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Face distortions in prosopometamorphopsia provide new insights into the organization of face perception

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ABSTRACT

Prosopometamorphopsia (PMO) is a striking condition of visual perception in which facial features appear distorted, for example drooping, swelling, or twisting. Although numerous cases have been reported, few of those investigations have carried out formal testing motivated by theories of face perception. However, because PMO involves conscious visual distortions to faces which participants can report, it can be used to probe fundamental questions about face representations. Here we review cases of PMO that address theoretical questions in visual neuroscience including face specificity, inverted face processing, the importance of the vertical midline, dissociable representations for each half of the face, hemispheric specialization, the relationship between face recognition and conscious face perception, and the reference frames that face representations are embedded within. Finally, we list and touch upon eighteen open questions that make clear how much is left to learn about PMO and the potential it has to provide important advances in face perception.

1. Introduction

In 1947, Bodamer (translated by Ellis and Florence, 1990) reported two patients with difficulty recognizing faces but no facial distortions and one patient with facial distortions but no difficulty recognizing faces. This third patient with facial distortions, patient B, reported that faces were “distorted or displaced, e.g. a nurse’s nose was turned sideways by several degrees, one eyebrow was higher than the other, the mouth was squinted, and the hair shifted like an ill-fitting cap.” Bodamer notes, however, that “he recognized the nurse by her face, and never mixed her up with others.” Based on the double dissociation seen in these patients, Bodamer concluded that the recognition of faces and the conscious perception of faces are separable processes. Since then, hundreds of cases of prosopagnosia, the condition exhibited by Bodamer’s first two patients, have been reported. These reports have played a critical role in shaping theories of face perception and the organization of the visual system (Bruce and Young, 1986; Farah, 2004; Kanwisher and Barton, 2011; Duchaine and Yovel, 2015). Much less studied but potentially no less important for understanding face processing is the condition exhibited by Bodamer’s third patient, prosopometamorphopsia (PMO). Over 80 cases of PMO have been reported (Blom et al., 2021), but few articles about PMO contain formal testing guided by theoretical questions from visual neuroscience. Rather than cover all of the PMO cases in this review (see Blom et al., 2021 for a comprehensive review of PMO), here we focus on cases that we believe shed light on theoretical questions about face perception.

Prosopometamorphopsia is a seemingly rare condition in which faces look distorted, often while other visual categories remain largely or entirely undistorted. Although some individuals with PMO see distortions on almost all faces (e.g. Anbarasan and Howard, 2012; Dalrymple et al., 2014), others see distortions on only a limited set of faces (e.g. Miwa and Kondo, 2007) Approximately two-thirds (34/51) of the PMO cases that met the selection criteria for our review involve distortions to only half of the face (i.e. left half or right half), a subcategory known as hemi-prosopometamorphopsia (hemi-PMO). Hemi-PMO distortions never switch sides on an upright face (e.g. a hemi-PMO participant who sees distortions to the right half of an upright face always sees distortions to the right half of any upright face that is distorted). Hemi-PMO contrasts with bilateral-PMO, in which features on both halves of the face are distorted.

Some of the most vivid illustrations of PMO come from patient TNP, an artist who developed hemi-PMO following the removal of a tumor in the left medial parietal-occipital region (Mooney et al., 1965). A few of the drawings he made while hospitalized can be found in Fig. 1. The

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majority of PMO cases, however, rely solely on verbal or written descriptions. One particularly evocative description of PMO comes from a patient who reported that the left halves of faces melted "like clocks in a Dalí painting" (Brust and Behrens, 1977). Table 1 provides a list of quotations describing the face distortions experienced by several different PMO cases. The distortions reported in PMO vary from participant to participant with some commonalities (e.g. drooping) but few clear patterns emerging.

Some of the cases we classify as PMO and the subcategories we use in our review (e.g., hemi-PMO, bilateral-PMO) differ from the other recent review (Blom et al., 2021). Cases where distortions frequently appeared on non-face objects, possibly indicative of lower-level visual problems, were excluded. In addition, we have tried to do an exhaustive search of the PMO literature, but it is possible we may have missed some cases. We included papers not written in English (the authors' native language) for which we were able to obtain an adequate translation, but this was not possible for some papers. With these limitations in mind, we believe this review can serve as an overview of PMO, the research questions raised and addressed, and a guide with advice for improving future PMO studies.

One issue that often produces confusion in discussions of PMO, and especially hemi-PMO, has been the simple question of what is left and what is right. The left half of a face has sometimes referred to the left half from the participant's perspective (the participant's left-hand side; Fig. 2a) (e.g. Nijboer et al., 2008; Almeida et al., 2020) while in other articles it has referred to the perspective of the face being observed (the participant's right hand side; Fig. 2b) (e.g. Grüsser and Landis, 1991; Trojano et al., 2009). Here, we use the participant's perspective (Fig. 2a). Using this convention places the emphasis on how the face appears to the participant who experiences the distortions. It also matches the side of the face to the visual field: when fixating a face centrally, the left side of the face falls in the left visual field and the right side in the right visual field. Regardless of the perspective used, we strongly encourage researchers working on future PMO publications to clearly state what perspective they are using and to keep that perspective consistent when describing the participant's distortions..

2. Characteristics of PMO

2.1. Face specificity

The question of whether face-specific processes exist has been a central question in work on face processing (Diamond and Carey, 1986; Duchaine et al., 2006; Haxby et al., 2000; McKone et al., 2007; Moscovitch et al., 1997; Tarr and Gauthier, 2000; Yin, 1969). Although PMO reports have received little attention in this debate, numerous PMO participants report distortions only for faces and not for objects (e.g. Almeida et al., 2020; Cho et al., 2011; Dalrymple et al., 2014; Ebata et al., 1991; Funatsu et al., 2017; Jiang et al., 2017; Kim et al., 2016; Lee, 2015; McCarty et al., 2017; Miwa and Kondo, 2007; Trojano et al., 2009). What makes these reports of face-specificity so revealing is that PMO participants are continually having the face-specificity of their distortions tested in the natural world with countless categories of stimuli (e.g. bodies, cars, houses, trees, tables, entire rooms or streets, etc.). Other studies of face-specificity (e.g. studies of prosopagnosia, stimulation of face-selective areas, psychophysics, or fMRI measurements) cannot come close to testing face-specificity in our natural world with the massive number of visual stimuli, the length of the exposure, nor the numerous visual manipulations the stimuli undergo in position, viewpoint, and retinal size. Unlike prosopagnosia where visual recognition must be assessed through testing, people with PMO are consciously aware of their distortions as they look around their visual world; if other categories of stimuli were distorting, PMO participants would report it. Thus, in our view, examples of face-specific PMO provide the strongest, most robust evidence available that face-specific processes exist.

2.2. The role of the vertical midline in face representations

Perhaps the most notable characteristic of hemi-PMO is the importance of the face's vertical midline, which divides the left and right halves of the face. The ability for hemi-PMO lesions to routinely cause distortions to only one half of the face strongly suggests that representations of the left and right half of the face are dissociable. For example, patient AD "reported that the right eye, right side of the nose, and the right corner of the mouth look like they were 'melted down' and that the two halves of the face did not fit together." In contrast, Saito et al. (2014) described a patient who saw that "the [left] eye and the [left] half of the mouth look slightly smaller than the [right] ones and appear to stretch away from the center of the face." Even basic features of the face thought of as a single part, such as the nose or mouth, can have distortions that affect only one side of the part as indicated by only half of the mouth being distorted in these two cases.

Some evidence suggests that the comparison of features on either side of the vertical midline plays a role in bilateral-PMO distortions. In Dalrymple et al. (2014), AS had bilateral-PMO but reported that it was asymmetries between the left and right halves of the face that drove her distortions, as the asymmetries become more and more magnified the longer she looked at a face. In recent unpublished testing with mirror symmetric and asymmetric faces, AS reported distortions on all of the asymmetric faces (10/10) and none of the symmetric faces (0/20). Similarly, when AS was presented with half faces, she no longer

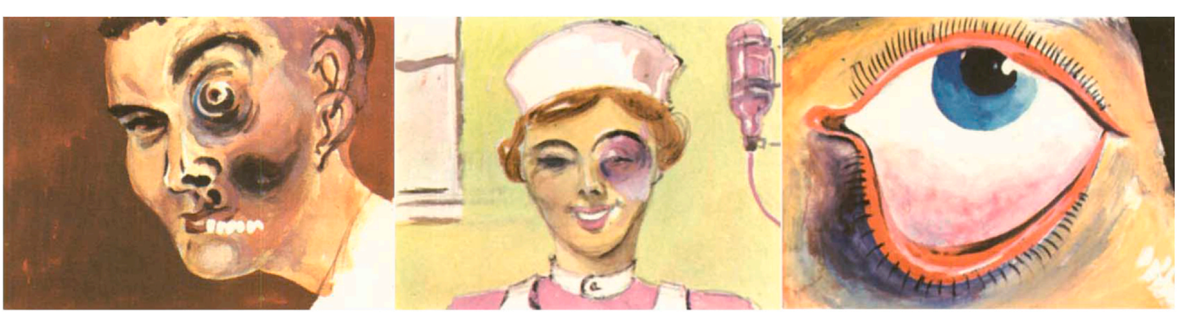

Fig. 1. Drawings made by patient TNP illustrating the distortions he saw on faces (Mooney et al., 1965). TNP's description of the distortion for each illustration are provided. (Left) Distortion to the right side of a doctor's face. According to TNP, "the eye became a ghastly staring hole, cheek bone a cavity; he had teeth on the upper lip, often had two ears." (Middle) Distortion to the right eye of a nurse. "When I was talking to a nurse standing at the end of my bed, her [right] eye became extraordinarily staring and fierce, the iris was of an unnatural cobalt blue and the white part very brilliant." (Right) A distorted eye TNP saw in his mind when he closed his eyes. "There was an eye which I saw quite often when my eyes were closed: the lid was shiny red, the iris vivid blue, the pupil jet black." Reprinted from American Journal of Ophthalmology, 59 (2), Alan J. Mooney, Patrick Carey, Max Ryan, Patrick Bofin, Parasagittal Parieto-Occipital Meningioma, 197–205, Copyright (1965) with permission from Elsevier.

Table 1
Quotations describing PMO, selected for illustrative purposes. These descriptions are directly quoted from the papers themselves, so left and right may refer to either the participant's perspective or the stimulus's perspective (Fig. 2). Direct quotations from participants are in quotation marks.

Paper	Distortion description
Bilateral-PMO Cases	
Bodamer (1947) (translation by Ellis and Florence, 1990)	A nurse's nose was turned sideways by several degrees, one eyebrow was higher than the other, the mouth was squint [sic], and the hair shifted like an ill-fitting cap.
Bala et al. (2015)	"I can see her eyes and smile quite different than usual, everything seems to be puffy, swollen, her smile is different than the one I remember, as if she was unnaturally baring her teeth, as if the smile would like to tell something, a grimace."
Dalrymple et al. (2014)	"Wow—large nose, prominent eyebrows. The eyebrows are coming towards me. And … strangely, his right eye is getting larger. Like, opening more … yeah, both brows are coming towards me and his- his right eye is getting larger, it's the most prominent thing and the nose is just really prominent, it's almost three dimensionally coming off the screen."
Hwang et al. (2012)	"The nose looks very narrow and lengthened toward the mouth, which looks small and round in shape" … According to her description, she appeared to see faces as if viewed through a convex lens.
Hemi-PMO Cases	
Almeida et al. (2020)	He reported that the right eye, right side of the nose, and the right corner of the mouth look like they were "melted down" and that the two halves of the face did not fit together.
Brust and Behrens (1977)	The right half of people's faces (i.e., to the patient's left) seemed to melt, "like clocks in a Dali painting," and took on yellow or violet colors.
Cho et al. (2011)	The left eyelid of people looked swollen as if they had undergone "failed eyelid surgery," while the nose appeared to be bent downward and the left facial outlines either bulged or writhed.
Grüsser and Landis (1991)	The left half of his face was distorted, the left part of his nose being swollen, the left eye and left corner of the mouth swollen and tilted downwards.
Jiang et al. (2017)	She noticed a "funhouse mirror effect" in the left half of the nurse's face, correlating to the patient's right visual field. This half of the face appeared to be laterally elongated, and the left eye appeared more oval than the right.
Nijboer et al. (2008)	"When looking at a face, the right side starts to distort within seconds; the right side becomes smaller and the eye starts to disappear outside the face. Nose, mouth, and eye brows are displaced as well and bulge, but are still seen inside the face."
Trojano et al. (2009)	"The left eye looks elongated towards left ear, the nose appears to be bended towards left cheek and the mouth towards the chin."

perceived distortions. Whether asymmetries across the midline of the face are important for other bilateral-PMO participants could be easily tested by showing half faces or mirror symmetric versions of faces that have previously produced distortions. If the distortions stop, then it would be strong evidence that asymmetries across the midline are important in driving that participant's distortions and would provide further evidence that face representations in the brain may be defined, in part, by the asymmetries of the face. Indeed, studies of facial attractiveness demonstrate the importance of facial symmetry in face perception (Rhodes, 2006).

The importance of the midline does not appear to be limited to face processing. Neglect dyslexia is a condition in which patients neglect a portion of a written word when reading it. For example, "stripe" may be read as "strip" (Caramazza and Hillis, 1990). For patient NG, nearly all the errors in a word reading task occurred on or to the right of the center of the word. Furthermore, there was a gradient such that letters further away from the center on the neglected side had a higher rate of errors.

The midline also appears to be important in cases of object neglect. When shown images of objects on both the left and right side of the screen, Patient PP would copy on the left halves of both objects (Driver and Halligan, 1991). In contrast to faces, words, and objects, there is little evidence for role of the midline in body representations. Grüsser and Landis (1991) report about a right hemi-PMO patient who also saw right hands as "enlarged and distorted" while left hands remained normal. However, patient TNP (Mooney et al., 1965)—who experienced right hemi-PMO—also experienced palinopsia for bodies and faces for which the face palinopsias were restricted to the same side as the distortions but the body palinopsias occurred on both sides of the body. The common role of the midline in face, word, and object representations suggests that while the brain may contain distinct networks for processing these different categories of stimuli, they may have similar (although not perfectly parallel) stages of processing (Almeida et al., 2020).

2.3. Face recognition

Because PMO reflects disruption to the face processing system and distortions might be expected to impact visual cues to identity, expression, or other aspects of faces, the question arises of how people with PMO perform on behavioral measures of face processing. For the 13 cases in which face recognition has been assessed through testing, no face recognition deficits were found in 10 of those cases (e.g. Almeida et al., 2020; Bala et al., 2015; Dalrymple et al., 2014; Grüsser and Landis, 1991; Hwang et al., 2012; Nijboer et al., 2008; Souza, 2018; Trojano et al., 2009) whereas three cases demonstrated impaired face recognition (Grüsser and Landis, 1991; Heutink et al., 2012; Whiteley and Warrington, 1977). For the three cases of impaired face recognition, it is possible that the damage was widespread enough to affect processes that independently caused distortions and impaired face recognition. Interestingly, all three cases of facial recognition deficits appear to involve damage to the cortex. Hwang et al. (2012) and Nijboer et al. (2008), however, both report patients with cortical damage and no face recognition deficits, so cortical damage alone is not sufficient to cause both face distortions and face recognition deficits. Although the patient in Hwang et al. (2012) appears to have damage to the right fusiform gyrus, the authors did not use a functional localizer to determine where the lesion was in relation to face-selective areas. All three cases with face recognition deficits were cases of bilateral-PMO. For cases of hemi-PMO, it is possible that participants can use the undistorted side of the face for facial recognition, thus preserving their facial recognition abilities.

To establish whether face recognition and conscious face perception have separate representations or share the same distorted representation, face recognition could be formally assessed in bilateral-PMO cases or with half faces in hemi-PMO. Three bilateral-PMO cases have been tested with the Cambridge Face Memory Test, and all three scored normally (Bala et al., 2015; Dalrymple et al., 2014; Souza, 2018). Two of these cases (Bala et al., 2015; Dalrymple et al., 2014), however, had distortions that built-up over time, raising the possibility that they relied on an initially undistorted or minimally distorted view of the face for face recognition. Even if that were not the case, it is difficult to assess how control participants might perform on a facial recognition task if they saw face stimuli distorted in the same way as the PMO participant saw them. To model distortions from PMO, Dear and Harrison (2022) distorted faces along two independent dimensions, with more severe distortions generally resulting in worse face recognition performance. However, even with an accurate method of generating distorted face stimuli, it would be challenging to match the degree of the model-generated distortion to that seen by a PMO participant and thus establish a baseline of face recognition performance for the PMO participant.

Although some evidence suggests that face recognition and the conscious visual perception of faces may not share the same facial representation, it does appear that familiarity can influence distortions in

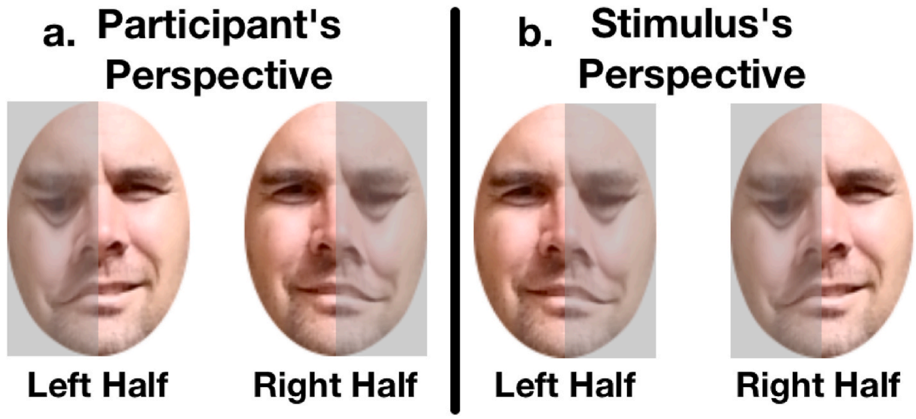

Fig. 2. Throughout this review, we use the participant's perspective (a) — rather than the stimulus's perspective (b) — when referring to the left and right half of a face. To maintain consistency when discussing publications that used the stimulus's perspective, we flip left and right such that these participants' distortions are reported from the participant's perspective.

some cases of PMO. In two cases of bilateral-PMO, familiarity increased the strength of the distortion, whereas in one case of right hemi-PMO, familiarity decreased the strength of the distortion. Patient JS, saw distortions only on the faces of close family members and reported that her grandchildren appeared "very overweight and had an extremely tanned skin as if they had spent too much time in a solarium" (Heutink et al., 2012). Meanwhile, she reported that it was easy to tell when she was looking at strangers because strangers "look like normal people." In Dalrymple et al. (2014), AS reported that all faces were distorted but that faces she had seen multiple times and thus recognized were more distorted. In contrast, the patient in Jiang et al. (2017) reported that seeing a face multiple times caused the distortion to lessen. That familiarity can modulate the strength of distortions in some cases of PMO suggests that the conscious face perception system interacts with the face recognition system or contains some degree of face recognition capabilities.

3. Locations of PMO lesions

One of the most striking findings from reviewing hemi-PMO cases with unilateral lesions is the relationship between the lesioned hemisphere and the side of the face that was perceived as distorted. Left hemisphere lesions were associated only with distortions to the right side of the face whereas right hemisphere lesions were associated with distortions to the left side, the right side, or both sides of the face (Table 2). This relationship suggests that the mechanisms generating our conscious visual experience of faces are organized in a novel and surprising manner. In this account, the processing of both halves of the face is split between the hemispheres, consistent with studies of half faces (Almeida et al., 2020; Blom et al., 2021; see also Chan et al., 2010). Left

Table 2
The relationship between lesion location and distortion location for all cases with clear information about both characteristics. Lesions to cortical areas and white matter (e.g. splenium) are both included. Cases with a unilateral left hemisphere lesion only reported distortions to the right side of the face. In contrast, unilateral right hemisphere lesions can result in distortions to either half of the face or even the entire face. This data suggests that in individuals with typically organized face processing systems the left hemisphere contains representations of the right face half and that the right hemisphere eventually contains representations of both halves of the face and joins them together into a bilateral face representation.

		Distortion Location		
		Left Face	Right Face	Bilateral Face
Lesion Location	Left Hemisphere	0	14	0
	Right Hemisphere	10	8	6

hemisphere face areas process the right half of the face before transferring that representation to the right hemisphere. The right hemisphere, meanwhile, processes the left half of the face and then unites the two representations into a bilateral face representation. Thus, lesions to the left hemisphere would only disrupt representations of the right half of the face while lesions to the right hemisphere could disrupt representations of the left face half, right face half, both the left and right face half before they are fused, or the fused bilateral face representation. As we discuss below in the section on intracranial stimulation studies and PMO, we suspect it is the fused, bilateral face representation in the right hemisphere that reaches consciousness. This account would explain the pattern of lesion and distortion locations seen in Table 2.

The majority of hemi-PMO cases (20/34) involve damage to the splenium, a posterior region of the corpus callosum (Fig. 3c). Because the corpus callosum carries information between the hemispheres, and because splenium lesions can cause face-selective distortions, the splenium appears to contain sections of white matter that selectively carry face information between the hemispheres. White matter tracts connected to a functionally-defined face-selective region have been identified in the fusiform gyrus (Gomez et al., 2015), and it is possible that similar functionally-defined white matter tracts in the splenium could be identified connecting face areas from each hemisphere.

In some cases, there is no apparent lesion or abnormality causing PMO. Cases of bilateral-PMO with unilateral lesions tend to involve the right hemisphere (Grüsser and Landis, 1991; Bala et al., 2015) but in Dalrymple et al. (2014) there were no detectable abnormalities in MRI, fMRI, or EEG analyses. Complicating matters further, patients with PMO often report their symptoms diminishing and eventually disappearing over time (*e.g.* Ebata et al., 1991; Ganssauge et al., 2012; Grüsser and Landis, 1991), sometimes after medication is provided (e.g. Blom, 2020). It is unclear if recovery is due to the medication administered, the lesion healing, or the face system adjusting its processing so faces appear normal again (Blom et al., 2021). Although recovery of face recognition abilities in prosopagnosics is limited, even with training (Davies-Thompson et al., 2017; DeGutis et al., 2014), it isn't clear how many individuals with lesions initially experience face recognition problems that they eventually recover from.

4. PMO as a window into representational spaces

Given the different manifestations of PMO and hemi-PMO, it seems likely that distortions in different individuals arise at different points in the face processing system. One way to examine the stage at which the distortions occur is to examine the reference frame within which the distorted representation is generated (Fig. 4). A reference frame is the spatial coordinate system used to encode the representation of a visual

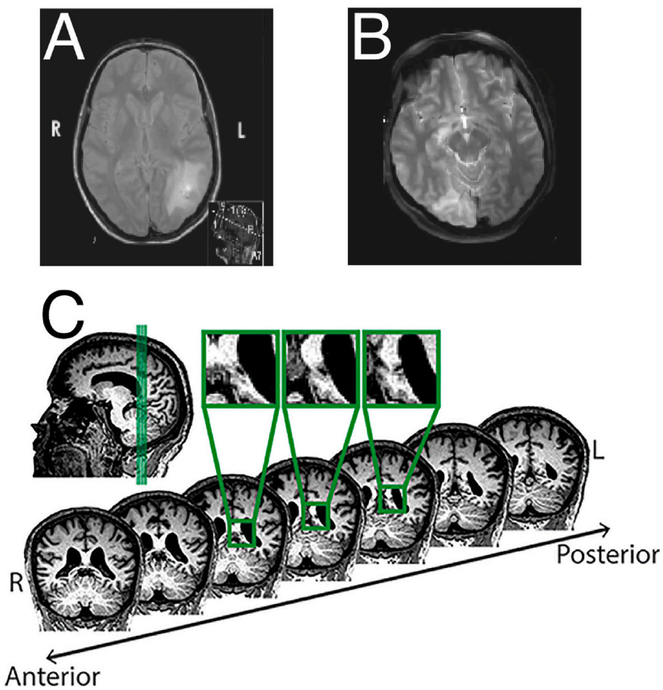

Fig. 3. Examples of lesions in PMO cases. All images display the right hemisphere on the left and the left hemisphere on the right. A) Patient MZ has a lesion to the left occipital-temporal cortex and experiences distortions to the right halves of faces (Nijboer et al., 2008). B) Patient CM has a lesion to the posterior right hemisphere and experiences distortions to the left side of the face (Nijboer et al., 2008). C) Patient AD has a lesion to the left splenium and experiences distortions to the right side of the face. A) and B) Reprinted from Journal of Neuropsychology, 2 (1), Tanja C. W. Nijboer, Carla Ruis, H. Bart Van der Worp, Edward H. F. de Haan, The role of Funktionswandel in metamorphopsia, 287-300, Copyright (2008) with permission from John Wiley and Sons.

stimulus (Caramazza and Hillis, 1990). For example, distortions occurring at an earlier stage of face processing in a retino-centered reference frame (Fig. 4a) would only occur in a particular part of the visual field. Disruptions to the retina-centered reference frame might occur when face-selective neurons with receptive fields encoding a particular portion of the visual field generate distorted representations. Such distortions would be both face-selective and position-dependent. These distortions may appear on only half the face if only that part of the face is in the distorted portion of the visual field during fixation, but we expect that patients would be likely to notice the distortion changing position as they fixated on different parts of the face. At a higher-level, stimulus-centered reference frames are centered on the face stimulus, but do not rotate as the face rotates in the picture plane (Fig. 4b). When the face is rotated, different features will enter the distorted region, thus making it look like the distortion is shifting around the face. If the distortion occurs even later in the face processing system when faces at different positions and orientations have been aligned to the same reference frame, then the distortions would be generated by a face-centered reference frame (Fig. 4c). In such a case, the distortions would be tied to specific features of the face and continue to affect the same features as the face is rotated.

Almeida et al. (2020) examined the reference frame involved in the distortions in a case of hemi-PMO, patient AD. For AD, the distortion occurred on the right side of the face regardless of position in the visual field, indicating that a retino-centered frame was not disrupted. When left and right halves of faces were shown, the distortions were only on the right face halves. If AD's disruption was to a stimulus-centered reference frame, then the right half of both the left and right half faces should have been distorted. Finally, AD saw distortions on the same set of facial features even when the face was rotated 90, 180, and 270°, consistent with a disrupted face-centered reference frame. Thus, at some point in the face system, faces are aligned to a position-, orientation-, and, presumably, size-independent template that may facilitate comparison between current percepts and stored face representations.

The existence of a face-centered reference frame also has implications for how inverted faces are processed. A substantial amount of evidence indicates that upright and inverted face perception depends on qualitatively different mechanisms (Tanaka and Farah, 1993; Yin, 1969; Young et al., 1987), but the strongest evidence comes from work with Mr. CK (Moscovitch et al., 1997). Following a closed head injury, CK developed object agnosia and dyslexia. Interestingly, although he showed normal performance on tasks with upright faces, his performance with inverted faces was severely impaired relative to controls. To account for these results, the authors proposed that upright faces initially enter the face system, which was intact in CK, whereas inverted faces first enter the object system, which was damaged in CK, before entering the face system. Although certain parts of the face system might encode only upright faces, AD's results are consistent with Moscovitch's hypothesis in that they demonstrate that inverted faces must enter the face system at some point.

To our knowledge, no other published studies of hemi-PMO have either explicitly examined the reference frame that was disrupted or thoroughly tested factors like face rotation and visual field position that would allow the reference frame being disrupted to be inferred. Stimulus-centered disruptions are consistent with findings from two hemi-PMO cases where the patients' distortions did not remain on the same features when the face was rotated and instead were always on the same side of the image (Nagaishi et al., 2015; Hishizawa et al., 2015). However, the testing in both cases was limited to a small number of stimuli, and no manipulations of the visual field position were reported. At the very least, hemi-PMO researchers can run two simple manipulations to test which reference frame is disrupted. In the first, the PMO participant should fixate while upright faces are shown at different positions in the visual field. If the distorted features change as the face is moved around the visual field, then the case involves a disruption to a retina-centered frame (Fig. 4a). In the second experiment, a face should be shown upright and then shown rotated at 90, 180, and 270° at

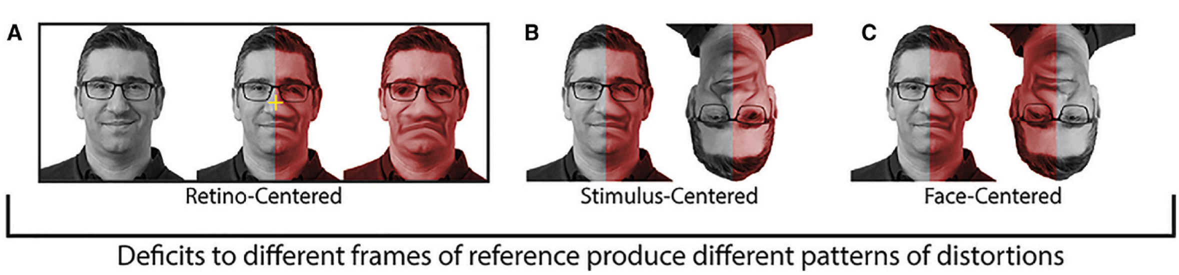

Fig. 4. Disruption to each putative reference frame produces a different pattern of distortions in hemi-PMO. The red region indicates the distorted portion of the face if that reference frame were disrupted. These predictions are for a person who sees distortions on the right half of upright faces. A person with hemi-PMO on the left side of the face would see the red and grayscale regions swapped. Reprinted from Almeida et al. (2020).

fixation. If the distortion affects the same side of the stimulus so that different features are distorted as the face is rotated, then representations within a stimulus-centered reference frame are generating the distortions (Fig. 4b). If the same features are distorted regardless of rotation, then representations in a face-centered reference frame are disrupted (Fig. 4c).

5. Comparison of PMO to intracranial stimulation of face areas

The distortions seen in PMO resemble distortions seen in some studies in which face-selective areas have been stimulated. For example, when a site on the fusiform gyrus of a patient in Rangarajan et al. (2014) was stimulated, the patient reported "You turned into someone else. Your face metamorphosed … your nose got saggy and went to the left." In the same paper, another patient with stimulation to the fusiform gyrus reported "Her nose looked different, larger … you looked harsher, more masculine." Hallucinations of faces are also commonly reported. In a different case where electrodes were implanted at a face-specific site in the ventral occipital-temporal cortex, stimulation "evoked imagery of an eye which changed into a right profile view of a face during stimulation" (Puce et al., 1999). The intracranial stimulation studies reviewed here all involve stimulation of the ventral occipital temporal cortex. Although some cases of PMO have lesions to this area (e.g. Patient MZ and CM of Nijboer et al. (2008), see Fig. 3a and b), many others involve damage to white matter like the splenium. However, white matter damage can affect the processing in cortical areas, particularly cross-area interactions (Fan et al. eLife, 2020).

Nine stimulation studies have examined face perception while stimulating face-selective regions (Allison et al., 1994; Puce et al., 1999; Jonas et al., 2012, 2014, 2015; Rangarajan et al., 2014; Rangarajan and Parvizi, 2016; Schalk et al., 2017; Schrouff et al., 2020). Pooling together stimulation sites across studies that reported which hemisphere was stimulated, face-related perceptual effects were found at 22 out of 47 right hemisphere sites and only 6 out of 50 left hemisphere sites. However, 5 of those perceptual effects following left hemisphere stimulation came from a single left-handed patient (Rangarajan and Parvizi, 2016) who may have had reversed laterality of his face areas (Bukowski et al., 2013). If his data is removed, only 1 out of 40 left hemisphere sites produced a face-related perceptual effect. Schrouff et al. (2020) also found that stimulation at face-selective sites produced face-related perceptual effects only in the right hemisphere except for a left-handed patient for whom stimulation of the left hemisphere produced face-related perceptual effects. Thus, the right hemisphere is much more likely to evoke visual perceptual effects in right-handed individuals.

As with PMO, interpreting what is changing on the face during stimulation can be difficult. Although patients may often mention individual face parts that are distorted, it is hard to quantify how many distortions are only to one side of the face. Two stimulation studies have reported distortions that were clearly to half of a face. Stimulation was delivered to the face-selective areas of the left fusiform gyrus in left-handed patients (Rangarajan and Parvizi, 2016; Schrouff et al., 2020). Upon stimulation, the patient in Rangarajan and Parvizi (2016) was looking at one researcher's face and described the effect, "It changed to someone else's face. Not the whole, but one side (her left) changed. When you clicked it, it changed, and then it changed back." On another trial, the patient remarked, "Very little [changed]–one side of her face. Not as much as the previous one. It was like it was the same person or something that I've seen in the movies before, it was less." Unfortunately, it's not clear from either study whether the distortion was tied to the half of the face or whether it was tied to a particular part of the visual field which that half of the face happened to be in. In some studies, stimulation to right hemisphere face-selective sites produced face-related perceptual effects that occurred for one eye only (Rangarajan et al., 2014; Schalk et al., 2017; Schrouff et al., 2020). These are technically half-face perceptual effects, although the extent of the effect is limited to a single feature of the face.

Comparing the effects of disruption to the left and right hemisphere is often done across patients, because patients usually have electrodes implanted in only one hemisphere. However, Schalk et al. (2017) had access to a patient with electrodes implanted in face-selective regions of the left and right fusiform gyrus, allowing comparison of the right and left hemisphere in a single patient. For this patient, stimulation to the right hemisphere caused either distortions to a face or face hallucinations on top of non-face objects. For example, when looking at a face, the patented reported, "How do I explain … it changed. Just the eye changed … the eye changed … picture? Like a picture or like a drawing. The shape of the eye didn't change, but it just looked different." When looking at a box, the patient reported that "just for the very first second I saw an eye, an eye, and a mouth." In contrast, stimulation to the left hemisphere in the same patient caused hallucination of faces and upper bodies that were positioned to the right side of faces and non-face objects. For example, when looking at a face, the patient reported "So your face and the color doesn't [sic] change, but for a brief moment, like very brief … even for the box and the ball, and this time with your face, I saw a flash of a face right next to it, and disappeared." The patient did not report any hallucinations of half faces. Although stimulation to the left hemisphere can generate hallucinations of faces, it is stimulation to the right hemisphere that consistently creates facial distortions and thus suggests that in PMO disrupted representations must arrive in the right hemisphere for face distortions to be perceived.

Future intracranial stimulation studies can address some of the questions raised by PMO and hemi-PMO through a similar testing structure. Researchers could present faces to the left and right of fixation to determine whether a retina-centered frame is involved. They could also show left and right half faces on separate trials and see if stimulation distorts them selectively. Finally, they could present faces at different orientations to determine whether upright and inverted faces are being represented together and whether a face-centered reference frame is being disrupted.

5.1. *Hallucinations in PMO*

Just as stimulation of face-selective areas can cause facial hallucinations, PMO is sometimes accompanied by facial hallucinations. Blom et al. (2014) described a patient with bilateral-PMO who saw distortions in which faces "turned black, grew long, pointy ears and a protruding snout, and displayed a reptiloid skin and huge eyes in bright yellow, green, blue, or red." However, this patient also hallucinated similar faces on walls, electrical sockets, computer screens, and in the dark. The patient had bilateral lesions to the centrum semiovale, a white matter region near the center of each hemisphere. Mooney et al. (1965) describe a patient with right-sided hemi-PMO (Fig. 1) who saw a wide variety of distortions on faces. However, he also experienced visual hallucinations: "If there were two or three people talking together in the ward, another person, either very much larger or very much smaller (a child), would appear about three feet from them on my right and disappear immediately I [sic] tried to see them clearly." Grüsser and Landis (1991) describe a patient with left hemi-PMO for whom "faces were swollen on the left side, and the mouths were grotesquely distorted in a frightening way." However, when presented with a face stimulus, he began to hallucinate "grotesquely distorted faces or parts of faces" across his entire visual field for up to a minute. This patient's lesion included the bilateral splenium, left occipital pole, and left parahippocampal gyrus. Interestingly, none of the cases with hallucinations appear to involve damage to the right hemisphere face areas, despite intracranial stimulation studies demonstrating that stimulation of right hemisphere face areas are the regions mostly likely to produce facial hallucinations (Rangarajan et al., 2014; Schalk et al., 2017).

6. Methodological challenges and improvements

6.1. Subjective interpretation

Unlike prosopagnosia which can be assessed through quantitative testing and comparison to control groups, PMO can be more difficult to classify given the reliance on subjective perceptual self-reports. For example, the second case in Bodamer (1947), patient A, was categorized as prosopagnosic and provided the following description of faces (translation from Ellis and Florence, 1990): "Apart from the eye I see the face blurred. I don't see that which marks out a face. I don't see a particular expression of a face, my eye always goes to the most striking part of the face, and with living people I find the eye the most striking expression." Patient A describes the face as "blurred," but it's not clear whether this is a literal blurring or whether it refers figuratively to the fact that the face no longer carries meaningful information about identity or other aspects of face perception. In contrast, the third patient in Bodamer (1947), patient B, has a clear distortion as he describes facial features as rotating and moving position.

The interpretation of PMO cases can change depending on how the perceptual self-reports are understood. One example comes from Dalrymple et al. (2014), where AS described one face, "It's whole lower face and chin are … almost ballooning. And his left eye is dropping down … still dropping down. It's really weird it's like I can tell it's not moving because I can look at it and see that but still it, it's moving down his face." Our original interpretation of AS's distortions was that she saw features moving on a face, almost like the face was a piece of clay being reshaped. However, in recent follow-up interviews we have conducted, it has become clear that AS does not see facial features become displaced. Instead, she sees what we call *illusory motions*, where the facial features have a constant direction of motion but don't actually move, as if they were running in place. In retrospect, this is apparent in some of AS's descriptions: she describes seeing a downward motion on the left eye but also mentions that she can see that the eye has not actually moved. In this case, the interpretation does not change the classification of this case as PMO, but it does change our understanding of the distortions themselves.

6.2. Data collection and annotation

Having PMO participants make written annotations on a face they are looking at (e.g. drawing on a printed picture or using a computer drawing tool on a computer image) can help participants physically show what they are seeing on a face without having to rely on subjective descriptions or analogies. This data collection method would also benefit intracranial stimulation studies. Because reporting any conscious, visual perceptual effects from intracranial stimulation can be difficult, giving patients a way to annotate any images of faces that were presented, either on paper or on the computer, can allow the patient to demonstrate exactly which parts of the face were affected, as well drawing any changes to the best of their ability. These annotations can also be accompanied by a verbal description from the patient. Given the brief, transitory nature of stimulated facial distortions, even with annotations it may be difficult for them to communicate their experience, but providing the patient with more tools for expression can help.

6.3. Low-level visual problems

Finally, just as a person with face recognition problems must not have low-level visual problems that can account for their face recognition deficits to be classified as prosopagnosic, it is important to assess potential low-level visual causes of face distortions. Safran et al. (1999) reported two patients with scotomas who said that when faces or the upper body of a person appeared within the area of the visual field affected by the scotoma, that portion of the face or upper body appeared contracted or "thin." Both patients, however, also reported that a line that crossed through their scotoma was smaller than it actually was, indicating that perceived distortions to faces may have been a lower-level issue. Nevertheless, we expect that face distortions caused by low-level deficits make up only a small proportion of cases reported as PMO. Indeed, several investigations of PMO have found no low-level visual issues (e.g. Nijboer et al., 2008; Trojano et al., 2009; Heutink et al., 2012), and Patient AD's face-centered and face-specific distortions demonstrate a high-level origin.

7. Open questions

Despite all of the cases that have been reported over the past century (Blom et al., 2021), research into PMO is only just beginning. Many open questions with important implications for face perception and visual recognition more broadly remain to be answered through in-depth testing. We provide a list of some of these questions below. We consider questions 1–3 about the face template and reference frames to be some of the most theoretically exciting issues as well as some of the easiest to investigate by performing basic manipulations like rotating the face stimulus or placing it in different regions of the visual field.

7.1. Questions about the face template and face representations

1. Do hemi-PMO cases exist that result from disruption to a stimulus-centered reference frame? Although results from two cases hint at stimulus-centered distortions (Nagaishi et al., 2015; Hishizawa et al., 2015), no cases have shown clear evidence of such distortions. Not only would stimulus-centered distortions reveal a particular type of face representation, they would also indicate face and word processing both involve stimulus-centered representations and face/word-centered representations (Hillis and Caramazza, 1995).
2. What stimulus properties are necessary to evoke distortions? Because PMO typically involves face-selective distortions, it may be possible to assess the presence or absence of distortions to infer what properties gain entry to the stages of the face processing system that are disrupted.
3. Can the nature of distortions in PMO (e.g., drooping features, stretched regions) be used to understand face representation at a fine-grained level?
4. How separable are the representations for conscious face perception and the representations used for face recognition? Do the representations that we are consciously aware of play a role in face processing decisions (e.g. identity or expression)? This question can be addressed via tasks that force reliance on the distorted part of the face, and in cases for whom distortions build up over time, by presenting test stimuli only after distortions are fully present.

7.2. Questions about brain regions and connectivity

5. What brain regions contain face-centered representations and (if they exist) stimulus-centered face representations?
6. Are the relationships between lesion location and distortion location seen in Table 2 maintained as more cases are thoroughly tested?
7. If the splenium carries face information between the two hemispheres, why would it matter which side of the splenium was lesioned? Lesions to the left splenium appear to cause distortions only to the right side of the face while right splenium lesions can cause distortions to the left or right side of the face. A telephone wire connecting two phones would be disrupted in the same way regardless of where the wire was cut. Similarly, a lesion to an axon extending across the corpus callosum seems like it should disrupt hemispheric communication the same way regardless of whether it is severed on the left or right side.
8. Why do white matter lesions produce face distortions? Perhaps damage to white matter produces inconsistent signal propagation

and thus introduces noise to the neural coding, leading to distortions similar to those produced by intracranial stimulation of face areas (Rangarajan et al., 2014; Rangarajan and Parvizi, 2016; Schalk et al., 2017; Schrouff et al., 2020).

9. Why is there little evidence that stimulation of the left hemisphere causes perceptual effects in right-handed people if left hemisphere cortical damage can cause PMO in right-handed people (Trojano et al., 2009)?
10. In one study (Bukowski et al., 2013), approximately one-third of left-handed individuals showed a reversed asymmetry for the fusiform face area (i.e. larger in the left hemisphere than right). Do PMO participants with reversed laterality of FFA (Bukowski et al., 2013) and lesions to the left hemisphere show distortions to the left face half or both face halves? Do cases with reversed laterality and right hemisphere lesions only see distortions to the left face half?

7.3. Questions about the condition of PMO itself

11. Is there a heritable or developmental component to some cases of PMO? Unlike developmental prosopagnosia, there have been no reports of people who have experienced PMO for much or all of their life. Furthermore, we were unable to find any cases of PMO where family members were also reported as having PMO, although such cases may exist. In contrast, developmental prosopagnosia has been reported for multiple family members (Duchaine et al., 2007; Schmalzl et al., 2008).
12. Why do distortions in PMO resolve in some cases but not others? Does recovery from PMO or prosopagnosia following a lesion occur in a similar proportion of cases? When recovery does occur, is the speed of recovery similar for PMO and prosopagnosia?
13. What role does asymmetry play in the evocation of distortions? What does the contribution of asymmetry reveal about the mechanisms supporting face processing? Do some individuals with PMO see distortions in symmetric stimuli such as car fronts or human/animal bodies?
14. What is the time course of distortions in PMO? Is build-up more likely to occur for certain types of PMO than other types?
15. Do individuals with PMO see distortions on imagined faces or faces in dreams? This fairly simple question will speak to whether representations driven by top-down processes access the disrupted mechanisms. At least one PMO case does not experience distortions when imagining faces (Trojano et al., 2009) while another does experience distortions for imagined faces (Mooney et al., 1965).
16. Do people with PMO see distortions on multiple faces simultaneously? This question will shed light on the capacity of the disrupted mechanism.
17. Is there any pattern or consistency to the distortions reported in PMO? Can the type of distortion reported (e.g. drooping of the eye) be used to create meaningful sub-types of PMO beyond bilateral-PMO and hemi-PMO (e.g. Blom et al., 2021)?
18. How many PMO distortions involve an actual displacement of features and how many involve illusory motions without displacement? The distortions reported by AS (Dalrymple et al., 2014) involve features that seem to move without being displaced from their location. We encourage researchers to ask PMO participants whether they are seeing what appear to be features changing their form like clay being shaped or whether they see illusory motions without displacement.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The list of PMO cases and information from those cases is included as an Excel file in the supplementary material.

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Appendix A. Supplementary data

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