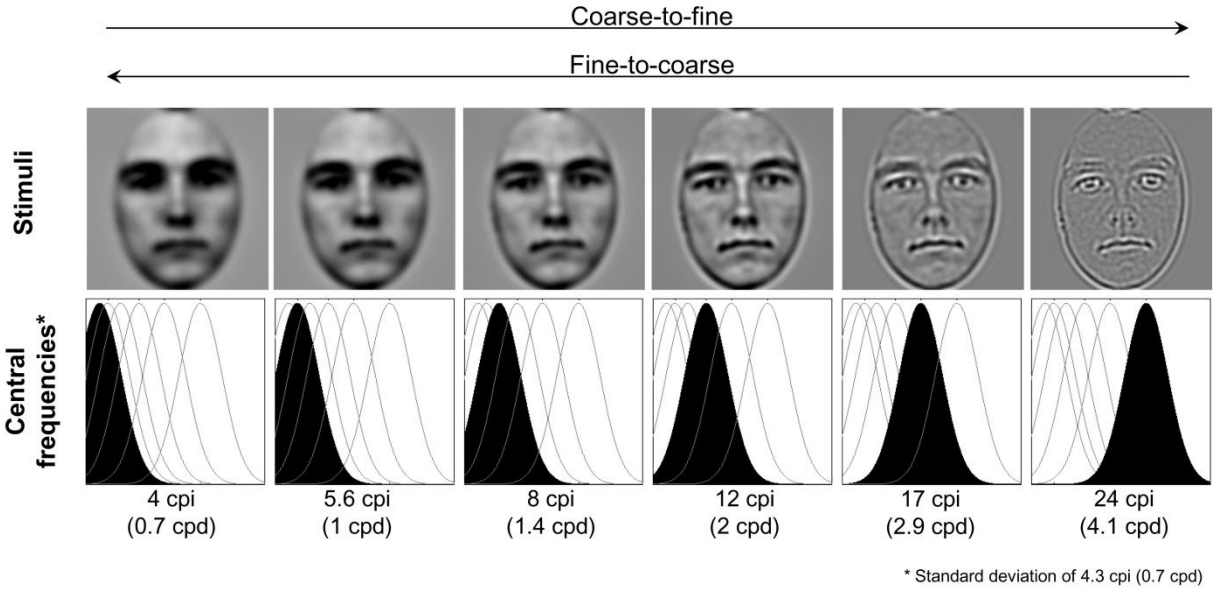

Figure 4.1. Example of the six spatial-frequency filtered versions that originated from a full-bandwidth image along with the information of their central frequency measured in cycles/image width (cpi) and cycles/degree of visual angle (cpd). One stimulus consisted of a brief succession of the filtered faces going from lower (left side) to higher (right side) spatial frequencies in the coarse-to-fine condition, or in the opposite direction going from higher to lower spatial frequencies in the fine-to-coarse condition.

The filtering process was performed using MATLAB 7.9.0 (MathWorks) as implemented by Kauffmann et al. (2015). Each image was filtered by six Gaussian band-pass filters with central frequencies set at 4, 5.6, 8, 12 17 and 24 cycles per image (cpi) and SD of 4.3 cpi, which corresponds to 0.7, 1, 1.4, 2, 2.9 and 4.1 cycles per degree (cpd) and SD of 0.7 cpd. We removed SF information below 1.2 cpi (0.2 cpd) and normalized the luminance (i.e., mean luminance of 128 on a 256 gray-level scale) among the filtered faces (see Kauffmann et al., 2015 for more details on the filtering procedure).

We used the filtered versions of the stimuli to create brief dynamic sequences. The six filtered versions of each face were assembled to create a sequence. They were presented in succession going from lower to higher SF (CtF sequences) or vice-versa (FtC sequences). Thus, only the order of presentation differentiated CtF from FtC sequences. The sequences lasted 141 ms and each one of the six filtered faces was displayed for an average time of 23.5 ms (refresh rate set at 85 Hz) on a 19" CRT monitor. Figure 4.1 shows examples of the stimuli used.

Procedure and experimental design

The experimental procedure was performed in an individual and single session in a dark and adapted room. Instructions were given by the researcher and the computer screen

and emphasized the importance of fixating at the central fixation point during the stimulus presentation.

Each trial began with the presentation of a central fixation point for 500 ms in order to drive the participant's gaze to the screen center. It was immediately followed by a dynamic sequence lasting 141 ms. The sequences could be presented either in the LVF, RVF or central visual field (CVF), in a CtF or FtC succession. When the stimulus was presented lateralized, the face's inner edge was 2.5 degrees of visual angle distant from the fixation point, which was still displayed on the screen. In addition, the opposite hemifield was filled by a mask (1/f noise) at the same size and eccentricity of the stimulus and presented for the same time period. This procedure improves fixation control over trials by avoiding that attention driven to a unilaterally presented stimulus initiates a saccade toward it (Carpenter, 1988). Next, the same mask covered the stimuli area for 35 ms to prevent retinal persistence. At the mask offset, participants had to categorize the face as male or female as fast and as accurately as possible. Figure 4.2 illustrates one trial. The answer was given by pressing a blue or red button with the index or middle finger, depending on the response category (button positions were counterbalanced across participants). An RB-730 response pad (Cedrus) registered the response and its latency during a maximum time gap of 1500 ms. The following trial started just after the response.

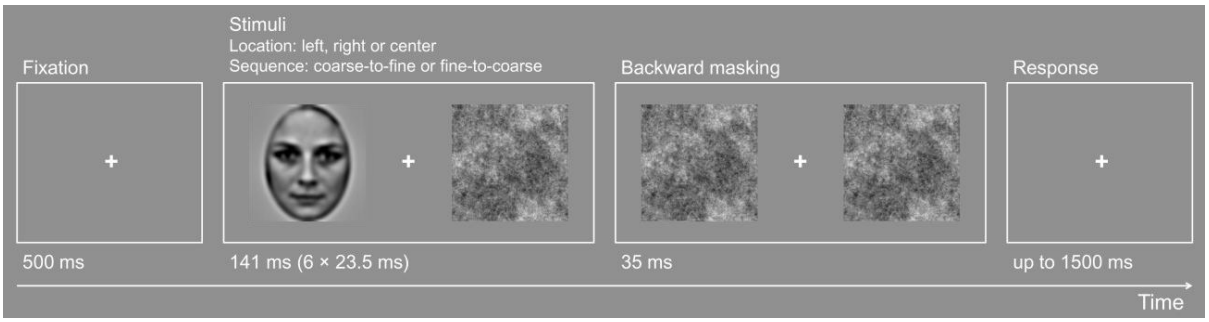

Figure 4.2. Illustration of one trial. A fixation screen was followed by the stimulus, a coarse-to-fine or fine-to-coarse dynamic sequence that was presented in the left, right or central visual field and immediately backward masked. At the mask offset, participants must categorize the face as male or female as fast and as accurately as possible.

All faces from the original stimuli set were presented twice in each condition. Thus, the design "3 Visual Field × 2 Sequence" had 80 trials per experimental condition, totaling 480 trials, randomly presented within and among conditions, plus 36 training trials at the beginning of the experiment. Stimuli used for training were not part of the experiment. The

entire experiment lasted approximately 15 min. E-prime 2.0 (Psychology Software Tools) displayed the stimuli and collected the data.

4.3 Results

We first analyzed the error rate (ER) and the response time (RT) for categorizing the faces. For the RT analysis only correct responses and latencies inside the boundaries of two SD units of the average correct RT in each condition for each participant were considered. This procedure excluded 19.89% trials for judgment errors and omissions and 3.67% for extreme values, totaling 23.56% of the overall trials. A two-way repeated-measures ANOVA ($\alpha = .05$) was performed with Visual Field (LVF, RVF and CVF) and Sequence (CtF and FtC) as within-participant factors for both ER and RT. We used the Bonferroni adjustment for multiple comparisons. Statistical analyses were conducted with SPSS PASW 18 (IBM). Figures 4.3a and 4.3b show the mean ER and the mean RT along standard errors of the mean for each experimental condition.

The ANOVA performed on ER revealed a significant main effect of Visual Field, $F(2,56) = 62.33$, $p < .001$, $\eta_p^2 = .69$. Participants made less errors when the faces were presented in the CVF (mean ± SE: 12.63 ± 1.05%) compared to lateralized presentations (LVF: 23.43 ± 1.60% and RVF: 22.59 ± 1.64%; $p < .001$ in both comparisons). There was no main effect of Sequence, $F(1,28) = 1.01$, $p = .324$, $\eta_p^2 = .04$. However, there was an interaction between Visual Field and Sequence, $F(2,56) = 3.49$, $p = .037$, $\eta_p^2 = .11$. Further comparisons revealed that when stimuli were presented in the LVF, participants were more accurate in categorizing faces in a CtF than FtC sequence (CtF: 22.03 ± 1.77%; FtC; 24.83 ± 1.64%; $p = .027$), whereas no difference was found between CtF and FtC sequences when stimuli were displayed in the RVF (CtF: 22.37 ± 1.66%; FtC: 22.80 ± 1.82%; $p = .711$) or in the CVF (CtF: 13.32 ± 1.09%; FtC: 11.94 ± 1.20%; $p = .154$).

The ANOVA performed on RT also revealed a significant main effect of Visual Field, $F(2,56) = 23.39$, $p < .001$, $\eta_p^2 = .46$. Participants categorized the faces more rapidly when they were presented in the CVF (405 ms ± 15 ms) than in the LVF (439 ± 17 ms) and RVF (439 ± 18 ms; $p < .001$ in both comparisons). There was a marginal main effect of Sequence, $F(1,28) = 3.89$, $p = .058$, $\eta_p^2 = .12$, favoring categorization of CtF (425 ± 16 ms) over FtC (430 ± 17

ms) sequences. The interaction between Visual Field and Sequence was not significant, F(2,56) = 0.01, p = .991, η_p^2 < .01.

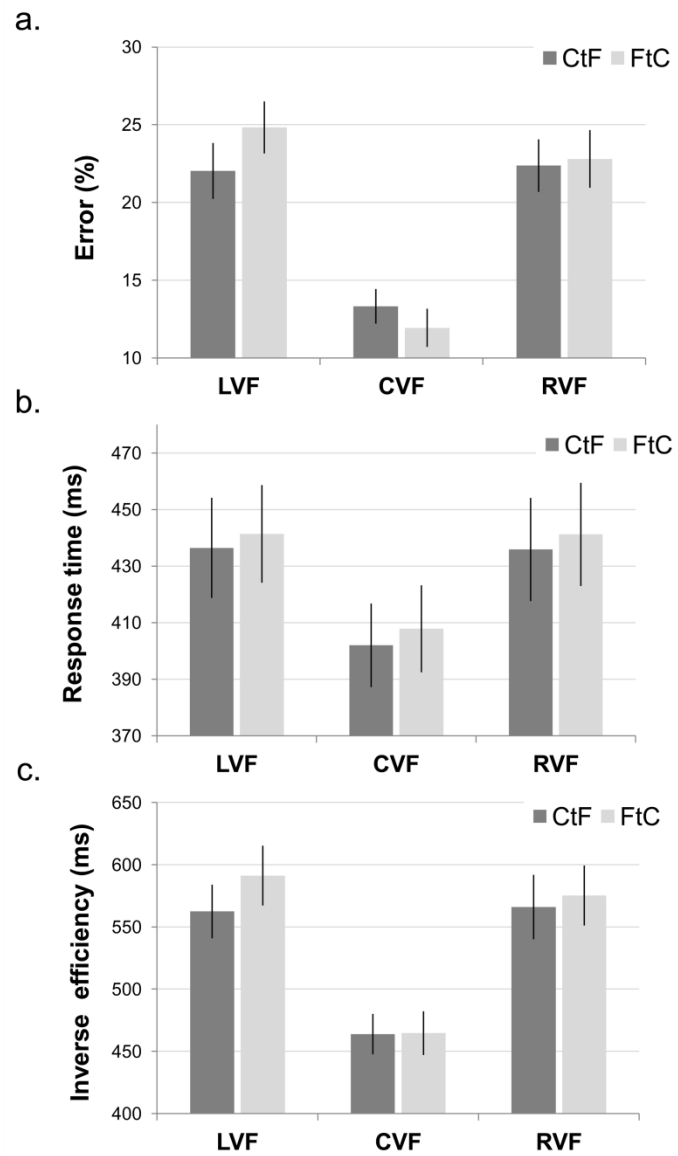

Figure 4.3. Averages of error rate (a), correct response time (b) and inverse efficiency score (c) for dynamic coarse-to-fine (CtF) and fine-to-coarse (FtC) sequences of faces presented in the left (LVF), central (CVF) and right visual field (RVF). Error bars indicate the standard error of the mean.

We also analyzed the inverse efficiency score (IES), proposed by Townsend & Ashby (1978). The IES combines the ER and the RT in a single dependent variable. Besides summarizing behavioral findings, the IES circumvent speed-accuracy trade-offs and individual differences in strategy (e.g., one is concerned with just speed or accuracy). The IES is computed individually per condition as follows: IES = RT / (1 - ER), and is expressed in

ms. Figure 4.3c shows the mean IES and the standard error of the mean for each experimental condition.

The IES received the same statistical treatment as the ER and RT. The ANOVA performed on IES revealed a significant main effect of Visual Field, $F(2,56) = 67.91$, $p < .001$, $\eta_p^2 = .71$. As expected, the efficiency in categorizing faces was greater in the CVF (CVF: 464 ± 16 ms; LVF: 577 ± 22 ms; RVF: 571 ± 24 ms; both comparisons with $p < .001$). The main effect of Sequence reached significance, $F(1,28) = 4.23$, $p = .049$, $\eta_p^2 = .13$, showing that face categorization was more efficient in CtF (531 ± 20 ms) than FtC (544 ± 20 ms) sequences. The interaction between Visual Field and Sequence was not significant, $F(2,56) = 1.98$, $p = .148$, $\eta_p^2 = .07$ (Greenhouse-Geisser corrected, $\varepsilon = .80$).

In short, the analysis of ER showed an interaction: when presentation occurred in the LVF, categorizations of CtF sequences were more accurate than categorization of FtC sequences, whereas there was no difference between categorization of CtF and FtC sequences when presented in the CVF or RVF. Results regarding the RT in the LVF showed the same pattern, but with no significant difference, as it can be seen by the flattened bars in Figure 4.3b. Both IES and RT analysis evidenced no interaction between factors Sequence and Visual Field. However, IES and RT showed a significant effect and a strong trend toward significance, respectively, for the main factor Sequence. Thus, results point toward the same direction: an overall advantage for CtF processing irrespective of the brain hemispheres.

4.4 Discussion

The present behavioral study aimed to provide supplementary arguments in favor of a predominantly CtF processing strategy carried out by the visual system to encode faces. We additionally examined whether this predominant CtF processing strategy could be reversed in favor of a FtC processing strategy depending on the brain hemisphere mainly used to perform the task. For this purpose we implemented the divided visual field method. Our results as measured by RT and IES showed an overall better efficiency in categorizing faces (male vs. female categorization) in a CtF than in a reverse FtC sequence, regardless of the visual field of presentation.

First, this overall CtF advantage suggests that the visual system initially extracts low SF conveyed by fast magnocellular pathways and builds a coarse face representation. This

representation is later on refined by high SF conveyed by slower parvocellular pathways. These data are consistent with a previous fMRI study conducted by Goffaux et al. (2011) wherein most face-sensitive sites produced a CtF activation in the brain hemispheres. Therefore, the above-mentioned study and our data agree that temporal integration of SF for face encoding is primarily unidirectional and stable across the brain hemispheres. Therefore, there is no evidence of an inversion in the temporal processing of SF in the left hemisphere as was found by Peyrin et al. (2005). In that study, FtC sequences of scenes revealed greater activation within the left occipito-temporal cortex; the right side revealed the default CtF preference.

However, RT and IES had modest mean differences between CtF and FtC conditions of the factor Sequence, at 5 ms and 13 ms respectively. Latency differences regarding manual responses in perceptual and cognitive tasks tend to be higher than the obtained values. Furthermore, the RT analysis reached a borderline significance trend, $p = .058$, and the IES p-value is just below the traditional significance threshold of 5%, $p = .049$, when comparing the general difference between CtF and FtC of the main factor Sequence. This is possibly related to the task's high difficulty level, as shown by the ER, and consequent additional computation due to decision-making processes. Nevertheless, four reasons make us confident that the output of the main analysis reflects the nature of the visual system: a default integration of SF in a CtF fashion. First, data collection was well conducted and the use of a response box ensured precision in timing and hence avoided random effects caused by the buffer of conventional keyboards. Second, a reliable *post-hoc* test (Bonferroni) was used, which controls familywise error. Third, a considerable effect size (partial eta-squared) was reported according Cohen's rules of thumb (Cohen, 1988) for the main factor Sequence for both RT and IES analyzes, .12 and .13, respectively. Fourth and lastly, as stated in the introductory section, previous studies suggest a general primacy of the CtF integration order for SF processing. Therefore we could have conducted planned comparisons by preregistering a hypothesis. Since data corroborated the initial hypothesis, a greater statistical significance could be achieved in this one-tailed procedure. However, we opted for the traditional two-tailed post-hoc test approach. All in all, the predominant CtF advantage observed in the present study appears to be a robust effect.

As a secondary result, the ER data showed that when presentation occurred in the LVF, participants were more accurate into categorizing CtF sequences. It suggests that the right hemisphere predominantly performs this strategy. This CtF advantage might be related to the holistic processing performed by the right hemisphere to encode faces (Jacques &

Rossion, 2015; Maurer et al., 2007; Renzi et al., 2013; Rossion et al., 2000). Holistic processing emerges very early during face processing (Ramon & Rossion, 2012; Richler, Mack, Gauthier, & Palmeri, 2009) and relies on low SF (Collishaw & Hole, 2000; Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux & Rossion, 2006; Goffaux, 2009, however, see Collin, Rainville, Watier, & Boutet, 2014). Therefore, taking together the results of RT, IES and ER, we can assume that both brain hemispheres preferentially integrate SF information in a CtF order, and that this process may be more pronounced in the right hemisphere.

Outside the scope of face perception, the present study supports influential and general CtF models on visual perception (e.g., Bar, 2003; Bullier, 2001; Marr, 1982). Here we provide a behavioral contribution to the field issuing laterality effects. In addition, we used a complex stimulus, the human face. Besides its biological and social relevance, the human face advantageously seems to be more sensitive to SF than other visual stimuli. Selective extraction of SF facial information impairs the execution of specific tasks more markedly than for most visual stimuli. For example, low SF are essential for configural representation, facial identity relies on intermediate SF, and perception of local elements is based on high SF (Collin, Liu, Troje, McMullen, & Chaudhuri, 2004; Goffaux, Gauthier, & Rossion, 2003; Yue, Tjan, & Biederman, 2006).

However, our assumptions are restricted to a single task: a male-female categorization. An alternative to the fixed and unidirectional CtF model, the diagnostic approach, states that differences in the task or in the stimulus drive the selection of specific SF ranges by the visual system. The diagnostic approach assumes a flexible usage of different spatial scales even in early stages of visual processing, since they carry different diagnostic cues (Morrison & Schyns, 2001; Schyns & Oliva, 1997, 1999). Previous studies have shown that a male-female categorization relies more on low than high SF (Deruelle & Fagot, 2005; Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003). In fact, many face-encoding tasks show this preference, since low SF has a general primacy over high SF in face encoding (Goffaux, Gauthier, et al., 2003; Goffaux & Rossion, 2006). Nonetheless, the literature reports face categorization tasks wherein a bias of high or middle SF was found (Gao & Maurer, 2011; Schyns & Oliva, 1999; Vuilleumier et al., 2003). Therefore, it would be of great value testing the visual stimulation we implemented here, brief dynamic sequences in CtF and FtC order, in categorization tasks other than the male-female we used. Likewise, this visual stimulation design could be used to investigate high-order face-processing paradigms, e.g., composite face effect and face inversion effect. Probably the CtF and the diagnostic approaches might coexist and

simultaneously operate in the visual system. It is unclear how they relate though. We expect that future studies bring a better understanding on this issue.

To summarize, here we aimed to behaviorally investigate which temporal strategy, i.e., CtF or FtC, each brain hemisphere performs to integrate SF information of human faces. To address this issue we conducted a male-female categorization task in a divided visual field. The CtF and FtC brief sequences of faces were presented in the LVF, RVF and CVF. The ER results showed that categorizations in the LVF were more accurate in CtF sequences. It suggests that the right hemisphere integrates information more efficiently in a CtF strategy. However, the right-hemisphere asymmetry in accuracy was not followed by a right-hemisphere asymmetry in response speed. In order to control speed-accuracy trade-off we analyzed the IES. The RT and IES results point toward the same direction: a small but significant primacy (borderline trend toward significance, in the case of RT) of CtF over FtC processing regardless of the visual field of presentation. In short, our results of the RT and IES suggest that there is an overall precedence of a CtF temporal integration of SF information for human faces regardless of the brain hemisphere. In addition, results of the ER also suggest a better efficiency of CtF processing in the right hemisphere.

The current work provides new evidence on the precedence of low over high SF in the processing time-course of human faces in both brain hemispheres. Our study gives behavioral support to a previous neuroimaging investigation. We used an interesting experimental design that simulates the default CtF processing and its FtC alternate mode in a divided visual field. It seems that face encoding is more stable across brain hemispheres and does not switch the order of SF integration, unlike other-stimuli processing does, such as in landscapes of natural scenes that might perform FtC processing in the left hemisphere. Beyond face perception, influential models assume that the CtF strategy is the default mode of the visual system. Therefore, the current study adds evidence at the behavioral level using a complex stimuli with ecological value. Future studies should be aware of the effects of the task's difficulty level when measuring RT. Furthermore, it would be of great value testing this experimental design using different face-processing tasks (e.g., recognition, identification, categorization of facial expression) and paradigms (e.g., composite face effect, face inversion effect).

5. Concluding remarks

This concluding section summarizes the main findings and contribution of this thesis. This section also shows how the chapters are connected and how they were conceived. Finally, we pointed out unsolved questions in the field.

In the first section, where the main theoretical framework of this work's research topic was presented, we discussed studies that corroborate a functional brain asymmetry to process spatial frequency information of human faces. A rich and recent literature on laterality of high-level face encoding was described, and then linked to lower-level asymmetry of spatial frequencies. Furthermore, we presented limitations of previous studies and highlighted the influence of the stimulus processing time.

This factor, the processing time, in addition to the task influence, led us to design Study 1. This study investigated laterality of low and high spatial frequencies in face recognition at different exposure times and in two different tasks. Besides the assumption of spatial frequency hemispheric specialization, we based our hypotheses and data interpretation in the light of the coarse-to-fine and the diagnostic approach frameworks. The first states a temporal precedence of low over high spatial frequencies processing. The second assumes a flexible usage of different spatial scales depending on the task. The d' data showed that the processing of low and high spatial frequencies are respectively lateralized in the right and left hemisphere for face recognition. However, their contribution is dependent on the task and the processing time-course. Study 1 provided insights on the mutual influence of spatial frequency sensitivity, temporal processing, hemispheric specialization, and task influence on face encoding.

The experimental design of Study 1 was sensitive to assay laterality effects. However, since speed processing varies in the population, fixed exposure constraints may impair observation of the processing time-course in perceptual and cognitive operations. We were also interested to verify if the left hemisphere could invert the default coarse-to-fine encoding for faces. Thus, we implemented a visual stimulation that simulated and imposed coarse-to-fine and fine-to-coarse processing in a face categorization task. The response time and the inverse efficiency score showed an overall coarse-to-fine advantage, irrespective of the brain hemisphere. Data support the notion that face encoding is more stable across brain hemispheres and does not switch the order of spatial frequency integration, unlike scene encoding might do in the left hemisphere.

After summarizing the studies, some words must be said specifically regarding the theoretical background that based our hypotheses. The experimental studies carried out for this doctoral thesis agree with the large amount of literature that supports an overall primacy

of low over high spatial frequencies for face processing. The low spatial frequencies may play an important role in configural face encoding. Study 1 supported two main assumptions regarding visual cognition. On the one hand, results supported the diagnostic approach proposed by Philippe Schyns and Aude Oliva, since spatial frequency sensitivity was modulated by the task. On the other hand, results supported the hypothesis of hemispheric specialization proposed by Justine Sergent: when information selection favored low spatial frequencies, the processing was carried out mostly by the right hemisphere, as occurred to the left hemisphere when information selection favored high spatial frequencies. Although we considered the coarse-to-fine framework, a coarse-to-fine pattern was not observed in Study 1. But when we ran Study 2 implementing a different design and collecting a different response variable, the results showed an overall and non-lateralized coarse-to-fine advantage for face categorization.

Taking into account our data and the theoretical frameworks we have just mentioned, i.e., hemispheric specialization of spatial frequencies, the diagnostic approach, and the coarse-to-fine temporal integration, at least two points must be raised. First and well known to experimental psychologists, factors such as study design, visual stimulation, experimental paradigm, and other methodological variables may be critical to the behavioral output. Second and more important for future research, many sensorial and cognitive operations work in parallel very efficiently without posing cognitive load. Therefore, lateralized, diagnostic-oriented, and coarse-to-fine operations may coexist in the human brain to process spatial frequency information for human faces, and for other types of visual stimuli as well. The work of Musel et al. (2013), that investigated categorization of spatial frequency filtered scenes, illustrates this possibility. Although the idea of retinotopic[5] and lateralized spatial frequency processing seems conflicting, they were observed in the same fMRI dataset by performing different analyses. Revealing how different operations of information processing work in parallel is a big challenge to understand the machinery of the human brain. Many questions still remain unsolved. How these different operations interact? In what conditions one type of operation overlaps another type? Are there specific brain networks or sensitive cortical sites for different operations?

This thesis provides a humble contribution to fields of visual cognition interested in functional brain asymmetry, high-level integration, and processing time-course of spatial frequency information, mainly for those interested in face perception. As can be seen, there is

[5] Cortical cellular organization that follows the retina mapping, which is respectively more sensitive to high and low spatial frequency bandwidths in medial and lateral areas.

still a long highway of research to go follow. What we have offered here is just an invitation to hit the road!

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[6] APA style, American Psychological Association.

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Supplement

Ethics committee approval letter - Universidade de São Paulo

FFCLRP

Universidade de São Paulo
Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto
Comitê de Ética em Pesquisa

Campus de Ribeirão Preto

Of.CEtP/FFCLRP-USP/016-jsl

Ribeirão Preto, 06 de março de 2013

Prezado Pesquisador,

Comunicamos a V. Sa. que o projeto de pesquisa intitulado **"ESPECIALIZAÇÃO HEMISFÉRICA E PROCESSAMENTO COARSE-TO-FINE DE FREQUÊNCIAS ESPACIAIS DE ESTÍMULOS VISUAIS COMPLEXOS EM HOMENS E MULHERES"** foi analisado pelo Comitê de Ética em Pesquisa da FFCLRP-USP, em sua 117ª Reunião Ordinária, realizada em 28.02.2013, e enquadrado na categoria: **APROVADO** (CAAE - 05168213.1.0000.5407).

Solicitamos que eventuais modificações ou emendas ao projeto de pesquisa sejam apresentadas ao CEP, de forma sucinta, identificando a parte do projeto a ser modificada e suas justificativas, e que, ao término do estudo, um relatório final seja entregue, via Plataforma Brasil.

Atenciosamente,

Prof.ª Dr.ª ANDRÉIA SCHMIDT
Coordenadora

Ao Senhor
Rui de Moraes Júnior
Programa de Pós-Graduação em Psicobiologia da FFCLRP USP

C/C:
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Ethics committee approval letter - Université de Montréal

Université de Montréal

N° de certificat
14-080-CERES-D

Comité d'éthique de la recherche en santé

CERTIFICAT D'APPROBATION ÉTHIQUE

Le Comité d'éthique de la recherche en santé (CERES), selon les procédures en vigueur, en vertu des documents qui lui ont été fournis, a examiné le projet de recherche suivant et conclu qu'il respecte les règles d'éthique énoncées dans la Politique sur la recherche avec des êtres humains *de l'Université de Montréal.*

Projet	
Titre du projet	**Processus latéral et temporal de visages filtrés à différentes fréquences spatiales**
Étudiant requérant	**Rui de Moraes Júnior** (20009890), Candidat à la M. Sc., étudiant visiteur de recherche, École d'optométrie
Sous la direction de	Jocelyn Faubert, professeur titulaire, École d'optométrie, Université de Montréal

Financement	
Organisme	CRSNG
Programme	Discovery grants
Titre de l'octroi si différent	
Numéro d'octroi	RGPIN-2014-04474
Chercheur principal	Jocelyn Faubert
No de compte	

MODALITÉS D'APPLICATION

Tout changement anticipé au protocole de recherche doit être communiqué au CERES qui en évaluera l'impact au chapitre de l'éthique.

Toute interruption prématurée du projet ou tout incident grave doit être immédiatement signalé au CERES

Selon les règles universitaires en vigueur, un suivi annuel est minimalement exigé pour maintenir la validité de la présente approbation éthique, et ce, jusqu'à la fin du projet. Le questionnaire de suivi est disponible sur la page web du CERES.

Dominique Langelier, présidente
Comité d'éthique de la recherche en santé
Université de Montréal

21 juillet 2014
Date de délivrance

1er août 2015
Date de fin de validité

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Funding during PhD

March/2012 - July/2012. Scholarship: Cotas do Programa de Pós-Graduação. Agency: Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq. Process number: 140667/2012-1.

August/2012 - February/2016. Scholarship: Programa Regular de Bolsas no País. Agency: Fundação de Amparo à Pesquisa do Estado de São Paulo, FAPESP. Process number 2012/00945-2.

April/2014 - March/2015. Scholarship: Bolsa de Estágio de Pesquisa no Exterior, BEPE. Agency: Fundação de Amparo à Pesquisa do Estado de São Paulo, FAPESP. Process number 2013/24558-0.

Publications during PhD

Perilla-Rodríguez, L. M., **de Moraes, R., Jr.**, & Fukusima, S. S. (2013). Lateral visual hemifield asymmetry and sex differences in recognizing low and high spatial frequency filtered faces. *Psychology and Neuroscience*, *6*(3), 253–250. PDF

de Moraes, R., Jr., Barbosa, B. F., Garcia, F. P., Silva, F. H. M., Ribeiro, J., Amaral, M. V., & Fukusima, S. S. (2014). Reconhecimento de expressões faciais e cenas de valência emocional apresentadas em alta restrição temporal. *Estudos de Psicologia (Natal)*, *19*(2), 110–1180. PDF

de Moraes, R., Jr., Sousa, B. M., & Fukusima, S. S. (2014). Hemispheric specialization in face recognition: From spatial frequencies to holistic/analytic cognitive processing. *Psychology and Neuroscience*, 7(4), 503-511. PDF