

Investigating face-specificity through congenital prosopagnosia: studies on perceptual phenomena and eye movement patterns

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Declaration

I confirm that the work presented in this thesis is my own.

Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

Congenital prosopagnosia consists of the failure to develop normal face recognition ability despite intact low-level perceptual and intellectual functioning, and in the context of normal exposure to faces throughout the individual's life. Typically, these individuals are able to perceive facial stimuli as faces but fail to identify a face as familiar or unfamiliar and to identify it. Despite the large amount of studies that have investigated face recognition in individuals with typical development and in congenital prosopagnosics over the last twenty years, we are still far from a complete understanding of the mechanisms underlying typical and atypical face recognition, and some research questions are still open.

For this reason, the present dissertation investigates some perceptual effects in individuals with a selective deficit in face recognition processing in order to reach a better understanding of what happens during a successful and unsuccessful face recognition process. In particular, by using a combination of behavioural and eye-tracking methods, I investigated whether the *left perceptual bias* and the *self-face advantage* are shown by individuals with congenital prosopagnosia and are truly face-specific or not.

My results demonstrate that, whereas the *left perceptual bias* seems to characterize the recognition of unfamiliar faces in good recognizers, individuals with congenital prosopagnosia seem to show an opposite bias (i.e., a *right perceptual bias*) during the recognition of the self-face. Moreover, despite their face recognition impairment, congenital prosopagnosics consistently show high accuracy in recognizing their own face (i.e., a *self-face advantage*). Furthermore, some of the studies I conducted on the visual scanning strategies of this population demonstrated that the *self-face advantage* phenomenon is not associated with a different exploration of the face stimuli, suggesting that it could reflect a more general *self-advantage* and not be face-specific. Finally, the evidence presented in this dissertation also highlights that individuals with face impairment from birth show some difficulties in recognizing stimuli with high degree of similarity (such as objects belonging to the same class), and that these difficulties are associated with a different pattern of visual exploration.

Overall, the evidence illustrated in the present thesis helps to shed light on the mechanisms characterizing face recognition and to expand our knowledge on the impairment affecting individuals with congenital prosopagnosia.

1. Introduction

Faces carry a lot of information that goes beyond the simple recovery of the physical characteristics and personal biographical information of others, allowing us to identify other important information for communication and survival, such as understanding and interpreting mood and intentions of others. Its relevance has been proposed as the reason for the specificity of a face as a visual stimulus (e.g., Farah, Wilson, Drain, & Tanaka, 1998).

Even though it is usually achieved effortlessly and instantaneously, face recognition is a complex and demanding task. Several authors have tried to account for this complexity by developing cognitive and neuro-anatomical models of face recognition; most of these models involve different series of cognitive operations including perception, visual memory, emotional processing and semantic knowledge. Indeed, before the identification of the person takes place, face recognition requires a series of multistage processes starting with the discrimination of subtle variations in facial features and in their spatial relationship. Face recognition and identification is possible regardless of the viewpoint and the lighting and even when the face presents dynamic changes because of expressions, leading to the matching of the stimulus with its specific facial representation in memory, among all the representations we keep in memory of all the people we have met during our life (Barton & Corrow, 2016). As further evidence of the specificity of face processing, the ability to recognize faces can be selectively disrupted, leading to a specific face recognition impairment known as prosopagnosia, which can be congenital or acquired, depending on its onset from birth or as consequence of brain lesion.

Therefore, because of the high impact of this ability on our daily lives, understanding the perceptual mechanisms underlying face perception and recognition in normal and pathological conditions represents nowadays one of the most exciting challenges of cognitive neuroscience. In this chapter, I will first provide an overview of the most recent and relevant models on face recognition; I will also introduce some perceptual effects that characterize face recognition in healthy individuals, in order to highlight their role as further proof of the specificity of face processing. Finally, I will present and describe the congenital form of prosopagnosia, by characterizing this deficit and highlighting some research questions still unsolved on this impairment.

1.1 Face recognition in healthy individuals

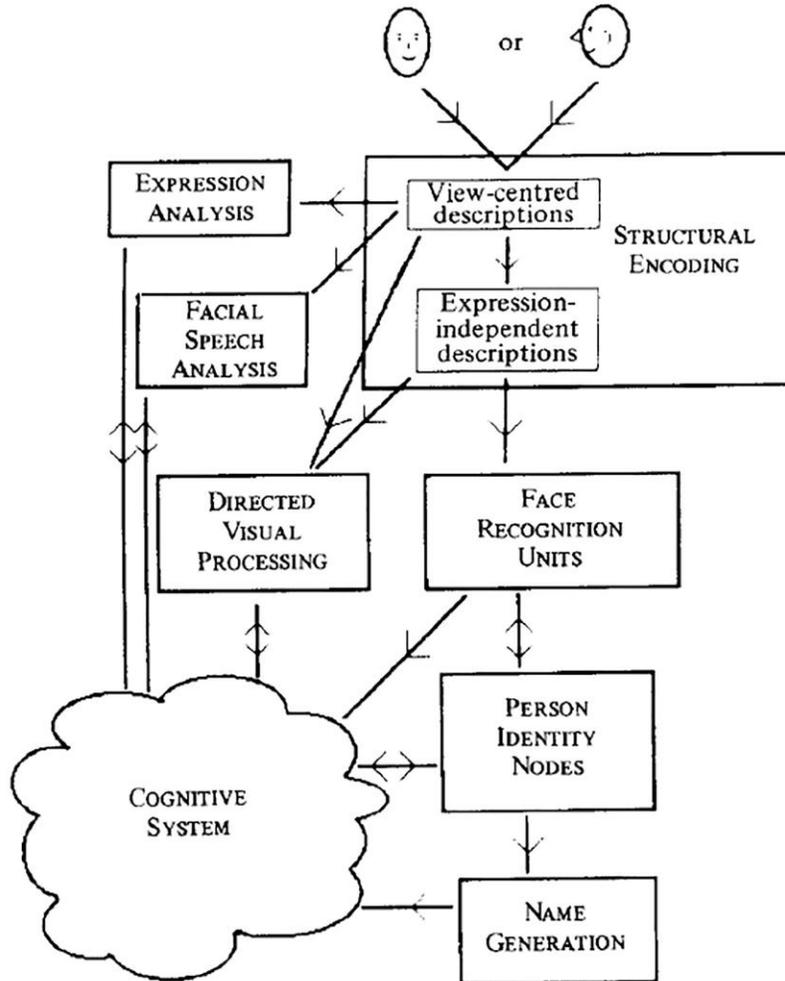
1.1.1 Models of face recognition

Among all the cognitive models of face recognition, probably the most influential is the one proposed by Bruce & Young (1986). By relying on the traditional “box-and-arrow” cognitive modeling, the authors describe face recognition as a series of multiple processing stages and parallel routes of information, which allows us to extract several kinds of information from faces. Particularly, two specific aspects characterize this model: (1) face identity is processed through a separate route in respect to other type of facial information (such as expressions, gaze, age, etc.) and, (2) face identity information are processed through a series of stages (see Figure 1a).

According to this model, when we see a face the first step consists of creating a facial percept through its *structural encoding*, which represents the extraction of both view-centered and abstract (or view-independent) representations of the facial information. According to the authors, whereas view-centered representations provide information for the analysis of facial speech and expressions, the more abstract view-independent descriptions provide information for the next step, in which the formed facial percept is matched with stored face memories called *face recognition units* (Bruce & Young, 1986). Each face recognition unit contains stored structural codes of the faces known to the individual, and the degree of resemblance during the matching between the coded percept and the stored perceptual representation will determine the level of activation of the face recognition unit’s signal and, thus, whether the seen face will be classified as familiar or not. However, it has to be noted that, according to the model, the level of activation of the recognition unit can also be raised by backward input from the next stage. Once the matching has been correctly operated, the information obtained from the face recognition unit can then activate a *person identity node*, which contains all the semantic and episodic information about that specific person. Finally, *names* are accessed only via the person identity node. Specifically, the main distinction between face recognition unit and person identity node is that, whereas face recognition units are modality specific (i.e., they respond only when the appropriate face is seen, but not in case the same individual’s voice or name is presented), person identity nodes are multi-modal and can be accessed also via voice and name (Bruce & Young, 1986).

Finally, the *cognitive system* includes all the other associative and episodic information that fall outside the scope of the person identity nodes, and one of its further functions consists of directing attention to other components of the system.

Figure 1a. Cognitive stages of face recognition in Bruce & Young (1986) model.



Interestingly, the existence of different stages in the face recognition process, as included in the first formulation of this model, has been confirmed by different studies showing that the inability to recognize familiar faces exists in multiple functional forms that correspond to different impairments at the various stages of the Bruce and Young's model (Adolphs, Tranel, Damasio, & Damasio, 1994; Barton, 2008; Damasio, Tranel, & Damasio, 1990; De Renzi, Faglioni, Grossi, & Nichelli, 1991). For example, it has been demonstrated that face recognition units can be selectively impaired, resulting in a deficit to identify a face as familiar but with intact structural encoding of the same face, leading to the associative variant of prosopagnosia (Damasio et al., 1990; De Renzi et al., 1991). On the other hand, the inability to encode the facial percept and, thus, to discriminate the subtle differences between faces, which would happen at the stage of the structural encoding, would lead to the apperceptive form of the impairment (De

Renzi et al., 1991). Similarly, the parallel routes involved in facial expression can be selectively damaged as well, resulting in an impaired recognition of emotion in facial expression despite preserved ability to recognize the identity of the face (Adolphs et al., 1994).

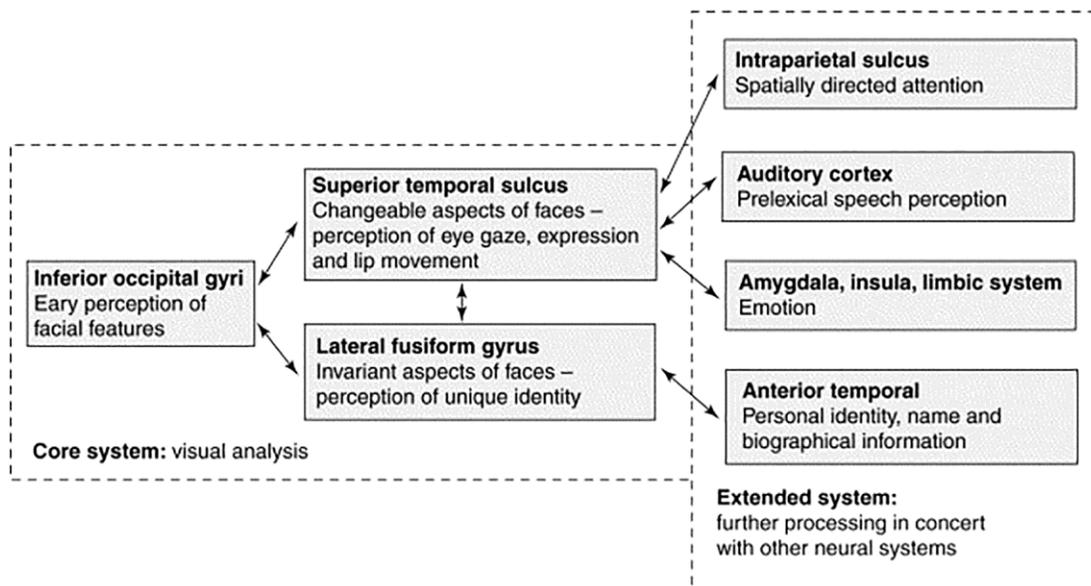
The relevance that Bruce and Young's model (1986) has acquired during the years is reflected by the fact that, after its first formulation, different authors have attempted to partially modify it while keeping its essential structure. In particular, in order to incorporate different and newly studied aspects of face recognition (such as covert face recognition or the information related to the dynamic aspects of the face), or to create more extensive multi-modal models of person recognition, different variations of the original model have tried to incorporate parallel sources of information from different cues, as voice and names.

Particularly, among the later modification of the model, Ellis and Lewis (2001) tried to account for the existence of a covert recognition route, which represents the specific case of recognition without awareness. Indeed, in the context of face recognition, covert recognition usually refers to the specific situation in which some individuals show behavioral, electrophysiological or autonomic indices of recognition in the absence of overt, conscious recognition (e.g., Rivolta, Palermo, & Schmalzl, 2013). Trying to account for this finding, Ellis & Lewis (2001) proposed a modified version of the original model by Bruce & Young (1986) in which the output from the face recognition unit has access to a module for *affective response to familiar stimuli* other than the person identity node. Particularly, the activation of this affective response module would be responsible for different covert recognition effects already demonstrated in the literature, such as increased skin conductance response following familiar faces (e.g., Tranel, Damasio, & Damasio, 1995), specific ERPs components (e.g., Eimer, Gosling, & Duchaine, 2012), and behavioral effects (e.g., Avidan & Behrmann, 2008; Rivolta, Palermo, Schmalzl, & Coltheart, 2012).

Another famous elaboration of the model is the one made by authors who incorporated parallel route for voice and name recognition, in order to create more extensive models of person recognition. Among these authors, Ellis, Jones, and Mosdell (1997) and Belin, Fecteau, and Bedard (2004) incorporated a parallel route for person identification from voice in the original model. In particular, similarly to what happens in the face recognition route, the voice recognition route would flow by stages, including voice structural encoding and voice recognition unit, and it would end in the multi-modal person identity node. Specifically, Belin et al. (2004) also included parallel processing for voice, such as voice expression and voice speech, similarly to the face parallel processing of expression and facial speech. Finally, a further important elaboration of Bruce and Young's model (1986) in the domain of models of person

recognition is the one proposed by Gainotti (2014), who also incorporated hemispheric lateralization of different modalities. In particular, according to the author, whereas the routes for face and voice recognition would be lateralized to the right hemisphere, the stream for name recognition would be lateralized to the left. Moreover, this model claims also that the feeling of familiarity with the face would be generated at the level of the modality-specific recognition units and before the level of the person identity nodes (PINs), and that cross-communication would be possible between the different perceptual channels (Gainotti, 2014).

Figure 1b. The distributed neural system for face recognition of Haxby, Hoffmann & Gobbini (2000) model.



Thus, as evident by this brief excursus of the literature, the Bruce & Young’s model (1986) continues to be useful and to influence new researchers belonging to different fields. In particular, one of its most famous neuro-anatomical adaptation is the one proposed by Haxby, Hoffman, and Gobbini (2000) (see Figure 1b). Using the fMRI technique, Haxby and collaborators (2000) proposed a distributed neural system model for face recognition with a hierarchical structure within which a *core system* for the visuo-perceptual analysis of a face is distinguished from an *extended system* that is involved in the extraction of other information gleaned from the face (such as semantics, speech, emotions). Specifically, according to the authors, the core system includes three bilateral regions with the inferior occipital gyrus,

providing input to the lateral fusiform gyrus and superior temporal sulcus. In particular, within the core system the authors emphasize a further distinction between the representation of invariant and changeable aspects of faces. Whereas the processing of the invariant aspects (i.e., eyes, nose, mouth, etc.) would be responsible for the recognition of the identity of a face, the processing of the changeable aspects would be involved in the perception of information that facilitates social interaction and communication (e.g., facial expression, eye-gaze direction, etc.). The functional distinction of these two aspects of a face would be also reflected by the anatomical dissociation within the core system; indeed, whereas the invariant aspects would be processed by the lateral fusiform gyrus, the changeable ones would be processed by the superior temporal sulcus (Haxby et al., 2000). Finally, the extended system would consist of additional brain regions that are usually involved in other cognitive functions, such as processing speech, directing spatial attention and analyzing facial expressions. According to the model, these brain regions become part of the face recognition system when they work together with the core system in order to extract additional information from a face, other than the identity.

Overall, independently of their specific elaborations, all the most relevant models of face recognition agree in seeing this process as multistage, and in identifying two main steps before the identification of the person: (1) the first one consisting of the visuo-perceptual analysis of a face, which results in a view-independent representation of the face, followed by (2) the matching of that representation to stored facial memories of people already encountered. However, even though this topic has received lot of interest in the past years and different theorizations can now explain what typically happens during the successful recognition of a face, we are still away from a comprehensive understanding of the impaired mechanisms underlying the case of an unsuccessful face recognition process, such as the one affecting individuals with congenital prosopagnosia. Furthermore, despite different perceptual effects during face recognition have been described in the literature, among which the left perceptual bias and self-face advantage, still we do not know so much about how their presence affects and influences the entire recognition process.

1.1.2. Perceptual biases in face recognition

The main models of face recognition (Bruce & Young, 1986; Gainotti, 2014; Haxby et al., 2000) describe all the steps necessary to recognize a face (or a person), from the first stage of its perceptual encoding, along the match with its representation in memory among all the faces we

have met during the lifetime, to the processing of other aspects of a face, such as facial speech or expression. However, face perception and face recognition are not always so straightforward, and the way we perceive and remember familiar and unfamiliar faces can be affected by the existence of some perceptual effects. Among these, one of the most interesting is the *left perceptual bias* (LPB).

The left and right parts of a face are not only less symmetrical than we think, but are also assigned different weights in face processing. Wolff (1933) was the first to confirm this observation experimentally, showing that one side of a face, usually the right side which falls in the observer's left visual field (hence the name "left perceptual bias") would resemble our idea of a specific person more than the other side. More recently, this effect has been detected in terms of improved accuracy in performance and in response times, and is still observed using Wolff's experimental procedure. This method is based on the use of chimeric images composed of two different half-faces. Frontal-view face photographs and their mirror images are divided along the vertical midline and then matched in order to obtain a composite made up of two left half-faces and another of two right half-faces.

Initial conjectures regarding the cause of this bias included hypotheses that expressiveness and disposition were more prevalent on the right side of the face. Subsequently another hypothesis was introduced based on the observation that after right brain lesions the ability to recognize a face is often impaired and that the right part of a face would be more relevant in these cases because it falls in the observer's left visual field (Gilbert & Bakan, 1973): when the observer looks straight at a face, the right side of the face lies in the left visual field, which directly projects to the right hemisphere. Assuming that this hemisphere mediates face recognition, input coming from the left visual field would be analyzed immediately by the appropriate hemisphere, while input coming from the right visual field would be slower and more sensitive to interferences, having to pass through the corpus callosum and the left hemisphere

Since Wolff's experiments, congruent findings with the right hemisphere dominance explanation of the left bias have been obtained by using different facial aspects, such as gender (e.g., Butler et al., 2005; Butler & Harvey, 2008; Ellis et al., 1997; Schyns, Bonnar, & Gosselin, 2002), facial expression (e.g., Schiff & Truchon, 1993), emotion (e.g., Bourne, 2008; Bourne & Maxwell, 2010; Coolican, Eskes, McMullen, & Lecky, 2008), age and attractiveness (e.g., Burt & Perrett, 1997). Moreover, this effect seems so robust to be detected also by using inverted faces in the context of a gender decision task, and it has been used as proof that inversion does not destroy the right hemisphere superiority for faces (Butler & Harvey, 2005; but see also Coolican

et al., 2008 for reduction of left perceptual bias in young adults and absence in older adults after face inversion during an emotion judgment task).

With regard to eye-movement patterns, a relationship between left perceptual bias and eye fixation pattern was reported by Butler et al. (2005), who demonstrated that on trials where participants showed a left perceptual bias they produced significantly more left saccades and fixated for longer on the left side of the chimeric face. Similarly, Guo, Smith, Powell, and Nicholls (2012) observed a consistent left gaze bias in face viewing irrespective of task demands, suggesting that the left gaze bias is an automatic reflection of hemispheric lateralization in face processing, and it is not necessarily correlated with the perceptual processing of a specific type of facial information.

In addition to behavioral results, neurological evidence seem also to support the attribution of the bias to the right hemisphere specialization in face processing, in that individuals with acquired prosopagnosia, normally involving damage to the right brain (Barton, 2008; Barton, Press, Keenan, & O'Connor, 2002; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994), and right brain patients do not show a left visual field bias in matching chimeric faces, while controls and patients with left-hemisphere lesions do (Kolb, Milner, & Taylor, 1983). The bias has also been found to be reduced in older adults and its reduction interpreted as consequence of the reduced right hemispheric function, or increased bilateral function (Butler & Harvey, 2005; Failla, Sheppard, & Bradshaw, 2003). Finally, supporting the hypothesis that the left perceptual bias is due to a right hemisphere dominance for face recognition, a recent functional magnetic resonance imaging study (Yovel, Tambini, & Brandman, 2008) has shown that the magnitude of the left bias was correlated with the asymmetrical activation of the face-selective area in the fusiform face area (FFA) across subjects (i.e., individuals with a stronger bias for the left than right half-face, during a matching task, had a larger face-selective activation over the right than the left fusiform gyrus).

Taken together, the evidence on the existence of this left bias seem to suggest that the structural encoding of a face might not be carried out symmetrically and, consequently, that the cognitive system could play a fundamental role in directing one's attention to particular parts of a face; indeed, the information coming from the left visual field seem to have more weight compared to the information coming from the right visual field, influencing not only the processing of the identity of the face, but also the processing of additional information that can be extracted from it (i.e., gender, age, emotions, etc.) and, thus, affecting the whole face recognition process.

Although the right hemisphere dominance explanation of the bias has been reported across different studies, another possible explanation that has been also considered takes into account the influence of cultural-based scanning habits, and specifically reading habits (Vaid & Singh, 1989); for this reason, different experimental studies have involved right to left script readers. Despite some first inconsistent results (Eviatar, 1997; Gilbert & Bakan, 1973; Vaid & Singh, 1989; Vaid, Singh, Sakhuja, & Gupta, 2002), partial support for the hypothesis that reading habits can determine our bias to process faces starting from the left side comes from a study by Heath, Rouhana, and Ghanem (2005) in which left-to-right readers showed the greatest leftward bias compared to right-to-left readers or bilateral readers. However, a more recent study by Megreya and Havard (2011) showed that also native readers of right-to-left exhibit a left perceptual bias, even if weaker compared to left-to-right readers. Thus, a reasonable explanation could be that although the left perceptual bias could be due to a right hemisphere advantage, scanning habits could control its consistency (Megreya & Havard, 2011). If so, the bias could be a structural effect, but susceptible to manipulation by environmental factors (such as reading habits).

Ultimately, as last hypothesis it has also been proposed that the left perceptual bias could be independent of scanning habits and right hemisphere dominance for face processing and, instead, be attributed to the involvement of right parietal mechanisms in control of spatial attention during visual processing, which could cause a bias to scan the left side of all visual stimuli (Burt & Perrett, 1997). Consistent with this hypothesis, a right hemisphere advantage in perceptual judgments has been found also for chimeric non-face patterns (Luh, Redl, & Levy, 1994), and a reduced left perceptual bias seems to persist even with tachistoscopic presentations, where eye movements are impossible, suggesting a central attentional mechanisms (Phillips & David, 1997).

To sum up the status of the research to date, the different experimental studies investigating the mechanisms underlying face recognition have yielded results that confirm the existence of a common trend to base judgments on facial stimuli on the hemi-face that, from the observer's perspective, falls in the left visual field, during face free viewing (e.g., Luh et al., 1994) and tachistoscopical viewing (e.g., Levy, Trevarthen, & Sperry, 1972), and during different tasks (e.g., Butler et al., 2005; Coolican et al., 2008; Guo et al., 2012). However, despite the relevance of this tendency during face recognition processing, all the results on the possible origin of the bias seem to point to different directions and it is still a matter of debate whether this perceptual bias is intrinsically linked to the face perception and recognition process (i.e., whether it is face-

specific or not), or whether it arises from reasons independent of face processing (such as scanning habits).

1.1.3. The specificity of self-face recognition

All the models that have been proposed in order to define the mechanisms underlying face recognition (Bruce & Young, 1986; Gainotti, 2014; Haxby et al., 2000) are thought to explain how both familiar and unfamiliar faces are recognized. Particularly, according to the influential model of Bruce and Young (1986), while familiar face recognition identification would depend on all the stages included in the model (i.e., structural encoding, face recognition units, person identity nodes, and name generation), the ability to match unfamiliar faces could be accomplished by relying only on the structural encoding process.

However, among all the familiar faces that an individual have met during life there is one stimulus that might be particularly different from the others, which is the self-face. Indeed, self-perception is unique and different from the perception of others. Human self-recognition seems to appear early in life, with infants between 3 and 5 months of age already showing the ability to implicitly discriminate their own body parts from someone's parts (e.g., Bahrick & Watson, 1985) and, in particular, by the age of 3 months the ability to discriminate their face from the face of a peer (Bahrick & Moss, 1996). Explicit mirror self-recognition, instead, seem to occur later, between 14 and 18 months of age (Amsterdam, 1972; Bertenthal & Fischer, 1978; Parker, Mitchell, & Boccia, 1994). Furthermore, evidence from recent studies on adults suggests that we are able to recognize our body and body parts more easily than the bodies of others in terms of accuracy (Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2008; Frassinetti et al., 2009), and that the right hemisphere could play a crucial role in this process, through a fronto-parietal network (Frassinetti et al., 2010; Frassinetti et al., 2008). All these results seem consistent with evidence suggesting that we have specific knowledge about the self, and that the processing of the self-information is distinct from the processing of other-information (Frassinetti, Ferri, Maini, Benassi, & Gallese, 2011; Kircher et al., 2000).

In particular, among all our body parts, the existence of a specific advantage for the self-face (i.e., the *self-face advantage*, SFA) has already been proven, and it consists of faster reaction times when participants have to recognize their own face compared to unfamiliar or familiar faces (Ma & Han, 2010; Sugiura et al., 2005). Different studies have already tried to investigate what would make the self-face so special, but the evidence collected so far is mixed. Indeed, whereas some studies found that the self-face advantage might be part of a right-dominated neural network devoted to the processing of self-information (Devue et al., 2007; Platek,

Keenan, Gallup, & Mohamed, 2004; Platek et al., 2006; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005), other studies have provided evidence for a specific representation of one's own face. The nature and the hemispheric lateralization (or absence of lateralization) of the self-face advantage is not so clear, showing in some cases left dominance (e.g., Brady, Campbell, & Flaherty, 2004; Turk et al., 2002), in other cases right dominance (e.g., Breen, Caine, & Coltheart, 2001; Keenan, Freund, Hamilton, Ganis, & Pascual-Leone, 2000; Keenan, Wheeler, Platek, Lardi, & Lassonde, 2003; Keenan, Wheeler, Gallup, & Pascual-Leone, 2000; Platek et al., 2004), and even no hemispheric dominance (Uddin, Rayman, & Zaidel, 2005).

However, at the same time, some authors (Brady et al., 2004; Brady, Campbell, & Flaherty, 2005; Devue & Bredart, 2011; Keyes & Brady, 2010) suggested the involvement of both hemispheres, as correlates of visual self-recognition, hypothesizing a complex bilateral network for self-recognition composed of the frontal, parietal and occipital areas (Devue & Bredart, 2011). In particular, it has been suggested that the bilateral representation of the self-face could result in a more robust representation of both the global and local aspects of the self-face, which could explain the self-face advantage (Brady et al., 2004, 2005; Keyes & Brady, 2010). According to this last hypothesis, while the right hemisphere would be responsible for the processing of the global aspects of the self-face, the left hemisphere might contribute by emphasizing the local aspects of it (Keyes & Brady, 2010). This prediction seems supported by the presence of the self-face advantage with both upright and inverted faces (Brady et al., 2004, 2005; Keyes & Brady, 2010), so that while the global aspects might play a central role in determining the advantage in the upright condition, the more robust representation of the local ones would allow the advantage for our face during inverted presentations. Particularly, despite face inversion usually disrupts the normal global face processing (Tanaka & Farah, 1993), the advantage would be still present in the inverted condition thanks to the enhanced representation of the local aspect in the left hemisphere.

Thus, identifying the actual origin of the specificity of the self-face has not been easy so far and clear evidence about its nature has not been provided yet. However, as further proof of the specificity of the self-face, while the recognition of familiar and unfamiliar faces seems characterized by a tendency to visually process the hemi-face that falls in the observer's left visual hemi-space (i.e., a left perceptual bias), self-face recognition seems to be related to the exact opposite bias. Good recognizers, indeed, tend to rely more on the right half-side of their face (i.e., a *right perceptual bias*), which falls in the right visual hemi-space looking at the mirror, when they are asked to recognize themselves (Brady et al., 2004), thus suggesting the existence of asymmetry in the perception and recognition of the self-face, and leading to

hypothesize a relation between the behavioral self-face advantage and a preference for the right-half of the facial stimulus.

In sum, whereas the presence of an advantage for recognizing one's own face is broadly accepted, there is currently little agreement in the literature about the underlying mechanism responsible for it, with some evidences suggesting that it could be face-specific (e.g., Keyes & Brady, 2010; Platek & Gallup, 2002; Platek et al., 2004), and other evidence demonstrating its relationship with self-recognition in general (Devue et al., 2007; Platek et al., 2004; Platek et al., 2006; Uddin, Kaplan, et al., 2005). Thus, it is still unknown whether the recognition of the self-face is supported by a face-specific mechanism or by a more general self-mechanism. Whereas in the former case one can speculate that the self-face advantage would arise as a consequence of the specificity of the self-information (and, thus, result in a more efficient extraction of the information during the structural encoding of the self-face), in the latter case the effect could probably be linked to the higher degree of familiarity of the self-face compared to other faces (which could be associated with lower threshold of activation in the face recognition units).

1.2. Abnormal face recognition: the case of congenital prosopagnosia

Typically, face recognition occurs rapidly and without particular efforts despite changes in viewpoints, expression and viewing conditions. However, there are still some cases in which the process is not so straightforward and does not end with a successful recognition; indeed, for individuals with prosopagnosia, who are selectively impaired in recognizing human faces, face recognition is a long and exhausting process. They are typically able to perceive facial stimuli as faces but fail to judge a face as familiar or unfamiliar and to identify it.

The term "prosopagnosia" derives from Classical Greek *πρόσωπον* (*prósōpon*) meaning "face" and *αγνοσία* (*agnōsía*) meaning "non-knowledge" and the impairment has been primarily described in individuals who have sustained cortical lesion in adulthood, often as a consequence of head trauma or stroke. In its acquired form (acquired prosopagnosia, AP) the face recognition deficit is attributed to a lesion in ventral occipito-temporal cortex, limited to the right hemisphere (De Renzi & di Pellegrino, 1998) or bilateral (Sergent & Signoret, 1992), and it is usually perceived by the patients, since they start to encounter some unexpected difficulties in recognizing familiar people after the trauma. In addition to this acquired form of prosopagnosia, it has become clear that some people can exhibit face processing impairment from birth, without suffering any brain damage (i.e. congenital prosopagnosia, CP; McConachie (1976)). In the case of congenital prosopagnosia (also known as developmental prosopagnosia; e.g., Susilo and

Duchaine (2013)), the failure to develop normal face recognition skills occurs despite intact low-level perceptual and intellectual functioning and in the context of normal exposure to faces throughout the individual's life (Schmalzl, Palermo, Green, Brunsdon, & Coltheart, 2008). On the contrary of acquired prosopagnosics, individuals with congenital prosopagnosia are often not even aware of their impairment because face perception was never normal in their lifetime (Behrmann & Avidan, 2005), so that they are not able to compare their actual face recognition abilities to previously normal abilities. Furthermore, congenital prosopagnosics have had the opportunity to develop different compensatory strategies in their lifetime, so that they are often able to recognize people, by using different types of cues such as physiognomic cues (e.g., clothing, posture and style of walking) or acoustic cues (e.g., voice; Palermo, Willis, et al. (2011)).

In the present thesis I will focus on the congenital form of prosopagnosia; I will first provide an overview of the most recent findings in the literature about the impairment, by focusing on its nature and selectivity. Finally, I will also introduce some open questions in the study of prosopagnosia, which will constitute part of the experimental section of the present thesis.

1.2.1. Nature and extent of the deficit

Although it is widely accepted that congenital prosopagnosia consists of a disorder characterized by severe face recognition problems (which results from a failure in the development of the necessary and typical mechanisms required for competent face processing), the exact nature of the deficit and the exact mechanisms underlying the face processing impairment in congenital prosopagnosics is still largely unknown. As described in paragraph 1.1, face recognition is not a monolithic process, but involves different stages, and impairment in face recognition could result from a failure of any of those stages.

Even though most of the individuals with congenital prosopagnosia are able to detect faces among other stimuli and to perform simple face matching task (e.g., de Gelder & Rouw, 2000; Humphreys, Avidan, & Behrmann, 2007; McKone et al., 2011), suggesting that their ability to encode the structure of a face is unimpaired, other studies found that even face detection or face matching can be impaired in some cases (e.g., Behrmann, Avidan, Marotta, & Kimchi, 2005; Bentin, Deouell, & Soroker, 1999; Garrido, Duchaine, & Nakayama, 2008; Kress, 2003). The ability to judge a face as previously seen or not is usually far below the normal range in these individuals, and these difficulties can be experienced with very familiar faces, famous faces or even newly learned faces, suggesting that facial memories are often impaired in

congenital prosopagnosia. Despite these individuals are also less likely to report a sense of familiarity for unrecognized faces (Palermo, Rivolta, Wilson, & Jeffery, 2011), congenital prosopagnosics usually show implicit or covert recognition as reflected in larger amplitude skin conductance responses after seeing familiar faces compared to unfamiliar ones (Jones & Tranel, 2001; Rivolta et al., 2013). Finally, some studies also showed that individuals with congenital prosopagnosia can be impaired in extracting non-identity information from a face, such as expression, gender, age and attractiveness, even though the processing of these parallel information is typically preserved in this population (Behrmann & Avidan, 2005; Bentin et al., 1999; De Haan & Campbell, 1991; Duchaine, Parker, & Nakayama, 2003; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Jones & Tranel, 2001; Kress, 2003). Thus, congenital prosopagnosia is an heterogeneous disorder, both in its features and in the severity of the deficit itself (e.g., de Gelder & Rouw, 2000; Duchaine, Germine, & Nakayama, 2007; Schmalzl, Palermo, Green, et al., 2008), and it is possible that, like other developmental disorders, congenital prosopagnosia could include different subtypes, rather than one prototypical form (Dalrymple & Palermo, 2016).

Recently, some studies involving the families of congenital prosopagnosics have shown the recurrent presence of the face recognition impairment in some prosopagnosics' relatives (e.g., Behrmann et al., 2005; Duchaine, Germine, et al., 2007; Lee, Duchaine, Wilson, & Nakayama, 2010; Schmalzl, Palermo, Green, et al., 2008; Wilmer et al., 2010), suggesting a genetic contribution to the impairment. These findings parallel evidence showing that also face recognition abilities have a heritable component, with monozygotic twins having more similar face recognition skills compared to dizygotic twins (Wilmer et al., 2010; Zhu et al., 2010). To shed light on the biological causes of the impairment, some authors have suggested the possibility of a simple autosomal inheritance pattern (Kennerknecht et al., 2006; Kennerknecht, Ho, & Wong, 2008), whereas other authors (e.g., Susilo & Duchaine, 2013) suggested that congenital prosopagnosia might result from the cumulative effect of multiple genes. Interestingly, a recent exploratory study (Cattaneo et al., 2016) indicates that the impairment could be associated with the DNA polymorphism of the receptor gene of oxytocin (a hormone that regulates basic social and reproductive behaviors) and the finding seems in accordance with previous evidence demonstrating that intranasal inhalation of the hormone is effective in improving face processing abilities in individuals with congenital prosopagnosia (Bate et al., 2014).

Finally, it is worth mentioning that, even if congenital prosopagnosics sometimes are not even aware of their deficit and may have developed successful strategies to overcome it during

the lifetime, prosopagnosia has usually a high impact in the life of individuals who have it. Indeed, some studies have demonstrated that congenital prosopagnosia can lead to elevated rates of anxiety and chronic stress and can also create traumatic social experiences resulting in a limited social circle (e.g., Yardley, McDermott, Pisarski, Duchaine, & Nakayama, 2008). Thus, investigating the mechanisms underlying this face recognition impairment is important not only to shed light on what stages of the face recognition process are affected, but also to find a way to significantly enhance the quality of life of these people.

1.2.2. Selectivity of the deficit

The defining feature of congenital prosopagnosia is a severe impairment in recognizing faces. However, the selectivity of this deficit has often been questioned, opening the possibility that individuals with congenital prosopagnosia could present an even broader deficit.

The face-specific hypothesis holds that faces are processed by specialized mechanisms. In particular, it has been shown that, whereas object recognition typically involves feature processing, through a recognition-by-components method (Biederman, 1987), face recognition requires both the sensitivity to the precise spatial layout of the facial features in the context of a facial image (configural processing) and the integration of facial information into a gestalt (holistic processing) (Duchaine & Nakayama, 2005; Freire, Lee, & Symons, 2000; McKone, Martini, & Nakayama, 2001; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). Thus, holistic processing is the parallel processing of a face as a whole, which combines the features and the spatial relationships between them, and is what characterizes expert face recognition processing (Farah, Wilson, Drain, & Tanaka, 1995; Farah et al., 1998; Van Belle, De Graef, Verfaillie, Busigny, & Rossion, 2010).

According to this hypothesis, different studies (e.g., Avidan, Tanzer, & Behrmann, 2011; Kimchi, Behrmann, Avidan, & Amishav, 2012; Palermo, Willis, et al., 2011; Ramon, Busigny, & Rossion, 2010; Richler, Cheung, & Gauthier, 2011) showed that individuals with congenital prosopagnosia fail in holistic processing. Particularly, the holistic processing impairment of these individuals would obligate them to over-rely on single features, as demonstrated by the presence of a local (rather than the normal global) superiority and precedence in a hierarchical Navon letter task (Behrmann et al., 2005), and to encode faces according to a feature by feature strategy, by focusing separately on the eyes, nose and mouth (Diamond & Carey, 1977; Verfaillie, Huysegems, De Graef, & Van Belle, 2014; however, see also Yovel & Duchaine (2006) for difficulties with part-based face processing in congenital prosopagnosia). Despite this evidence, some studies have not found impaired holistic processing in congenital prosopagnosics while

they found normal global processing in these individuals (e.g., Duchaine, Yovel, & Nakayama, 2007; Le Grand, Mondloch, Maurer, & Brent, 2004; Schmalzl, Palermo, & Coltheart, 2008; Susilo et al., 2010; M. A. Williams, Berberovic, & Mattingley, 2007).

The face-specific hypothesis seems supported by studies investigating: (1) the role of eye movements during face processing in this population, and (2) the existence of a dissociation between face and object recognition in individuals with congenital prosopagnosia. Indeed, some studies demonstrated that congenital prosopagnosics have anomalous scan path behavior during the exploration of faces (Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007). Good recognizers direct their gaze primarily at the central part of the face and its core features (Schwarzer et al., 2007), suggesting that these regions convey the largest amount of information about a human face (Schmalzl, Palermo, Green, et al., 2008), and are the optimal locations for holistic processing (Hsiao & Cottrell, 2008; Peterson & Eckstein, 2012). By contrast, individuals with congenital prosopagnosia usually show a more dispersed gaze, focused not only on central but also on external features (Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007). Furthermore, some studies have demonstrated that despite their severe face recognition impairment, individuals with congenital prosopagnosia have no problem in recognizing and processing object recognition (Bentin et al., 1999; Duchaine & Nakayama, 2005; Farah, Levinson, & Klein, 1995; Farah, Wilson, et al., 1995; Nunn, Postma, & Pearson, 2001), further supporting the specificity of their impairment.

One of the most powerful arguments typically used to support the presence of holistic processing impairment in congenital prosopagnosia is the absence of inversion effect for faces in these individuals. The face inversion effect consists of better performance for upright compared with inverted faces (e.g., Farah, Wilson, et al., 1995; Yin, 1969) and it is usually explained by the fact that normal recognizers perceive a face holistically by using expert face analysis that relies on a whole-based analysis for upright faces, whereas they switch to a non-expert part-based analysis in the case of inverted faces (Tanaka & Farah, 1993). This difference between the processing of the two face orientations is related to the holistic processing being active and functional with only upright and not inverted faces, because of our way of acquiring face expertise through continuous exposure to upright faces (Barton, Radcliffe, Cherkasova, & Edelman, 2007). Accordingly, some studies (e.g., Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006) have shown that normal recognizers scan upright faces differently from inverted faces, with a more random sequence of fixations in the latter condition. By contrast, it seems that congenital prosopagnosics do not show the normal face inversion effect during behavioral tasks (Behrmann et al., 2005; Duchaine, Germine, et al., 2007; Russell, Duchaine, &

Nakayama, 2009) because they process both upright and inverted faces in the same non-expert part-based way (e.g., Behrmann & Avidan, 2005; Gauthier & Tarr, 1997). Nevertheless, mixed results are reported in the literature regarding the inversion effect in this population (Behrmann et al., 2005; Duchaine, Yovel, et al., 2007; Le Grand et al., 2006), thus suggesting that the holistic processing might not be always impaired.

The alternative view, instead, asserts that both objects and faces are sub-served by a single visual processing and that the dissociations between those two class of stimuli would arise as a consequence of the higher cognitive demand requested by face processing (Behrmann & Avidan, 2005); indeed, face processing involves individual identification, requiring fine grained discrimination of perceptually similar exemplars within a category, whereas other objects are typically recognized at a more basic level (Tarr & Cheng, 2003). Accordingly, some authors have argued that the impairment shown by congenital prosopagnosics is the result of a problem in subordinate-level object discrimination (e.g., Behrmann et al., 2005). This alternative hypothesis, usually referred to as the “within-class hypothesis” (Damasio, Damasio, & Van Hoesen, 1982), states that the impairment of congenital prosopagnosic, would be evident in face recognition because of the greater degree of difficulty in discriminating visually similar exemplars of the same class (faces) compared with the recognition of objects of different classes (Behrmann et al., 2005; Farah, Levinson, et al., 1995), and that a similar impairment would be detectable in the recognition of objects within the same class (within-class object).

Supporting this “within-class” hypothesis, some studies (Behrmann et al., 2005; De Haan & Campbell, 1991; Duchaine, Germine, et al., 2007; Duchaine & Nakayama, 2005; Gauthier & Tarr, 1997; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002) have shown that some congenital prosopagnosics show within-class object recognition deficits (e.g. birds, flowers, cars, horses, guns, houses and tools) and are impaired in discriminating between novel objects (Greebles), especially when the discrimination is at the individual level and even when the pair to be discriminated is visually available to the individual for unlimited time. However, on the other side, some studies found that congenital prosopagnosics perform within the normal range for tasks involving the recognition of within-class objects, supporting the specificity of face recognition (Bentin et al., 1999; Duchaine et al., 2006).

Therefore, despite the general agreement that prosopagnosia is a discrete condition, dissociable from other forms of agnosia, the existence of a clear dissociation between face and within-class object recognition is still a matter of debate and the controversy between a domain-specific organization of faces versus a within-class recognition system has not been resolved yet.

1.2.3. Tools for the assessment of congenital prosopagnosia

Congenital prosopagnosia is not only a disorder that might cause difficult social experiences, but it is also quite common. Indeed, some studies reported that as many as 2-2.5% of the population has congenital prosopagnosia (Kennerknecht et al., 2006; Kennerknecht et al., 2008). Despite defining congenital prosopagnosia might seem straightforward (i.e., a life-long impairment in recognizing faces), establishing widely accepted criteria to diagnose it has been more challenging. In one of the first attempt, (Behrmann & Avidan, 2005) identified three important diagnostic criteria for congenital prosopagnosia: (1) no positive evidence for any neurological or neuropsychological alteration should be present; (2) face perception was never normal in the lifetime of these individuals; and (3) face processing impairments can be present also in family members. Not surprisingly, however, there is considerable variation between studies on how congenital prosopagnosia is assessed. Furthermore, making the diagnosis of congenital prosopagnosia even more difficult, there are large individual differences in face recognition ability in good recognizers as well as in individuals with congenital prosopagnosia (e.g., Bowles et al., 2009; Herzmann, Danthiir, Schacht, Sommer, & Wilhelm, 2008; McKone & Palermo, 2010; Wilmer et al., 2012; Wilmer et al., 2010); indeed, as evident from the overview of the literature in the last two sections, congenital prosopagnosia is a very high heterogeneous disorder, whose features and their severity might vary across individuals.

Usually, cases of congenital prosopagnosia are first identified following self-reports or questionnaires in which people state their poor face recognition abilities, followed by a formal testing using neuropsychological tests assessing different dimensions of face recognition (e.g., famous face recognition, newly learned faces recognition). However, different studies have advised caution on relying on self-reports of face recognition difficulty (e.g., De Haan, 1999); indeed, people have typically very little insight of their face recognition skills, as demonstrated by evidence proving that people reporting poor face recognition abilities performed at typical level on a battery of behavioral tests (e.g., De Haan, 1999). Similarly, people classified as prosopagnosic because of test scores can be even not aware of their deficit (Bowles et al., 2009; De Haan, 1999; Grueter et al., 2007). Furthermore, individuals with congenital prosopagnosia are not the only ones showing poor face recognition abilities; for example, patients who were deprived of early visual input as consequence of bilateral cataracts during childhood usually show low performance when assessed with face recognition tests (de Heering & Maurer, 2014), highlighting that the simple report of impaired face recognition abilities during self-assessment can be due to different reasons. However, some studies demonstrated that individuals with very poor face recognition skills can actually have insight into their deficit, on the contrary of those

with less severe or no difficulties (e.g., de Heering & Maurer, 2014). In particular, individuals who score in the normal range on face tests may have less insight into their face recognition abilities for different reasons. For instance, whereas we often received clear and consistent feedback in education settings for a series of abilities, such as language competence, the same is not true for face recognition abilities, which are not typically measured and/or reinforced (Zell & Krizan, 2014). Moreover, when people give feedbacks about their perceptual abilities in face recognition, they can often confound it with the ability to remember a person's name after they have recognized her. Thus, overall typical adults seem to have only minimal insight into their face recognition ability, suggesting that self-report measures have to be used carefully while diagnosing congenital prosopagnosia.

The key diagnostic tests used in the diagnosis of congenital prosopagnosia involve the ones assessing people's abilities to match unfamiliar faces and to recognize previously seen faces as familiar. Common tests probing these abilities include the Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006), the Cambridge Face Perception Test (CFPT, Duchaine, Germine, et al., 2007), the Benton Facial Recognition Test (BFRT, Benton, 1994; Benton & Van Allen, 1968) and the Warrington Recognition Memory Test (Warrington, 1984). However, some studies (e.g., Duchaine & Nakayama, 2004; Duchaine & Weidenfeld, 2003) have highlighted that results from some of these tests (i.e., the Benton Facial Recognition Test and the Warrington Recognition Memory Test) have to be taken carefully. Indeed, it has been shown that, despite their face recognition impairment, both cases of acquired prosopagnosia (e.g., Busigny & Rossion, 2010; Delvenne, Seron, Coyette, & Rossion, 2004) or congenital prosopagnosia (Duchaine & Nakayama, 2004) can sometimes reach almost normal performance in these tests by using unusual strategies and/or taking abnormally long response times (Busigny & Rossion, 2010; Delvenne et al., 2004). Accordingly, when questioned at the end of the testing, some individuals with congenital prosopagnosia reported that their performance on these tests relied heavily on feature matching and on non-internal facial feature information (Duchaine, 2000; Duchaine & Weidenfeld, 2003; Nunn et al., 2001). Thus, since alternative strategies can be used to achieve normal performance, it has been suggested that normal scores on these tests do not require normal face recognition abilities. Consequently, whereas impaired score can actually reflect impairment in face recognition processing, normal score on either instruments do not always demonstrate preserved face recognition abilities, suggesting that results from these tests should be interpreted cautiously and should be supplemented with other tests of face recognition.

Therefore, because of the high incidence rate of congenital prosopagnosia, its correct and prompt diagnosis is necessary to help these individuals facing the impairment and its related difficult social experiences, before the deficit undermines their self-esteem and social relationships. To this aim, essential for a correct diagnosis is the use of sensitive and reliable tools, whose results can be interpreted straightforwardly.

1.3. Concluding remarks and specific aims

Face recognition is a form of “expert” visual processing. We can recognize an incredible number of faces rapidly and without any particular efforts. Different models have been proposed to account for the specialization of face processing, and several studies have shown that face recognition abilities can be selectively disrupted. However, despite the large amount of studies that have investigated face recognition in individuals with typical development and in congenital prosopagnosics over the last twenty years, we are still far from a complete understanding of the mechanisms underlying normal and atypical face recognition, and some research questions are still open. For instance, whether the face recognition deficit is category-selective or common to all within-category objects is still a matter of debate, as well as whether some of the perceptual biases that characterize face processing are face-specific or not.

For this reason, the following chapters will try to answer some of these open questions. To this aim, in the present work I have used different paradigms (such as matching or recognition tasks) and, along with the recording of the behavioural results, I have also taken advantage of the eye-movement methodology. In particular, in the first part of this thesis I will provide a characterization of the impairment presented by individuals with congenital prosopagnosia, by comparing their ability to recognize faces and other classes of objects, and I will investigate the reliability of some of the tests most commonly used in the diagnosis of congenital prosopagnosia. Afterwards, in the second part of this work, I will investigate the face-specificity of some of the perceptual biases (i.e., left-perceptual bias and self-face advantage) that characterize face recognition; indeed, the study of these perceptual effects in individuals with a selective deficit in face recognition processing can help us to reach a better understanding of the mechanisms underlying typical and atypical face recognition.

2. The characterization of congenital prosopagnosia: open questions

2.1. Study I: The reliability of self-report measurements in the diagnosis of congenital prosopagnosia

Self-reports are commonly used to identify people with congenital prosopagnosia, as part of the screening process during the neuropsychological assessment or even on websites recruiting those individuals with face recognition impairment. Typically, self-report measurements are used as a first step in the diagnosis of this disorder, followed by a formal assessment by means of face recognition tests. The underlying assumption is that people should have insight into their face recognition abilities and, thus, be able to detect if they encounter specific difficulties while they try to recognize the others. However, some authors have advised caution on relying on self-reports, suggesting that people have actually very little insight of their face recognition skills (e.g., De Haan, 1999).

Many studies that have used self-report questionnaires as part of screening routine for congenital prosopagnosia reported the score obtained by participants on both self-assessment and psychometric tests, allowing to run some correlations among those. For instance, Bowles et al. (2009) asked participants to rate their ability to recognize faces in everyday life as “compared to the average person“ on a 10-point scale, where 0 was much worse than average, and 10 was much better than average. In this study participants were also asked to undergo two of the most commonly used and most reliable tests to assess prosopagnosia, namely the Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006) and the Cambridge Face Perception Test (CFPT, Duchaine, Germine, et al., 2007). The analyses on a possible correlation between the self-report measurement and the two tests revealed in that case only a significant but small correlation between self-report and overall score on the CFMT, and no significant association between the self-rating and the performance on the CFPT. Similarly, Bindemann, Attard, and Johnston (2014) asked participants four single questions to rate their ability to recognize famous faces, familiar faces, unfamiliar faces seen several times and unfamiliar faces seen only once; the rating was performed on a 7-point scale from “very bad” to “very good”. Self-report ratings of the ability to recognize unfamiliar faces and familiar faces did not correlate with the ability to recognize famous faces assessed by standard tasks, except, moderately, on two tests. In another study, Rotshtein, Geng, Driver, and Dolan (2007) asked participants to rate their ability

to recognize faces on a scale from 1 (“I cannot remember faces at all”) to 10 (“I never forget a person’s face once I met him or her”). The authors found that self-reported ability did not correlate with behavioral measures of face memory performance. Similarly, McGugin, Richler, Herzmann, Speegle, and Gauthier (2012) measured participant’s self-reported experience on a 9-point scale where 1 was the lowest expertise, and in this case better performance on the CFMT was weakly associated with greater experience with faces.

Thus, evidence from studies using self-report questions demonstrated that these measurements do not always correlate with score on formal face recognition test, suggesting that typical adults have only minimal insight into their face recognition ability. However, in the attempt to create more reliable self-report measures, recently some authors have tried to develop short questionnaires for screening the presence of congenital prosopagnosia (e.g., Kennerknecht et al., 2008; Shah, Gaule, Sowden, Bird, & Cook, 2015). Among these, the most popular one is the questionnaire created by Kennerknecht et al. (2008). This questionnaire is composed of 15 questions, which can be answered on a 5-point rating scale, resulting in scores between 15 and 75 points, with higher scores indicating more difficulty in recognizing faces. In particular, in order to control for other deficit that can mimic prosopagnosia, 3 items not related to face recognition were specifically included as control questions. In their original study, Kennerknecht et al. (2008) showed the presence of a significant difference between the average score of eight individuals with congenital prosopagnosia (diagnosed as prosopagnosic on the basis of another more detailed questionnaire and a semi-structured interview) and the average score of 186 non-prosopagnosic people reported. Furthermore, in a second study, a significant correlation was found between scores on the questionnaire for 15 individuals with congenital prosopagnosia and face recognition performance (z-score of performance combined over multiple tests) (Stollhoff, Jost, Elze, & Kennerknecht, 2011). However, it was not reported whether a similar correlation was also present in the case of people who did not report long-life difficulties in face recognition.

Therefore, most studies suggest that there is minimal, if any, relationship between one’s self-evaluation of face recognition ability and the more standardized behavioral measures of face recognition performance, further highlighting how these scores should be interpreted carefully when screening for prosopagnosia. To further investigate this topic, in the present chapter is reported the outcome of a study we conducted in which face recognition performance was assessed in a large cohort of participants with typical face recognition ability, in parallel with self-reports of their face recognition abilities. Particularly, both face recognition and face perception abilities were formally assessed by means of the Cambridge Face Memory Test

(Duchaine & Nakayama, 2006) and the Benton Facial Recognition Test (Benton, 1994; Benton & Van Allen, 1968), whereas the questionnaire developed by Kennerknecht et al. (2008) was used as self-report measure.

Finally, the results of eight people formally diagnosed as congenital prosopagnosics on the basis of behavioral tests are also reported, in order to examine whether very poor performance in face recognition is linked to increased insight compared to those with typical face recognition ability, as suggested by some authors (de Heering & Maurer, 2014). This combination of measures and participant groups will provide a better understanding of people's belief and insight into their face recognition abilities.

2.1.1. Participants

The Kennerknecht et al. (2008) questionnaire (translated into Italian) was administered to 490 psychology students of the University of Milan-Bicocca. Ninety-six of these (16 males), aged between 19 and 28 years ($M = 21.69$, $SD = 1.98$), volunteered to return at a later time and complete computerized tests for course credit. All had normal or corrected-to-normal vision and no evidence of neurological deficit.

Eight individuals with congenital prosopagnosia also took part in this study (see next chapters for a more detailed description of these individuals). All of them were female, aged between 19 and 26 years ($M = 21.25$, $SD = 2.49$). All had normal or corrected-to-normal vision, no evidence of neurological deficit and all of them reported a long-life difficulty in recognizing faces.

2.1.2. Material and Methods

The initial sample of 490 participants completed only the Kennerknecht et al. (2008) questionnaire, whereas the 96 participants that agreed to come back underwent also the Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006), both in the upright and inverted face conditions, and the Benton Facial Recognition Test (BFRT, Benton, 1994; Benton & Van Allen, 1968). The order of test administration was counterbalanced.

The questionnaire developed by Kennerknecht and colleagues (2008) contains 15 questions, which can be answered on a 5-point rating scale. The total score varies between 15 and 75 points, with higher scores indicating more difficulty in recognizing faces. Examples of questions are: "I can easily follow actors in a movie" and "I recognize famous people immediately".

In the Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006), participants have to study six greyscale male target faces that have been cropped to remove non-face cues, and then select each of those faces from two distractors. The test section consists of three stages that increase in difficulty, for a total score of 72. In the first “learn” stage the target faces are the same as those studied (maximum score of 18), in the second “novel” stage all the faces are seen under different lighting conditions and viewpoints (maximum score of 30), and in the third “noise” stage, visual noise is overlaid on all the faces (maximum score of 24). Both the upright and inverted conditions of this test were administered and an additional index was calculated, namely the inversion effect. The inversion effect is the difference between the total score of the upright and inverted faces (i.e., the ‘cost’ for recognizing inverted faces) and was included because it represents a qualitative index of face processing (e.g., Behrmann & Avidan, 2005). The Cambridge Face Memory Test (Duchaine & Nakayama, 2006) is one of the most commonly used tests for assessing prosopagnosia (Wilmer et al., 2012). It has been proven to be the most sensitive test for detecting face recognition impairment and to have impressive and test-retest reliability (Bowles et al., 2009; Duchaine & Nakayama, 2006; Duchaine & Nakayama, 2004; Wilmer et al., 2010).

The Benton Facial Recognition Test (BFRT, Benton, 1994; Benton & Van Allen, 1968) is a classical test to assess face recognition impairments in brain-damaged patients. It involves the matching of a target face to either one face under the same viewpoint and lighting (6 items) or three of six faces that vary in viewpoints and lighting conditions (16 items). All faces are presented simultaneously. The maximum score is 54, with a score between 41 and 39 considered as mildly impaired, and below 39 as severely impaired. Note that despite the difficulty of this test, cases of patients with acquired prosopagnosia (Busigny & Rossion, 2010; Delvenne et al., 2004) or congenital prosopagnosics (Duchaine & Nakayama, 2004) can reach almost normal performance by using unusual strategies and taking abnormally long response times (Busigny & Rossion, 2010; Delvenne et al., 2004).

2.1.3. Results

Table 2a displays descriptive statistics for the three tests in individuals with typical face recognition skills. Importantly, average performance was neither at floor nor at ceiling, and all participants showed sufficient range. Descriptive statistics are also shown for the self-report questionnaire (Kennerknecht et al., 2008). Cronbach’s alpha, a measure of internal consistency, was average to high for all of the measures. Cronbach’s alpha values were also used to calculate

the theoretical upper bound (UB) of a correlation that could be obtained between two tests, calculated as the geometric mean of the two reliabilities (R. M. Kaplan & Saccuzzo, 2012)).

First, we examined the relationships between the tests to determine whether they were measuring similar aspects of face recognition. If so, we would expect self-report measures to correlate with both tests similarly. Then, we focused on our primary question: the relationship between test scores and self-report questionnaire. Here I reported both Pearson's r and Spearman's ρ (ρ), as in some cases the distributions were not normal, or suffered from significant skew or kurtosis (Table 2a).

Table 2a. Descriptive statistics for all tests administered to individuals with typical face recognition skills: N, possible and observed range, mean and standard deviation, Cronbach's alpha, skew, and kurtosis. CFMT = Cambridge Face Memory Test; IE = Inversion effect; BFRT = Benton Facial Recognition test; Q = Questionnaire.

Measure	N	Chance -ceiling	Observed range	Mean (SD)	Cronbach's α	Skew	Kurtosis
Kennerknecht Q	490	15-75	15-44	27.72 (5.54)	0.88	0.21	-0.26
Kennerknecht Q	96	15-75	17-44	27.57 (7.24)	0.86	0.38	-1.15
CFMT upright	96	24-72	35-72	56.18 (9.58)	0.90	-0.66	-0.50
CFMT inverted	96	24-72	30-58	41.17 (6.06)	0.86	0.58	0.34
IE	96	-72/+72	-9/+32	14.99 (8.88)	-	-0.40	-0.21
BFRT	96	25-54	38-53	46.42 (3.31)	0.69	-0.33	-0.71

Performances on the formal test commonly used to evaluate face recognition abilities significantly correlated with each other, suggesting that, even if they assess different stages of the face recognition process (i.e., the BFRT assesses face perception, whereas the CFMT assesses face familiarity), they still tap into similar aspects of it. Indeed, the upright condition of the CFMT correlated with the inversion condition of the same test ($r(94) = 0.43$, $p < .001$, $UB = 0.88$; $\rho = 0.41$, $p < .001$) and the BFRT ($r(94) = .49$, $p < .001$; $UB = .79$; $\rho = .50$, $p < .001$). A modest, but significant correlation was also found between the BFRT and the inverted condition of the CFMT ($r(94) = 0.22$, $p = 0.031$, $UB = 0.77$; $\rho = 0.24$, $p = 0.016$), as well as between the BFRT and the inversion effect ($r(94) = 0.38$, $p < .001$; $\rho = 0.41$, $p < .001$).

Higher scores on the Kennerknecht et al. (2008) questionnaire indicated more difficulties with face recognition. Thus, a negative correlation indicates a relationship between self-report scores and ability. However, the scores obtained by participants in the questionnaire

did not correlate with the upright ($r(94) = -0.002, p = 0.99, UB = 0.88; \rho = -0.02, p = 0.97$) or inverted condition of the CFMT ($r(94) = -0.07, p = 0.48, UB = 0.86; \rho = -0.08, p = 0.44$), nor with the inversion effect ($r(94) = 0.04, p = 0.67; \rho = 0.02, p = 0.85$). Finally, once again, the scores on the BFRT were not associated with the Kennerknecht et al. (2008) questionnaire ($r(94) = -.00, p = .99, UB = 0.77; \rho = .00, p = .97$). Overall, none of the formal measures of face recognition abilities correlated significantly with the self-report questionnaire.

Second, we examined how people who report everyday face recognition difficulties and perform poorly on formal tests assessing face recognition ability respond on self-report questionnaires. Individuals with congenital prosopagnosia performed poorly on the face recognition tests, especially on the CFMT (see Table 2b). However, they showed similar ratings of their face recognition abilities ($M = 27.00, SD = 8.38$) as the controls' ones ($M = 27.57, SD = 7.24; t(102) = -0.21, p = 0.83$). In order to further investigate whether individuals with face recognition impairments have more insight of their actual face recognition abilities compared to normal recognizers, as already suggested by some authors (e.g., de Heering & Maurer, 2014), we correlated the questionnaire scores with the face recognition tests within the group of congenital prosopagnosics. As a result, scores on the Kennerknecht et al. (2008) questionnaire were not significantly associated with the BFRT ($r(6) = -0.45, p = 0.26$) or the upright condition of the CFMT ($r(6) = 0.45, p = 0.26$); however, the questionnaire showed a trend to a significant correlation with the inverted condition of the CFMT ($r(6) = -0.66, p = 0.08$) and, more interestingly, proved a significant strong relationship with the inversion effect ($r(6) = 0.72, p = 0.04$).

Table 2b. Raw scores for each CP. CFMT = Cambridge Face Memory Test; IE = Inversion effect; BFRT = Benton Facial Recognition test; Q = Questionnaire. * indicates a pathological score according to the z-scores from Duchaine & Nakayama, 2006 for the CFMT and according to the cut-off values from Benton et al., 1983 for the BFRT; No normative data exists for the IE, even though it has to be noticed that all the 8 individuals with congenital prosopagnosia showed a reduced IE compared to the value reported in Table 2a.

Subject	Age	Kennerknecht Q	BFRT	CFMT upright	CFMT inverted	IE
A.M.	20	19	41*	38*	40	-2
C.S.	19	20	49	37*	45	-8
C.R.	21	36	40*	36*	30*	6
E.S.	24	19	48	37*	37	0
F.C.	26	26	45	38*	42	-4
M.D.A.	21	39	42	40*	34	6
P.C.	19	35	44	40*	32*	8
P.V.	20	22	41*	38*	33	5

2.1.4. Conclusion

The aim of the present study was to investigate how much insight individuals have in their ability to recognize faces. In order to do so, we collected data from nearly 100 participants with typical face recognition abilities and 8 individuals with congenital prosopagnosia, who completed three face recognition tests and one self-report questionnaire. Overall, our results suggest that individuals with typical face recognition abilities have only minimal (if not at all) insight into their face recognition abilities. Indeed, in this population no relationship was found between the Kennerknecht et al. (2008) questionnaire and any of the formal tests assessing face recognition ability (i.e., CFMT and BFRT).

Moreover, the individuals with congenital prosopagnosia did not score differently in the Kennerknecht et al. (2008) questionnaire from our group of good recognizers. This result seems in contrast with recent findings showing that individual with poor face recognition abilities have more insight into their abilities (de Heering & Maurer, 2014; Shah et al., 2015). However, it is important to note that we found a significant correlation between their scores on the tests and their self-report scores on the Kennerknecht et al. (2008) questionnaire, suggesting that, even though their overall score did not differ from the one obtained by good recognizers, congenital prosopagnosics are still aware of the relative severity of their impairment. In sum, results from our group of individuals with congenital prosopagnosia revealed better insight into face recognition ability compared to the population with typical face recognition skills.

One possible explanation of the limited relationship between the Kennerknecht et al. (2008) questionnaire and the face recognition tests could lie in the content of some of the items included in the questionnaire itself, despite its good internal consistency. Indeed, in an attempt to exclude individuals who have other difficulties in addition to congenital prosopagnosia, the Kennerknecht et al. (2008) questionnaire includes items that are not really related to face identity recognition and that are unrelated to the core face recognition impairment in congenital prosopagnosia (e.g., “I can easily form a mental picture of a red rose”). Accordingly, the validity of the Kennerknecht et al. (2008) questionnaire to tap into the self-awareness of one’s own face recognition ability has been previously criticized (e.g., Shah et al., 2015). Trying to avoid this issue, Shah et al. (2015) recently developed a new questionnaire, the Prosopagnosia Index 20 (PI20), composed of 20 items all focused on face recognition ability. During the validation of this questionnaire, a group of people recruited on the basis of their suspected congenital prosopagnosia scored significantly higher on the PI20 than controls, indicating that this self-report measure could actually tap into the everyday face recognition difficulties characterizing the impairment and prove itself to be relevant for screening purposes. Furthermore, scores on

the PI20 from good recognizers correlated highly with scores on a famous face task, suggesting that people could really show insight into their abilities when asked a large number of very specific questions.

In summary, the ability of self-report questionnaires to measure insight into face recognition ability appears often limited. However, because they are actually struggling in some daily situations, it appears that people with poor face recognition skills seem to be more aware of their difficulties compared to the rest of the population. However, this result has to be confirmed by other studies, given the limited number of participants with congenital prosopagnosia that was included in this study (8). Overall, the results of this first study further confirm that, in order to correctly make diagnosis of prosopagnosia, self-report measurements are not sufficient. Indeed, even though they could be used to screen the general population on a first step, to correctly identify individuals with congenital prosopagnosia it is still necessary to assess face recognition abilities by means of formal and validated behavioral tests that can actually account for everyday face recognition difficulties.

2.2. Study II: A comparison between the Benton Facial Recognition Test and the Cambridge Face Memory Test

In the previous chapter the reliability of self-report measurements has been investigated, demonstrating that these measurements have only limited ability to reflect people's face recognition skills. However, this conclusion is based on the assumption that the common behavioral tests used to measure face recognition abilities truly reflect daily-life face recognition skills. Regarding this point, among the most used tests there are the Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006) and the Benton Facial Recognition Test (Benton, 1994; Benton & Van Allen, 1968). Whereas the former one tests the ability to recognize as familiar previously seen faces, the latter one assesses the ability to match unfamiliar faces under different viewpoints and lighting conditions (see chapter 2.1 for a more detailed description of these tests).

The CFMT has been shown to be one of the most sensitive tests in detecting face recognition impairment (Duchaine & Nakayama, 2004, 2006). This test has been used widely (Wilmer et al., 2012) in studies of congenital prosopagnosia and is known for having impressive internal (0.86; Wilmer et al., 2010; 0.88; Bowles et al., 2009) and test-retest (0.70; Wilmer et al., 2010) reliability. Also, performance on the CFMT correlates with performance on a face matching test without any learning component (i.e., CFPT; Bowles et al., 2009; Duchaine et al.,

2007) but the test displays only modest correlations with measures of non-face visual memory (Dennett et al., 2012; Wilmer et al., 2010) and even weaker correlations with measures of verbal memory (Wilmer et al., 2012), supporting its efficacy to specifically tap into face recognition processing. Finally, the CFMT has been validated also on the basis of its ability to diagnose people with acquired prosopagnosia (Susilo, Yovel, Barton, & Duchaine, 2013).

On the other side, the BFRT is another test often used to assess whether individuals with congenital prosopagnosia show impairment in face discrimination in addition to face memory. The BFRT internal (0.72; Christensen, Riley, Heffernan, Love, & McLaughlin Sta Maria, 2002) and test–retest (1 year: 0.71; Christensen et al., 2002) reliability is good, even if lower than the CFMT reliability. The correlation between the Short and the Long Form of this test is very high across studies and participant samples (.88, .92 and .93 for healthy subjects, neurological subjects and both samples, respectively; Benton (1994); Benton and Van Allen (1968); Ferracuti and Ferracuti (1992)). However, some studies have argued that the scores of the BFRT have to be interpreted carefully (e.g., Duchaine & Weidenfeld, 2003; Duchaine & Nakayama, 2004). Indeed, as already highlighted in paragraph 1.2.3, it has been shown that, despite their face recognition impairment, individuals with congenital prosopagnosia (Duchaine & Nakayama, 2004) can sometimes reach almost normal performance in this test by using unusual strategies and/or taking abnormally long response times (Busigny & Rossion, 2010; Delvenne et al., 2004). In fact, since the target face and the test faces are presented simultaneously, participants can rely heavily on feature matching and on non-internal facial feature information (Duchaine, 2000; Nunn, et al., 2001; Duchaine & Weidenfeld, 2003). Similarly, cases of patients with acquired prosopagnosia (e.g., Busigny & Rossion, 2010; Delvenne et al., 2004) also can perform in the normal range by using similar unusual strategies. Thus, since normal performance can be achieved in unusual ways, it has been suggested that normal scores on the BFRT do not require normal face recognition abilities and, thus, do not always demonstrate preserved face recognition abilities. Consequently, results from this test should be interpreted carefully and should be supplemented with other tests of face recognition (Duchaine & Nakayama, 2004).

Furthermore, recent studies have demonstrated large individual differences in face identity recognition ability (e.g., Bowles et al., 2009; Herzmann et al., 2008; McKone & Palermo, 2010; Wilmer et al., 2010; Wilmer et al., 2012) and, more interestingly, have shown that age, gender and participant-stimulus ethnic match have to be taken into account in interpreting results from tests assessing it (Bowles et al., 2009; Christensen et al., 2002); for instance, some studies showed that face recognition ability peaks at around age 30 and then slowly declines (Susilo, Germine, & Duchaine, 2013), and that women tend to outperform men

in face recognition abilities (e.g., Herlitz, Nilsson, & Backman, 1997; Herlitz & Yonker, 2002; Lewin, Wolgers, & Herlitz, 2001), even though some studies found this to be true only for women's faces (Lewin & Herlitz, 2002; McKelvie, Standing, Jean, & Law, 1993). Regarding the CFMT, two studies found that adult women have a small advantage compared to men (which was significant in only one of the studies), but that this difference was not associated with a change in the cut-off score for the diagnosis of prosopagnosia on the CFMT (Duchaine & Nakayama, 2006; Bowles et al., 2009). The original norms for the CFMT all come from Caucasian participants in the USA; however, participant-stimulus ethnicity match also plays a role in influencing participant's performance on face recognition tests, and this is true not only across races, but also within the same race (e.g., Caucasians) (Bowles et al., 2009; Chiroro, Tredoux, Radaelli, & Meissner, 2008), raising the possibility that country-specific norms may be needed to ensure a correct diagnosis of prosopagnosia (Bowles et al., 2009).

Thus, considering the importance of having norms derived from controls with a similar experience of faces as the 'potential' prosopagnosic individuals, and in order to obtain more appropriate control and normative data for an Italian sample, in the present chapter I report the results of one study we conducted in which the CFMT and the BFRT were administered to a large cohort of young adult individuals, who were not selected on the basis of their face recognition abilities. Finally, I also report the results from a sample of 23 individuals diagnosed with congenital prosopagnosia, in order to examine the sensitivity of both the CFMT and BFRT in detecting the prosopagnosic impairment once the two tests have been validated on a normative sample with characteristics similar to the ones of the potential prosopagnosics.

2.2.1. Participants

Participants were 272 students (56 males, mean age of 22.86 ± 2.66 y/o, age range 19-31 y/o, 5 left-handed) recruited from the University of Milan-Bicocca. All participants had normal or corrected-to-normal vision and no evidence of neurological or neurophysiological alterations. Participants received university course credit for taking part in the experiment. The ethics committee of the University of Milan-Bicocca approved the study, and an informed consent was obtained from all participants prior to the onset of the experiment.

Data from an additional 23 participants were included and composed the sample of congenital prosopagnosics (all females, mean age of 21.87 ± 2.91 y/o, age range 19-30, all right handed) (see next chapters for a more detailed description of these participants).

2.2.2. Material and Methods

Data came from different research projects, investigating other theoretical questions within the normal population, and in some cases they were obtained from participants tested as matched-controls for specific individuals with congenital prosopagnosia, but were all collected from the same laboratory in Italy. All participants were tested on the BFRT and most of them underwent also the CFMT (both in the upright and inverted face conditions). An additional index was calculated from the CFMT, which is the difference between the total score of the upright and inverted faces, namely the *inversion effect* (IE) (Yin, 1969). In their original study Duchaine and Nakayama (2006) demonstrated that inversion lowered the performance by 22% (i.e., 15 points). All the research projects involved also additional cognitive tests (e.g., object recognition) in addition to those reported here.

2.2.3. Results

Benton Facial Recognition Test

All 272 healthy participants completed the BFRT. The average total scores for the long form, as well for the short and the different parts of the test are reported in Table 2c. Overall, despite slightly shifted to the upper limit, the average performance of this sample was either at floor or at ceiling, and showed a sufficient range (with the only exception of Items 1-6). Cronbach's alpha was poor to average for all the subparts of the test. Previous studies provided an alpha of 0.71 for the long form of the BFRT and showed that the Short and the Long Form highly correlate (.88, .92 and .93, Christensen et al., 2002; Benton, 1994; Ferracuti & Ferracuti, 1992); in this study we found a slightly smaller alpha for the long form (0.608), but a significant large correlation was confirmed between the two forms of the test ($r(272) = 0.88, p < .001$).

In order to investigate the effect of sex, independent t-tests were carried out on the average scores. No difference between the male and female participants were found in any of the average scores (Items 1-6: $t(270) = -0.71, p = 0.48$; Items 7-13: $t(270) = 0.77, p = 0.44$; Items 14-22: $t(270) = 0.93, p = 0.35$; Short form: $t(270) = 0.72, p = 0.47$; Long form: $t(270) = 0.95, p = 0.34$; Modified short version (Christensen et al., 2002): $t(270) = 1.10, p = 0.27$; Modified short form (item 7-22): $t(270) = 0.99, p = 0.32$).

In order to overcome the poor internal reliability of the existing short and long forms of the BFRT, a new subset of items was examined. To do so, we correlated each item score with the total score in the BFRT and only the items with a significant item-scale correlation were selected. Not surprisingly all the items of the first part (items 1-6) were discarded and only the

items involving a change in the luminance or in the viewpoint were selected (items 7-22). The Cronbach's alpha of this new subset of items was 0.616, only slightly better than the reliability of the long form.

Table 2c. Descriptive statistics for the BFRT in typical individuals: chance/ceiling scores and observed range, mean and standard deviation, Cronbach's alpha. ^aSince items 1-6 are dichotomous items reliability for this part of the test tests was calculated by using the KR20 developed by Kuder and Richardson (1937).

	<i>Chance- ceiling</i>	<i>Observed range</i>	<i>Mean (SD)</i>	<i>Cronbach's α</i>
Items 1-6	1-6	5-6	5.97 (0.18)	-0.027 ^a
Items 7-13	10.5-21	12-21	17.58 (1.84)	0.439
Items 14-22	13.5-27	18-27	23.57 (1.62)	0.445
Short form	11.5-27	18-27	23.59 (1.86)	0.408
Long form	25-54	38-54	47.12 (2.99)	0.608
Christensen et al. (2002) short form	6-36	25-36	31.8 (2.12)	0.543
Modified short form (items 7-22)	24-48	32-48	41.15 (2.97)	0.616

In the original report of Benton (1984) a score equal or lower than 40 is reported as pathological and, thus, revealing a face recognition impairment. Our data on 272 healthy Italian participants showed very similar results, with a score equal or lower than 41 as pathological; by contrast, in the modified short form (items 7-22), that is - the version with the highest internal reliability, the cut-off score was 35.

Cambridge Face Memory Test

Data for the CFMT were obtained from 217 participants (39 males, mean age of 22.75 ± 2.67 y/o, age range 19-31 y/o, 5 left handed). Average scores are shown in table 2d; once again, average performance was either at floor or at ceiling, and showed a sufficient range. Confirming previous findings (Bowles et al., 2009; Herzmann et al., 2008), Cronbach's alpha was average to high for both the upright and inverted versions, and for all the subparts of the CFMT; indeed, the alpha for the upright CFMT was 0.897 when calculated on all 72 trials and 0.893 when calculated on the 54 trials from 'noise' and 'no noise' stages, whereas the alpha for the inverted

CFMT was 0.858 and 0.846, respectively. Only the ‘intro’ stage of the upright condition of the CFMT showed poor reliability because participants performed at ceiling. Further confirming the high reliability of the CFMT, accuracy on ‘noise’ and ‘no noise’ stages highly correlated both in the upright ($r(271) = 0.72, p < .001$) and in the inverted version ($r(271) = 0.41, p < .001$).

Table 2d. Descriptive statistics for the CFMT and the IE in typical individuals: chance/ceiling scores and observed range, mean and standard deviation, Cronbach’s alpha.

	<i>Chance-ceiling</i>	<i>Observed range</i>	<i>Mean (SD)</i>	<i>Cronbach’s α</i>
CFMT upright				
intro	6-18	15-18	17.78 (0.59)	0.474
no noise	10-30	8-30	22.66 (5.03)	0.844
noise	8-24	6-30	16.79 (3.80)	0.756
total	24-72	31-72	57.21 (8.51)	0.897
CFMT inverted				
intro	6-18	10-18	15.29 (2.08)	0.684
no noise	10-30	5-25	15.52 (3.39)	0.823
noise	8-24	4-19	10.78 (2.64)	0.797
total	24-72	25-61	41.59 (6.03)	0.858
Inversion effect	0/72	-4/+34	15.86 (7.32)	-

Two previous studies reported that young women perform 2.5 and 2.7 points better than men in mean performance (Duchaine & Nakayama, 2006; Bowles et al., 2009), even though these differences were not significant. More importantly, despite the detected difference in performance between women and men in these studies, it was not possible to find a difference in the cut-off scores for these two groups. In our sample of 217 participants we found a 2.94 points advantage for women in the upright version of the CFMT (female = 57.74 ± 8.09 ; male = 54.79 ± 10.03) and a 2.24 points advantage in the inverted version (female = 41.99 ± 6.01 ; male = 39.74 ± 5.81), and in both cases the difference was significant ($p = .050$ and $p = .035$). By contrast, no sex differences were found on the average score of the inversion effect (female = 15.75 ± 7.64 ; male = 15.05 ± 8.01 ; $p = .609$), which was very similar to the one detected in the original study of Duchaine and Nakayama (2006). In combination with a larger standard deviation in males, the gender difference in the average performance translated into a quite big difference in the cut-off score between males and females: females’ cut-off is 41.6, whereas the males’ cut-off is 34.7. In the case of the inverted version of the CFMT the difference in the average performance

translated in a 1.8-point difference in the cut-off score between males (28.1) and females (29.9). Finally, data on the inversion effect revealed that a score of 1 can be considered as cut-off to distinguish between normal and pathological performances.

One previous study (Bowles et al., 2009) has highlighted that country-specific norms may be needed to ensure a correct diagnosis of prosopagnosia. In order to further confirm this hypothesis, we compared the cut-off score for the upright version of the CFMT obtained in the present study with the data published by different authors (Duchaine & Nakayama, 2006; Bowles et al., 2009; Herzmann et al., 2008). Since in the previous studies only one cut-off score is calculated for both male and female participants, the same procedure was adopted also here. As evident from table 2e, the CFMT total score of this study was similar to the total score of the USA and Israeli samples, but was better than the German and Australian samples. In combination with different variances in the different samples, the average total scores in these studies produced different cut-off scores; for instance, whereas a 1-point difference is found between the present study and the Israeli sample, a larger 5-points difference exists between the Italian and German samples. These differences should be considered of strong theoretical and practical relevance: indeed, the use of wrong cut-off scores can result in underestimating or overestimating the cases of prosopagnosia.

Table 2e. Effect of the country of origin of the participant on the average performance and on the cut-off score of the upright version of the CFMT. USA data are from Duchaine & Nakayama, 2006; Israel and Australia/New Zealand data are from Bowles et al., 2009; Germany data are from Herzmann et al., 2008. The cut-off score is calculated as mean performance minus 2 standard deviations.

<i>Country</i>	<i>N</i>	<i>Age (range)</i>	<i>Mean (SD)</i>	<i>Cut-off</i>
USA	50	20.3	57.9 (7.9)	42
Israel	49	22.0 (18-31)	57.6 (8.4)	41
Italy	217	22.7 (19-31)	57.2 (8.5)	40
Australia/New Zealand	117	23.0 (19-32)	55.2 (8.6)	38
Germany	153	24.0 (18-35)	52.0 (8.5)	35

Relationship between the CFMT and the BFRT

The CFMT assesses the ability to learn new faces and to later recognize them under different viewing conditions (i.e., lighting, viewpoints and noise). On the other side, in the BFRT participants are presented with a target face above six test faces, and they are asked to indicate

which of the six images matches the target face; also in this test the six test faces can vary in viewpoint and lighting conditions. Finally, the inversion effect is usually taken as index of the expert mechanism that characterizes face recognition. Thus, in order to assess whether the BFRT, the CFMT and the inversion effect tap into the same underlying ability, I investigated the correlation between these three scores. The long form of the BFRT significantly correlated with the total score of the CFMT upright ($r(217) = 0.40, p < .001, UB = 0.738$), the total score of the CFMT inverted ($r(217) = 0.19, p < .01, UB = 0.722$) and with the inversion effect score ($r(217) = 0.30, p < .001$). Furthermore, as expected, the total score of the upright version of the CFMT correlated with its inverted version ($r(217) = 0.48, p < .001, UB = 0.877$). Thus, these results seem to suggest that, despite the BFRT and CFMT assess different and dissociable skills (e.g., face perception and face memory), they also tap into overlapping abilities. However, the fact that the correlations are not at maximum carries the theoretical implication that face perception and face memory are partially dissociable skills.

Participants with face recognition impairment

As stated in the introduction of this study, the BFRT and the CFMT are two of the most used tests for the diagnosis of prosopagnosia. However, as highlighted by this and previous studies, different factors, such as participant's gender and participant-to-stimuli ethnicity match, can affect the normative score used to define the cut-off scores for the diagnosis of the impairment. Thus, I examined the BFRT, CFMT and inversion effect scores of 23 individuals with congenital prosopagnosia. All these individuals were recruited because they reported face recognition problems in everyday life.

Only 5 out of the 23 congenital prosopagnosics showed a pathological score in the BFRT, supporting previous findings showing that some, but not all, individuals with this impairment experience difficulty in face discrimination in addition to face memory (e.g., de Gelder & Rouw, 2000). Furthermore, as already demonstrated by some studies, individuals with prosopagnosia may achieve normal scores on the BFRT given the availability of external cues for recognition (e.g., Duchaine & Nakayama, 2004); in the attempt to overcome some of the limitation of the BFRT we proposed a modified total score for this test, by excluding items 1 to 6 in which the test and the target stimuli consist of the same exact pictures. However, even when considering this new modified score, still only 5 congenital prosopagnosics showed a pathological score. This result suggests that (1) not all individuals with prosopagnosia have difficulties in face discrimination, and that (2), given its low reliability and the fact that alternative strategies can be used in order to complete the task, normal scores on the BFRT do not necessary reflect

normal face discrimination abilities. For these reasons, we suggest that alternative tests, such as the Cambridge Face Perception Test (CFPT, Duchaine et al., 2007), should be used in the evaluation of face discrimination abilities.

In the upright version of the CFMT all 23 individuals with congenital prosopagnosia showed a pathological score, both considering the overall cut-off score or the female cut-off score. By contrast, none of the congenital prosopagnosics showed a score below the cut-off score of 29 in the inverted version of the test. These results confirm the reliability of the CFMT in the diagnosis of prosopagnosia, but also show that individuals with congenital prosopagnosia do not have difficulties in processing inverted faces, further suggesting that upright and inverted faces are processed in a qualitative different way. As a consequence, most of our individuals with congenital prosopagnosia do not have an inversion effect or show a reduced one.

Table 2f. Scores of the 23 individuals with congenital prosopagnosia in the BFRT, CFMT and inversion effect. * = pathological score according to the relative cut-off score.

<i>Participant</i>	<i>Age</i>	<i>BFRT total</i>	<i>BFRT modified</i>	<i>CFMT upright</i>	<i>CFMT inverted</i>	<i>IE score</i>
AS	23	47	41	40*	39	1*
AM	20	41*	35*	38*	40	-2*
AD	22	45	39	40*	34	6
CS	19	49	43	37*	45	-8*
CR	21	40*	34*	36*	30	6
ES	24	48	42	37*	37	0*
EB	20	40*	34*	36*	35	1*
FC	26	45	39	38*	42	-4*
GM	19	50	44	37*	31	6
LC	24	44	38	35*	35	0*
LP	26	38*	32*	40*	39	1*
MBR	19	47	41	40*	39	1*
MB	19	47	41	34*	37	-3*
MDA	21	42	36	40*	34	6
MF	26	46	40	40*	38	2
MP	22	45	39	40*	45	-5*
NS	20	48	42	40*	40	0*
PC	20	44	38	40*	32	8
PV	20	41*	35*	38*	33	5
RB	22	46	40	40*	44	-4*
SE	20	46	40	37*	44	-7*
VT	30	47	41	37*	38	-1*
VF	20	47	41	32*	34	-2*

2.2.4. Conclusion

The aim of the present study was to provide better normative data for two of the most widely used tests to diagnose prosopagnosia. Indeed, some studies have suggested that in order to have adequate normative data it is necessary to gain these data from controls with a similar experience of faces as the ‘potential’ prosopagnosic individuals.

Regarding the BFRT, the results presented here from a large sample of 272 Italian students show that the validation of the test in a different sample from the original one results in a very similar cut-off score. This suggests that face discrimination abilities seem not to be affected by the participant-stimulus ethnicity match. Furthermore, no sex differences were found in the BFRT score, with males and females performing similarly. However, confirming previous results, the BFRT showed only a slightly acceptable reliability and, when individuals with face recognition impairments in everyday life are tested on this test, the BFRT classifies as impaired only 5 out of 23 congenital prosopagnosics. Although not all individuals with prosopagnosia may be impaired in face discrimination, the low reliability of the BFRT suggests that results from this test have to be interpreted cautiously and that alternative tests might be preferred to assess face perception/discrimination abilities.

On the other side, the results from the CFMT confirm the high reliability of this test, both in its upright and inverted conditions. Moreover, the CFMT results seem to be affected both by participant’s gender and participant-stimulus ethnicity match. Indeed, not only females significantly outperform males in both the upright and inverted orientations, but the difference in the average performance between the two samples is also reflected in different cut-off scores: whereas quite small for the inverted version, the difference is larger for the upright one. However, it is worth mentioning that in our sample female and male participants were not balanced, and the female participants represented around 80% of the total sample. Thus, it is possible that the difference we found regarding both the average performance and, especially, the cut-off score can be affected by the different numerosity of the male and female subgroups.

The results presented here also confirm that ethnicity match between the participant and the stimulus face matters, not only across races, but also within the same race - i.e., Caucasians. Indeed, as reported in table 2e, five different cut-off scores for the CFMT were found in five studies (including the present one) on different samples, confirming that norms for the CFMT should be derived from countries with a stimulus–participant match in ethnicity similar to that of the potential prosopagnosic, even where participants and faces are matched for race - i.e., all Caucasian. Finally, the present study further confirms the sensitivity of the CFMT in identifying congenital prosopagnosia; indeed, supporting previous studies (e.g., Duchaine & Nakayama,

2006; Bowles et al., 2009), when individuals reporting face recognition impairments in everyday life were tested, they all performed poorly in the upright version; interestingly, when tested in the inverted version of this test, their performance was not different from the controls' one, confirming that (1) they have a specific deficit in processing upright faces, and that (2) upright and inverted face are processed qualitatively differently, at least in the general population.

Overall, the present study provides more appropriate control and normative data for the BFRT and the CFMT for an Italian sample. Whereas the scores of the BFRT are not affected by participants' gender and are only slightly affected by participant-stimulus ethnicity match, both these factors seem to influence the scores of the CFMT. Finally, confirming previous studies, our results showed that the low reliability of the BFRT affects its sensitivity in identifying individuals with congenital prosopagnosia, raising questions about the pertinence of its use to detect the face recognition impairment.

2.3. Study III: Investigating face-specificity in congenital prosopagnosia: an eye-movement study

In chapters 2.1 and 2.2 two studies investigating the reliability of some of the most common tests used to assess prosopagnosia are described. In the present chapter, instead, I will report one eye-movement study we conducted in order to investigate face-specificity in congenital prosopagnosia. Even though designed and conducted at different times, and in the context of different research projects, all the three studies reported in chapter 2 shed light on some interesting topics and help us to understand the mechanisms underlying congenital prosopagnosia.

The defining feature of the congenital prosopagnosic deficit consists of a failure in recognizing faces. However, as already reported in the first chapter, the selectivity of the deficit has often been questioned. In particular, whereas the face-specific hypothesis claims that the core deficit of congenital prosopagnosia is a deficit in holistic processing of a face (e.g., parallel processing of a face as a whole, which combines the features and the spatial relationships between them), the alternative view considers it a problem in subordinate-level object discrimination and, thus, that difficulties would be detectable not only with face but also in the recognition of objects within the same class (within-class hypothesis).

In particular, one of the most common arguments typically used to support the presence of holistic processing impairment in congenital prosopagnosia is the absence of inversion effect

for faces in these individuals. The face inversion effect is usually explained by the fact that good recognizers use an expert holistic processing for upright faces, whereas they switch to a non-expert part-based analysis in the case of inverted faces (Tanaka & Farah, 1993). Accordingly, some studies (e.g., Barton et al., 2006) have shown that good recognizers scan upright faces differently from inverted faces, with a more random sequence of fixations in the latter condition. By contrast, congenital prosopagnosics do not show the normal face inversion effect during behavioral tasks (Behrmann et al., 2005; Duchaine et al., 2007; Russell et al., 2009) and, according to some authors (e.g. Behrmann & Avidan, 2005; Gauthier & Tarr, 1997), they process both upright and inverted faces in the same non-expert part-based way. In particular, abnormal gaze behavior in congenital prosopagnosia has already been demonstrated during the processing of upright faces (Schwarzer et al., 2007; Schmalzl, Palermo, Green, et al., 2008), but no studies have taken advantage of the eye tracking technique to shed light on congenital prosopagnosics' processing of inverted faces. In fact, despite eye movements can give us information about how the efficiency and distribution of gaze control affect the perception (and recognition) of a stimulus (Bloom & Mudd, 1991), and provide insights into how prosopagnosic individuals process the information in faces (Barton et al., 2007) and other objects, no one has ever investigated the effect of face inversion on scanning strategies in congenital prosopagnosia, and proof of dispersed gaze behavior also during the processing of inverted faces has not yet been provided.

Furthermore, since previous studies showed the existence of an inversion effect also for non-face objects in normal recognizers, although to a lesser extent compared with faces (e.g., de Gelder & Rouw, 2000; Diamond & Carey, 1986; Gauthier & Tarr, 1997; Scapinello & Yarmey, 1970), in order to support the face-specific nature of the impairment of congenital prosopagnosics, it is necessary also to investigate whether the lack of inversion effect is face-specific or whether it is also visible with objects other than faces.

For these reasons, in this study we investigated the scanning pattern during face and non-face stimulus processing in 12 individuals with congenital prosopagnosia and 13 controls during the encoding of both upright and inverted faces (Experiment 1) and various objects (Experiment 2). The comparison between the two orientation conditions during the recording of eye movements could provide useful information to determine the strategy that individuals with congenital prosopagnosia use to acquire visual-sensory information related to faces and objects, and shed light on the consistency of their impairment by analysis of their anomalous scan path behavior. Particularly, if the lack of inversion effect in congenital prosopagnosic is face-specific, a similar exploration and inversion effect to controls during the recognition of objects should be

found, suggesting that the lack of inversion effect for faces in these individuals could be actually due to a deficit in holistic processing. On the other side, congenital prosopagnosics could also fail to show an inversion effect in the case of objects other than faces, by not showing any advantages in the processing of objects in their canonical perspective; in this case, this result might suggest that their impairment is not face-specific and could actually be related to a more general mechanism affecting every kind of visual stimulus. Moreover, the few existing studies that have investigated scanning strategies in this population included only a small sample of four individuals with congenital prosopagnosia (Schwarzer et al., 2007) or even a single case (Schmalzl, Palermo, Green, et al., 2008). By contrast, in this study we were able to take advantage of a larger sample size that is more representative of this population, and which could lead to a more accurate investigation of their gaze behavior.

Finally, the key prediction of the within-class hypothesis is that individuals with congenital prosopagnosia should be impaired every time they have to recognize perceptually similar exemplars within a category. Supporting the within-class hypothesis, some studies (de Haan & Campbell, 1991; Gauthier & Tarr, 1997; Rossion, et al., 2002; Behrmann et al., 2005; Duchaine & Nakayama, 2005; Duchaine, et al., 2007) have shown that some congenital prosopagnosics have within-class object recognition deficits (e.g., birds, flowers, cars, horses, guns, houses and tools). However, other studies found that these individuals perform within the normal range for tasks involving the recognition of within-class objects, supporting the specificity of face recognition (Bentin et al., 1999; Duchaine et al., 2006).

Nevertheless, out of all the existing studies that have shed light on this subject (e.g., Duchaine & Nakayama, 2005; Behrmann et al., 2005; de Haan & Campbell, 1991; Bentin et al., 1999; Duchaine et al., 2006), again, none that investigated within-class recognition in congenital prosopagnosics has taken advantage of eye movement recording technology to address this issue. In this case, recording the eye-movements made during within-class object recognition can allow us to overcome the limits of an accuracy-based approach and, hence, highlight any possible impairments in object recognition that are not detectable in other measurements (i.e. accuracy and RT). Therefore, taking into consideration the mixed results reported in the literature on this topic, in the last part of this study we investigated the scan pattern of both controls and congenital prosopagnosics during the encoding of within-class objects (Experiment 3). Individual-item object recognition is similar to facial identity recognition in that it requires the recognition of individual items within a category (Galaburda & Duchaine, 2003). Therefore, if congenital prosopagnosics' impairment affects individual-item recognition within a class (irrespective of what the class is), they would perform significantly

worse than controls in this task and show a different eye-movement pattern in comparison, supporting the within-class hypothesis. Conversely, if their impairment is exclusively face-selective, a performance similar to that of controls without an anomalous eye movement pattern would be expected.

2.3.1. Participants

All participants had normal or corrected-to-normal vision and no evidence of neurological or neurophysiological alterations. All were right-handed. The study was approved by the ethics committee of the University of Milan-Bicocca, and an informed consent was obtained from all participants prior to the onset of the experiment. Participants received university course credit for taking part in the experiment.

Congenital prosopagnosics

Twelve females (all right-handed, age range 19-30, mean age 22.92 ± 3.37) with congenital prosopagnosia participated in the study and composed the experimental group (CP group). All were undergraduate students recruited from the University of Milan-Bicocca.

All these participants underwent a semi-structured interview conducted by an experienced neuropsychologist to assess the presence of congenital prosopagnosia and to exclude possible alternative explanations for face recognition impairment (i.e., brain damage). All reported significant difficulty in recognizing people starting from face information alone (i.e., situations in which people wear similar clothes, such as swimwear or uniforms), life-long impairment in face recognition, and common symptoms of prosopagnosia (i.e., reliance on non-face cues to recognize others). All individuals underwent a neuropsychological battery for the assessment of face recognition abilities (see next section).

Control participants

To select individuals who did not have face recognition difficulties, 41 participants (10 males, all right-handed, age range 19-31, mean age 23.95 ± 2.97) were recruited and underwent a neuropsychological battery composed by four tests (see next section). All were undergraduate students from the University of Milan-Bicocca who were recruited through the Milan-Bicocca Sona System©. These participants' scores were then used as normative data to calculate the z-scores for participants with congenital prosopagnosia on each test.

On the basis of the participants' agreement to come back to undergo the second part of the experiment, 13 out of the 31 female participants returned for the three main experiments

and composed our final control group (all females, all right-handed, age range 19–29 years, mean age 23.08 ± 2.93). None of them reported face recognition impairments or difficulties at any point in their lives.

2.3.2. Material and Methods

Neuropsychological assessment

Initially, all participants underwent a neuropsychological battery composed of four tests: the Benton Facial Recognition Test (BFRT; Benton & Van Allen, 1968; Benton, 1994), the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006a), the Boston Naming Test (BNT, J. T. Kaplan, Goodglass, & Weintraub, 1983) and the Famous Faces Recognition Test (FFRT). All tests were administered in counterbalanced order during a single session. In addition to this test, we calculated another index from the CFMT, which is the difference between the total score of the upright and inverted faces, namely the *inversion effect* (IE) (Yin, 1969). These tests were selected to evaluate the presence of prosopagnosia by assessing participants' ability to recognize unfamiliar and familiar faces (i.e., BFRT and CFMT, and Famous Face Recognition Test, FFRT, respectively) and by assessing their visual object recognition (i.e., the Boston Naming Test, BNT, Kaplan et al., 1983; for a more detailed description of the CFMT and BFRT see previous chapters).

The BNT (Kaplan et al., 1983) was used to assess visual object recognition and visual naming ability by using black and white line drawings. It consists of 60 line-drawn pictures presented with increasingly difficulty (e.g., from “tree” to “abacus”). Participants have 20 seconds to name each item. Phonemic cues are given after a failure to respond or an incorrect response. A new test of famous face recognition, the FFRT, was created to assess participants' ability to identify famous people from their faces; it is composed of 43 trials of current celebrities (21 males and one practice trial). The celebrities were taken from different professional categories (e.g., entertainers, actors, politicians, singers, athletes) and different nationalities. A frontal picture of each celebrity, among the ones labelled for reuse with modification, was downloaded from the Internet, then converted to grayscale and cropped into an oval (345 x 470 pixels) to exclude all the external features (such as hair and ears). On each trial, participants were presented with the celebrity's picture at the center of a computer screen (1366 x 768 pixels, 31 x 17.5 cm, 60 Hz refresh rate) at a viewing distance of approximately 60 cm (so that the picture size was approximately $7.5^\circ \times 10^\circ$ of visual angle) and were required to explicitly identify the celebrity by name or other uniquely identifying semantic information. The

celebrities' pictures were presented in the same order for all the participants. At the end of the test, the 42 names of celebrities were read to the participants to verify that none of the celebrities was unknown to them.

For each test, we calculated the normative data based on the performance of the 41 initial participants who underwent the neuropsychological assessment. The mean scores for each test (\pm SD) were as follows: 46.66 ± 2.66 for the BFRT, 56.17 ± 8.01 for the upright version of the CFMT, 41.32 ± 5.51 for the inverted version of the CFMT, 14.85 ± 6.34 for the inversion effect (i.e., the difference between the scores of the upright and inverted versions of the CFMT), 31.78 ± 5.49 for the FFRT and 55.75 ± 2.75 for the BNT. The individual raw scores for each congenital prosopagnosic, as well as their z-scores calculated on the data of the initial group of 41 participants, are shown in Table 2g.

All our 12 congenital prosopagnosics were clearly impaired in face recognition: they all performed 2 SD below the mean of the control group in both the CFMT and the FFRT. The exact individuation of congenital prosopagnosia was also confirmed by comparing the CFMT z-scores calculated on our data with the published controls scores for this test (Duchaine & Nakayama, 2006) (See Table 2g). Moreover, further supporting the correct selection of the congenital prosopagnosia sample, all these individuals showed a reduced inversion effect compared to the control group: in particular, 10 out of 12 had an inversion effect score 2.0 SD lower than controls, whereas in the case of the remaining two congenital prosopagnosic participants the inversion effect was still reduced even if to a lesser extent (i.e., 1.0 SD lower than controls). Finally, 3 out of the 12 congenital prosopagnosic participants performed pathologically in the BFRT, supporting previous findings that some, but not all, individuals with this impairment experience difficulty in face discrimination in addition to face memory (e.g., de Gelder & Rouw, 2000). Furthermore, it has to be mentioned that some studies have demonstrated that individuals with prosopagnosia may achieve normal scores on the BFRT given the availability of external cues to recognition (e.g., Duchaine & Nakayama, 2004), which may explain why 9 out of 12 congenital prosopagnosics performed normally on this test.

As regards to non-face stimuli recognition, none of the congenital prosopagnosics performed pathologically on the BNT, showing no impairment or difficulties in general visual processing. None of the control participants who agreed to come back (13 females) showed any impaired performance, and they all scored within the normal range on each test.

Table 2g. Demographic details and scores (raw values and z-scores) at the neuropsychological tests for the 12 CPs. BFRT = Benton Facial Recognition Test; CFMT = Cambridge Face Memory Test; IE = Inversion Effect; FFRT = Famous Face Recognition Test; BNT = Boston Naming Test; * = pathological score

	Age	BFRT		CFMT upright			CFMT inverted		IE		FFRT		BNT	
		raw score	z-score	raw score	z-score	z-score (Duchaine & Nakayama, 2006)	raw score	z-score	raw score	z-score	raw score	z-score	raw score	z-score
CPs														
A.S.	23	47	0.13	40	-2.02*	-2.27*	39	-0.60	1	-2.18*	16	-2.87*	54	-0.64
C.R.	25	40	-2.50*	36	-2.52*	-2.77*	30	-2.05*	6	-1.40	11	-3.79*	58	0.82
E.B.	20	40	-2.50*	36	-2.52*	-2.77*	35	-1.15	1	-2.18*	14	-3.24*	56	0.09
G.M.	20	50	1.26	37	-2.39*	-2.65*	31	-1.87	6	-1.40	17	-2.69*	54	-0.64
L.C.	24	44	-1.00	35	-2.64*	-2.90*	35	-1.15	0	-2.34*	15	-2.51*	55	-0.27
L.P.	26	38	-3.26*	40	-2.02*	-2.27*	39	-0.42	1	-2.18*	8	-4.33*	55	-0.27
M.B.R.	19	47	0.13	40	-2.02*	-2.27*	39	-0.42	1	-2.18*	18	-2.51*	54	-0.64
M.B.	20	47	0.13	34	-2.77*	-3.03*	37	-0.78	-3	-2.82*	18	-2.51*	58	0.82
M.F.	26	46	-0.25	40	-2.02*	-2.27*	40	-0.24	0	-2.34*	17	-2.69*	57	0.45
M.P.	22	45	-0.62	40	-2.02*	-2.27*	45	0.67	-5	-3.13*	18	-2.51*	56	0.09
S.E.	20	46	-0.25	37	-2.39*	-2.65*	44	0.49	-7	-3.45*	18	-2.51*	57	0.45
V.T.	30	47	0.13	37	-2.39*	-2.65*	38	-0.60	-1	-2.50*	18	-2.51*	57	0.45
Controls'														
mean ± SD	23.1 ± 2.93	48.00 ± 2.52		65.08 ± 5.14			44.15 ± 4.67		20.92 ± 4.61		33.08 ± 5.42		56.15 ± 1.68	

Stimuli

Three different types of stimuli were created and used in the present study:

(1) *Face stimuli* consisted of a set of 39 frontal-view photographs of neutral female faces. All the depicted models gave their informed consent for the use of their photographs for the purpose of this experiment. Models were photographed under symmetrical ambient light on a white background with a neutral expression and looking directly at the camera (Nikon d5100). At the next stage, photographs were then converted into black and white images using Adobe Photoshop CS4®, and to adjust eye collinearity between the two hemi-faces, the whole image (3648 x 2736 pixels) was rotated between -1° and 1° and scaled. Then, an oval size-defined frame was fitted so that external features, such as hair, were excluded. Any subject-specific traits (pimples, moles, scars) that could facilitate recognition were also removed. The final oval face image was fully included in a 384 x 486-pixel rectangle ($12^\circ \times 15^\circ$ of visual angle; see Figure 2a for an example of stimulus).

(2) *Non-face stimuli* were high-resolution photographs of 13 different stimuli (both living and non-living) in their most conventional perspectives (e.g. watering can, mobile phone, cat, etc.). All pictures were taken from the Internet among the ones labelled for reuse with modification. The target items were selected partially based on the example stimuli used by Biederman (1987), so they differed in complexity because of their different number of components (geons) and because of the category they belonged to. For each target stimulus, we selected two different pictures (e.g., two different lamps with almost the same global shape), so that one picture was shown during the encoding phase and the other one during the recognition phase. We used two different pictures of the same stimulus during the two phases to make sure the participants visually explored the stimulus in the most “ecological” way possible and to ensure that they did categorize the target item and did not focus only on specific and task-dependent details of the picture. For each target stimulus, two distractors were shown during the recognition phase: a perceptual distractor, perceptually similar to the target stimulus (in shape, dimension and complexity), and a semantic distractor, perceptually different from the target stimulus but semantically related to it. The initial image of each stimulus was isolated from the background, converted into black and white using Adobe Photoshop CS4® and adjusted so that the whole stimulus was fully included in a 486 x 486 pixels square ($15^\circ \times 15^\circ$ of visual angle).

(3) *Within-class stimuli* consisted of a set of 39 high-resolution photographs of different gerberas in their frontal view. Pictures were taken from the Internet among the ones labelled for reuse with modification; as for the other stimuli, the initial images of the flowers were cropped from their background, converted into black and white images using Adobe Photoshop CS4® and reduced so that the whole flower was fully included in a 486 x 486 pixels square (15° x 15° of visual angle). This time, on each trial, the picture used as the target flower was the same in both the encoding and recognition phases.

Procedure and eye-movement recordings

Participants sat in a comfortable chair 57 cm away from a Sony Trinitron monitor (60 x 34 cm, 1920 x 1080 pixels, and a refresh rate of 120 Hz) in a quiet room. Participants' eye movements were monitored via an SR Research EyeLink 1000 eye tracker (SR Research Ltd., Mississauga, Ontario, Canada) sampling at 1000 Hz and with a spatial resolution of less than 0.2°. Although viewing was binocular, only the right eye was tracked, and the recording concerned only the encoding phase of the target stimulus. Head movements were restrained by the use of a chin and a forehead rest. Before the experiment began, participants underwent a nine-point calibration procedure. The calibration started with the presentation of a white dot in the center of a black screen, which afterward moved around the edge of the screen, until an adequate corneal lock was achieved in each location. The calibration was accepted when the worst error point in the calibration was less than 0.75° and the average error for the nine-points less than 0.5°. The experiment was controlled by Experiment Builder software (SR Research Ltd., Mississauga, Ontario, Canada). Responses were collected using a keyboard. The instructions of the task were displayed by using a self-paced presentation on the screen at the beginning of the experiment.

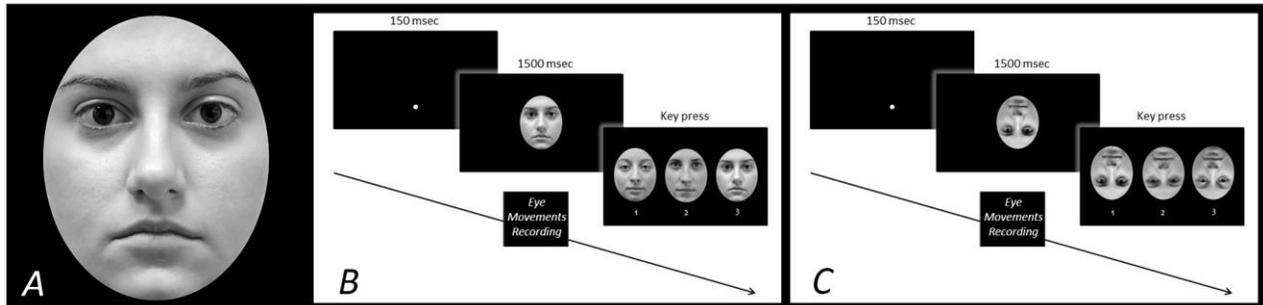
In this study, participants underwent three matching tasks (face, non-face and within-class stimuli) requiring them to discriminate an encoded target within a group of three stimuli displayed horizontally. During the task, each trial started with a fixation point located at the bottom part of the screen (approximately 10.5° below the center of the screen and 3° under the target stimulus) to control the initial point of retinal attention. If the participant's fixation remained stable within 1° of this fixation point for at least 150 ms, a target stimulus was presented for 1500 ms at the center of the screen (encoding phase), and the participant was instructed to watch it closely to memorize it. If

the fixation criterion was not met within 5 s, the trial was stopped, and the calibration procedure was repeated.

After the 1500 ms of stimulus presentation during the encoding phase, three stimuli appeared horizontally aligned in the center of the screen. Participants were asked to press the “1” key (right index finger placed on the 1 of the keypad) to choose the leftmost stimulus, the “2” key (right middle finger placed on the 2 of the keypad) to choose the stimulus in the center, or the “3” key (right ring finger placed on the 3 of the keypad) to choose the rightmost stimulus. The target stimulus and the two distractor stimuli remained on the screen until the participant provided a key-response (see Figure 2a for an example of trial procedure). Participants were asked to be as fast and as accurate as possible.

The presentation order of the stimuli was randomized, as were the positions of the target face and distractors. Each participant completed 12 trials for the upright block first and then 12 trials for the inverted block in the case of the face and non-face stimuli. By contrast, in the case of the within-class stimuli, the orientation presentation of the stimuli was unique (neither upright nor inverted) because of the nature of the stimulus itself which does not have a vertical orientation. Before each block, a practice trial was run to let the participants familiarize themselves with the task and response modality. Practice trials were not counted for statistical analysis.

Figure 2a. Example of upright stimulus (A), and example of trial procedure for the upright (B) and inverted (C) conditions in Experiment 1.



Data analysis

The proportion of correct responses and reaction times (RTs) from correct trials only (measured from the onset of the response screen to response emission) were analyzed. RT outliers (2.5 SDs above or below the mean for each participant) were

discarded and not analyzed. The proportion of correct responses and the RTs were adopted as dependent variables in a repeated-measures ANOVA with a between-subjects factor, “group” (control group, CG, vs. congenital prosopagnosia group, CP), and a within-subjects fixed factor, “stimulus orientation” (upright vs. inverted), as well as their mutual interaction. Significant differences were further explored by Bonferroni post hoc multiple comparisons, and corrected *p*-values are reported.

Eye movement data were pre-processed using EyeLink Data Viewer software (SR Research Ltd., Mississauga, Ontario, Canada). Among all the eye movement parameters, mean fixation number, mean fixation duration per stimulus, and mean first fixation duration were analyzed in order to have information about the efficiency of the stimulus encoding (i.e., an increase in the number of fixation or in their duration are usually associated with more demanding tasks or less efficient processing; Irwin (2004); Just and Carpenter (1993); Yarbus (1967)); mean saccade length was analyzed in order to obtain information about the exploration of the stimulus (e.g., Liversedge & Findlay, 2000; Yarbus, 1967) - that is, longer saccades would suggest a broader and larger exploration of the stimulus compared to smaller saccades. These parameters were analyzed using the linear mixed-effects model (Baayen, Davidson, & Bates, 2008) as the primary statistical tool. The effects of interest were group (control group, CG, vs. congenital prosopagnosia group, CP), stimulus orientation (upright vs. inverted), and their mutual interaction. Random intercepts for participants were also introduced. Significant differences were further explored by Bonferroni post hoc multiple comparisons, and corrected *p*-values are reported (see details in each of the Results sections below).

The distribution of fixations over the stimulus was analyzed by creating heat-maps computed on the regions of interest (ROIs) resulting from the eye movement data of controls and congenital prosopagnosic participants. This analysis, used by Primativo et al. (2015), has the advantages of combining both the temporal and the spatial features of the fixation distribution pattern over the stimulus to obtain each participant’s cumulative fixation time and to avoid any issues due to the use of predefined ROIs (Caldara & Miellet, 2011) by providing a completely data-driven way to analyze the scanning distribution.

First, we identified the areas (ROIs) in which controls spent most of their fixation time during the encoding of the stimulus, and then we looked at the individual fixation distributions within those ROIs. For each control participant, we plotted each fixation,

weighted for its duration, to obtain a 2D matrix (of the same dimensions of the stimulus) of the cumulative fixation distribution for each stimulus. Then, each fixation was associated with a 2D Gaussian, centered at the fixation location; the sigma value of the 2D Gaussian was set to of 0.2° (equal to the eye tracker spatial error) around the fixation location, and the height of the Gaussian was weighted by the duration of the single fixation.

After this procedure was applied to all fixations, for each participant, we obtained a map showing the cumulative fixation time on each pixel of each stimulus. Thus, we pooled these individual maps across the control participants to obtain a control activity map for each stimulus. Afterwards, for each of these maps, we calculated the threshold value that corresponded to the mean value of the fixation activity calculated for the control participants, and we selected as ROIs those regions where the fixation time contribution was larger than this threshold value.

Finally, for each participant (both controls and congenital prosopagnosics), we measured the proportion of total fixation time (calculated on the single stimulus map) spent within the ROIs previously obtained. Later, we averaged the proportion of fixations within the ROIs across the stimulus and condition to obtain a single value for each participant indicating her mean proportion of fixations within the ROIs (i.e., overlapping fixations) in both the upright and inverted conditions. In this way, we drew the specific ROIs for the upright and inverted conditions. The maps obtained with this procedure allowed us to compare the eye movement patterns of the two groups to examine whether the two groups' scanning distribution was the same or different with upright and inverted stimuli.

To examine if, within each group, congenital prosopagnosics and controls employed different strategies during the encoding of upright and inverted stimuli, we repeated all the procedures described so far to identify the areas (ROIs) in which congenital prosopagnosics spent most of their fixation time. Thus, we estimated different ROIs for controls and congenital prosopagnosics, and for each participant, we measured (1) the proportion of total fixation time spent within the ROIs previously obtained for each upright stimulus (upright condition) and (2) the proportion of total fixation time spent within the same ROIs for each inverted stimulus after all the fixations of the inverted condition were flipped to be overlapped and comparable to the upright ones (inverted-flipped condition).

2.3.3. Results

Experiment 1 – Face task

Behavioral data: The results of the ANOVA on accuracy revealed that both the main effect of group ($F(1, 23) = 6.672, p < 0.05, \eta^2 = 0.77$) and the main effect of stimulus orientation were significant ($F(1, 23) = 26.986, p < 0.001, \eta^2 = 0.354$). By contrast, the interaction between the two main factors was not significant ($F(1, 23) = 0.008, p = 0.931, \eta^2 = 0.0009$). Congenital prosopagnosics were significantly worse than the control group in recognizing faces ($M = 0.873 \pm SE = 0.019$ and 0.904 ± 0.018 , respectively), but overall, the inverted condition was significantly more difficult than the upright one for both groups (0.799 ± 0.024 and 0.942 ± 0.012 , respectively; Table 2h). The analysis of variance on RTs, by contrast, showed a significant main effect of the stimulus orientation ($F(1, 23) = 37.404, p < 0.01, \eta^2 = 0.001$), but neither the main effect of group ($F(1, 23) = 2.67, p = 0.116, \eta^2 = 0.087$) nor the interaction between the two main factors was significant ($F(1, 23) = 1.584, p = 0.221, \eta^2 = 0.004$). In this case, both groups were significantly slower in recognizing inverted than upright faces (inverted: 1579 ± 101 and upright: 1288 ± 73 ms).

Table 2h. Mean values (standard error in parentheses) of proportion of correct responses, RTs and eye movement data for the controls and congenital prosopagnosics in Experiment 1.

Experiment 1 – Face Recognition				
	<i>Upright</i>		<i>Inverted</i>	
	<i>Mean CP</i>	<i>Mean CG</i>	<i>Mean CP</i>	<i>Mean CG</i>
<i>Accuracy</i>	.910 (.017)	.974 (.016)	.764 (.35)	.833 (.033)
<i>RTs (ms)</i>	1458 (105)	1119 (101)	1695 (146)	1479 (141)
<i>Fixation number</i>	5.14 (.270)	4.90 (.254)	5.16 (.270)	5.24 (.259)
<i>Fixation duration (ms)</i>	238 (16)	252 (15)	235 (16)	229 (15)
<i>First fixation duration (ms)</i>	177 (18)	155 (18)	172 (18)	183 (18)
<i>Saccade length (deg)</i>	2.26 (.115)	2.34 (.112)	2.23 (.116)	2.31 (.111)

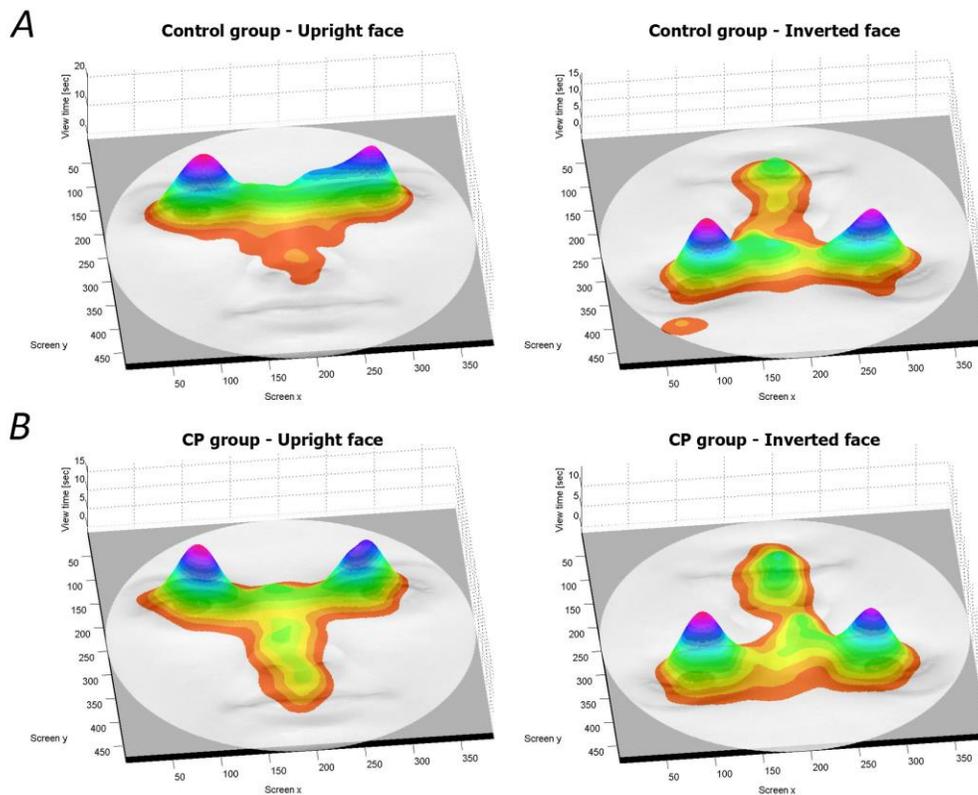
Eye movement data: We analyzed the basic eye movement information obtained from the participants while they were encoding the target face stimuli (see Table 2h). A significant main effect of the stimulus orientation was found in the mean number of

fixations per stimulus ($F(1, 569) = 6.502, p < .05$), in the mean fixation duration ($F(1, 3018) = 7.321, p < .01$) and almost in the mean first fixation duration ($F(1, 569) = 3.686, p = .055$). However, the interaction between stimulus orientation and group was also significant for all these three measures (mean fixation number per stimulus: $F(1, 569) = 4.663, p < .05$; mean fixation duration: $F(1, 3018) = 4.839, p < .05$; mean first fixation duration $F(1, 569) = 7.325, p < .01$). The interaction showed that control participants increased their number of fixations on inverted faces compared to upright faces (5.24 ± 0.26 and $4.90 \pm 0.25, p = .001$, respectively), but at the same time they shortened their duration (inverted 229 ± 15 ms, upright 252 ± 15 ms; $p < .001$). In contrast, congenital prosopagnosics made a similar number of fixations (upright 5.14 ± 0.27 and inverted $5.16 \pm 0.27; p = .83$) of similar duration (upright 239 ± 15 ms and inverted 235 ± 15 ms; $p = .72$) in both conditions. This suggested that even though controls changed their gaze behavior during the two conditions of presentation, highlighting their need for a greater visual exploration of the inverted stimuli during the encoding, congenital prosopagnosics kept constant their scanning strategy with both orientations. No significant effects were found in the saccade amplitude.

Scanning distribution: First we compared the scanning distribution of controls and congenital prosopagnosics with both upright and inverted faces in order to confirm the presence of an abnormal scan pattern in individual with congenital prosopagnosia. To this aim, we compared the mean proportion of fixations within the ROI of the two groups using an independent t-test. This analysis showed that the two groups differed significantly in their proportion of fixations within the ROIs only in the upright condition (CG = 0.941 ± 0.015 ; CP = 0.849 ± 0.029 ; $t(23) = 2.774, p = .011$). In the inverted condition, by contrast, congenital prosopagnosics and controls showed a similar proportion of fixations within the ROIs (CG = 0.926 ± 0.027 ; CP = 0.854 ± 0.029 ; $t(23) = 1.795, p = .086$). Afterwards, we compared the proportion of the overlapping ROIs between the upright and the inverted (flipped) conditions within each group. These comparisons allowed us to investigate whether controls and/or congenital prosopagnosics looked at different parts of the face and if they used different scanning strategies during the exploration of upright and inverted stimuli. A dependent t-test was carried out within each group to test if the difference between the upright and inverted conditions was significant. The control group showed a significant change in the scanning distribution, whereas congenital prosopagnosics did not. In fact, controls' proportion of overlapping fixations was significantly different between the inverted

condition and the upright one (upright = 0.941 ± 0.015 , inverted-flipped = $.788 \pm .053$; $t(12) = 3.25$, $p < .01$), but the same was not true for the congenital prosopagnosic participants (upright = 0.947 ± 0.009 ; inverted-flipped = 0.930 ± 0.014 ; $t(11) = 1.154$, $p = .273$).

Figure 2b. 3D representation of (A) controls' and (B) congenital prosopagnosics' scanning pattern during face encoding in the upright and inverted conditions. Notes: Areas of the same background color indicate those areas that were fixated upon for a time less than or equal to the threshold value. Areas of progressively colder colors indicate the areas that were fixated upon the most.



Experiment 2 – Object task

Behavioral data: The results of the ANOVA on accuracy revealed a significant effect of the group ($F(1,23) = 8.195$, $p < .01$, $\eta^2 = 0.148$), with congenital prosopagnosics performing worse than control participants (0.958 ± 0.01 and 0.997 ± 0.01 , respectively; see Table 2i). The main effect of the stimulus orientation did not reach statistical significance ($F(1, 23) = 2.155$, $p = .156$, $\eta^2 = 0.33$), whereas the interaction between the

group and the stimulus orientation was almost significant ($F(1, 23) = 4.006, p = .057, \eta^2 = 0.057$). Post hoc comparisons showed that congenital prosopagnosics were significantly worse in recognizing upright than inverted stimuli (0.938 ± 0.016 and 0.979 ± 0.009 , respectively; $p = .010$) and that the difference between the two groups was significant only in the upright condition. By contrast, the analysis of variance on RTs showed a significant main effect of the stimulus orientation ($F(1, 23) = 5.203, p < .05, \eta^2 = 0.029$), but neither the main effect of group ($F(1, 23) = 0.911, p = .35, \eta^2 = 0.032$) nor the interaction between the two main factors was significant ($F(1, 23) = 0.046, p = .832, \eta^2 = 0.0002$). Both groups were significantly slower in recognizing upright than inverted stimuli (827 ± 28 and 776 ± 33 ms, respectively).

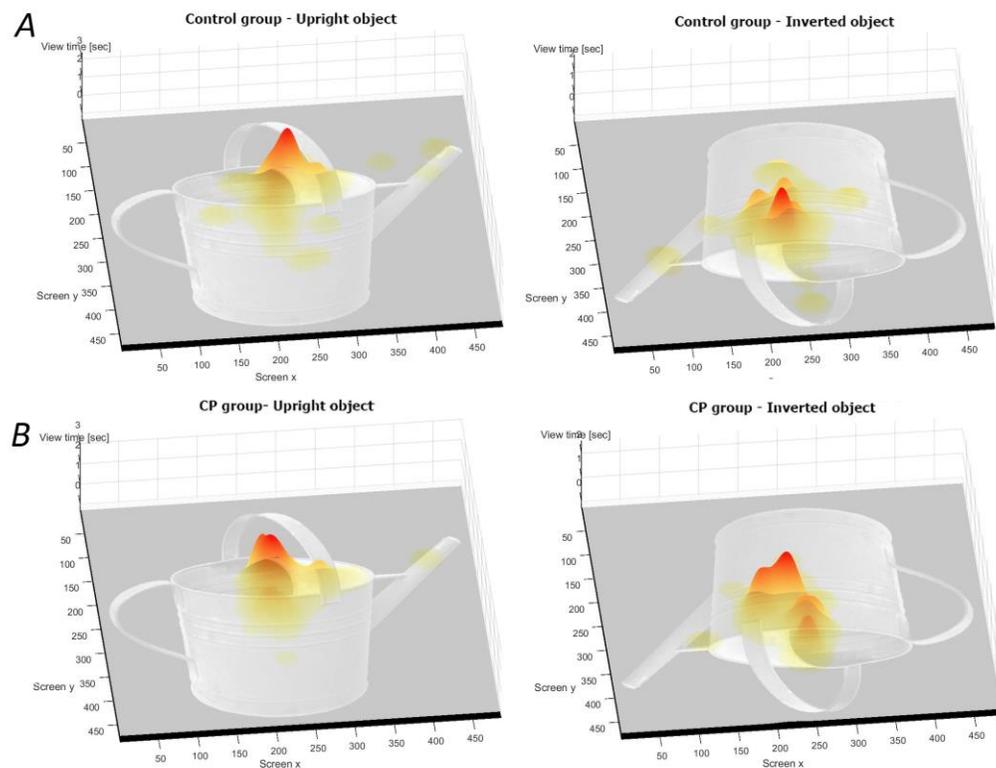
Table 2i. Mean values (standard error in parentheses) of the proportion of correct responses, the RT and the eye movement data for the controls and congenital prosopagnosics in Experiment 2.

Experiment 2 – Object Recognition				
	<i>Upright</i>		<i>Inverted</i>	
	<i>Mean CP</i>	<i>Mean CG</i>	<i>Mean CP</i>	<i>Mean CG</i>
<i>Accuracy</i>	.938 (.016)	1.00 (.015)	.979 (.009)	.994 (.009)
<i>RT (ms)</i>	803 (41)	853 (39)	746 (47)	806 (45)
<i>Fixation number</i>	3.42 (.162)	3.55 (.141)	3.37 (.164)	3.58 (.140)
<i>Fixation duration (ms)</i>	343 (18)	356 (17)	348 (19)	338 (16)
<i>First fixation duration (ms)</i>	259 (32)	222 (29)	317 (33)	349 (28)
<i>Saccade length (deg)</i>	2.65 (.197)	2.34 (.191)	2.52 (.200)	2.69 (.187)

Eye movement data: To obtain a general indication about the scanning strategies, we looked at the basic eye movement information obtained from participants while they were processing the stimulus during the encoding phase (see Table 2i). Congenital prosopagnosics and controls were not significantly different in terms of mean number of fixations per stimulus (CPs 3.39 ± 0.14 ; CG 3.56 ± 0.13 ; $F(1, 262) = 1.42, p = .234$) or in the mean fixation duration (CPs 345 ± 16 ms; CG 347 ± 14 ms; $F(1, 329) = 0.009, p = .926$). The main effect of the stimulus orientation was significant only in the mean first fixation duration, showing that both groups were inclined to make shorter first fixations during the upright condition (240 ± 24 ms) than during the inverted one (333 ± 24 ms; $F(1, 575) = 17.566, p < .001$). Moreover, the interaction between the two main factors on the length of the saccades was close to significant ($F(1, 1698) = 3.416, p$

= .065), showing that the control group made longer saccades in the inverted condition (2.7 ± 0.18 deg) than in the upright condition (2.3 ± 0.19 ; $p = .04$ deg). The congenital prosopagnosic participants did not show any difference in the length of saccades in the two conditions (upright = 2.6 ± 0.2 deg, inverted = 2.5 ± 0.2 deg; $p = .51$).

Figure 2c. 3D representation of (A) controls' and (B) congenital prosopagnosics' pattern of exploration during object encoding in the upright and inverted conditions. Notes: Areas with the same background color indicate parts that were fixated on for a time less than or equal to the threshold value. Areas of progressively colder colors indicate the areas that were fixated on the most



Scanning distribution: First, to examine which areas of the stimulus were visually more salient for the task and to investigate if congenital prosopagnosic participants scanned those stimuli differently from controls, the mean proportion of fixations within the control ROIs of the two groups was compared by using an independent t-test, which showed the absence of a significant difference between the two groups both in the upright (CG = 0.935 ± 0.016 ; CP = 0.943 ± 0.016 ; $t(23) = -0.342$, $p = .735$, $d = 0.14$) and inverted conditions (CG = 0.932 ± 0.011 ; CP = 0.928 ± 0.023 ; $t(23) =$

0.135, $p = 0.894$, $d = 0.06$);). Second, a dependent t-test was carried out within each group to test if any differences between the upright and the inverted (flipped) conditions were significant. Both controls and congenital prosopagnosics showed a significant change in their scanning distribution; in fact, the proportion of overlapping fixations was significantly different between the inverted (flipped) condition and the upright one for each group (CG upright = 0.935 ± 0.016 , CG inverted = 0.647 ± 0.021 , $t(12) = 12.419$, $p < .001$; CP upright = 0.975 ± 0.003 , CP inverted = 0.655 ± 0.029 , $t(11) = 11.991$, $p < .001$).

Experiment 3 – Within-class stimuli task

Behavioral data: congenital prosopagnosics performed significantly worse than controls in recognizing a within-class stimulus (0.924 ± 0.024 and 0.981 ± 0.010 , respectively; $t(23) = 2.26$, $p < 0.05$, $d = 0.255$), but the independent t-test on the RT data did not show any significant difference between the two groups (CP 851 ± 118 ms, CG 933 ± 188 ms: $t(23) = 1.29$, $p = 0.21$, $d = 0.53$; Table 2l).

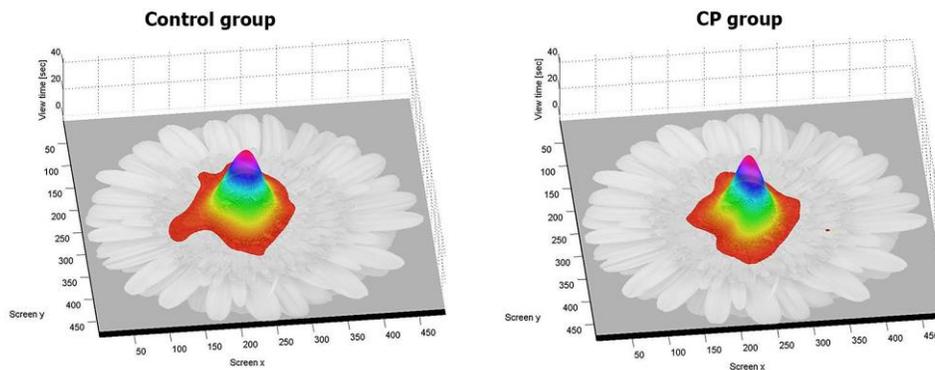
Eye movement data: When performing the task, congenital prosopagnosic participants made more fixations per stimulus than controls (3.48 ± 0.16 and 3.03 ± 0.14 , respectively; $F(1, 56) = 5.308$, $p < .05$; Table 2l). The analyses on the fixation duration showed that congenital prosopagnosics made shorter fixations, even if this effect was significant only for the first fixation duration (CPs 270 ± 36 ms, CG 376 ± 32 ms, $F(1, 47) = 5.32$, $p < .05$) and was nearly significant in the overall mean fixation duration (CPs 362 ± 21 , CG 410 ± 19 ms, $F(1, 49) = 3.193$, $p = .08$). No significant effect was found on the mean saccade length ($F(1, 23) = 2.285$, $p = .144$).

Table 2l. Mean values (standard error in parentheses) of the proportion of correct responses, the RT and the eye movement data for the controls and congenital prosopagnosics in Experiment 3.

Experiment 3 – Flower Recognition		
	<i>Mean CP</i>	<i>Mean CG</i>
<i>Accuracy</i>	.924 (.024)	.981 (.010)
<i>RT (ms)</i>	851 (34)	933 (52)
<i>Fixation number</i>	3.48 (.159)	3.03 (.139)
<i>Fixation duration (ms)</i>	362 (21)	410 (19)
<i>First fixation duration (ms)</i>	270 (36)	376 (32)
<i>Saccade length (deg)</i>	1.45 (.146)	1.76 (.135)

Scanning distribution: By using the same procedure as Experiment 1 and Experiment 2, we analyzed congenital prosopagnosics' fixation distribution over the stimulus to understand whether they scanned the within-class stimulus (i.e., a flower) differently from control participants. The mean proportion of fixations within the ROI of the two groups was compared by dependent t-test, which showed the absence of any significant differences between the two groups (CPs = 0.939 ± 0.015 , CG = 0.924 ± 0.019 ; $t(23) = -0.613$, $p = .546$, $d = 0.25$; see Figure 2d).

Figure 2d. 3D representations of the patterns of exploration during flower encoding for the controls and congenital prosopagnosics. Notes: Areas of the same background color indicate those areas that were fixated for a time less than or equal to the threshold value. Areas of progressively colder colors indicate areas that were fixated upon most.



Comparing Experiments 1, 2 and 3

Our results suggest that, even if congenital prosopagnosics' main impairment affects the processing of faces, there is also some evidence of difficulties with stimuli other than faces. To examine if congenital prosopagnosics' performance during these three experiments was related, their behavioral and eye movement data were correlated across the three tasks. Our underlying hypothesis was that, if congenital prosopagnosics showed a selective face recognition impairment only, their performance in each task would be independent of the others; otherwise, if congenital prosopagnosics' impairment reflected a more general deficit in subordinate-level object processing, we would expect to detect more similarities between congenital prosopagnosics' performance during experiment 1 (face task) and 3 (flower task) than between experiment 1 and 2 (object task).

As for the behavioral data, we found that the average accuracy and RT in the object task was correlated with the average accuracy in the face task (accuracy: $r = .61$, $n = 12$, $p = .037$; RTs: $r = .80$, $n = 12$, $p = .002$) and that RT in the within-class stimuli task correlated with RT in the face task ($r = .75$, $n = 12$, $p = .005$). This result suggests that, even though the three tasks involved different types of stimuli, the performance in the three conditions was not completely independent.

Furthermore, the correlation between the eye movement data revealed that the mean number of fixations per stimulus ($r = .57$, $n = 12$, $p = .05$), the mean fixation duration ($r = .66$, $n = 12$, $p = .019$), the mean first fixation duration ($r = .63$, $n = 12$, $p = .028$) and the mean saccade amplitude ($r = .71$, $n = 12$, $p = .01$) in the flower task and in the face task were highly correlated. By contrast, the same measurements between the face and the object tasks were not correlated (mean number of fixations: $r = .38$, $n = 12$, $p = .23$; mean fixation duration: $r = .33$, $n = 12$, $p = .29$; mean first fixation duration: $r = .25$, $n = 12$, $p = .43$; mean saccade amplitude: $r = .28$, $n = 12$, $p = .38$), and the same was true also between the flower and the object tasks (mean number of fixations: $r = .29$, $n = 12$, $p = .36$; mean fixation duration: $r = .29$, $n = 12$, $p = .35$; mean first fixation duration: $r = .51$, $n = 12$, $p = .10$; mean saccade amplitude: $r = .13$, $n = 12$, $p = .68$). These findings further support the hypothesis that, even if congenital prosopagnosics' main impairment involves face recognition, they can experience difficulties during the processing of other types of stimuli. In particular, looking at congenital prosopagnosics' eye movement pattern, it seems plausible that there exists a relationship between the way they process face stimuli and the way they process within-class stimuli, further supporting the previous finding that these individuals are behaviorally impaired in individual-item discrimination within the same class (Behrmann et al., 2005; Gauthier, Behrmann & Tarr, 1999). In conclusion, congenital prosopagnosics' impairment was not strictly related to faces, and it is likely that it involves the more general subordinate-level object processing.

2.3.4. Conclusions

In the present study we conducted three experiments to investigate how congenital prosopagnosics acquire visual sensory information related to different types of stimuli in different orientations, in order to shed light on the relationship between object and face processing and on the nature of their impairment.

In particular, the aim of experiment 1 was to investigate the effect of face inversion on scanning strategies in congenital prosopagnosics, in order to obtain proof that their dispersed gaze behavior reflects the use of the same non-expert part-based strategy in both conditions. As expected, congenital prosopagnosics performed significantly worse than controls in recognizing faces, even though it must be mentioned that they performed relatively better in experiment 1 than in the neuropsychological tests of the screening part to assess face recognition abilities. However, in this experiment (as well as in experiment 3), the same image was used both for the encoding and testing phases and this could have reduced the difficulty of the recognition task. Thus, it could be possible that accuracy and RTs data were affected by our design and that the use of different pictures for the encoding and testing phases would have shown further differences. However, even if this were true, the same cannot be said about the eye movement data. In fact, the eye-movements of the participants were recorded only during the encoding phase and could not have been affected by the repetition of the target picture. Accordingly, the results from experiment 1 first confirm the findings of previous studies showing that, when faces are presented upright, congenital prosopagnosics show a more dispersed gaze behavior (with more frequent, shorter and more distant fixations) compared to controls (Schmalzl et al., 2008; Schwarzer et al., 2007). This could reflect their need to sample more information to encode the stimulus properly, compared with good recognizers, and their attempt to use extra-facial cues to recognize the face correctly. More interestingly, the scanning patterns of controls and congenital prosopagnosics were affected in different ways by the inversion of the face stimulus. Indeed, consistent with the results of previous studies (e.g. Barton et al., 2006), our controls scanned upright faces differently from inverted ones, with a more random sequence of fixations in the latter condition. Furthermore, a visual inspection of their heat-maps highlighted that controls explored different regions of the face depending on the orientation condition, by focusing more on the region between the eye in the upright condition (i.e., one of the optimum locations for holistic processing; Hsiao & Cottrell, 2008; Peterson & Eckstein, 2012), and increasing the time spent exploring the mouth region when faces were presented inverted. These results could suggest that good recognizers use an expert holistic processing only in the case of faces in the canonical upright perspective. By contrast, congenital prosopagnosics explored the face stimulus in the same way, independently of its orientation. In particular, they made a similar number of fixations of the same duration and focused on all the features of the

face (i.e. eyes, nose and mouth) under both sets of conditions, suggesting their use of a part-based strategy. Accordingly, congenital prosopagnosics differed significantly from controls only when presented with upright faces, suggesting that the holistic processing impairment that characterizes these individuals (e.g., Avidan et al., 2011; Ramon et al., 2010; Richler, et al., 2011; Palermo, et al., 2011; Kimchi, et al., 2012) is also reflected by their eye movement pattern. Conversely, when faces were presented upside-down, a part-based strategy had to be used, and therefore the eye movement performance of congenital prosopagnosics is comparable to the one of controls. Thus, the results from experiment 1 suggest that the absence of face inversion effect in congenital prosopagnosics during behavioral tasks (e.g., Avidan et al., 2011) could be due to the use of a part-based exploration of the face stimulus for both upright and inverted faces, as demonstrated by the analysis of their gaze behavior during the encoding of upright and inverted faces.

In experiment 2 we asked whether the lack of inversion effect in congenital prosopagnosics is face-specific or if it can also be visible with objects other than faces. Indeed, some studies have shown that some individual with congenital prosopagnosia can also be impaired in object recognition (e.g., Duchaine et al., 2003; Behrmann et al., 2005; de Haan & Campbell, 1991), even though objects are usually processed accurately in a part-based way (Biederman, 1987). In this task, congenital prosopagnosics exhibited a lower performance compared with controls. Nevertheless, the performance of these individuals still showed high accuracy and reduced variability, suggesting that they are not impaired in the recognition of stimuli other than faces. Supporting this evidence, the analyses of the eye movement data did not highlight any significant differences between scanning patterns in congenital prosopagnosics and controls, either in the upright or the inverted condition, suggesting that the processing was more effective in controls but was not qualitatively different in the two groups. Indeed, even if less effective than controls, the recognition process of congenital prosopagnosics was successful enough to allow them to use a “typical” visual exploration strategy. Conversely, in the case of faces, where congenital prosopagnosics’ performance is much lower, their impaired recognition process induced a change in their scanning strategy in the attempt to improve their performance (e.g., by looking at single features). Thus, in this latter case, the presence of a different exploration of the visual stimulus could be both a consequence of and a compensation for the reduced efficacy of their visual processing and behavioral performance.

Therefore, the results of experiment 2 seem to suggest that congenital prosopagnosics are not impaired in object recognition and that the lack of inversion effect in this population is face-specific. Interestingly, even though they did not differ from each other, both congenital prosopagnosics and controls changed their scanning strategies significantly for the upright compared with the inverted orientation. In fact, during the exploration of inverted stimuli, both groups tended to make shorter and more dispersed fixations, suggesting the use of an even more part-based strategy with these stimuli.

The presence of an inversion effect in terms of eye movements also during the encoding of objects could be explained by the possibility that even objects can be processed according to some types of orientation-dependent effect, as expert face processing does, and this result seems to be in agreement with other previous behavioral studies, which demonstrated that inversion can also disrupt the recognition of stimuli other than faces (e.g. de Gelder & Rouw, 2000; Diamond & Carey, 1986; Gauthier & Tarr, 1997). In fact, even though objects can be presented and handled upside-down, or even be seen in several different perspectives, they still have a canonical orientation in everyday life as faces do and could require the sampling of more visual information when presented in an unusual way. However, with the exception of people who develop a particular expertise for a specific object (e.g., Diamond & Carey, 1986; Gauthier, Williams, Tarr, & Tanaka, 1998), the magnitude of the inversion effect is typically larger for faces than for objects (e.g. de Gelder & Rouw, 2000; Diamond & Carey, 1986; Gauthier & Tarr, 1997), with the suggesting that the mechanisms underlying the two effects are different. Our results seem to support this hypothesis; indeed, since congenital prosopagnosics performed in a manner that was comparable to controls in the object task, the expert processing involved in object recognition seems to be independent of the expert face processing, further supporting the specificity of faces.

Finally, in experiment 3 we investigated the possibility that face impairment in congenital prosopagnosics could be the result of a problem in subordinate-level object discrimination, more than a face selective impairment, and that their processing impairment could also be evident in individual-item recognition within a class. Indeed, even though some studies (Gauthier & Tarr, 1997; Rossion et al., 2002; Behrmann et al., 2005; de Haan & Campbell, 1991; Duchaine & Nakayama, 2005) have shown that some congenital prosopagnosics have within-class object recognition deficits, other studies could not find any evidence (Bentin et al., 1999; Duchaine & Nakayama, 2006), proving

that the existence of a clear dissociation between face and within-class object recognition is still a matter for debate. However, as a result, our congenital prosopagnosics have performed worse in the recognition of within-class objects when compared with controls. Moreover, individuals with congenital prosopagnosia tended to make more frequent, shorter and more dispersed fixations compared with controls, suggesting their requirement for a deeper exploration of the within-class stimulus in order to encode it properly compared with good recognizers. Thus, the results for experiment 3 seem to confirm that impairment in congenital prosopagnosics is not strictly limited to faces but it could affect individual-item recognition within a class (irrespective of what the class is).

Confirming this hypothesis, we found similar gaze behavior characteristics between the face and the within-class object tasks. In particular, the shorter fixations made by congenital prosopagnosics during these two tasks could be explained in two different ways: 1) they focused on one particular area of the stimulus without being able to identify whether the information was relevant and then moved to another part of the stimulus; or 2) they processed all the separate parts correctly, without being able to integrate them and process the stimulus globally. Therefore, they adopted a more distributed scanning pattern (the greater the amount of collected information, the higher the chance of finally encoding the stimulus satisfactorily). Our results seem to point in the direction of the second hypothesis. In fact, during experiment 2, we found that congenital prosopagnosics did not show any impairment during the exploration of various objects; particularly, by using a part-based strategy similar to the one adopted by controls, they were able to extract all the information needed to correctly recognize the object, suggesting that the extraction of critical information from single features is not a problem for them. This result seems to be consistent with previous findings showing intact single-feature processing in congenital prosopagnosia (e.g., Avidan et al., 2011), the existence of a local bias in this population, and their lack of sensitivity to the composite face effect (Behrmann et al., 2005; Lê, Raufaste, & Démonet, 2003) (i.e., they exhibit equivalent performance with aligned and misaligned hemi-face images and are impervious to the normal interference from the task-irrelevant bottom sections of faces; Palermo et al., 2011). Therefore, because they can encode single parts correctly and the constituent parts of every example are similar in the case of within-class stimuli, whereas what change the most are the relationships between them, it seems unlikely that impairment in congenital prosopagnosics is related to the processing of the single parts

of the stimulus. What seems most plausible is that their failure in holistic processing (Avidan et al., 2011; Palermo et al., 2011; Tanaka & Farah, 1993) could affect their eye movement during these tasks, confirming that their main deficit could be an impaired subordinate-level object discrimination, as already suggested by other authors (e.g. Behrmann et al., 2005).

As further evidence, we found a clear relationship between the performance of the face and within-class objects tasks in both the behavioral performance and all the eye movement data, reconfirming that the performance in the two tasks was not independent. At the same time, the lack of any correlation between the object and the other two tasks strengthens the idea that the significant correlation we found is not simply due to a generic “scanning factor” detectable during any visual stimulus exploration, but rather, it highlights how these results are linked to the specificity of within-class stimuli.

In summary, this investigation of the behavioral performance and scan patterns in 12 individuals with congenital prosopagnosia has revealed that (i) congenital prosopagnosics use the same part-based strategy in encoding both upright and inverted faces, suggesting a possible interpretation for the lack of inversion effect in this population; (ii) the lack of inversion effect is face-specific and does not affect objects; (iii) however, the deficit in congenital prosopagnosics is not strictly limited to faces, but it also seems to extend to individual-item recognition within a class. Furthermore, our data show how the distribution and organization of scanning fixations can provide information about the face processing of individuals with congenital prosopagnosia and about their processing of non-facial stimuli, and can shed light on the ongoing debate about object and face recognition in prosopagnosia.

3. Self-recognition and lateralization biases in congenital prosopagnosia

3.1. Study IV: Right perceptual bias during self-face recognition in congenital prosopagnosia

As highlighted in chapter 1, the left and right parts of a face are not only less symmetrical than we think, but are also assigned different weights in face processing. Indeed, the right side of the face that falls in the observer's left visual field seems resemble our idea of a specific person more than the other side (Wolff, 1933). This bias, called *left perceptual bias* (LPB), has been detected in terms of improved accuracy and faster reaction times in different studies investigating different facial aspects, such as gender (e.g. Butler & Harvey, 2005, 2008; Schyns et al., 2002; Burt & Perrett, 1997), facial expression (e.g., Rhodes, 1993; Schiff & Truchon, 1993), emotion (e.g. Bourne, 2008; Bourne & Maxwell, 2010; Coolican et al., 2008), age and attractiveness (e.g., Burt & Perrett, 1997). Whether this effect is face-specific or not is still a matter of debate. One of the most accredited hypotheses links the left perceptual bias to the right hemisphere superiority for faces: when the observer looks straight at a face, the right side of the face lies in the left visual field, which directly projects to the right hemisphere. Thus, input coming from the left visual field would be analysed immediately by the appropriate right hemisphere, while input coming from the right visual field would be slower and more sensitive to interferences, having to pass through the left hemisphere and the corpus callosum. An alternative possible explanation for the left perceptual bias that has been also considered takes into account the influence of cultural-based scanning habits, and specifically reading habits (Vaid & Singh, 1989). Indeed, some studies (Heath et al., 2005; Megreya & Havard, 2011) have demonstrated that left-to-right readers showed the greatest leftward bias compared to right-to-left readers or bilateral readers, supporting the hypothesis that reading habits can determine our bias to process faces starting from the left side. However, the fact that also native readers of right-to-left exhibit a left perceptual bias, even if weaker compared to left-to-right readers, could suggest that, although the left bias could be a structural effect linked to the right hemisphere advantage for faces, environmental factors such as scanning habits could control its consistency (Megreya & Havard, 2011).

The left perceptual bias seems to characterize the perception of both unfamiliar and familiar/famous faces (e.g., Brady et al., 2004; Brady et al., 2005; Keyes & Brady, 2010). However, when we are asked to recognize our own face, the face recognition process seems to be characterized by an opposite bias. Indeed, the recognition of the self-face seems to be related to a *right perceptual bias*, which consists of a tendency to rely more on the right half-side of the face that falls in the right visual hemi-space when we look at ourselves in the mirror (Brady et al., 2004). In particular, the existence of a different perceptual effect during the self-face recognition process further confirms the specificity of the self-face as visual stimulus and might also suggest the existence of an asymmetry in the perception and recognition of self-related facial information.

Thus, in the present study we aimed to verifying the existence of the left perceptual bias and right perceptual bias in a group of participants with congenital prosopagnosia. In particular, by using this population we would be able to test the face specificity of these biases; indeed, since individuals with congenital prosopagnosia are specifically impaired in recognizing faces and process them differently compared to normal recognizers (e.g., Behrmann & Avidan, 2005), neither the left nor the right perceptual biases should be detectable in this population if they are linked to the specific processing that characterizes faces. By contrast, if these biases are not face-specific but are due to other factors (e.g., scanning habits), individuals with congenital prosopagnosia should show these effects as well.

3.1.1. Participants

Fifty-eight students from the University of Milan-Bicocca were recruited in two ways: 44 through the University of Milan-Bicocca Sona System© and 10 volunteers who responded to an advertisement recruiting participants with familiar face recognition impairment. Those who participated received university course credit. Each participant provided informed consent and written permission for the use of their photographs for the purposes of this study, in accordance with ethical guidelines by the University of Milan-Bicocca ethical committee. All participants had normal or corrected-to-normal vision and reported no known neurological damage.

All participants underwent two neuropsychological tests to assess their ability to recognize unfamiliar faces: the Cambridge Face Memory Test, (CFMT; Bowles et al., 2009; Duchaine & Nakayama, 2006) and the Benton Facial Recognition Test (BFRT; Benton, 1994; Benton & Van Allen, 1968). Moreover, to further confirm the presence of

prosopagnosia in the experimental group, the inversion effect was also calculated as additional index for all participants (as the difference in accuracy between the total score of the upright and inverted faces in the CFMT) and our z-scores were compared with published control scores for this test (Duchaine & Nakayama, 2006), as shown in Table 3a.

Control participants

Forty-four healthy control participants took part in the screening phase (all females, right-handed, age range 19–27, mean age 21.5 ± 1.87). All performed in the normal range in all tests (higher than 2.0 standard deviations below the mean). The scores obtained by these 44 participants formed the sample for the calculation of z-scores for the screening phase.

Twenty-one of the original 44 control participants returned for the experimental phase (all females, right-handed, age range 19–23 years, mean age 20.9 ± 1.34) and served as the final control group for the experimental phase. All the healthy controls included in the final control group scored within the normal range (± 2 SD) on the CFMT, and on the BFRT, and showed a positive inversion effect (i.e., they all performed better with upright faces compared to the inverted ones).

Participants with congenital prosopagnosia

Ten females (all right-handed, age range 19–24, mean age 20.8 ± 1.55) with congenital prosopagnosia participated in the study and composed the experimental group (CP group). All were undergraduate students recruited from the University of Milan-Bicocca. All participants were administered the two neuropsychological tests mentioned above (CFMT and BFRT) and underwent a semi-structured interview conducted by an experienced psychologist in order to assess the presence of congenital prosopagnosia and to exclude possible alternative explanations for face recognition impairment (i.e., brain damage). They all reported significant difficulty in recognizing people starting from face information alone, life-long impairment in face recognition and common symptoms of prosopagnosia – that is, reliance on non-face cues to recognize others. In addition, many of the participants reported that at least one additional family member has difficulty with face recognition. Furthermore, none of the participants reported a concomitant neurological disorder.

All 10 participants demonstrated performance below the normal range (less than 2.0 SD below the mean) on the CFMT. By contrast, only three of them showed a borderline or impaired score in the BFRT, suggesting impairment in face discrimination. These results are consistent with the data of the previous chapters and other studies showing that some, but not all, individuals with congenital prosopagnosia experience difficulty with face discrimination in addition to face memory (Ariel & Sadeh, 1996; de Gelder & Rouw, 2000). All our participants with congenital prosopagnosia showed an inversion effect that was smaller than that of the control group (below 1.0 SD): in particular, 5 out of 10 had an inversion effect score 2.0 SD lower than controls.

In Table 3a, the individual test scores for each participant with congenital prosopagnosia are shown, as well as the z-scores calculated for the data of each participant with congenital prosopagnosia.

Table 3a. Demographic features of the 10 individuals impaired in recognizing familiar faces and their performance scores (raw data and z scores) at neuropsychological tests of episodic face recognition.

Subject	Age	Benton			CFMT			Inversion Effect	
		raw score	z	cut-off	raw score	z	z (Duchaine & Nakayama, 2006)	raw score	z
C.S	19	49	0,42	normal	37	-2,71*	-2,65*	-8	-3,30*
M.D.A.	21	42	-1,68	normal	40	-2,35*	-2,27*	6	-1,35
P.C.	20	44	-1,08	normal	40	-2,35*	-2,27*	8	-1,07
C.R.	22	40	-2,28*	borderline	36	-2,83*	-2,77*	6	-1,35
E.S.	24	48	0,12	normal	37	-2,71*	-2,65*	0	-2,19*
P.V.	21	41	-1,98	normal	38	-2,59*	-2,52*	5	-1,49
A.M.	20	41	-1,98	normal	38	-2,59*	-2,52*	-2	-2,47*
R.B.	22	46	-0,48	normal	40	-2,35*	-2,27*	-4	-2,74*
S.E.	20	46	-0,48	normal	37	-2,71*	-2,65*	-7	-3,16*
G.M.	19	50	0,72	normal	37	-2,71*	-2,65*	6	-1,35
<i>CP mean ± SD</i>		<i>44,7 ± 3,62</i>			<i>38 ± 1,49</i>			<i>1 ± 5,96</i>	
<i>Controls mean ± SD</i>		<i>47,61 ± 3,34</i>			<i>59,64 ± 8,36</i>			<i>15,7 ± 7,18</i>	

3.1.2. Material and Methods

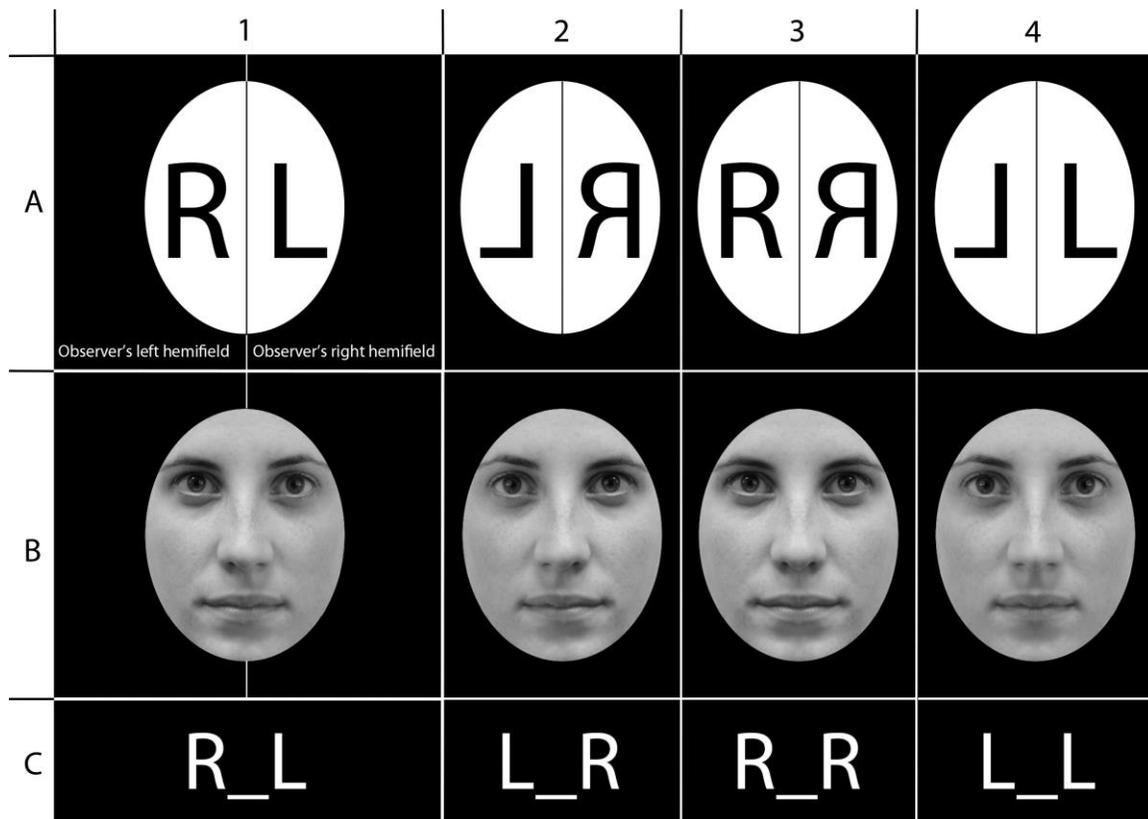
A unique face stimuli set was created for each participant. These stimuli included the participant's own face and three additional faces, matched for hair and eye colour of the participant. To create each unique stimulus set, the participant and three models

were photographed under symmetrical ambient light on a white background, with a neutral expression and looking directly at the camera (Nikon d5100).

In the final experiment, four versions of each photograph were used: (1) the original photograph, (2) the left-right reversal, or mirror image, of the original photograph, (3) a left-half-of-model's-face chimeric and (4) a right-half-of-model's-face chimeric. To create each of these stimuli, each photograph was converted into greyscale using Adobe Photoshop CS4® and any specific traits (e.g., pimples, moles and scars) that could facilitate self-recognition were also removed. In order to facilitate the later creation of the chimeric faces, we ensured proper collinearity of each photograph by rotating the face -1° to 1° , if needed, and centred the image on the screen on the basis of the face midline. Then, faces were scaled to provide consistency in the height of the face across different models; in the end, each face was 14.5 cm in height on the screen and subtended $\approx 14.5^\circ$ of visual angle. Finally, each face was cropped into an oval shape so that external features such as hair, were excluded. This oval was 12×14.5 cm on the screen and subtended $\approx 12 \times 14.5^\circ$ of visual angle, respectively. To create the two chimeric images, a vertical line passing through the face midline divided the face in half, allowing us to obtain the right and left sides of the model's face (192×486 pixels each). Starting from the obtained hemi-faces, two chimeric face stimuli were created of each face: a composite face made by two left half-faces, later referred to as L_L chimeric, and a composite face made by two right half-faces, later referred to as R_R chimeric (Figure 3a). The L_L chimeric was designed by creating a mirror image duplicate of the left side of the model's face and combining it with the left-half-of-face original. The same was done for the R_R chimeric. In the end, each image was 384×486 pixels (approximately $12 \text{ cm} \times 14.5 \text{ cm}$ on the screen). These steps resulted in 4 images (original-R_L, reversal-L_R, left-chimeric-L_L and right-chimeric-R_R) of each person's face (participant and 3 matched models) for a total of 16 images in each unique stimulus set — 4 images of the participant's face and 12 belonging to matched models.

As each participant only viewed their own stimulus set and none of the participants were familiar with any of the other participants or models (each participant provided a familiarity judgment for each photograph in their set), some photographs were used in more than one participants' stimulus set. For example, in the event of having two participants with the same hair and eye colour, the same models could be used for both participants.

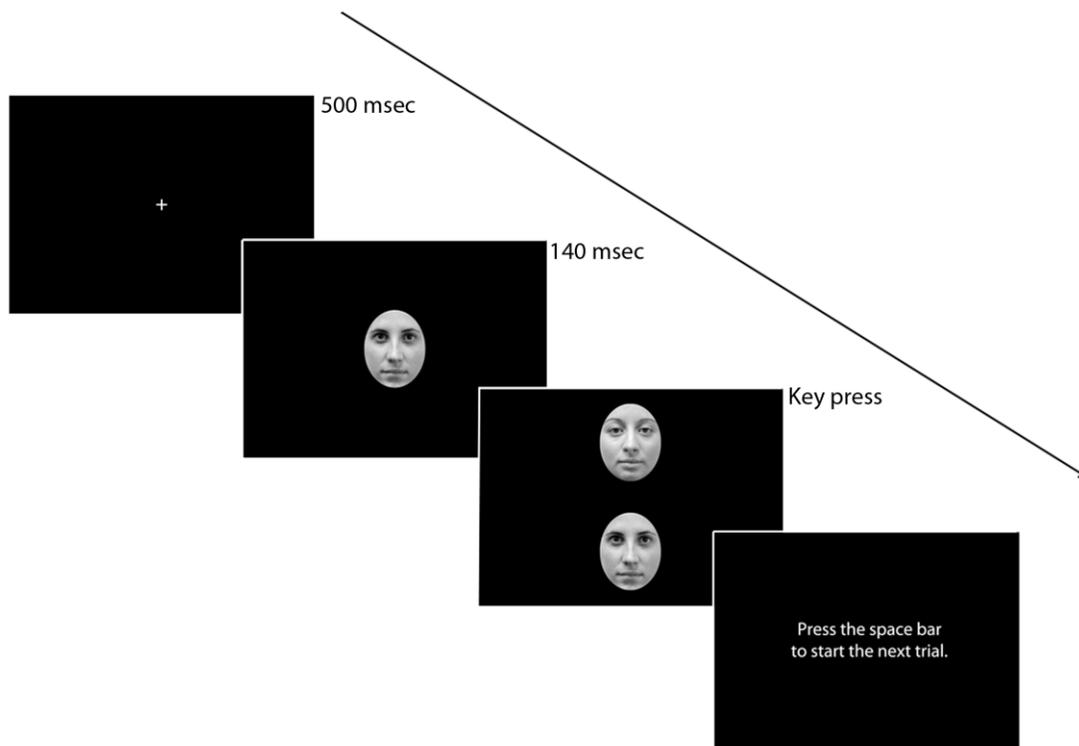
Figure 3a. Examples of Chimeric Stimuli. (A) Letters “R” and “L” refer to side of the model’s face from the model’s perspective. For example, the farthest left image in (A1) demonstrates the layout of an original photograph with the right side of the models face in the observer’s left hemi-field and the left side of the models face in the observer’s right hemi-field. “R–L” means that the stimulus was composed of the Right half-face falling in the observer’s LVF and the Left half-face falling in the observer’s RVF. Images (A2)–(A4) demonstrate how each image was modified relative to the original layout (A1). (B) Examples of four stimuli used in the experiment for one model. (A1) The original photograph, (A2) the left-right reversal, or mirror image, of the original photograph, (A3) a right-half-of-model’s-face chimeric, (A4) the left-half-of-model’s-face chimeric. (C) The labels used for each type of stimulus.



Participants sat in a comfortable chair approximately 57 cm from the monitor (40.5 cm × 30.5 cm, 1280 × 1024 pixels) in a dark silent room and a chin rest supported their head. The experiment was controlled by E-Prime 1.0 Software. All images were presented on a black background. Before starting, the experimenter explained to the participant that the procedure was self-paced: participants were explicitly informed to press the space bar to continue the task following each trial and were asked to be as accurate and as fast as possible. Each trial (Figure 3b) started with a fixation cross at the

centre of the screen for 500 ms. Immediately following the fixation cross, a target face was presented for 140 ms at the centre of the screen; participants were instructed to closely watch the face. After that, two faces (the target and a distractor) appeared at the centre of the screen aligned vertically, one above the other. Participants were asked to press the “↑” key (right index finger placed on the 9 of the keypad) if the target face appeared in the upper half of the screen, or the “↓” key (right thumb finger placed on the 3 of the keypad) if the target face appeared in the lower half of the screen. The faces were presented vertically to ensure that the spatial layout of the faces on the screen did not influence the participants’ tendency to look at the right or left sides of the face. The test stimuli remained on the screen until the participant provided a key-response.

Figure 3b. Example of an experimental trial. Trials began with a fixation cross that ended after 500 ms. Then, observers were presented with a target face for 140 ms followed by a test trial in which they were asked to select which face was the one previously seen. This test trial ended when the participant pressed a key, indicating their response.



Each of the 16 stimuli described above appeared as the target stimulus 10 times, in randomized order, for a total of 160 trials. On each trial, the distractor stimulus was chosen randomly from the 12 images of the remaining three identities, so that target face

and distractor face always depicted different identities. The target face appeared in the upper and lower part of the screen in randomized order.

Before the experimental phase, to familiarize the participant with the brief presentation time of the target stimulus during the test trials and to practise key press responses, all participants performed 10 practice trials in which they were asked to categorize a stimulus, presented for 140 ms, as male or female by pressing a button with their right index finger (number pad button 8) and right thumb finger (number pad button 2). Practice trials were not counted for statistical analysis.

3.1.3. Results

The percentage of correct responses and the reaction times from correct trials only (RTs) were used as dependent measures in Linear Mixed Models (LMM). This design was used because the different conditions included in our experiment were not fully balanced in terms of numbers of trials; each participant performed 120 trials in which the target face was unfamiliar and 40 trials in which the target face corresponded to their own face. Furthermore, we used unbalanced sample sizes, with roughly two control participants for each participant with congenital prosopagnosia. A General Linear Model (GLM) could be affected by the unbalance in trials and sample size (and by the subsequent violation of the normality distribution), thereby increasing the possibility of type I and type II error. On the other hand, the LMM allows for an unequal number of repetitions, given that it directly takes into account the imbalance in the number of trials and group numerosity. The LMM is better suited for data with potentially correlated residuals and unequal variance between conditions (Judd, Westfall, & Kenny, 2012). LMM avoid the problems associated with analysing within-participant or within-stimulus mean scores by explicitly modelling these dependencies (Baayen et al., 2008; Kliegl, Wei, Dambacher, Yan, & Zhou, 2010). LMMs, in fact, divide the error term into several different “errors”, including the usual residual error term plus a number of random effect errors that account for participant variance by adjusting the predicted values of the model separately for each level of the grouping factors (e.g., for each participant) (Judd et al., 2012).

We ran preliminary analyses evaluating the presence of any response biases across the upper and lower visual fields. Therefore, we compared both accuracy and RTs between the trials in which the target appeared in the upper visual field and the trials in which the target appeared in the lower visual field; results revealed no effect of the

upper/lower hemi-field neither in the control group (Accuracy: $t(20) = 1.636$, $p = .118$; RTs: $t(20) = 1.023$, $p = .319$) nor in the group of participants with congenital prosopagnosia (Accuracy: $t(9) = -0.432$, $p = .676$; RTs: $t(9) = -1.658$, $p = .132$). These data suggest that there was no upper versus lower hemi-field bias for either group of participants; therefore, the upper/lower visual hemi-field factor was excluded in subsequent analyses

Accuracy

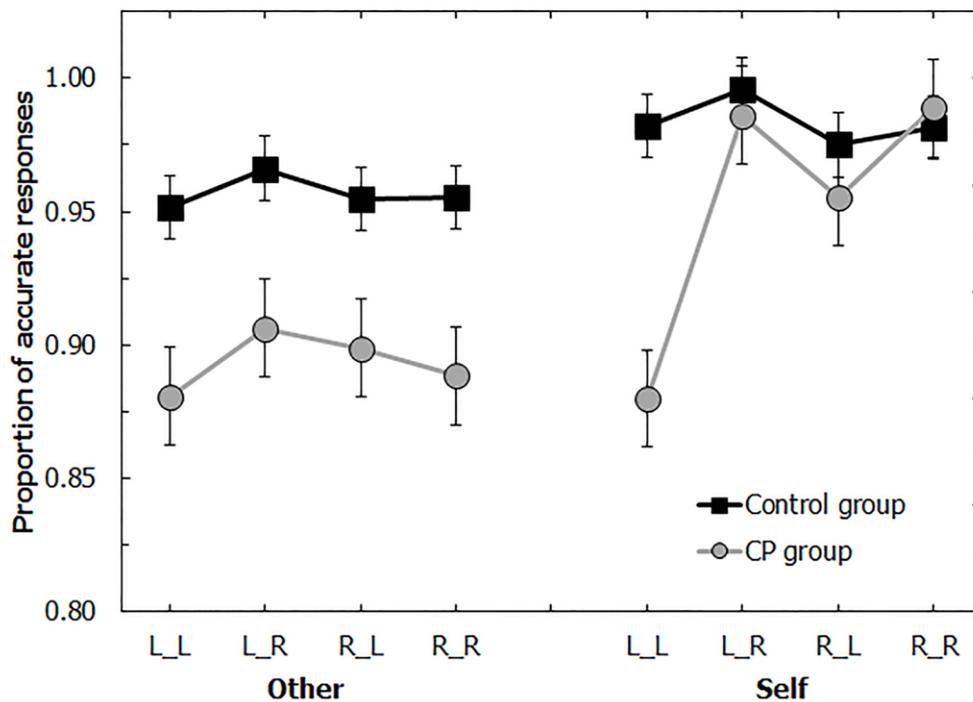
To examine the effect of stimulus type on self and other-face recognition in each group of participants, we conducted a $2 \times 2 \times 4$ ANOVA (software IBM SPSS Statistics 20) with Stimulus Type (L_L, L_R, R_L and R_R), Group (control group and CP) and Face Identity (Self and Other) as the main fixed effects and a by-subjects random intercept. Significant differences were further explored by post hoc multiple comparisons and to account for multiple testing, we used the Bonferroni correction.

As expected, significant main effects of both Group ($F(1, 29) = 21.97$, $p < .001$) and Face Identity ($F(1, 203) = 33.95$, $p < .001$) were found, showing a self-face advantage (SFA) - that is, greater accuracy in recognizing one's own face than the faces of others (mean accuracy of 96.4% and 92.3%, respectively) and, overall, better performance by the control group ($M = 97.0\%$) than the group of participants with CP ($M = 91.7\%$). The interaction between Group and Face Identity was also significant ($F(1, 203) = 4.13$, $p < .05$), highlighting a significantly larger self-face advantage in the participants with congenital prosopagnosia (Self $M = 94.5\%$; Other $M = 89.0\%$; $p < .001$) compared with the control group (Self $M = 98.4\%$; Other $M = 95.7\%$; $p < .001$). The main effect of Stimulus Type ($F(3, 203) = 5.07$, $p < .01$) was also significant: both groups, independently of Face Identity, had a worse performance with the L_L stimulus type relative to all other stimulus types. However, the significant two-way interactions between Group and Stimulus Type ($F(3, 203) = 3.07$, $p < .05$) and between Face Identity and Stimulus Type ($F(3, 203) = 2.71$, $p < .05$) highlighted that Stimulus Type became relevant only when participants had to recognize their own face, an effect that differed between the two groups.

This result was confirmed also by the three-way interaction of Group, Stimulus Type and Face Identity ($F(3, 203) = 2.75$, $p < .05$; Figure 3c). In the Other-Face condition the group of participants with congenital prosopagnosia demonstrated significantly ($p < .05$) worse performance compared to the control group for all four

stimulus types. Moreover, in the Other-Face condition, neither of the two groups seemed to be significantly influenced by the Stimulus Type. On the other hand, in the self-condition the participants with congenital prosopagnosia demonstrated worse performance for the L_L stimulus (M = 88.1%) compared with the L_R (M = 97.6%; $p < .001$) and R_R (M = 99.0%; $p < .001$) stimuli. Comparing the performance of the two groups, in the self-condition the congenital prosopagnosic group demonstrated worse performance than the control group only with the L_L stimulus (CP M = 88.1%, CG M = 98.2%, $p < .001$). By contrast, in the L_R, R_L, and R_R conditions the group of participants with congenital prosopagnosia did not significantly differ from the control group ($p > .05$). Furthermore, in the L_L condition congenital prosopagnosics showed performance similar ($p > .05$) to the analogue stimulus type in the Other-Face condition. Taken together, these results suggest that the group of participants with congenital prosopagnosia showed a self-face advantage only when their own right hemi-face was present; this effect was strongest when the right hemi-face fell in the right hemi-field. Finally, the performance of the control group did not seem to be significantly influenced by the Stimulus Type, both in recognizing their own face and the faces of others.

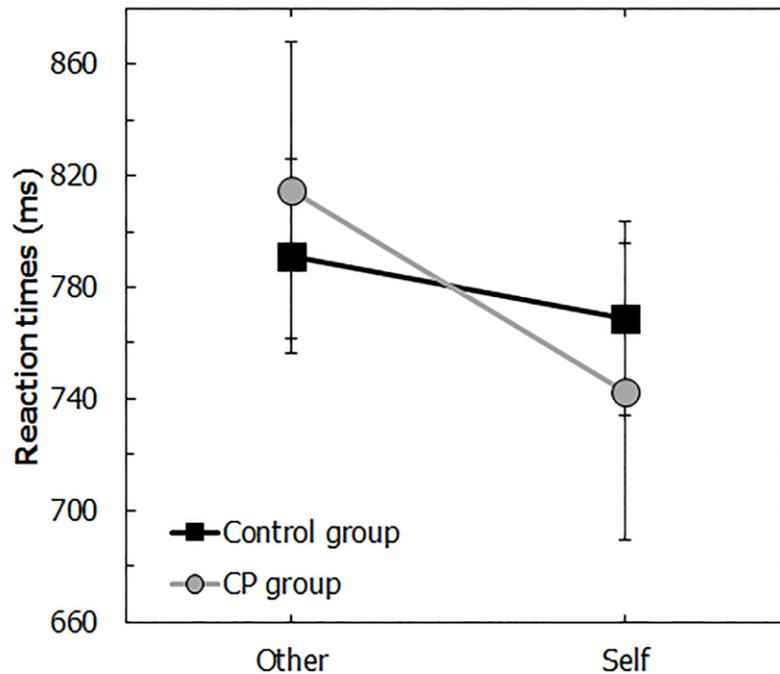
Figure 3c. Proportion of correct responses of the two groups for the Other/Self-conditions and for the four Stimulus Types. Vertical lines indicate ± 1 SE.



Reaction times

RTs were analysed as a dependent variable in a mixed effect model for repeated measures data (software IBM SPSS Statistics 20) with Stimulus Type (L_L, L_R, R_L, and R_R), Group (control group and congenital prosopagnosics) and Face Identity (Self and Other) as fixed effects and a by-subjects random intercept. Significant effects were further explored using Bonferroni post hoc multiple comparisons. Atypical outliers were excluded from the RT analyses (employing 2.5 SDs above or lower the mean as a criterion; a mean of $2.68\% \pm 0.96\%$ trials were excluded for each participant).

Figure 3d. Mean reaction times in the Other and Self-conditions for the two groups. Vertical lines indicate ± 1 SE.



The main effect of Face Identity was significant ($F(1, 203) = 21.52, p < .001$) showing that both groups were faster in responding to their own faces ($M = 764$ ms) than to the faces of others ($M = 807$ ms). The main effect of Group was not significant ($F(1, 29) = 0.03, p = .857$), but a significant interaction was found between Group and Face Identity ($F(3, 203) = 4.97, p < .05$; Figure 3d) with the group of participants with congenital prosopagnosia showing a greater difference in RT between self and other-face conditions (64 ms; $p < .001$) than in the control group (22ms; $p < .05$). This interaction emerged even though the two groups did not differ either in the self (CG $M = 769$ ms; CP

M = 759 ms; $p=.875$) or in the other conditions (CG M=791 ms; CP M=823 ms; $p=.608$), and that both groups showed a significant temporal advantage in recognizing their own face. Nevertheless, this advantage was very similar to the data seen for accuracy, with participants with congenital prosopagnosia showing a greater difference between the self and other conditions as compared to the control group.

Finally, no significant effect of the Stimulus Type was found, neither as main effect nor in interaction with the other factors (Stimulus Type \times Group, Stimulus Type \times Face Identity and Stimulus Type \times Group \times Face Identity).

3.1.4. Conclusions

The purpose of this study was to examine the existence of a left and a right perceptual bias in the performance of individual with congenital prosopagnosia and participants with typical development during the recognition of unfamiliar faces and the recognition of the self-face. In particular, we studied the effect through an indirect face recognition task (visual matching) by using chimeric facial stimuli involving self-face and unfamiliar faces.

A newer and significant result of this study is the one coming from the self-face condition: indeed, both groups performed better in recognizing their own faces than the faces of others, demonstrating the presence of a self-face advantage (Ma & Han, 2010; Sugiura et al., 2005) both in terms of accuracy and reaction times, and suggesting that in individuals with congenital prosopagnosia self-face recognition is spared. One possible explanation of this phenomenon could be that congenital prosopagnosics may employ an alternative strategy in the recognition of the self-face compared to the recognition of other faces, using mechanisms responsible for more general self-body recognition in order to achieve self-face recognition. This could demonstrate the existence of an advantage for the self-body that goes beyond the self-face advantage described in the literature (Ma & Han, 2010), consistently with some studies showing the existence of a specific neural network devoted to the processing of self-information (Platek et al., 2004; Uddin, Kaplan, et al., 2005; Platek et al., 2006; Devue et al., 2007).

An opposite hypothesis, instead, could be that the advantage of the self-face is less a result of a whole-body self-recognition advantage, but rather, more specific to faces. Following Keyes and Brady's results (2010), the self-face advantage can be found also with inverted faces, due to the more bilateral and robust representation of the global and local details of the self-face compared to the faces of the others. In our case, this

stronger representation of the self-face (and in particular of the local aspects of the face) could have helped our congenital prosopagnosic participants in overcoming their face-recognition impairment at least with this kind of stimulus. Unfortunately, it is not possible to disentangle between these two hypotheses on the basis of our data only, whereas a further study involving the perception of the self-body could help in clarifying this issue (see chapter 3.3).

Noteworthy, individuals with congenital prosopagnosia demonstrated accurate indirect judgments of self-recognition equivalent to that of the control group, but only when their right half-face fell in the right visual field, an effect that we called *right perceptual bias* (RPB). As further proof of the importance of the right half-face for self-face recognition in these individuals, the chimeric stimulus characterized by the absence of the right half-face (i.e., the composite face made up of two left half-faces) led to worse performance by the congenital prosopagnosics relative to the controls and relative to their own performance in other conditions. In fact, performance in the L–L condition was comparable in terms of accuracy to that of an unknown face. By contrast, in the case of the chimeric stimulus depicting their face as viewed in a photograph (i.e., their right hemi-face falling in the left hemi-space and the left one in the right hemi-space, R–L), the presence of their right half-face on the left side was insufficient to produce accuracy equivalent to the control group, suggesting the importance not only of the right half-face but also of the right hemi-space.

Thus, our data suggest that individuals with congenital prosopagnosia may rely more on their right half-face for self-face recognition, in terms of both object-centred spatial coordinates (as the right side of the face) and ego-centric coordinates (as the right side of visual space). In other words, best performance is seen for the participants with congenital prosopagnosia only when the right half-face is located in the right visual hemi-space. To our knowledge, this is the first time that the right perceptual bias effect for the self-face has been observed in a population affected by face impairment. On the contrary, in healthy participants this perceptual asymmetry has already been described by Brady et al. (2004), who showed a dissociation between self and others' recognition in a task requiring participants to judge the likeness of chimeric faces that depicted their own face and the face of a close friend. In particular, as reported in chapter 1.1, the authors demonstrated a right bias for the self-face and a left bias for others' faces. Even though Brady and colleagues' study (2004) involved different control stimuli (unknown and other friends' faces, respectively), their data concerning the right half-face advantage

for self-face recognition in healthy participants are consistent with what we found in the performance of congenital prosopagnosics for self-recognition. On the other side, our controls did not show a right bias for the self-face condition; however, in the case of the self-face condition the control group showed a ceiling effect that could have hidden any possible lateralization bias, suggesting that probably our task was not sensitive enough to detect subtle effects on good recognizers. Another possible explanation for the differences between our study and Brady et al. (2004) could lie in the different paradigm we used, but which was chosen because of the population we were studying, in order to avoid to ask prosopagnosics to explicitly identify stimuli they are usually impaired with.

Finally, it is worth mentioning that in the other-face condition, neither the control group nor the congenital prosopagnosics showed a difference in performance across any of the four chimeric conditions. Thus, we failed to find a left perceptual bias in both groups: whether the lack of the left bias in the congenital prosopagnosia group might prove the face specificity of this bias (i.e., the left perceptual bias is linked to the specificity of the face recognition processing and, thus, is not detectable in individuals with an atypical face recognition process), this result is more surprising in the case of the control group. One possible explanation for this finding is linked to methodological factors. In the literature, the left perceptual bias has typically been investigated in studies of gender, age and race processing. In these studies, tasks using unknown faces typically involve ambiguous stimuli in which there is no objectively correct answer (e.g., Burt & Perrett, 1997; Butler & Harvey, 2008; Luh et al., 1994; Turk, Handy, & Gazzaniga, 2005). For example, a study examining the left perceptual bias in conjunction with emotion processing might present chimeric faces consisting of a left smiling-right neutral stimulus that can be judged as either happy or neutral, the former being consistent with the left perceptual bias, but not the latter (e.g., Coolican et al., 2008). Even in the single study that found a left perceptual bias in a task involving matching of unknown face identities, the task itself was ambiguous (with no clear correct answer), as participants were asked to match an original face to one of two chimeric faces that were L-L and R-R composites of the original (Coolican et al., 2008). In our study, however, each matching trial included an objectively correct target and incorrect distractor (with a different identity) and the left perceptual bias was determined based on accuracy performance across conditions - L-L and L-R for the left perceptual bias versus R-R and L-R for the right perceptual bias.

In conclusion, our study has shown the existence of a self-face advantage in participants affected by congenital prosopagnosia, which manifests itself in a right advantage for self-face stimuli. Our findings provide interesting insights into the self-recognition of those with congenital prosopagnosia with regards to both half-face and hemi-space, without evaluating what would happen in the case of familiar face recognition. To further explore this topic, it would be intriguing to verify if this advantage in congenital prosopagnosics could be detectable also with familiar faces and other body parts recognition (e.g., hands, feet, etc.). If a perceptual bias appears also with faces familiar to the congenital prosopagnosic participant, rather than with the self-face only, it would suggest a differential processing strategy in individuals with congenital prosopagnosia compared to people with typical development in terms of face recognition. On the other hand, if the right perceptual bias is not tied to faces, relying instead on a more general self, it should be detectable also with other self body-parts. In the latter case the existence of a right perceptual bias during self-hands and self-feet recognition, for instance, would highlight how the right bias is tied and specific to the self-processing and not to the face processing only. The chance to investigate these two hypotheses could allow us to better understand the functional and non-functional aspects linked to congenital prosopagnosia. In particular, the question of whether the self-face advantage and the right perceptual bias are face specific or not will be the topic of the next two chapters describing, respectively, two studies on eye-movements and self-body parts recognition in congenital prosopagnosia.

3.2. Study V: How do individuals with congenital prosopagnosia look at themselves? An eye-movement study on self-face recognition

In the previous chapter I described a study that demonstrated how, despite their face recognition impairment, congenital prosopagnosics show a preserved performance both in terms of accuracy and reaction times when they have to recognize their own face, demonstrating that also these individuals can show a self-face advantage (Ma & Han, 2010; Sugiura et al., 2005). Moreover, in the case of congenital prosopagnosics the self-face advantage seems to be linked to the presence of the right-half face, an effect that we called *right perceptual bias*. A similar results was already described in good recognizers: indeed, they tend to rely more on the right half-side of their face (i.e., a right perceptual

bias), which falls in the right visual hemi-space looking at the mirror, when they are asked to recognize themselves (Brady et al., 2004), whereas they tend to rely more on the hemi-face that falls in the observer's left visual hemi-space (i.e., a left perceptual bias) during the recognition of unfamiliar or familiar faces.

Considering this evidence, in the present study we aimed at investigating whether the self-face advantage (SFA) and the right perceptual bias (RPB) showed by good recognizers and individuals with congenital prosopagnosia during self-face recognition is also reflected in their scan path behaviour. Indeed, some studies have suggested that individuals with congenital prosopagnosia explore every face in the same way, independently whether the face is familiar (or famous) to them or not (Barton et al., 2007; Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007). In particular, there seems to be a general agreement about the relationship between the face recognition impairment of this population and their anomalous scan path behaviour during the exploration of faces (Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007). Indeed, while good recognizers focus their gaze primarily on the central facial features, suggesting that these regions are the most informative regions in a human face (Hsiao & Cottrell, 2008; Peterson & Eckstein, 2012; Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007), individuals with congenital prosopagnosia tend to show a more dispersed gaze, directing their attention not only on the central features but also on external features with both unfamiliar and famous faces (Barton et al., 2007; Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007). Furthermore, congenital prosopagnosics typically show no or weaker familiarity modulation in their scan path behaviour: whereas good recognizers use fewer fixations and less viewing time to identify famous faces compared to unfamiliar faces, individuals with congenital prosopagnosia typically use a similar number of fixations and viewing time in exploring both unfamiliar and famous faces (Barton et al., 2007; Schmalzl, Palermo, Green, et al., 2008; Schwarzer et al., 2007), resulting in both cases in a poor recognition performance. As a possible explanation for this behaviour, it has been suggested that the lack of a familiarity modulation in congenital prosopagnosics' eye movements could be due to the absence of residual facial memories or internal viewing schema in these individuals (Barton et al., 2007; Lê et al., 2003; Schmalzl, Palermo, Green, et al., 2008), because they never developed normal face recognition abilities. However, congenital prosopagnosics' performance is comparable to the one of the good recognizers when they have to recognize their own face, leading to question whether this enhanced performance in the

case of the self-face is detectable also in terms of eye-movements - that is, in a different exploration of the self-face compared to unfamiliar faces.

For this reason, we recruited a group of congenital prosopagnosics and healthy controls who underwent a simple recognition task involving different facial stimuli depicting the participant's self-face and another unfamiliar face. First, we wanted to compare the eye movements made by the two groups on these two types of stimuli to investigate whether the self-face advantage is detectable also as a change in gaze behaviour. Moreover, since in the previous chapter the advantage in the congenital prosopagnosic population was demonstrated by using an indirect task, here, by means of a direct task "me/not me", we tested if these individuals still show the same advantage also when asked to consciously identify themselves. In particular, in this case, the use of both eye movement and behavioural measurements could allow us to obtain information on both the online visual processing of the stimulus, as well as on the resulting outcome. Eye movements can give us information about how the efficiency and distribution of gaze control affect the perception (and recognition) of a stimulus (Bloom & Mudd, 1991), and provide insights into how prosopagnosic individuals process the information in faces (Barton et al., 2007). Furthermore, since the advantage for the self-face has been demonstrated with both upright and inverted faces (Keyes & Brady, 2010), here we decided to test both orientations of presentation as well.

Finally, we also asked whether the rightward bias characterizing "indirect" self-face perception is also detectable in a "direct" task and whether it is linked to a different visual exploration of the two halves of the facial stimulus. Thus, we used chimeric stimuli created from the original picture of the face of each participant (i.e., a composite face made of two right half-faces and a composite face made of two left half-faces) in addition to the original face and mirror-reversed face. In particular, we would expect the right perceptual bias to be present and reflected in an increased visual exploration of the right self hemi-face, independently of its position in the visual field.

3.2.1. Participants

A total of thirty-eight participants (recruited as described below) took part in the experiment. All participants had normal or corrected-to-normal vision, and each of them received course credits for participation in two one-hour sessions. An informed consent form for the processing of personal data and for the use of their photographs was

obtained from all participants before testing, and the ethical approval for this study was specifically granted by the Ethics Committee of the University of Milan-Bicocca.

Control participants

In order to select individuals with no face recognition difficulties, thirty-one undergraduate students of the University of Milan-Bicocca (all females, right-handed, age range 19-27, mean age 22.23 ± 2.43) were recruited through the Bicocca Sona System[®] and underwent a battery of tests assessing face and object recognition (see below). After the screening phase, on the basis of the participants' agreement to come back to undergo the second part of the study, 13 out of the initial group of 31 participants returned for the main experiment and served as the final control group for the experimental phase, CG group (all females, right-handed, age range 19-23, mean age 21.46 ± 1.56). None of them experienced face recognition difficulties during their lives.

Congenital prosopagnosics

Seven females (all right-handed, age range 20-25, mean age 21.23 ± 1.89) with congenital prosopagnosia took part in this study and composed our experimental group, CP group. As the controls, all the congenital prosopagnosia participants underwent a battery of tests investigating face and object recognition, and a semi-structured interview conducted by an experienced neuropsychologist in order to assess the presence of congenital prosopagnosia and to exclude possible alternative explanations for face recognition impairment. All congenital prosopagnosics reported significant difficulty in recognizing people starting from face information alone and provided detailed examples about it. They also reported no known history of brain damage, that their impairment was present from birth and other common symptoms of prosopagnosia, as their strategy of relying on non-facial cues to recognize the others.

Face and object recognition abilities assessment

All participants underwent a first screening session during which their face and object recognition abilities were assessed. In particular, our battery was composed of five tests: the Benton Facial Recognition Test, BFRT (Benton, 1994; Benton & Van Allen, 1968), the Cambridge Face Memory Test, CFMT (Duchaine & Nakayama, 2006), the Boston Naming Test, BNT (J. T. Kaplan et al., 1983), a Famous Faces Recognition Test (FFRT) and a Famous Monuments Recognition Test (FMRT). These tests were selected

to determine the presence of prosopagnosia, by assessing participants' ability to recognize unfamiliar and familiar faces (i.e., BFRT and CFMT, and FFRT, respectively), their visual object recognition and general visual processing abilities (i.e., BNT and FMRT, respectively). We also calculated an additional index from the CFMT: the inversion effect (IE) (Yin, 1969). The Famous Monuments Recognition Test (FMRT) consists of 30 pictures of Italian and international monuments presented in their most conventional perspective; each monument remains visible until the participant provides its name or as much information as possible about it in order to prove correct recognition; the maximum score possible is 30 (see previous chapters for a more detailed description of the other tests).

The scores obtained in these tests by the 31 initial healthy participants who took part in the screening phase formed the sample for the calculation of z-scores for the congenital prosopagnosics and control group participants. The mean scores for each test (\pm SE) were as follows: 47.61 ± 3.12 for the BFRT, 58.29 ± 8.99 for the upright version of the CFMT, 43.39 ± 5.95 for the inverted version of the CFMT, 14.90 ± 6.44 for the inversion effect, 23.81 ± 4.09 for the FFRT, 20.68 ± 5.42 for the FMRT and 55.55 ± 3.13 for the BNT. In Table 3b, the individual test scores for each congenital prosopagnosic and the z-scores calculated for each individual CP against the data from the initial group of 31 participants are reported (to further confirm the presence of prosopagnosia in the CP group, our z-scores from the CFMT upright were compared with the published control scores for this test).

All our 7 congenital prosopagnosics were impaired in face recognition; indeed, they all performed poorly (i.e., 2 SD below the mean of the control group) in the upright version of the CFMT (both considering our control sample and the published data of the controls from Duchaine & Nakayama, 2006) and the FFRT. Furthermore, all the congenital prosopagnosics showed a smaller inversion effect compared with the control group and, particularly, 4 of them had an inversion effect score 2 SDs lower than controls. In the BFRT only 2 out of 7 congenital prosopagnosics performed pathologically, consistently with other studies proving that some individuals with congenital prosopagnosia can experience difficulty with face discrimination in addition to face memory (Ariel & Sadeh, 1996; de Gelder & Rouw, 2000).

By contrast, in the tests investigating object recognition abilities (FMRT and BNT) all congenital prosopagnosics performed in the normal range, further confirming

the selectivity of their impairment. None of the controls who agreed to come back for the second part of the study (13 females) showed any impaired performance in any tests.

Table 3b. Demographic details and scores (raw and z-scores) at the tests investigating face and non-face object recognition for the 7 congenital prosopagnosics (CP) and average score for the control group (CG). BFRT = Benton Facial Recognition Test; CFMT = Cambridge Face Memory Test; IE = Inversion Effect; FFRT = Famous Face Recognition Test; FMRT = Famous Monuments Recognition Test; BNT = Boston Naming Test. * = pathological score

	Age	BFRT		CFMT Upright			CFMT Inverted		Inversion Effect		FFRT		FMRT		BNT	
		raw score	z-score	raw score	z-score	z-score (Duchaine & Nakayama, 2006)	raw score	z-score	raw score	z-score	raw score	z-score	raw score	z-score	raw score	z-score
A.D.	22	45	-0.84	40	-2.03*	-2.14*	34	-1.58	6	-1.38	14	-2.40*	20	-0.13	53	-0.81
C.R.	25	40	-2.44*	36	-2.48*	-2.77*	30	-2.25*	6	-1.38	13	-2.64*	18	-0.49	58	1.10
E.B.	20	40	-2.44*	36	-2.48*	-2.77*	35	-1.41	1	-2.16*	6	-4.35*	17	-0.68	56	0.46
G.M.	19	50	0.77	37	-2.37*	-2.65*	31	-2.08*	6	-1.38	11	-3.13*	18	-0.49	54	-0.50
M.B.	19	47	-0.20	34	-2.70*	-3.03*	37	-1.07	-3	-2.78*	13	-2.64*	27	1.17	58	1.10
R.B.	22	46	-0.52	40	-2.03*	-2.27*	44	0.10	-4	-2.93*	8	-3.87*	18	-0.49	55	-0.18
S.E.	20	46	-0.52	37	-2.37*	-2.37*	44	0.10	-7	-3.30*	12	-2.89*	24	0.61	57	0.78
CP mean ± SD		44.86 ± 3.67		37.14 ± 2.19			36.43 ± 5.68		0.71 ± 5.47		11.00 ± 2.94		20.29 ± 3.77		55.86 ± 1.95	
CG mean ± SD		48.62 ± 2.99		65.62 ± 4.68			46.54 ± 3.71		19.08 ± 4.77		24.46 ± 2.90		20.85 ± 5.56		56.00 ± 2.20	

3.2.2. Materials and Methods

Stimuli

A unique set of face stimuli was created for each participant, following the same procedure described in paragraph 3.1.2. However, in this case, each set included four facial stimuli built starting from the participant's own face and four facial stimuli created starting from a control face (unknown to the participant). A participant's face could also be used as control face for another participant. In this case, it was verified that our participants did not know one another before the experiment. Moreover, the control face was always matched so that it looked as similar as possible to the participant's face (i.e., eyes and eyebrows colour, skin texture).

Summarising (see paragraph 3.1.2. for further details), 4 images (original face-R_L, mirror face-L_R, left-chimeric-L_L and right-chimeric-R_R) of each person's face were created (participant and matched control) and each unique stimulus set was composed of a total of 8 images – 4 images of the participant's face and 4 belonging to the matched control – which could be presented also upside-down depending on the block of the experiment.

Apparatus and procedure

Participants sat in a comfortable chair approximately 57 cm from a Sony Trinitron monitor (27-inch, 1920 x 1080 pixels, refresh rate of 120 Hz in 32-bit color) in a silent room and with their head stabilized with a chin and forehead rest. Participant's eye movement were monitored at a rate of 1000 Hz with a spatial resolution of 0.2° by an Eye-Link 1000 eye-tracking system (SR Research, Mississauga, Ontario, Canada). Before the experiment began, participants underwent a 5-points calibration (calibration target of 0.15° diameter black circle overlaid on a 0.35° diameter white circle). The calibration was accepted when the worst error point in the calibration was less than 0.75° and the average error for the five-points less than 0.5° .

The experiment was controlled by Matlab R2012a and a Microsoft video-game controller was used to collect participants' responses. The instructions of the task were displayed by using a self-paced presentation on the screen at the beginning of the experiment. Each trial began with a central drift correction circle (0.5°), which participants were asked to accurately fixate on, in order to check fixation drift for minor changes in head position (in the case that the drift correction error was larger than 0.5° the calibration procedure was repeated). When participant's fixation remained stable within 0.75° of this drift correction circle for at least 200 ms, one of the possible facial stimuli appeared on a black background and remained on the screen for as long as the participant responded. Participants were instructed to freely look at the stimulus and to decide whether the chimeric face represented the self-face or another individual's face by pressing one of two keys on the video-game controller. They were asked to be as accurate and as fast as possible. Participant's response was then followed by a 500 ms random noise mask, in order to eliminate any possible

afterimage before the beginning of the next trial. Although viewing was binocular, only the right eye was tracked, and the eye-movements were recorded from the stimulus onset until participant's response.

The experiment consisted of two blocks: a first block (Upright condition), during which the original, mirror-image and two composite faces of the participant and matched control were presented in the canonical perspective, and a second block (Inverted condition), involving the same stimuli but presented upside-down. Each condition (upright and inverted) consisted of 80 randomised trials depicting the 4 facial stimuli of the participant and 4 facial stimuli of the control unknown to the participant. The order of the two tasks was counterbalanced across participants. Furthermore, in order to avoid possible differences due to stimulus-response spatial compatibility, also response key buttons were counterbalanced across participants.

Before each condition, a practice session was run in order to let the participants familiarize themselves with the task and to practice making responses. This practice session consisted of 8 trials depicting all the possible facial stimuli used for the experiment and gave the participants the opportunity to take a first look at each of them. Practice trials were not counted for statistical analysis.

3.2.2. Results

Behavioural data

The proportion of correct responses and response times (RTs) from correct trials only (measured from the stimulus onset until participant's response) were analysed. RT outliers (2.5 SDs above or below the mean for each participant) were discarded and not analysed. In order to provide a better summary of our findings, by taking into account both measurements, we also analysed the inverse efficiency score (IES), defined as RT/accuracy (Bruyer & Brysbaert, 2011).

The behavioural data (i.e., accuracy, RTs and IES) from the control and congenital prosopagnosic groups were analysed using a linear mixed model with the lme4 package (Bates, Maechler, Bolker, & Walker, 2013) in R (<https://www.r-project.org/>; R Development Core Team, 2008). A first model was run including as factors *Face Identity* (Self vs. Other), *Orientation* (Upright vs. Inverted), *Group* (CG vs. CP) and a random intercept for each participant. Then, a second model was run, in order to investigate any possible effect of the four facial stimuli (L_L, L_R, R_R, and R_R) on participants' performance only in the Self condition (i.e., in the familiar face condition, since no effect should be expected in the case of an unfamiliar face). Thus, in this second model the factors included were *Stimulus* (L_L, L_R, R_R, and R_R), *Orientation* (Upright and Inverted), *Group* (CG and CP) and a random intercept for each participant. For both models, F tests from the LMER results are presented (type III with Satterthwaite approximation for degrees

of freedom), and significant differences were further explored by Bonferroni post hoc multiple comparisons (corrected *p-values* are reported).

Accuracy analysis revealed significant main effects of *Orientation* ($F(1, 294) = 22.80, p < .001$) and of *Face Identity* ($F(1, 294) = 8.65, p < .01$), showing that, overall, both groups were more accurate in recognizing upright than inverted faces (0.966 ± 0.01 and 0.914 ± 0.03 , respectively), and in recognizing the self-face compared to the other-face (0.951 ± 0.02 and 0.928 ± 0.03 , respectively). The interaction between the *Face Identity* and the *Group* was also significant ($F(1, 294) = 4.99, p < .05$), highlighting that, in terms of accuracy, the SFA was significant only in the congenital prosopagnosia group (see Table 3c).

Table 3c. Mean values (standard error in parentheses) of proportion of correct responses, RTs and IES for the control group (CG) and congenital prosopagnosia group (CP), separately for the self and other condition.

	Accuracy		RTs		IES	
	<i>self</i>	<i>other</i>	<i>self</i>	<i>other</i>	<i>self</i>	<i>other</i>
CP group	0.96 (0.03)	0.91 (0.06)	653 (39)	751 (50)	681 (42)	925 (68)
Control group	0.95 (0.03)	0.94 (0.02)	629 (29)	661 (25)	677 (45)	713 (38)

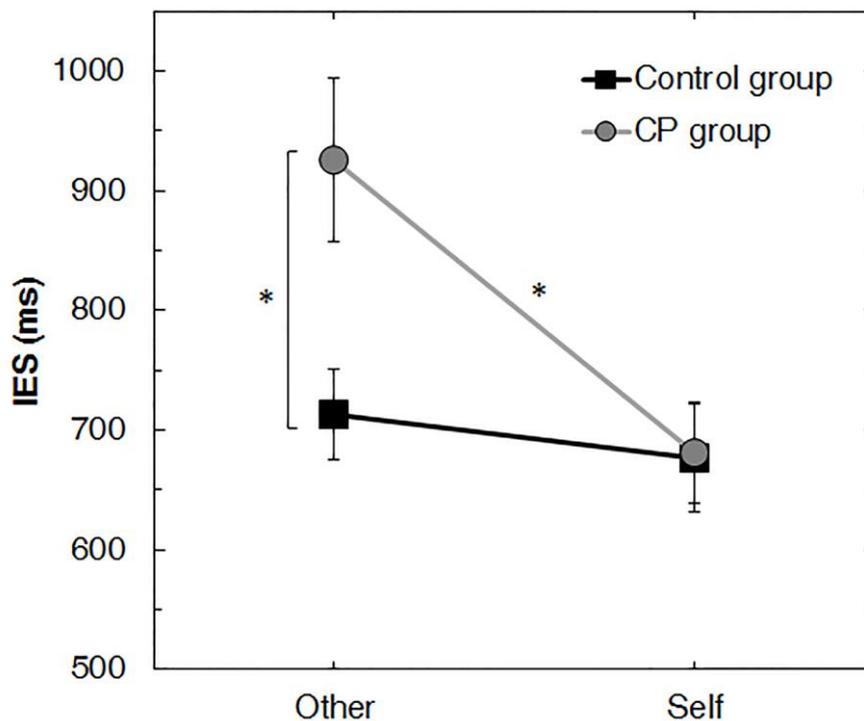
Analysis on RTs showed that the main effects of *Face Identity* ($F(1, 294.13) = 71.11, p < .001$) and *Orientation* ($F(1, 294.13) = 165.79, p < .001$) were significant, showing that both groups were faster in responding to their own face (637 ± 24 ms) than to the other's face (693 ± 26 ms), and that they were also faster in responding to upright faces (619 ± 19 ms) than to inverted faces (711 ± 27 ms). More interestingly, the interaction between *Group* and *Face Identity* ($F(1, 294.13) = 18.34, p < .001$) was also significant: the congenital prosopagnosia group was significantly slower than the control group only in the Other condition (751 ± 50 ms and 661 ± 25 ms, respectively, $p < .001$) but not in the Self condition (653 ± 39 ms and 629 ± 29 ms, respectively, $p = 1.00$; see Table 3c). This result suggests that in the Self-condition participants with congenital prosopagnosia improved their performance to the point that it could be comparable to the one of controls. Finally, the interaction between *Group* and *Orientation* was significant ($F(1, 294.13) = 11.85, p < .001$), showing that congenital prosopagnosics were significantly slower than controls only with inverted faces (765 and 682 ms, respectively).

The analysis on the IES confirmed the presence of a significant effect of *Orientation* ($F(1, 291.42) = 26.99, p < .001$) and *Face Identity* ($F(1, 291.42) = 13.69, p < .001$): both groups performed better with upright than inverted faces (647 ± 27 ms and 810 ± 97 ms, respectively), and in the self-condition compared to the other-condition (678 ± 32 ms and 787 ± 101 ms, respectively). However, once again, the interaction between *Group* and *Face Identity* was significant ($F(1, 291.42) = 6.94, p < .01$), highlighting that congenital prosopagnosics showed a performance comparable to controls in the self-condition, whereas in the other-condition they

performed significantly worse than controls (see Figure 3e and Table 3c). The type of facial stimulus (L_L, L_R, R_R, and R_R) did not seem to influence participant's performance neither in terms of accuracy ($F(3, 126) = 1.11, p = .348$) nor RTs ($F(3, 125.93) = 0.274, p = .844$), or IES ($F(3, 125.98) = 1.01, p = .392$).

Taken together, these results confirmed the findings of previous studies showing that the self-face advantage is detectable both in good recognizers and individuals with congenital prosopagnosia. In particular, the self-face advantage is detectable in terms of RTs in the control group and in terms of accuracy, RTs and IES in the congenital prosopagnosia group. Moreover, the self-face advantage in the congenital prosopagnosia group is so effective that in the self-face condition their performance is comparable to the one of controls.

Figure 3e. Mean inverse efficiency score of the control group (CG) and congenital prosopagnosia group (CP) for the Other/Self conditions. Vertical lines indicate ± 1 SE.



Eye-movements data

Eye movement data were pre-processed using EyeLink Data Viewer software (SR Research Ltd., Mississauga, Ontario, Canada). All fixations were recorded from the beginning to the end of each trial. Since the initial fixation was always at the centre of the screen, superimposed on the fixation dot, it was discarded, and the fixation following this first fixation was taken as the onset of the scanning sequence.

First, we looked at the basic characteristics of the eye-movements made by participants while they were encoding the face. The total scan time per stimulus (i.e., the sum of the durations of all fixations) was analysed in order to investigate the amount of scanning that the participants needed to recognize the face; mean fixation number and duration per stimulus were also examined to determine if any change in total scan time was due to an increase in the number or the length of fixations. Finally, mean first fixation duration was also analysed as indicator of participants' preference when starting to explore the facial stimulus.

Second, we explored the scanning distribution over the face stimulus. Fixation distribution was analysed by iMap4 (Lao, Mielle, Pernet, Sokhn, & Caldara, 2016), which has the advantage to avoid any issues due to the use of predefined ROIs (Caldara & Mielle, 2011) by providing a completely data-driven way to analyse the scanning distribution.

Fixation features. Eye-movement data were analysed using a linear mixed model with the lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in R (<https://www.r-project.org/>; R Development Core Team, 2008). The same models tested on the behavioural results were run also on the eye-movement data. Again, for both models, F tests from the LMER results are presented (type III with Satterthwaite approximation for degrees of freedom) and significant differences were further explored by Bonferroni post hoc multiple (corrected *p-values* are reported).

The main effect of the *Group* was significant in the total scan time ($F(1, 18) = 5.13, p < .05$), in the mean number of fixations per stimulus ($F(1, 18) = 6.50, p < .05$) and in the mean first fixation duration ($F(1, 18) = 7.02, p < .05$), showing that congenital prosopagnosics differed in the way they explored the facial stimulus. Indeed, participants with congenital prosopagnosia needed more time (735 ± 39 ms) and more fixations (3.70 ± 0.25) in order to encode the stimulus compared to controls (668 ± 26 ms and 3.06 ± 0.17 , respectively); accordingly, they also made shorter first fixations (253 ± 40 ms) and overall fixations (307 ± 29 ms) than controls (356 ± 31 ms and 361 ± 24 ms, respectively).

The *Face Identity* factor significantly influenced the total scan time ($F(1, 294.2) = 18.87, p < .001$) and the mean number of fixation per stimulus ($F(1, 294) = 6.82, p < .01$), highlighting that the self-face advantage is evident also in terms of eye-movements. Indeed, participants needed less time and less fixations in order to recognize their own face (675 ± 21 and 3.24 ± 0.16) compared to an unfamiliar face (708 ± 23 ms and 3.33 ± 0.15). By contrast, the analysis on the fixation duration did not show any difference between the self- and other- condition, suggesting that even though the self-face requires less information in order to be recognized, the amount of information extracted within each fixation is similar in the two conditions.

Interestingly, the interaction between *Group* and *Face Identity* was nearly significant in the total scan time ($F(1, 294.2) = 3.19, p = .07$), showing that, similar to the IES results, the difference between congenital prosopagnosics and controls was bigger in the other-condition (762 ± 39 and 679 ± 26 ms) than in the self-condition (709 ± 37 and 657 ± 25 ms).

Finally, the main effect of the *Orientation* was significant in the total scan time ($F(1, 294.2) = 28.99, p < .001$), in the mean number of fixations ($F(1, 294) = 71.28, p < .001$), in the mean fixation duration ($F(1, 294.02) = 22.29, p < .001$) and in the mean first fixation duration ($F(1, 294.11) = 12.92, p < .001$). Both congenital prosopagnosics and controls used more scan time and more (and shorter) fixations in the inverted conditions (scan time: 713 ± 23 ms; mean fixation number: 3.45 ± 0.16 ; mean fixation duration: 328 ± 83 ms; mean first fixation duration: 304 ± 25 ms) compared to the upright one (scan time: 670 ± 22 ms; mean fixation number: 3.12 ± 0.14 ; mean fixation duration: 356 ± 91 ms; mean first fixation duration: 337 ± 28 ms). The interaction between *Group* and *Orientation* was also significant in the mean number of fixations per stimulus ($F(1, 294) = 6.06, p < .01$), showing that the difference between the two groups was greater in the inverted condition.

In accordance with the behavioural results, the type of facial stimulus (L_L, L_R, R_R, and R_R) did not seem to influence participant's eye-movements neither in terms of total scan time ($F(3, 126.08) = 0.33, p = .804$), nor in mean number of fixations ($F(3, 126) = 0.27, p = .848$) or in fixation duration (first fixation duration: $F(3, 126.01) = 1.65, p = .18$; overall fixations duration: $F(3, 125.93) = 0.37, p = .77$).

Taken together, these results showed that congenital prosopagnosics required longer scan times to recognize faces, not because of the use of longer fixations, but because they used a greater number of them. Furthermore, both groups made fewer fixations and had shorter scan time with upright faces than inverted faces, reflecting the presence of an inversion effect in the characteristics of their eye-movements. Finally, all participants required fewer fixations and less viewing time to recognize their own face than the unfamiliar face - that is, they showed a self-face advantage.

Spatial fixation mapping using iMap4. The spatial mapping of the fixation distribution was performed using *iMap4* (Caldara & Miellet, 2011; Lao et al., 2016). *iMap4* is a data-driven analysis framework for statistical fixation mapping, in which fixation distribution is modelled using Linear Mixed Model (LMM) and hypothesis testing is performed using non-parametric statistics based on resampling and spatial clustering (Lao et al., 2016).

iMap4 projects the fixation durations into two-dimensional space according to the x - and y -coordinates at the single-trial level. The sparse fixation duration maps were then smoothed with a 2D Gaussian Kernel function of full width at half maximum (FWHM) around 1° of visual angle. The smoothed fixation map for each condition is then estimated within each participant by taking the mean of the trials in the same condition. To model the spatial pattern of fixation pattern, the conditional mean fixation maps were normalized using z -score (Figure 3A). The resulting 3D matrix (trials \times x -Size \times y -Size) was then modelled as the response variable in *iMap4*. Each pixel in the smoothed fixation map was fitted with a linear mixed model using the following formula:

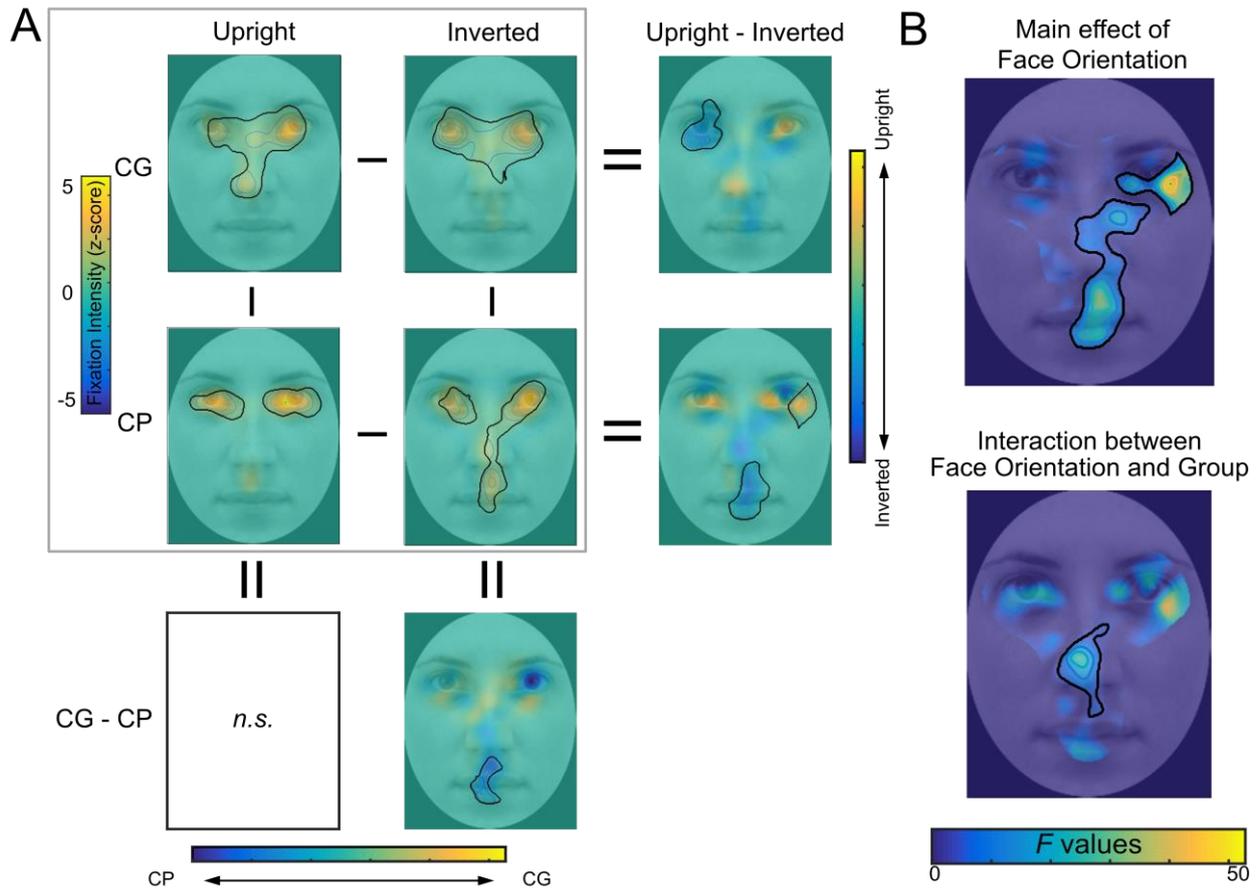
$$\begin{aligned}
\text{Fixation Intensity}_{(x,y)} &\sim 1 + \text{Group} + \text{Face Identity} + \text{Face Orientation} + \text{Group} \\
&\quad * \text{Face Identity} + \text{Group} * \text{Face Orientation} + \text{Face Identity} \\
&\quad * \text{Face Orientation} + \text{Group} * \text{Face Identity} * \text{Face Orientation} \\
&\quad + (1 \mid \text{Subject}), 1 \leq x \leq x\text{Size}, 1 \leq y \leq y\text{Size}
\end{aligned}$$

Thus, the fixation duration at different spatial locations (e.g., eyes, nose, or mouth) was fitted as a linear function of *Group* (CG or CP), *Face Identity* (Self or Other), *Face Orientation* (upright or inverted face), and their *interactions*. The effect of subject was fitted as a random intercept. *iMap4* uses the *LinearMixedModel* class from the Statistics Toolbox™ in Matlab for model fitting. The linear mixed model coefficients were estimated using Restricted Maximal Likelihood (ReML) with the default *iMap4* settings. A bootstrap spatial clustering procedure threshold on the cluster size was applied for the null hypothesis significance testing and for multiple comparison corrections (Lao et al., 2016).

An ANOVA on the linear mixed model revealed a significant main effect of *Face Orientation* on the right eye and the mouth region, and a significant interaction of *Group* and *Face Orientation* around the right eye and nose (see Figure 3f). The effect of *Face identity* does not modulate the fixation pattern, as its main effect and interaction are not significant after multiple comparison correction using bootstrap clustering. Overall, participants fixated more the mouth and nose areas with inverted faces compared to upright faces (local maximum within the significant cluster: $F(1, 280) = 33.88$, $\beta_{\text{upright}} = 0.17 [-0.338, 0.670]$ and $\beta_{\text{inverted}} = 1.08 [0.577, 1.586]$; local minimum: $F(1, 280) = 3.88$, $\beta_{\text{upright}} = -0.09 [-0.202, 0.022]$ and $\beta_{\text{inverted}} = 0.07 [-0.043, 0.181]$; $p < 0.05$ cluster corrected; brackets show 95% confidence interval); whereas the eye region was fixated more in the upright than in the inverted condition (local maximum within the significant cluster: $F(1, 280) = 53.99$, $\beta_{\text{upright}} = 1.07 [0.570, 1.568]$ and $\beta_{\text{inverted}} = 0.08 [-0.418, 0.579]$; local minimum: $F(1, 280) = 3.90$, $\beta_{\text{upright}} = 2.93 [2.062, 3.796]$ and $\beta_{\text{inverted}} = 2.34 [1.472, 3.206]$; $p < 0.05$ cluster corrected; brackets show 95% confidence interval).

To clarify the significant main effect and interaction, we mapped the fixation area above chance level of the following predictors: CG_upright, CG_inverted, CP_upright, and CP_inverted, and then performed linear contrasts among these conditions (see Figure 3f). The main effect of face orientation was mostly driven by the change of fixation pattern between the upright and inverted condition in individuals with congenital prosopagnosia: they fixated more on the nose and mouth area in the inverted condition, while in the upright condition they were heavily biased towards the eye region only. Moreover, the significant *Group * Face Orientation* interaction around the nose region ($F_{\text{max}}(1, 280) = 27.93$ and $F_{\text{min}}(1, 280) = 3.88$ within the significant cluster; $p < 0.05$ cluster corrected) was driven by the higher fixation duration in the upright condition compared to the inverted one in CG, and the reverse pattern in CP.

Figure 3f: *i*Map4 results of the spatial fixation pattern. A) Conditional z-score fixation duration map estimated from the linear mixed model: control group (CG) viewing upright and inverted faces, and congenital prosopagnosics (CP) viewing upright and inverted faces. Linear contrasts of the conditional fixation maps were performed for all the possible 2*2 combinations. Significant clusters are outlined with black lines in the map (cluster corrected $p < .05$). B) ANOVA result output from *i*Map4: F-value map of the significant main effect of *Group* and significant interaction of *Group* and *Face Orientation*.



3.2.4. Conclusions

The aim of the present study was to test whether the self-face advantage (SFA) showed by congenital prosopagnosics in an indirect task (see chapter 3.1) could also be detected by asking participants an explicit recognition of their face and, if so, whether this advantage would be reflected by a specific gaze behaviour, distinct from the one characterizing the exploration of unfamiliar faces. In the present study we asked the participants to explicitly discriminate the face stimuli and to judge them as “Me”/”Not me”, whereas previous evidence of the advantage in congenital prosopagnosics was obtained by means of a visual matching task in which the discrimination between the self and the other faces was indirectly required. In particular, in order to study the possible presence of the self-face advantage during this explicit task, here we took advantage of both behavioural and eye movement measurements because, while the former could

confirm its presence also during explicit self-face recognition, the latter ones could provide us information about how efficiency and distribution of gaze could account for its possible presence.

Specifically, the behavioural data corroborated the results of the previous chapter and previous findings (Keyes & Brady, 2010; Ma & Han, 2010) showing that the self-face advantage is detectable both in people with good recognition ability and individuals with congenital prosopagnosia, with both groups performing better and faster in the self-face condition. In particular, while congenital prosopagnosics performed significantly worse than controls with unfamiliar faces, their performance was comparable to controls with the self-face, suggesting that the self-face advantage may act as a compensatory process to overcome their face recognition impairment.

The eye movement results confirmed that overall congenital prosopagnosics show abnormal gaze behaviour compared to good recognizers during the exploration of facial stimuli; in particular, congenital prosopagnosics needed more fixations and more scanning time to recognize faces. Moreover, both groups exhibited a self-face advantage in their gaze behaviour; indeed, all our participants required less time and less fixations in order to recognize their self-faces compared to the unfamiliar faces. Interestingly, this advantage was not associated with a different spatial distribution of their fixations, suggesting that, whereas the information from the self and other was sampled in a similar way (same spatial fixation mapping), the processing of the information extracted within each fixation must have been different in the two conditions in order to give the different behavioural results. This evidence seems to support the idea that what is special about the self could be not 'what' is processed but 'how' efficiently the information sampled is processed. Indeed, even though the exploration of familiar faces is usually characterized by a different distribution of scanning compared to unfamiliar faces (Heisz & Shore, 2008; Stacey, Walker, & Underwood, 2005), this did not happen in our study.

Accordingly, the possibility that the self-face could be characterized by a specific processing has been already addressed in the literature, but the evidence collected so far is mixed. Indeed, as reported in paragraph 1.1.3, whereas some studies found that the self-face advantage might be part of a right-dominated neural network devoted to the processing of self-information (Devue et al., 2007; Platek et al., 2004; Platek et al., 2006; Uddin, Kaplan, et al., 2005), other studies have provided evidence for a specific bilateral representation of one's own face, suggesting that the advantage might be due to a more robust representation of the global and local aspects of the self-face across the brain (Brady et al., 2004, 2005; Keyes & Brady, 2010).

Particularly, according to this last hypothesis, while the right hemisphere would be responsible for the global aspects of the self-face, the left hemisphere might contribute by emphasizing the local aspects of it (Keyes & Brady, 2010). This prediction seemed supported by the presence of the self-face advantage with both upright and inverted faces (Brady et al., 2004, 2005; Keyes & Brady, 2010), so that while the global aspects might play a central role in determining the advantage in the upright condition, the more robust representation of the local ones would allow

the advantage for our face during inverted presentations. In particular, despite face inversion usually disrupts the normal global face processing (Tanaka & Farah, 1993), the advantage would be still present in the inverted condition thanks to the enhanced representation of the local aspect in the left hemisphere.

However, the results of the present study seem to support the first hypothesis emphasizing that the self-face could be characterized by an enhanced processing of self-information and, specifically, we believe that the self-face advantage could reflect a more general enhanced processing of self-related information. In fact, the advantage for the self-face affected the performance of controls and congenital prosopagnosics similarly in terms of behavioural and eye movement data and, because of the face recognition impairment characterizing the latter ones, this lack of difference between the two groups seems to suggest that the advantage could be not related to any face-specific mechanisms. Accordingly, if the self-face advantage was face-specific we would have expected a different modulation of it in the two groups, which we could not find.

In particular, recent findings supported the idea that in individuals with congenital prosopagnosia face recognition impairments arises from a failure in global/holistic processing (Avidan et al., 2011; Kimchi et al., 2012; Palermo, Willis, et al., 2011; Ramon et al., 2010; Richler et al., 2011), which obligate them to rely on single feature. Thus, if the self-face advantage is due to a more robust representation of the global aspects of the face when the stimulus is presented upright, and local aspects of the face when it is turned upside-down, then we would expect congenital prosopagnosics to take advantage of their spared feature-based processing and show a self-face advantage in the inverted condition, but not in the upright one, because of their impairment in global processing. However, this was not the case in our study, since the self-face advantage was present in both conditions of orientation and was not associated with any change in terms of spatial fixation distribution. Furthermore, although some authors (Brady et al., 2004, 2005; Keyes & Brady, 2010) interpreted the presence of the self-face advantage in both upright and inverted faces as proof of the more robust and bilateral representation of the local and global aspect of the face, we believe that this evidence could actually support the opposite hypothesis. In fact, it is well accepted that face inversion disrupts the expert face recognition processing and that, when inverted, faces are processed like any other object - that is, feature by feature (Tanaka & Farah, 1993); thus, for this reason, the presence of an advantage for the self-face in the inverted condition does not seem to be attributable to a face-specific mechanism but, by contrast, it seems more in favour of a generic self-advantage. In particular, as suggested by others (Blanke, 2012; Frassinetti et al., 2011; Frassinetti et al., 2008), the self-advantage may rely upon the integration of multisensory signs of the self-body involving a fronto-parietal network in the right hemisphere and, in our case, this multisensory representation of the self could act as a compensatory process to overcome the face recognition impairment in individuals with congenital prosopagnosia. However, additional studies will be needed to further investigate whether the self-face advantage is face specific or linked to self-related material in general; specifically, since previous studies have

demonstrated that prosopagnosics can be impaired in body and body motion perception (Lange et al., 2009; Moro et al., 2012; Righart & de Gelder, 2007; Rivolta, Lawson, & Palermo, 2017), it might be critical to investigate whether these individuals show also a self-advantage for their body parts, and, if so, if this advantage differs from the one characterizing the self-face (and this will be the topic of chapter 3.3).

A significant result of this study concerns face inversion. Indeed, in accordance with previous evidence (Barton et al., 2006; Farah, Wilson, et al., 1995), upright faces were easier to recognize compared to inverted faces and required fewer fixations and shorter scanning time. Surprisingly, in this case individuals with congenital prosopagnosia showed an inversion effect similar to controls both in terms of accuracy and reaction times. However, despite congenital prosopagnosics typically show a similar performance between upright and inverted faces (de Gelder & Rouw, 2000; Righart & de Gelder, 2007), it is worth mentioning that the studies reporting a lack of inversion effect in these individuals usually have used only unfamiliar faces as stimuli. By contrast, in this case both the inclusion of the self-face in the experimental paradigm and, thus, the presence of a self-face advantage in the congenital prosopagnosic group might have played as a confound factor, preventing the absence of inversion effect in this group. Confirming this hypothesis, the analysis on the spatial fixation mapping revealed that face inversion affected the two groups differently. In particular, whereas controls tried to encode both upright and inverted faces in a similar way, congenital prosopagnosics made significantly more fixations on the nose area and the mouth region in the inverted condition compared to the upright one.

Particularly, the fact that controls focused their fixations on the eyes and nose areas in both conditions is in accordance with previous evidence showing that the eye region contains the most diagnostic information for face identification (Sadr, Jarudi, & Sinha, 2003; Vinette, Gosselin, & Schyns, 2004), and that good recognizers look mostly at the eyes and they scan the upper half-face more than the lower half when recognizing faces (Barton et al., 2006; Blais, Jack, Scheepers, Fiset, & Caldara, 2008; Henderson, Williams, & Falk, 2005; Miellet, Vizioli, He, Zhou, & Caldara, 2013). However, whereas focusing around the eye region allows us to extract critical information in the upright condition, the same does not seem to work as efficiently when faces are presented upside-down. Previous evidence in good recognizers has also shown that the face inversion effect is not strictly a consequence of anomalous eye movements (C. C. Williams & Henderson, 2007), whereas it might be linked to a different efficiency in the extraction of information between the two conditions (Sekuler, Gaspar, Gold, & Bennett, 2004), and our data seem to point in the same direction. In addition, the mouth is also fixated more in the inverted than upright condition (Rodger, Kelly, Blais, & Caldara, 2010). However, in our experiment, the control group continued to focus on the same eye region also when faces were presented upside-down and, because this area does not seem to be so informative in this orientation, they showed a typical inversion effect.

By contrast, individuals with congenital prosopagnosia changed their fixation pattern between the upright and inverted condition, focusing only on each one of the two eyes in the first

case, while extending their focus also on the nose in the latter one. Despite face inversion is one of the most powerful arguments used to support the presence of face-specific impairment in congenital prosopagnosia, to the best of our knowledge only this study and the study described in chapter 2.3 have investigated how face inversion affects the gaze behavior of congenital prosopagnosics. Specifically, results from both these studies show that individuals with congenital prosopagnosia tend to explore upright and inverted faces in a very similar way, by focusing only on facial features and, despite some differences probably due to the additional inclusion of the self-face here, the results of both studies seem coherent. Indeed, even if with a different distribution between the upright and inverted conditions, during this task the congenital prosopagnosic group directed overall their attention on the single features of the face (eye, nose, or mouth), while ignoring the region between the eyes, crucial for expert processing. In particular, as also suggested by a previous study (Righart & de Gelder, 2007), the use of a same feature-based strategy with both upright and inverted faces could partially explain why congenital prosopagnosics often show a similar accuracy in recognizing upright and inverted faces. Specifically, whereas the feature-based strategy could also be optimal in the inverted condition (as also confirmed by the fact that sometimes congenital prosopagnosics perform even better than normal recognizers with inverted faces; e.g., (Farah, Wilson, et al., 1995)), the same is not true for upright faces, which require holistic processing; moreover, even though face recognition can be achieved also by using a feature-based strategy, this kind of processing is typically less efficient, requires more time, and it could explain why congenital prosopagnosics struggle so much with upright faces.

Lastly, since previous studies and the data presented in chapter 3.1 suggested that the self-face advantage could be linked to the preference for the right-half of the face (Brady et al., 2004), another aim of this study was to investigate whether the right perceptual bias (RPB) described in the literature in both good recognizers and congenital prosopagnosics would be detectable also in terms of eye movements. However, the analyses on the chimeras did not prove any influence of the type of chimeric stimulus on the behavioural performance of the two groups in the self-condition, so that no preference for one specific half of the self-face was found. In particular, we could not find a right perceptual bias in the behavioural or in the eye movement results of the two groups. Nevertheless, the lack of right perceptual bias is still very informative about, at least, two aspects: (1) since neither of the two groups showed a preference for the right-half of the self-face, despite showing a significant self-face advantage, this could suggest that the two effects are independent of each other and further support the hypothesis that the self-face advantage can be due to a more general enhanced processing of self-related information; (2) furthermore, the lack of right perceptual bias in a task requiring a direct and explicit recognition of the self-face could also suggest that the bias toward the right-half of the self-face could be sensitive to the task demand. Indeed, whereas the previous studies demonstrating the existence of the rightward bias have used indirect tasks, not requiring an explicit recognition of the self-face, in this study participants had to explicitly judge the face stimulus as “Me”/”Not me” (Brady et al., 2004). Accordingly, the study

that has used more direct and explicit task to test self-face recognition has failed to observe a right perceptual bias in good recognizers (Brady et al., 2005), suggesting that the rightward bias characterizing the self-face might be detectable only during indirect tasks probably because these tasks require to maintain a short memory representation of the self-face, which might elicit a different exploration of this stimulus.

In conclusion, the present study corroborated further the presence of a self-face advantage in both congenital prosopagnosics and good recognizers also during an explicit recognition task, and both in the case of upright and inverted face processing; particularly, the self-face advantage was not related to any change in the spatial fixation distribution, suggesting that it could be related to a more general enhancement of the self-information processing, instead of being due to face-specific mechanisms. However, contrary to what found in previous studies (Brady et al., 2004, 2005), the self-face advantage was not driven by the preference to the right-half face, suggesting that these two effects are separate and independent of each other, and that the right perceptual bias characterizing the self-face is sensitive to the task demand, being more evident when an explicit recognition of the self-face is not required. Finally, we showed that face inversion affects differently controls and congenital prosopagnosics. On the contrary of controls who explored mostly the eyes and the area between them in both conditions of orientation, congenital prosopagnosics made more distributed fixations in the non-canonical inverted condition, by focusing more on the nose and the mouth in this orientation. This observation could explain why congenital prosopagnosics sometimes can perform even better with inverted compared to upright faces. Altogether, the data presented in this study reveal a new oculomotor signature of the congenital face processing impairment.

3.3. Study VI: Self body-parts recognition in congenital prosopagnosia

As demonstrated in the studies described in chapters 3.1 and 3.2, both people with typical development and congenital prosopagnosia show an advantage in recognizing their own face during an indirect and direct task. In the first study, confirming previous evidence (Brady et al., 2004, 2005), we found this advantage to be related to a preference for the right part of the self-face, which falls in the observer's right visual field when looking at the mirror. However, in the second study asking participants to consciously judge the face stimulus as "Me/Not me", this right bias was not confirmed by means of a direct task, neither in terms of accuracy and reaction times nor eye movements. Moreover, in this last case, the self-face advantage showed by both controls and congenital prosopagnosics was not related to any specific change in the spatial fixation distribution, which may suggest that this effect could be related to a more general enhancement of the visual self-information processing, instead of being due to face-specific mechanisms. In order to verify this hypothesis, it would be critical to test the existence of a more general self-advantage

related also to the recognition of body parts other than the face in the congenital prosopagnosic population, which could explain their ability to recognize their own faces despite the face recognition impairment affecting them.

In particular, some recent findings suggest that individuals with congenital prosopagnosia can show difficulties in body perception (Rivolta et al., 2017) and atypical body motion perception (Lange et al., 2009). By contrast, other studies found normal body perception (Duchaine et al., 2006) and normal activation of the body-selective brain regions (Van den Stock, van de Riet, Righart, & de Gelder, 2008), further confirming the selectivity of the deficit of these individuals. However, besides the mixed results, none of these studies has investigated self-body recognition in congenital prosopagnosics and, thus, these results do not help us in clarifying the possible nature of the self-advantage.

To this aim, we recruited a group of congenital prosopagnosics and healthy controls that underwent a simple matching task involving the presentation of chimeric face and body-part stimuli (hands and feet), belonging to the participant or to other unfamiliar controls. We first wanted to compare the performance of the two groups with these three types of stimuli to further investigate whether individuals with congenital prosopagnosia are impaired in body-parts recognition as well as in face recognition and, in case they are, whether their impairment is of similar magnitude of the one for faces or not. Second, we wanted to investigate the nature of the self-face advantage that we found in the two previous studies. In particular, if this effect is not due to face-specific mechanisms we would expect both groups to show an advantage also in recognizing their own body parts, and to find that the advantage with these stimuli is similar to the one shown in recognizing the self-face. By contrast, if the self-face advantage is linked to mechanisms specific to self-face recognition, one could expect these individuals to show an advantage in recognizing their own faces but not necessarily their body parts.

Finally, since chapter 3.1 and previous evidence (Brady et al., 2004, 2005) suggest that the self-face advantage is linked to a rightward bias, we also wanted to investigate the possible presence of such bias also during the recognition of other body parts. For this reason, we used chimeric stimuli created from the original picture (face, hands or feet) of each participant (i.e., a composite made of two right half-faces or two right hands/feet and a composite made of two left half-faces or two left hands/feet) in addition to the original picture and mirror-reversed picture of all these stimuli. In particular, according to the results obtained in chapter 3.1, we would expect the right perceptual bias to be present and reflected in an increased performance in the presence of the right self hemi-face and in the presence of the right hand and foot.

3.3.1. Participants

Twenty-two students from the University of Milan-Bicocca were recruited through the University of Milan-Bicocca Sona System© and composed our control group (11 males, all right-

handed, mean age of 23.5 ± 2.3 years old, age range 20-30). The recruitment of these students was based on the absence of perceived life-long face recognition impairment and each of them received university course credit for taking part in the study. In addition, six congenital prosopagnosics (1 male, all right-handed, mean age of 24.8 ± 1.7 years old, age range 23-28; see Table 3d for more information) took also part in this experiment. All participants had normal or corrected-to-normal vision and reported no known neurological damage. Each participant provided informed consent and written permission for the use of their photographs for the purposes of this study, in accordance with ethical guidelines by the University of Milan-Bicocca ethical committee.

Face and object recognition abilities assessment

All participants underwent a first screening session during which we assessed their face and object recognition abilities. In particular, this time our battery was composed of two tests assessing participants' ability to recognize unfamiliar and familiar faces (i.e., the Cambridge Face Memory Test, CFMT, Duchaine & Nakayama, 2006, and the Famous Faces Recognition Test, FFRT, respectively), a test on visual and object recognition and general visual processing abilities (i.e., the Boston Naming Test, BNT, Kaplan et al., 1983; Famous Monuments Recognition Test, FMRT), and a self-rating report on face recognition ability (PI20, Shah et al., 2015). Similarly to the screening phase of the previous studies, here we derived again the inversion effect (IE) (Yin, 1969) as additional index from the CFMT, in order to obtain the "cost" for recognizing inverted faces for our participants (see previous chapters for a more detailed description of these tests).

The scores obtained in these tests by the 22 control participants formed the sample for the calculation of z-scores for the congenital prosopagnosic participants. The mean scores for each test (\pm SE) were as follows: 56.86 ± 7.03 for the upright version of the CFMT, 41.77 ± 5.56 for the inverted version of the CFMT, 15.09 ± 7.06 for the inversion effect, 33.59 ± 5.18 for the FFRT 24.04 ± 3.55 for the FMRT and 57.27 ± 1.98 for the BNT. The individual test scores for each congenital prosopagnosic and the z-scores calculated for each individual congenital prosopagnosic against the data from the group of 22 control participants are reported in table 3d. In addition, to further confirm the presence of prosopagnosia in the experimental group, our z-scores were compared with the published control scores for this test (Duchaine & Nakayama, 2006).

All our 6 congenital prosopagnosics were impaired in face recognition; indeed, they all performed poorly (i.e., 2 SDs below the mean of the control group) in the upright version of the CFMT (both considering our control sample and the published data of the controls from Duchaine & Nakayama, 2006) and the FFRT. Furthermore, all congenital prosopagnosics showed a smaller inversion effect compared to controls and, particularly, 5 of them had an inversion effect score 2 SDs lower than controls.

By contrast, in the tests investigating object recognition abilities (FMRT and BNT) all congenital prosopagnosics performed in the normal range, further confirming the selectivity of

their impairment. None of the controls showed any impaired performance in any tests or reported any life-long face recognition impairment.

Table 3d. Demographic features of the 6 individuals impaired in recognizing familiar faces and their performance scores (raw data and z scores) to neuropsychological tests of episodic face recognition. PI20 = Prosopagnosia Index 20; CFMT = Cambridge Face Memory Test; IE = Inversion Effect; FFRT = Famous Face Recognition Test; FMRT = Famous Monuments Recognition Test; BNT = Boston Naming Test. * = pathological score

Participant	EC	LS	RB	CR	VT	SE
Gender	F	M	F	F	F	F
Age	25	24	25	28	24	23
PI20	73	45	69	79	76	64
CFMT upright						
raw score	40*	40*	40*	36*	37*	37*
z-score	-2.40*	-2.40*	-2.40*	-2.97*	-2.83*	-2.83*
z-score ⁽¹⁾	-2.27*	-2.27*	-2.27*	-2.77*	-2.65*	-2.65*
CFMT inverted						
raw score	41	39	44	30*	38	44
z-score	-0.14	-0.50	0.40	-2.12*	-0.68	0.40
IE						
raw score	-1*	1*	-4*	6	-1*	-7*
z-score	-2.28*	-2.00*	-2.71*	-1.29	-2.28*	-3.13*
FFRT						
raw score	21*	21*	12*	13*	18*	12*
z-score	-2.43*	-2.43*	-4.17*	-3.98*	-3.01*	-4.17*
FMRT						
raw score	21	28	18	18	21	24
z-score	-0.86	1.11	-1.70	-1.70	-0.86	-0.01
BNT						
raw score	54	56	55	58	57	57
z-score	-1.65	-0.64	-1.15	0.37	-0.14	-0.14

3.3.2. Material and Methods

Since the experiment was composed of three different conditions involving the presentation of three different body parts (face, hands and feet), three unique stimuli sets were created for each participant. Each set included the participant's own face, hands and feet and two additional people's faces, hands and feet who were used as control stimuli consistently across the experiment (i.e., two female models for all female participants, and two male models for all male participants, whose body parts worked as control stimuli for all the experiments). To create each unique stimulus set, the participant and the two gender-matched models (unknown to the participants)

were photographed under symmetrical ambient light on a white background. In the case of the face, participants were required to look directly at the camera (Nikon d5100) with a neutral expression, whereas in the case of hands and feet they were asked to place those on a specific position outlined on a white cardboard.

For stimuli construction, in this experiment we used the same procedure already described in paragraph 3.1.2, this time involving not only the participants' faces, but also hands and feet. All the steps resulted in 4 images (original-R_L, reversal- L_R, left-chimeric-L_L and right-chimeric-R_R) of each person's body parts. In particular, while the face of the participant was divided in half in order to obtain the left and right sides necessary to create the chimeric faces, in the case of hands and feet we used the left and right hand, as well as the left and right foot singularly, to create the chimeric stimuli. In this latter case the single body parts were arranged side by side in the picture, horizontally aligned at a fixed distance of 4 pixels for the distance between the thumbs of two hands, and 40 pixels for the distance between the soles of the two feet (see figure 3g for an example of chimeric hand stimuli). Prior to the construction of the chimeric stimuli, the image properties of the three original pictures belonging to the participant and two matched controls (original-R_L of the face, hands, and feet) were equalized within each specific set of stimuli by using the SHINE toolbox for Matlab (Willenbockel et al., 2010), in order to minimize potential low-level confounds.

In the end, each face image was 288×384 pixels (approximately 9 cm \times 14.5 cm on the screen), whereas hands images were 446×384 pixels (approximately 14.5 cm \times 14.5 cm on the screen), and feet images were 326×384 pixels (approximately 10.5 cm \times 14.5 cm on the screen). Summarizing, all the procedure resulted in 4 images of the body part of each participant (participant and 2 gender-matched models) for a total of 12 images in each unique stimulus set — 4 images of the participant's body part and 8 belonging to matched models.

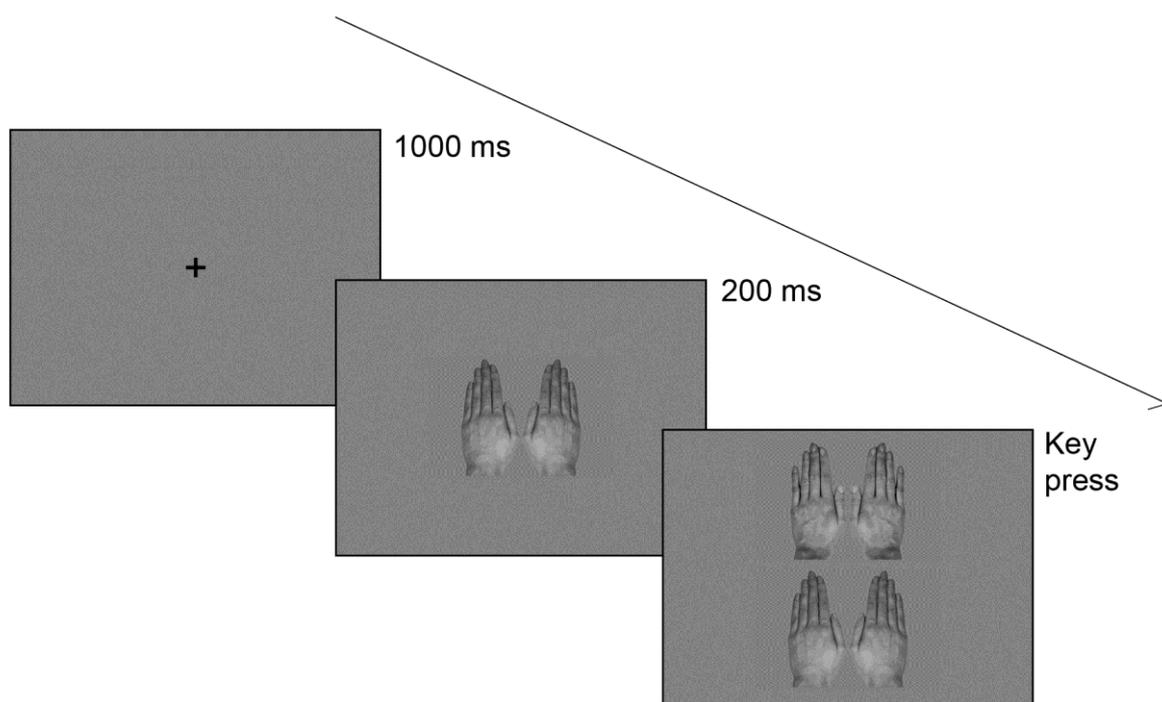
Participants sat in a comfortable chair approximately 57 cm from the monitor (40.5 cm \times 30.5 cm, 1280×800 pixels) in a dark silent room and a chin rest supported their heads. The experiment was controlled by OpenSesame 3.1.1 Software. All images were presented on a grey background. The experiment was composed of 3 blocks, one for each body part: block "A" for faces, block "B" for hands and block "C" for feet. The three blocks were administered according to an ABC CBA scheme, and specifically A1, B1, C1, C2, B2, and A2, in order to prevent any possible effects of presentation order.

Within each block, each trial (Figure 3g) started with a fixation cross at the centre of the screen, replaced after 1 sec from one of the possible stimuli (face, hands, or feet, depending on the block) for 200 ms. After that, two stimuli (the target and a distractor) appeared at the centre of the screen aligned vertically, one above the other. Participants were asked to press the "↑" key (right index finger placed on the 9 of the keypad) if the target stimulus appeared in the upper half of the screen, or the "↓" key (right thumb finger placed on the 3 of the keypad) if the target stimulus appeared in the lower half of the screen. Participants were asked to be as accurate and as fast as possible. The stimuli were presented vertically to ensure that the spatial layout of the body parts on

the screen did not influence the participants' tendency to look at the right or left sides of the stimulus. The test stimuli remained on the screen until the participant provided a key-response. There were no inter-stimulus intervals in this paradigm and participant's response triggered the presentation of the next trial.

Within each block, each of the 4 participant's stimuli described above appeared as the target stimulus 12 times, while the 4 stimuli of the two controls 6 times (resulting in 48 "self" target stimuli and 48 "other" target stimuli) for a total of 96 trials per single block, and 192 for each condition (i.e., face, hands and feet). All the stimuli were presented in randomized order. On each trial, the distractor stimulus was chosen pseudo-randomly from the 8 images of the remaining two control identities so that all pictures were used as distractor stimulus an equal number of times. For example, if the target hands were the L_L image of the participant, the distractor hands could be any one of the image types (R_L, L_R, R_R, or L_L) of the two models. Likewise, if the target hands were the R_L image of one of the models, the distractor hands could be any one of the image types of either the participant or the remaining model. In other words, target stimulus and distractor stimulus always depicted different identities. The target stimulus appeared in the upper and lower part of the response screen in randomized order.

Figure 3g. Example of an experimental trial. Trials began with a fixation cross that ended after 1 sec. Then, observers were presented with a target stimulus (face, hands or feet depending on the block) for 200 ms followed by a test trial in which they were asked to select which stimulus was the one previously seen. This test trial ended when the participant pressed a key, indicating their response.



Before the first block of each condition, to familiarize the participant with the brief presentation time of the target stimulus during the test trials and to practise key press responses, all participants performed a practice following the same procedure of the actual experiment. During these three practices participants were also given self-paced instructions. In particular, each one of these practises involved the presentation of the same body part stimulus of the following experimental block, and was composed of 12 trials depicting three models' body-parts (faces, hands, or feet, depending on the practice block) unknown to the participant. Participants were asked to reach 80% accuracy during the practice, in order to switch to the corresponding experimental block; otherwise, the practice part was repeated until the criterion was met. These trials were not counted for statistical analysis.

3.3.3. Results

The proportion of correct responses and response times (RTs) from correct trials only (measured from the stimulus onset until participant's response) were analysed. RT outliers (2.5 SDs above or below the mean for each participant) were also discarded and not analysed. In order to provide a better summary of our findings, we also analysed the inverse efficiency score (IES), defined as RT/accuracy (Bruyer & Brysbaert, 2011). Focusing not only on accuracy is also critical to detect differences between typical and atypical populations (Duchaine & Garrido, 2008).

The accuracy, RTs and IES data from the control and congenital prosopagnosic groups were analysed using a linear mixed model with the lme4 package (Bates, Maechler, Bolker, & Walker, 2013) in R (<https://www.r-project.org/>; R Development Core Team, 2008). A first model was run including as factors *Identity* (Self vs. Other), *Condition* (Face vs. Hands vs. Feet), *Group* (CG vs. CP), their mutual interactions and a random intercept for each participant. Then, within each condition and for the self stimuli only (i.e., in the familiar stimulus condition, since no effect should be expected in the case of an unfamiliar stimulus), a second model was run, in order to investigate any possible effect of the four stimuli (L_L, L_R, R_R, and R_R) on participants' performance. Thus, in this second model the factors included were *Stimulus* (L_L, L_R, R_R, and R_R), *Group* (CG and CP), their mutual interaction and a random intercept for each participant. For both models, F tests from the LMER results are presented (type III with Satterthwaite approximation for degrees of freedom), and significant differences were further explored by Bonferroni post hoc multiple comparisons (corrected *p-values* are reported).

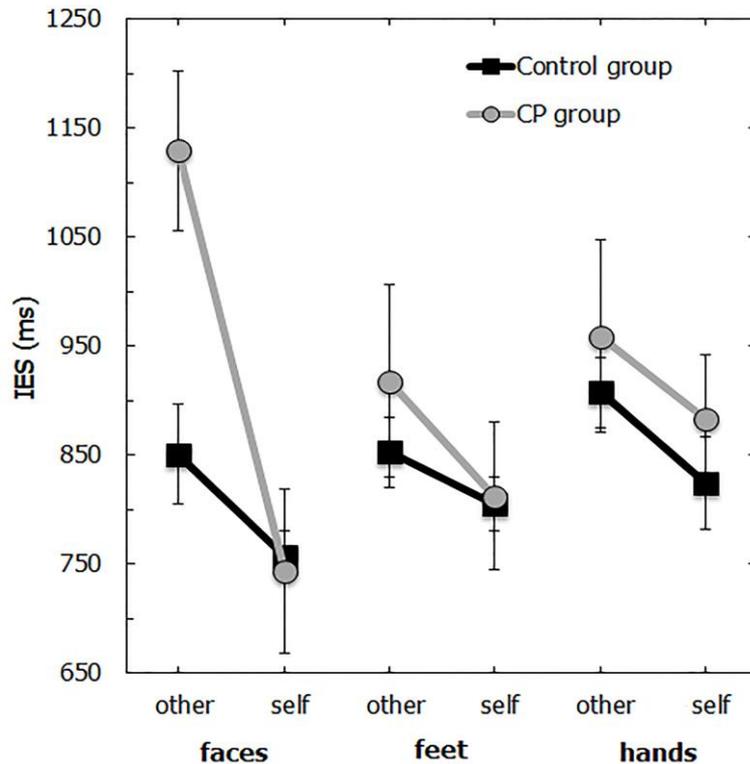
Results from the first model reveal that the main effect of the *Group* was significant on the accuracy data ($F(1,26) = 5.55, p < .05$), whereas the main effect of the *Condition* was significant only on RTs ($F(2,130.06) = 5.39, p < .005$), demonstrating that overall individuals with congenital prosopagnosia have lower accuracy compared to controls (0.87 ± 0.04 and 0.92 ± 0.01 , respectively) and that the hand condition was the one associated with the slower RTs (face: 757 ± 28 ; hands: 789 ± 26 ; feet: 753 ± 22). By contrast, the main effect of the *Identity* was significant on

accuracy, RTs and IES ($F(1,130) = 37.81, p < .001$; $F(1,130.06) = 12.37, p < .001$ and $F(1, 130.02) = 36.78, p < .001$, respectively), demonstrating the presence of a significant self-advantage in all measurements.

The interaction between *Group* and *Identity* was also significant on both accuracy ($F(1,130) = 14.20, p < .001$) and IES ($F(1,130.02) = 6.88, p < .01$). Confirming the results of chapter 3.2, whereas both controls and congenital prosopagnosics had a significant advantage in recognizing their body parts, this advantage was larger in the congenital prosopagnosia group (accuracy: CP = 0.10, $p < .001$; CG = 0.02, $p = .26$; IES: CP = 189 ms, $p < .005$; CG = 75 ms, $p < .05$). Accordingly, individuals with congenital prosopagnosia performed significantly worse than controls only in the other condition (accuracy: CP = 0.82 ± 0.03 , CG = 0.91 ± 0.02 , $p < .001$; IES: CP = 1002 ± 98 ms, CG = 870 ± 37 ms, $p < .05$), whereas in the self one they were comparable to controls (accuracy: CP = 0.92 ± 0.01 , CG = 0.93 ± 0.01 , $p = 1.00$; IES: CP = 813 ± 98 ms, CG = 795 ± 31 ms, $p = 1.00$).

The interaction between *Group* and *Condition* was also significant on accuracy ($F(2,130) = 10.92, p < .001$) and the interaction between *Identity* and *Condition* was significant on both accuracy ($F(2,130) = 16.08, p < .001$) and IES ($F(2,130.02) = 6.19, p < .005$): individuals with congenital prosopagnosia performed worse than controls only when they had to recognize faces, and the self-advantage was larger for faces compared to hands and feet (particularly in the IES data).

Figure 3h. Mean inverse efficiency score of the control group and congenital prosopagnosia group for the Other/Self in the different stimulus conditions. Vertical lines indicate ± 1 SE.



Finally, the triple interaction between *Group*, *Condition* and *Identity* was significant on accuracy ($F(2,130) = 15.72, p < .001$) and IES data ($F(2,130.02) = 4.36, p < .05$; Figure 3h). This interaction highlighted that in both cases controls and congenital prosopagnosics showed a similar performance for feet and hands, and a similar advantage for the self-version of these stimuli. In the face conditions, instead, individuals with congenital prosopagnosia differed from controls only when they had to recognize unfamiliar faces, while they performed as controls in recognizing their own faces.

By contrast, the results from the second model (i.e., the one investigating the effect of the different chimeras) failed to reveal any significant effect of the type of stimulus in all conditions (face, hands, and feet), neither as main effect nor in interaction with the group factor.

Taken together, these results confirmed the findings of previous studies showing that the self-face advantage is detectable both in good recognizers and individuals with congenital prosopagnosia, and that the self-face advantage in the congenital prosopagnosia group is so effective that in the self-face condition their performance is comparable to the one of controls. Furthermore, these results highlight that both groups show a similar advantage in recognizing their body parts compared to unfamiliar ones.

3.3.4. Conclusions

The aim of the present chapter was to investigate whether individuals with congenital prosopagnosia are impaired in recognizing body-parts as well as faces, and to test whether the self-face advantage (SFA) showed by congenital prosopagnosics in the two previous studies is face-specific or not, by investigating whether they show a similar advantage also in the recognition of other self body-parts. Similarly to the study of chapter 3.1, here we used again an indirect face recognition task (visual matching) asking participants to match a previously seen stimulus to one of two possible stimuli, and we used again chimeric stimuli, this time involving self body-parts and unfamiliar body-parts in addition to chimeric faces.

First, according to our data, individuals with congenital prosopagnosia have no difficulties in recognizing body parts. This result seems in contrast with some recent evidence showing that both individuals with acquired and congenital prosopagnosia can show difficulties in body perception (Rivolta et al., 2016; Moro et al., 2012; Susilo et al., 2013) and atypical body motion perception (Lange et al., 2009). However, whereas in this study we used body parts (face, hands, and feet), all the studies mentioned above investigated the recognition of the whole body. In particular, these different results could leave open the possibility of a dissociation between the recognition of body parts and whole body in this population. Similarly, indeed, despite they show difficulties in recognizing whole faces, congenital prosopagnosics are still able to recognize the local aspects of a face (i.e., nose, mouth, and eyes) individually when required (e.g., Diamond & Carey, 1977; Verfaillie et al., 2014). Typically, this dissociation between the spared face-parts and the

impaired whole-face recognition abilities in individuals with congenital prosopagnosia has been linked to a deficit in holistic processing (i.e., the parallel processing of a face as a whole, which combines the features and the spatial relationships between them; Avidan et al. (2011); Kimchi et al. (2012); e.g., Palermo, Willis, et al. (2011); Ramon et al. (2010); Richler et al. (2011)). In particular, some studies have suggested that holistic processing could be not specific to faces only, but it could apply also to some other type of stimuli, such as body and objects belonging to the same class (Behrmann et al., 2005; Damasio et al., 1982; Farah, Levinson, et al., 1995; Robbins & Coltheart, 2012). In support of this hypothesis, when typical individuals are asked to recognize bodies they are better with upright than inverted ones, and this effect is of similar extent to the one shown for faces (Minnebusch, Keune, Suchan, & Daum, 2010; Minnebusch, Suchan, & Daum, 2009; Reed, Stone, Bozova, & Tanaka, 2003). Thus, the existence of a similar inversion effect for both bodies and faces might suggest that face and body processing might share similar cognitive, and eventually neural, processing (Rivolta et al., 2016; Robbins & Coltheart, 2012). In particular, the results from this study, together with this previous evidence present in the literature, may suggest that holistic processing can be applied also to bodies (Robbins & Coltheart, 2012); accordingly, individuals with congenital prosopagnosia show spared performance in recognizing the single parts of a face or of a body, while being impaired in the recognition of the whole stimulus.

However, according to an alternative hypothesis, each body part we tested here could be considered as within-class stimulus, similarly to the ones we used in chapter 2.3 (i.e., gerberas). In this case, we would expect individuals with congenital prosopagnosia to show a worse performance compared with controls during the recognition of unfamiliar body-parts, because of their possible deficit in individual-item recognition. Despite we did not find a significant difference between congenital prosopagnosics and controls in the unfamiliar feet and hands conditions, a closer look at figure 3h could confirm the presence of such trend, which could have been hidden by the small sample size of our group of congenital prosopagnosics. For this reason, it is possible that the inclusion of more individuals with congenital prosopagnosia into the experimental group would let the effect emerge, further supporting the possible within-class impairment in this population (previously described in chapter 2.3).

As second result, we found that good recognizers showed a self-advantage for all the types of stimuli we tested (face, hands, and feet). This result confirms previous findings demonstrating that normal individuals are more accurate in processing their own body parts compared to other people's body-parts (Frassinetti et al., 2008; Frassinetti et al., 2009; Frassinetti et al., 2010). In particular, the fact that normal recognizers show an advantage of the same magnitude for the self-face, hands, and feet seems to suggest that the same mechanisms could underlie the recognition of all three types of stimuli, supporting the existence of a general self-advantage for the own body and claiming against the face specificity of the self-face advantage. Specifically, this general self-advantage might arise from a right-dominated fronto-parietal network devoted to the processing of

self-information (Devue et al., 2007; Platek et al., 2004; Platek et al., 2006; Uddin, Kaplan, et al., 2005) and it may rely upon the integration of multisensory signs of the self-body.

Similarly to controls, individuals with congenital prosopagnosia showed an advantage in recognizing their own body parts compared to unfamiliar ones. In particular, in this population the self-advantage was larger in the case of faces compared to hands or feet. It could be argued that this result might support the face-specificity of the self-face advantage, at least in the case of individuals with congenital prosopagnosia. However, another more plausible explanation of this result could be that, in this population, the self-advantage is larger for faces compared to other body parts simply because of their impairment in recognizing faces, which leads them to show a much lower performance with unfamiliar faces compared to their performance with other unfamiliar body-parts. Furthermore, the existence of a face-specific mechanism responsible for the self-face advantage in a population characterized by a selective face recognition impairment seems unlikely; more plausible is that a more general enhancement of the self-processing could underlie both the self-face and the self body-part advantages. In particular, confirming the results of chapter 3.1 and 3.2, the self-advantage in the congenital prosopagnosia group could act as compensatory process to overcome their face recognition impairment so that in the self condition their performance is comparable to the one of controls.

Finally, since previous evidence (Brady et al., 2004; chapter 3.1) suggested that the recognition of the self-face could be linked to a preference for the right-half of it, in this study we used chimeric stimuli to test whether a similar bias was detectable also during the recognition of other body parts. However, analyses on the different type of chimeric stimuli failed to reveal any preference for any of them. In particular, we could not find any rightward bias in the present study, neither for faces nor for hands or feet stimuli. Taken together, these results confirm that the self-advantage and right perceptual bias could be independent of each other; indeed, neither of the two groups showed a preference for the right-half of the face or body-part stimuli, despite showing a significant self-advantage. Furthermore, the lack of a right perceptual bias with body-parts might highlight the face-specificity of this effect. Moreover, it is possible that in this study the use of multiple conditions (face, hands and feet) might have hidden the right perceptual bias we previously found in chapter 3.1 by using a similar paradigm. An additional limit of the present study is represented by the limited sample size of individuals with congenital prosopagnosia; indeed, whereas in chapter 3.1 the right perceptual bias was found with a sample of 11 congenital prosopagnosics, in this study only 6 individuals with face recognition impairment were tested. Thus, it is possible that this effect could emerge by increasing the sample size.

In conclusion, despite some previous evidence reporting that individuals with congenital prosopagnosia can be impaired in body perception and recognition, the present study demonstrated that at least self body-part recognition is spared in this population, suggesting that body-parts and whole-body processing might be dissociable in this population and further supporting that holistic processing could be applied also to bodies recognition (Robbins &

Coltheart, 2012). Moreover, we showed that the self-advantage was similarly present for all types of stimuli, indicating that the same mechanism could be responsible for both the self-face and self body-part advantage. Particularly, this general enhancement of the self-information processing might be due to the integration of multisensory signs of the self-body relying on a fronto-parietal network. Finally, we failed to find any rightward bias in the recognition of the self body-parts, further confirming that the right perceptual bias characterizing the recognition of the self-face (Brady et al., 2004) is an effect completely independent of the self-advantage, and that it might concern the memory representation of the self-face.

4. Conclusions and general discussions

The series of studies described in the present doctoral thesis deal with some of the open issues about congenital prosopagnosia, and provided some answers and new insights about the face-specificity of some of the perceptual biases characterizing face recognition (i.e., left-perceptual bias and self-face advantage).

In particular, the first part of the present thesis investigated some of the open questions still present in the literature about face recognition and, especially, congenital prosopagnosia. Chapter 2.1 and 2.2 described two studies examining in depth some of the most common tools used in the assessment of congenital prosopagnosia. Indeed, previous evidence showed that not all tools are equally reliable in assessing the face recognition deficit in this population (e.g., Duchaine & Nakayama, 2006; Duchaine & Weidenfeld, 2003; Duchaine & Nakayama, 2004) and, particularly, that relying on self-report is not enough (e.g., De Haan, 1999; Bowles et al., 2009; Grueter et al., 2007). Results from our studies show that, despite individuals with impaired face recognition have more insight about their abilities compared to good recognizers, self-reports or questionnaires alone do not represent reliable measurements that can be used to identify the presence of the impairment. By contrast, the use of formal tests assessing face recognition abilities is critical, but even among those tests it is important to select tools sensitive enough to identify individuals with poor face recognition abilities, and to compare the data of the potential prosopagnosic individual to adequate normative sample.

Chapters 2.3, instead, investigated the selectivity of the deficit that characterizes congenital prosopagnosia. Indeed, some studies (e.g., Behrmann & Avidan, 2005; Damasio et al., 1982) have questioned the face-selectivity of the impairment affecting congenital prosopagnosics. By examining both the behavioural performance and the scanning strategies of these individuals, our study demonstrated that congenital prosopagnosics might be characterized by a broader deficit affecting not only faces but also individual-item recognition within a class; particularly, the deficit in congenital prosopagnosia would be evident every time a fine-grained discrimination of perceptually similar exemplars within a category is required.

In the second part of the present thesis (chapter 3), I addressed the question whether some of the perceptual biases (e.g., *right perceptual bias* and *self-face advantage*) that characterize face recognition in normal individuals, are detectable also in individuals with congenital prosopagnosia. In particular, whereas the self-face advantage consists of a better performance when participants have to recognize their own face compared to unfamiliar or familiar faces (Ma & Han, 2010; Sugiura et al., 2005), the right perceptual bias refers to one's tendency to rely more on the right half-side of the face, which falls in the right visual hemi-space looking at the mirror, when asked to recognize the own face (Brady et al., 2004).

Results described in chapter 3.1 demonstrated the existence of a self-face advantage also in participants affected by congenital prosopagnosia. Thus, despite their face recognition impairment, individuals with congenital prosopagnosia can achieve normal performance in recognizing their own face. In particular, results from this study suggested that this advantage was linked to the presence of the right-half of the self-face, suggesting that a right perceptual bias could act as a compensatory strategy that allows this population to overcome their face recognition deficit.

Since it is well accepted that the face recognition impairment shown by congenital prosopagnosics is reflected in their anomalous scan path behavior during the exploration of faces (e.g., Schwarzer et al., 2007; Schmalzl, Palermo, Green, et al., 2008), in chapter 3.2 I described a study that investigated whether the enhanced performance that these individuals show in the case of the self-face is detectable also in terms of eye-movements (that is, in a different exploration of the self-face compared to unfamiliar faces). Moreover, since they seem to over-rely on the right-half of the self-face, in chapter 3.2 I described a study that tested also whether they explore the two half-parts of the face differently. However, results from this study demonstrated that both the self-face advantage and the right perceptual bias were not related to any change in the spatial fixation distribution. Thus, this evidence suggests that the self-face advantage we found could be related to a more general enhancement of the self-information processing, instead of being due to face-specific mechanisms, and that the right perceptual bias and the self-face advantage are two separate and independent effects.

These findings are further corroborated by the study reported in chapter 3.3. In order to examine the nature of these two effects, in chapter 3.3 I reported the comparison between normal individuals and congenital prosopagnosics on face and body-part recognition. Indeed, results from that study showed that the self-advantage was detected similarly for both the self-face and self body-parts, indicating that the same mechanism could be responsible for both advantages. Moreover, the findings from that study confirmed that the right perceptual bias characterizing the recognition of the self-face is an effect independent of the self-advantage, and that it might only concern the memory representation of the self-face. Finally, this study also demonstrated that self body-part recognition is spared in individuals with congenital prosopagnosia, leaving open the possibility that body-parts and whole-body processing might be dissociable in this population.

Collectively, the evidence presented in the present thesis help us in shedding light on the mechanisms underlying typical and atypical face recognition. In particular, congenital prosopagnosia seems not to be limited to face processing difficulties, but it may also extend to within-category recognition. On the other side, congenital prosopagnosics' ability to recognize body-parts seems preserved. Finally, despite their inability to recognize themselves in the mirror is often reported as anecdotal prove of the severity of their impairment, the present thesis demonstrates that, thanks to the use of a more general self-recognition processing, individuals with congenital prosopagnosia can achieve considerably high performance when recognizing their own face and, thus, that self-face recognition is spared in this population.

Considering that all the studies we conducted for this doctoral thesis involved the use of self-related and unfamiliar stimuli, it would be a challenge for future research to better characterize the effects we found here by taking advantage also of other stimuli with different degrees of familiarity to the participant. However, the involvement of individuals close and familiar to the participants in studies has proven to be challenging; for this reason, the possibility to have access to potential funding for participant recruitment and multiple resources could help us in overcoming this issue in the next future. Moreover, since some of the studies reported in this doctoral work underline that eye movements could be used as marker of the congenital face processing impairment, further studies could help to verify whether this technique could prove useful also during the assessment and diagnosis of the prosopagnosic deficit.

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