Orientation advantage in human face recognition: Why so horizontal?

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Abstract

Face processing is a core component of human social interactions, from the ability to detect a face to the comprehension of what it conveys, in terms of age, identity, emotion... This work aims at further the understanding of the diagnostic information at play in such essential processes. Previous studies demonstrated that face processing differed as a function of the orientation of face information, with an advantage for the horizontal range. In line with these results, we focused on the orientation of face information, to determine how this advantage could be explained. Along 4 different angles, we aimed at extending the comprehension of the horizontal advantage through thorough investigation of oriented face information.

First, we focused on the reference frame of this horizontal advantage. More specifically, we dissociated the observer's reference frame and the face's reference frame during a face recognition task. We found that albeit a small influence of the observer reference frame, the horizontal advantage of face identity categorization is image centered.

Having determined that it was the face information and not the orientation per se that was important, we then focused in the two following chapters on this oriented information, and why it is more diagnostic of identity than other ranges. First, in an identity recognition task, through the use of inversion and negation, disrupting shape and surface-shading cues processing, we found that the horizontal was the orientation range that was the most affected by these manipulations. As shape and surface-shading cues have been demonstrated to be essential sources of information in face identity categorization, we demonstrated that the horizontal range, more than other orientation ranges of information, conveys essential face perception cues. In a second phase, through analysis of the orientation dependency of identity recognition across views, we showed that it was the horizontal range that yielded best view-tolerant recognition. Further analysis of the image content enabled to conclude that the horizontal range conveys the most informative identity cues at frontal views, and the most stable ones across different views.

Finally, we tested whether the horizontal preference was solely found at finer categorization levels like identity and emotion processing, or whether basic-level

categorization was also tuned to the horizontal information. Using fast periodic visual stimulation coupled with EEG and a similar behavioral experiment, to measure face categorization amongst various stimuli, we found that the horizontal and neighboring ranges yielded better basic-level categorization. These results suggest that the horizontal and neighboring ranges of face information convey better diagnostic cues for basic-level face categorization than the vertical range.

In summary, the horizontal face information conveys face processing essential cues to a greater extent than other orientation ranges. This information is also the most informative at full front views as well as the most stable, enabling view-tolerant face recognition, thus accounting for the horizontal preference of face processing. As this horizontal advantage is found at multiple levels of face processing, the horizontal range seems to conveys diagnostic cues enabling the recruitment of face specialized mechanisms.

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Chapter 1: General Introduction

A few months ago, I came across the picture of a famous actress. No caption below the picture, no movement nor voice. Without any hesitation, nor any need to think about it, I could tell it was Tilda Swinton. I had never seen her with similar haircut, hair color or make-up, yet it did not raise any issue in my finding of her identity. Of course, she is very famous and has quite a peculiar face. This would not be different for anyone trying to find a colleague of them on a university graduation photo. For most with normal face recognition skills, it would be quite easy, even though the colleague was only met years after university or if everyone on the class photo was dressed in the same uniform and wore similar haircuts. That is because familiar face recognition is a very efficient process, very resistant to changes in appearances like age, facial hair, pose, lighting… (see examples in Fig 1.1). In the following thesis, I will try to explain some of the processes in place enabling such face identity recognition abilities.

The main focus of the thesis is face categorization. A face can be categorized at multiple levels, from the basic level: e.g. faces versus other body parts, to more complex levels like expression or emotion categorization, identity categorization… Face categorization in fact covers any process of comparing a face input with an internal representation whether it is the representation of a face, an emotion expression or an identity. In the following chapters of the thesis, our main focus is on face identity categorization i.e. recognition of a face by matching it to an internal representation. The last chapter will investigate basic-level face categorization. In all chapters, face categorization is studied under the prism of horizontal face information. We will therefore introduce these two aspects of face categorization, tie them together to link all the chapters and explore the influence of information orientation in face categorization.

Figure 1.1. Figure taken from (Mileva et al., 2020) of Paul McCartney through different ages, poses and lighting. Although he is very different across picture, his identity is recognizable from each.

1. Face identity categorization

Humans are generally considered to be accurate in face identity categorization (Young & Burton, 2018). Excluding some people with neurological disorders, such as people with prosopagnosia –a disorder either congenital or following a brain trauma resulting in the inability to recognize face identity– everyone is thought to be able to recognize each other's identity and many studies seem to go in that direction. Yet, when it comes to face identity recognition, humans only seem accurate for familiar face recognition. Indeed, familiar and unfamiliar face recognition are thought to rely on different processes (Johnston & Edmonds, 2009) and have been shown to rely on different brain regions (Dubois et al., 1999). The high accuracy in unfamiliar face matching tasks have been attributed to image recognition more than actual face recognition (V. Bruce & Young, 1986; Logie et al., 1987; Rossion, 2018; Young & Burton, 2018). Experiments with unfamiliar face identity recognition usually involve the presentation of an unfamiliar probe followed by presentation of a target and a decision about whether both target and probe are the same or different identity(ies). In these experiments, unfamiliar face recognition performance is very sensitive to any deviation between probe and target such as changes in viewpoint, in face expression or emotion (V. Bruce, 1982), or changes in dimension (e.g. picture to video or picture to real life; Bruce et al., 1999, 2001; Burton, Wilson, et al., 1999; Hancock et al., 2000; Kemp et al., 1997; Logie et al., 1987; Patterson & Baddeley, 1977). In contrast, familiar face recognition is highly robust to deviations between probe and target (although with familiar faces experiments do not necessarily include probes). Participants have indeed been found to recognize familiar faces, albeit less accurately, even when the images were pixelized, blurred or distorted, or with a very low resolution (V. Bruce et al., 2001; Burton, Wilson, et al., 1999a; Harmon, 1973; Hole et al., 2002; Lander et al., 2001). Furthermore, such distorted familiar faces yield similar neural responses to their intact version (Bindemann et al., 2008). More ecologically speaking, humans are able to recognize familiar faces through different ages, haircut, lighting poses and viewpoints. These changes in the physical appearance of one’s face is such that pictures of the same person taken under different conditions might be further apart than pictures of different persons taken under the same conditions (Adini et al., 1997a; Jenkins et al., 2011). Familiar face identity recognition therefore lies in the ability to link together various presentations of one identity in an internal representation (Andrews et al., 2015; Burton, 2013), and to match a given face or face-image with this internal representation. Hence, face identity recognition of a familiar face is its categorization as one known identity compared to other known identities. Studies have shown the necessity of presenting face identities under different viewpoints, either through several images or videos (Andrews et al., 2015; Etchells et al., 2017; Lander & and Bruce, 2003; Pike et al., 1997) for face familiarisation. Such encoding of multiple views of the same face could then constitute an internal representation, or face recognition unit (V. Bruce & Young, 1986; Burton et al., 1990; Burton, Bruce, et al., 1999; Burton et al., 2011). Burton et al. (2005) suggested that this internal identity representation was a sort of average of multiple presentations of the same face, which would constitute a good statistical summary of an identity. Such an average would indeed cancel non-diagnostic variations due to external factors, age, lighting, hair… while including the diagnostic elements of identity. For instance variability due to age would be blended together to give an age-invariant representation and enable familiar recognition through time (Mileva et al., 2020). Recognition of average faces made out of multiple instances of the same identity demonstrated better recognition than with single face images, both for human and artificial face recognition (Jenkins et al., 2006; Jenkins & Burton, 2008, 2011; R. A. Johnston & Edmonds, 2009a). This hypothesis was further supported by the finding that participants presented with four different images of the same identity believed the average of these images was presented as part of the initial images, demonstrating the ability to extract summary information as an average (Kramer et al., 2015).

There is no reported limit to the amount of familiar faces one can know, i.e., no reported limit of internal identity representations. Jenkins et al. (2018) evaluated the average of known identities to 5000, with a high inter-individual variability, including faces of personally familiar individuals and of celebrities. Such an ability to discriminate between so many identities is rendered possible because of the high anatomical variability between faces. Indeed, and contrary to the rest of human body parts, faces have evolved to be greatly different. A study focusing on the high phenotypic variability in human faces measured, among other things, the correspondence between fingers and palms of individuals and demonstrated a high correlation between the size of both for most people. Yet, the similar size comparison between face features did not show any correlation. In other words, a big nose does not mean big eyes but usually, big fingers mean big palms (Sheehan & Nachman, 2014). This means that all face features can vary independently, which gives rise to an infinite possibility of faces with only a limited number of features and therefore makes it possible to differentiate each known individual based on their face. Indeed, the more distinctive a face is, the easier it is to remember and recognize it later (Light et al., 1979; Valentine & Bruce, 1986a).

Although we saw the efficiency of familiar face identity categorization, it is important to note that a face’s identity can only be recognized if the face has been categorized at a basic-level first. It therefore seems quite accurate that both face detection in scenes and their basic categorization are also rapid and efficient processes that we will introduce in the next section.

1.2 Face detection and basic-level categorization

Face detection is the process of finding a face in a scene. Face basic-level categorization is the categorization of a face as one and not another object category. In a laboratory setting the use of extended scenes for visual search is limited and face detection and basic-level categorization are thus often measure together, which is the case in most studies presented in the following section.

Behaviorally, in a saccadic choice task, where participants are shown two images at the same time in the left and in the right visual fields and tasked to look towards a specific object category (faces, animals, cars…), Crouzet et al. (2010) recorded saccades towards faces as fast as 100ms, with a mean reaction time of 140ms, which was faster and more accurate than with other image categories. In the same study, the authors showed that even when asked to attend to a different object category, participants still did some saccades toward faces. Similar results were found in a search task where participants were told their target would *not* be on faces but still, saccades toward faces were measured (Cerf et al., 2009), illustrating how humans are drawn to faces.

Using magnetoencephalography (MEG), an activity increase was measured 100ms (or sooner) after presentation of various object categories, with a larger amplitude elicited by faces than other objects (J. Liu et al., 2002). More specifically, this face specific increase in activity was associated with the presence of features, irrespective of their configuration. This event-related potential (ERP) elicited after face presentation was larger in the case of successful face categorization but not identification. However this response has also been found to be based on the low-level characteristics of images rather than face images themselves, as shown by the similar activity amplitude elicited by scrambled and intact images (Rossion & Caharel, 2011). Another neural evidence of face detection, the N170 (or M170) has been recorded as early as 130ms post stimuli, with EEG and MEG (Bentin et al., 1996). Contrary to the M100, configuration but not features elicited a larger M170 amplitude. Like the M100, M170 is correlated with successful face categorization but also with successful identification (J. Liu et al., 2002). Indeed, face identity discrimination was also recorded in the same time range, as experiments where participants viewed faces in pairs, one after the other, also showed a modulation of this ERP with identity. The recorded N170 amplitude was larger when both faces were perceived as different identities than when they were perceived as the same identity (Jacques et al., 2007; Jacques & Rossion, 2006).

Face basic-level categorization has also recently been measured implicitly using frequency tagging: as brain activity synchronizes with the frequency of periodic stimulation (Norcia et al., 2015), regular stimuli will elicit brain activity at the stimulation frequency. Following this, if face images are presented periodically among other images and are categorized as such, brain activity will synchronize with the face images frequency. Coupling this paradigm with EEG measures, analysis of the signal in the frequency domain demonstrated the brain’s ability to both detect face stimuli and generalize it across multiple face exemplars (Rossion et al., 2015). Temporal analysis of the face categorization response demonstrated a progressive activation of the cortex, from the medial occipital cortex, to the lateral occipital cortex with a right lateralization up to the occipitotemporal cortex. These regions have been widely studied, and contain areas referred to as face specific, which we will try to detail in the next section.

1.3 Face specialized network

To better understand the basic-level face categorization response, we will report here a few studies focusing on the face neural network, i.e., the neural response to face stimulus.

The existence of a brain network specialized for face processing was suggested after the study of patients with similarly located brain lesions resulting in prosopagnosia. Prosopagnosia is an inability to recognize known faces sometimes even one's own, but not objects. Patients in question did not have any other visual problem and could, for instance describe a face and its features without recognizing its identity. They could however recognize people from their voices, clothes, gate…, indicating a problem for face processing but not for identity retrieving itself, which suggested that the damaged regions were areas dedicated to faces (Damasio et al., 1990; Hecaen & Angelergues, 1962; Tranel et al., 1988). Most of these observed patients had lesions in the close vicinity of the bilateral or right parieto-occipital or temporo-occipital regions, more precisely at the junction between occipital and temporal lobes: the fusiform gyrus (Damasio et al., 1990; Hecaen & Angelergues, 1962; Meadows, 1974; Tranel et al., 1988). Using fMRI and PET, these regions have been discovered to react more strongly to faces.

The fusiform gyrus, an area, later named the fusiform face area (FFA), demonstrated stronger activation during passing viewing of faces than other objects (Kanwisher et al., 1997) and during a face identity recognition task but not for an object recognition task (Sergent, Ohta, et al., 1992). For instance FFA exhibited a six-time-stronger activation for passive viewing of faces than houses (Kanwisher et al., 1997). The increased response to faces is not dependent on low-level characteristics of the face image, as intact faces were shown to elicit greater activation than scrambled faces (Kanwisher et al., 1997; Puce et al., 1995). Furthermore, this response was found selective to faces only and not other body elements as face images elicited stronger activation than hands both during passive viewing and while performing a task. In these studies using passive viewing of faces, strong activations (although weaker and recorded earlier after stimulus onset than for the FFA) were also recorded in an area of the occipital lobe, later named the Occipital Face Area (OFA) (Gauthier et al., 2000). While both OFA and FFA demonstrate higher activation for faces than other stimuli, OFA's activity is more related to low-level properties of the face images while FFA is more related to high-level properties (Rotshtein et al., 2005; Tsantani et al., 2021). OFA's activity is also related to face features perception, more than perception of the face as a whole (Pitcher et al., 2007, 2011). Together, OFA and FFA constitute the ventral pathway of face processing, in relations to the dorsal pathway, which projects to the superior temporal sulcus (STS). The STS also demonstrates greater activity elicited by faces than objects (Kanwisher et al., 1997; Puce et al., 1995). The specificity of the STS it the sensitivity to moving features, with an increased activity measured for eyes and mouth movement, that was not recorded when eyes and mouths were replaced with moving checkers, excluding an effect of movement alone (Puce et al., 1998). Furthermore, greater activation in STS has been recorded when presented with faces displaying expression of emotion compared to neutral faces, with activation intensity following the perceived emotion intensity (Bernstein & Yovel, 2015; Engell & Haxby, 2007). The STS, is indeed thought to process the dynamic aspects of faces like facial expression, and gaze direction.

The greater response to faces compared to other objects of these regions is thought to be due to the presence "face-cell" clusters in these areas. Studies with single cell recordings in monkeys described neurons, grouped in clusters, with selective receptive fields that were best activated by faces in the superior temporal sulcus and the inferior temporal cortex (C. Bruce et al., 1981; Desimone et al., 1984; Perrett et al., 1982, 1984). Single cell studies in monkeys also suggest differential selectivity of these faces cells, with those in STS more sensitive to changing aspects of faces, like facial expression, gaze direction or head orientation, while those in the inferotemporal cortex had selective responses to face identity (Hasselmo et al., 1989; Perrett et al., 1990). The possibility of such face selective cells in the face selective areas of the human brain, with differential roles in different brain areas pairs well with Bruce & Young (1986)'s theoretical model of a cognitive system for face processing. In this model, they expect face processing along two different axes, one for the fixed elements of faces, like identity, and the other for moving aspects of faces like speech or expression, as well as information such ad age or gender. Going back to prosopagnosia patients, most had severe trouble with face identity recognition but not with face expression, age or gender categorization (Tranel et al., 1988), observing the same dichotomy as face selective cells and the face processing theoretical model. Haxby et al. (2000) proposed a similar anatomical model of the human face processing. In this model, OFA, FFA and STS are considered the core of the model, although other brain areas can be recruited through these 3, as part as of the extended system. This model is hierarchical and proposes the OFA as the first step in face processing, followed by STS for dynamic face aspect and FFA for the fixed aspects. Temporal studies coupling EEG with fMRI seem to validate this hierarchical hypothesis, or at least suggest a temporal difference between these regions, by measuring a correlation between the P100 and the OFA (J. Liu et al., 2002; Pitcher et al., 2007, 2011) and between a later ERP, the N170, and the STS and FFA, but not the OFA (Sadeh et al., 2010).

However, more recent studies are in favor of a less specialized face network. Instead of it being a solely hierarchical model with face processes secluded to the highly face specific OFA, FFA and STS, the face network is seen as more diffuse. For instance, single cell recordings in humans midfusiform gyrus demonstrated a great proportion of face-selective neurons, as well as about 30% place-selective cells (Quian Quiroga et al., 2023). Face and place cells, while responding to different stimulus categories had similar activation patterns, hinting at similar categorization processes. This demonstrates that FFA is not only activated by faces, yet it is more responsive to faces because of a higher proportion of face cells, not because of a differential activation between different category specific cells. Furthermore, an overlap between face and other object categories regions was observed, and distinctive face neural responses compared to other stimuli was found even when excluding so-called face selective areas (Haxby et al., 2001). Regarding face selective regions themselves, Bernstein & Yovel (2015) also explained that while we tend to attribute distinct roles to different face areas, functions of brain specialized regions demonstrate some overlap. For instance, FFA demonstrates similar emotion perception related activity pattern as the STS (Engell & Haxby, 2007; Ganel et al., 2005). Finally, the temporality of the aforementioned model was also challenged by an fMRI study of a prosopagnosic patient without an OFA, who had normal FFA, however, this activation was not enough for efficient face recognition in the patient. This study established both, that FFA does not need input from OFA to be activated, but that OFA's activation seems necessary for face categorization, thus suggesting feedback from FFA to OFA in healthy face networks (Rossion et al., 2003).

Although the face neural network might not be as delineated as previously thought, face specialized activation seems to be due to the presence of face-cells. To enable face categorization these cells must be quickly activated by any face, most likely based on an internal representation. In the following sections we will take an interest in the information conveyed by most faces that would enable basic-level face categorization, i.e. comparison with a general face internal representation; as well as characteristics shared by different representations of the same identity that would enable identity categorization, i.e. comparison with an individual face internal representation.

2. Face natural statistics

A reasonable assumption for face basic categorization would be that it is based on what faces look like most of the time, i.e., based on the regularities in the appearance of faces we encounter. Although, as we previously saw, there are many ways for faces to vary between individuals, faces also have a lot in common, especially as we encounter most faces upright, and lit from above.

2.1 Feature configuration

An element that is part of natural face statistics is the configuration of the face features. That is, in an upright face –as most often seen– the eyebrows, above the eyes, above the nose, above the mouth, as we can see in

Figure 1.2. As an example, objects presenting a similar configuration to upright faces can elicit face pareidolia. Face pareidolia is the perceptual illusion of a face in another object or scene. A study with these face-like objects determined that perception of "faceness" is correlated with eyes, mouth, expression, proportion and symmetry of the features, forehead and frame with the presence of eyes and mouth being critical in the illusion of "faceness" (Omer et al., 2019). This illusion is not only behavioral as these face-like objects elicit an activation of face specialized regions, albeit less strongly (Cerrahoğlu et al., 2025), before redirecting the activation towards object specialized regions once the error is noticed (Wardle et al., 2020). These studies demonstrate that face configuration is such a strong signal that even without a face, it is sufficient to elicit a basic-level face categorization response.

Another way to study the tuning of face mechanisms to natural face statistics is to reverse these natural statistics and study the results in terms of face processing. Face inversion has been very extensively studied in the face recognition field. Hochberg & Galper (1967) showed that when inverted upside down, a face was much harder to recognize than when upright and that faces are disproportionally affect by inversion compared to other mono-oriented object (Yin, 1969). The face inversion effect is found at the neural level, with a delayed N170 and a smaller FFA activation compared to upright faces but a stronger activation in object selective regions (Rossion et al., 2000; Rossion & Gauthier, 2002). Behaviorally on top of identity categorization, the face inversion effect also disrupts, for instance, sex categorization (V. Bruce et al., 1993) and basic-level categorization (Garrido et al., 2008). Studies gradually manipulating face orientation showed that the further from the upright a face is, i.e. the further away from the face usual presentation it is, the harder it is to recognize (Jacques & Rossion, 2007; Rossion, 2008; Rossion & Boremanse, 2008). All these past studies illustrate that deviation from natural upright face configuration hinders all face categorization processes.

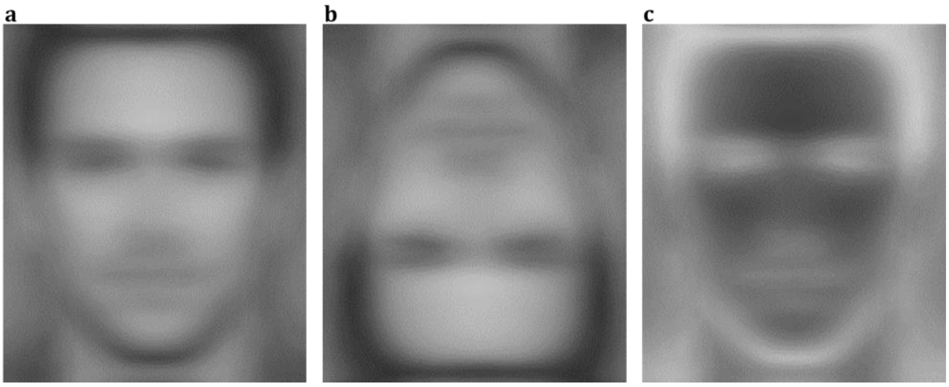


Figure 1.2. **a**. Average of 72 images take from 18 white male actors. Images were controlled in size and face size, and rotated to align the eyes with the horizontal. Images were between full front and ¾ faces. **b.** Same image as in a. inverted. **c.** Same image in a. contrast negated.

What happens is that inversion prevents the access to face specialized mechanisms, because these mechanisms are tuned to upright face configuration and do not seem to be activated by representation that deviates too much from it. It is the case for face mechanisms like holistic processing (Rossion, 2008). Holistic face processing supposes the integration of the parts and their relationship into a unified representation that will be considered and analyzed as such (Farah et al., 1998; Maurer et al., 2002). The composite face illusion is a great example of holistic processing and its disruption with inversion. In this paradigm, subjects compare face images made with the same identity for the top of the face, but a different one from the bottom and as a result of holistic processing, perceive the top halves as being different

(Hole, 1994; Young et al., 1987). However, when faces are inverted, the illusion disappears and the top halves of the faces are indeed perceived as identical (Rossion, 2013). This finding that deviation from the upright face configuration prevents holistic processing demonstrates the tuning to this upright face configuration of face specialized mechanisms, following statistical face presentations. Other studies focused on the neural aspect of face mechanisms: activation of face specialized brain regions. For instance, the FFA has a greater activation with upright than inverted faces (Rossion & Gauthier, 2002; Yovel & Kanwisher, 2005b, 2005a). However, brain regions that normally respond to nonface objects have an increased activity with inverted compared to upright faces (Rossion & Gauthier, 2002) and inactivation of these regions hinders inverted but not upright face recognition (Pitcher et al., 2011).

These studies indicate that face specialized mechanisms are tuned to the face configuration with the highest statistical probability: that of an upright face. This configuration is necessary for face specialized mechanisms and was even found to elicit them on its own.

2.2 Contrast distribution

Another common occurrence in all face is the light and dark regions distribution on the face : the features tend to be darker while the rest of the face is lighter (Watt, 1994). For instance, the eye region is always darker than the cheekbones, no matter the skin color or ethnicity even in different lighting conditions, except with lighting from below (Gilad et al., 2009; Liu-Shuang et al., 2022). Faces are most often perceived that way because all faces share similar feature positions and are seen under similar lighting condition with light coming from above (Hill & Bruce, 1996a; Hong Liu et al., 1999). Going back to pareidolia studies, it was hypothesized that the high contrast around the eyes and mouth is driving the illusory face effect (Wardle et al., 2020).

As with inverted faces, one manipulation can reverse faces natural statistics and move the face-image away from usual face representations: contrast polarity reversal, or contrast negation. Like inversion, it has a great impact on face recognition (Galper, 1970) and the deleterious effects of contrast negation are specific to faces (Nederhouser et al., 2007). Detrimental effects of contrast negation are found for face basic categorization (M. Lewis & and Edmonds, 2005; M. B. Lewis & Edmonds, 2003; Liu-Shuang et al., 2015a, 2022) and face identity recognition (V. Bruce & Langton, 1994a; Galper, 1970; Gilad et al., 2009; Nederhouser et al., 2007). With contrast negation it is the surface cues (V. Bruce & Langton, 1994a; Russell et al., 2006a; Vuong et al., 2005a) as well as shape-from-shading information (V. Bruce & Langton, 1994a; Kemp et al., 1996a; C. H. Liu et al., 2000a) that cannot be accessed, yet this information is necessary for efficient face recognition (C. H. Liu et al., 2000a; Russell & Sinha, 2007).

As seen with inversion, contrast negation has also been found to disrupt face holistic processing. A study demonstrated this using the Thatcher illusion. The Thatcher illusion consists in inverting the eyes and the mouth's relative to the face's orientation. When Thatcherized faces are seen inverted (with eyes and mouth seen upright) and therefore with a disruption of holistic processing, faces are perceived as normal and similar to unaltered faces. Seen upright, with eyes and mouth inverted, however, these faces are perceived as grotesque because processed holistically and the inverted features distort the perceived face (Bartlett & Searcy, 1993; Thompson, 1980). With contrast negated faces, this illusion also showed similar albeit weaker results to inversion, with contrast negated Thatcherized face perceived as less grotesque than their upright counterpart (M. B. Lewis & Johnston, 1997). In the second study, participants are asked to recognize the identity of fully or partly contrast negated faces. In the partly contrast negated conditions, features were kept with positive contrast. Recognition of all contrasted faces was decreased, yet recognition of negated faces with eyes in positive contrast was slightly better. This recognition improvement of changing the eyes back to their natural contrast was only found when the eyes were embedded in the face and not isolated (Sormaz et al., 2013). This study showed that contrast negation prevents holistic processing mainly due to the contrast inversion of eye region. However, studies using the face composite illusion only found a weak effect of contrast negation that disappeared when faces were shifted from full front to ¾ (Hole et al., 1999), or not effect at all (Taubert & Alais, 2011). Neuraly speaking, contrast positive faces elicit a stronger response in the FFA than contrast negative faces (Gilad et al., 2009; Yue et al., 2013). In macaques a study of face selective neurons response to contrast manipulated faces showed that contrast modulated the cell response and that these face selective neurons were tuned to natural contrast distribution between face parts (Ohayon et al., 2012). It has also been suggested that differential mechanisms are in place for positive and negative faces (Liu-Shuang et al., 2015a; Wiese et al., 2019). In light of these results it seems that the difference between natural face contrast statistics and contrast negative faces prevents an efficient face detection and therefore the activation of face specialized mechanisms (Liu-Shuang et al., 2015a).

As with face configuration, it seems that natural face statistics encompass faces' natural contrast distribution, as surface and shading information. Deviation from this natural presentation prevents the activation of faces specialized mechanisms. In light of these elements, the next question that arises is how these face natural statistics could be represented in the brain.

2.3 Face natural statistics processing

From the experiments described above, it seems that most faces encountered in our daily life, although different from one another share highly similar characteristics. This consistency of faces defines the natural statistics of this category. Here we take an interest in how these natural statistics could be represented in the brain and enable the activation of face cells when in presence of a face. Is this representation innate, or is it built through experience with faces?

In favor of an innate internal face representation, research has shown an attraction toward face-like object, compared to their scrambled version, from the first day of life (Johnson et al., 1991). A similar study has been done with unborn fœtus using three light dots projecting through maternal tissue either in a face-like disposition: two dot above one dot, or in an inverted face-like disposition : one dot above two dots, and demonstrated a preference for face-like signal compared to the inverted one even before birth (Reid et al., 2017). Newborns demonstrate a stronger cortical activation for upright than inverted face-like pattern (Buiatti et al., 2019). A complete study on newborns (a few hours after their birth) demonstrated the same pattern of preference of upright faces and face-like objects compared to inverted ones as well as a preference for natural face contrast in faces and face-like objects compared to inverted ones and lit from below faces (Farroni et al., 2005). By describing a preference for face-like patterns before any possible influence of experience, these studies hint at an innate face representation. Based on their results, this internal representation includes faces natural statistics in terms of configuration as well as contrast distribution. However, these conclusions do not exclude a potential role of visual experience as refinement or upkeep of the internal face representation. To explore the possible contribution of experience, monkeys were raised in a face-deprived environment and tested in face perception. They did not exhibit usual face processing regions, but instead regions for hand and scene perceptions were strongly developed (Arcaro et al., 2017). Another similar study with face-deprived monkeys did not show such drastic results, but demonstrated differences in face perception compared to control monkeys, as well as an evolution of their face processing after face exposure (Sugita, 2008), leading the authors to conclude towards a mixture of both innate and acquired face mechanisms. In human research, face deprivation is more complicated, preventing the execution of such studies. The only possible studies are thus of specific subjects, like one tested in face recognition by Duchaine et al. (2023), who, because of a joint disability, had more experience with inverted than upright faces. He had no preference for upright face perception compared to inverted face perception, leading the authors to conclude in favor of a mixture of innate and acquired mechanisms as well. Finally, research with three-month-old children also concluded towards acquired mechanisms, especially for face categorization and a face template base on experience (Macchi Cassia et al., 2006). Taken together, it seems that humans have an innate preference for faces underlying the existence of an innate component of face processing and thus of an internal face representation. Face processing mechanisms however also appear to be refined by experience. The following question would then be how would an internal face representation be adjusted through experience. We hypothesized earlier that the internal face representation would have similar characteristics to face natural statistics. If that is the case it seems logical to take an interest in the brain's ability to summarize several stimuli of the same category into one representation. In vision sciences, this subject received some interest, and has been widely studied and is described as ensemble coding. Research on ensemble coding showed that when participants are presented with several, distinctive objects of the same category, the mean (in terms of position, orientation, velocity, color or identity) of all the objects is more accurately recalled than the objects themselves (for a few examples : Albrecht & Scholl, 2010; Ariely, 2001; Chong & Treisman, 2003; de Gardelle & Summerfield, 2011). Research on ensemble coding for faces has also demonstrated the ability to extract mean information from a group of faces, in terms of emotion (Haberman & Whitney, 2007, 2009), and identity (de Fockert & Wolfenstein, 2009; Kramer et al., 2015; Neumann et al., 2013). Similar ensemble coding mechanism might be involved in the creation of internal face representations, although it is to be mentioned here that the time in ensemble coding is shorter (a few seconds) while we talk here about a process built over a lifetime. We can however imagine that every face encountered is blended in with previous face exemplars, which would smooth distinctive individual-specific information and reinforce elements found common in most. This hypothesis fits with behavioral observations, as it was found that face distinctiveness makes basic-level face categorization harder (Valentine & Bruce, 1986b). In other words, the further a face is from natural face statistics, the harder it is be to categorize as a face, suggesting that face categorization relies on a natural statistics' internal representation. Additionally, Prunty et al. (2023)showed faster and more accurate detection of subjects' "ingroup" faces than "outgroup" faces, suggesting that face cell respond more to "ingroup" faces and implying that different people differently detect faces and therefore that their internal face representations are different. These results thus support the role of experience in the establishment of this representation, and that an internal representation for basic-level categorization would have common cues from faces met in our daily lives. Pushing further their study of internal representation, Prunty et al. (2024) showed that averaging only 20 different faces in one image was sufficient to smooth out individualities and keep only common features, shape and configuration. Moreover, different averages made from 20 different faces were so similar, that they were perceived as being images of the same identity. Further demonstrating that averaging multiple faces can form an accurate generic face representation reflecting faces natural statistics, these averages yielded better basic-level face categorization than individual faces. These results also suggested the possibility that face processing mechanisms could rely on such representations.

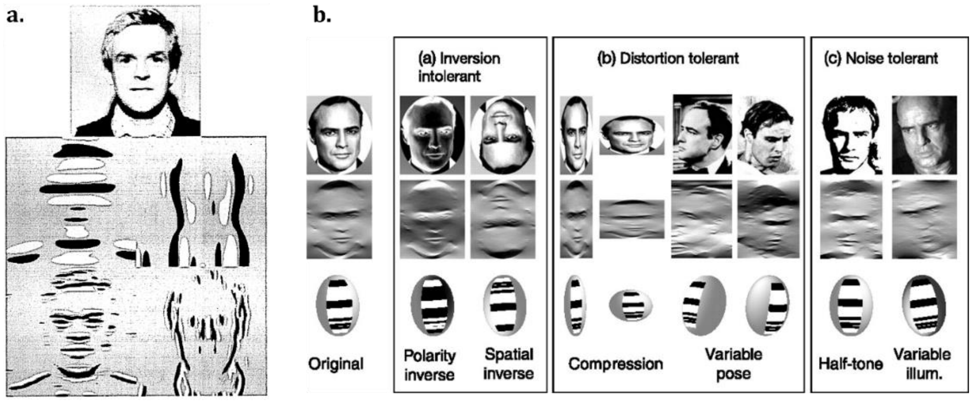
As the natural statistics of our visual environment have influenced the development of our visual system (Geisler, 2008), it is likely that faces natural statistics have influenced face specialized mechanisms. Studying faces properties conjointly with their processing thus enables better understanding of our visual system and more specifically of the face processing mechanisms.

3. The horizontal advantage in face processing

Up to this point, we have ventured the hypothesis that the faces we come across in our lives are averaged to build an internal representation of the human face, comprising face natural statistics. In the rest of this thesis, we will explore the possibility that similarly to basic-level categorization, identity categorization relies on representations highlighting identity diagnostic information while smoothing out other appearance variability (lighting, pose, haircut…). We take this interest under the lens of oriented information, more specifically the horizontal range of face cues. We examine the possibility of this range conveying diagnostic category and identity information privileged by face specialized mechanisms.

In taking an interest in object segmentation, Watt, (1994) proposed a novel idea. Until then, models for object segmentation in the visual system were mostly edge-based and therefore only worked at fine spatial frequency with sharply defined edges. Instead, Watt proposed a segmentation model based on orientation filtering, following the visual system organization and orientation selectivity. He demonstrated that the orientation-filtered outputs were blobs of alternating contrast, either vertical or horizontal, depending on the filter used, spread along the axis perpendicular to the filter used: e.g. horizontal filtering would give horizontal blobs spread along the vertical axis. Thank to Gestalt-like object properties, these blobs form clusters covering the general shape of the object, which could also serve as a segmentation basis. Instead of being purely edge-based, this proposed segmentation would involve whole objects. We take an interest here, because in testing this method on face images, Watt found that this segmentation method worked for faces and that horizontal filtering highlighted both the configuration and contrast distribution of face features (Fig 1.3a). The horizontal range therefore seems to carry natural face statistics necessary for basic-level face detection. Years later, Dakin & Watt, (2009), used the same methodology : they filtered faces in orientation, and showed that faces can be summed up as parallel horizontal blobs, piled along the face elongation axis. Furthermore, these alternations between light and dark horizontal stripes form a pattern that the authors refer to as the face “bar code”. The same manipulation over 300 faces resulted in an identical structure. Orientation filtering of both coarse and fine face images results in this face bar code. However, the same manipulation on scenes and flower images, did not yield this strong horizontal structure nor the same regularity between images of the same category. That is because faces all have a common structure and features disposition that result in a specific alternation of contrast under natural lighting, as mentioned above. Based on results described earlier in this chapter, such cues, common to all faces would constitute a candidate as a face internal representation for basic-level face categorization. In the same paper, the authors demonstrated that at the identity categorization level, the horizontal information enabled better performance than other orientation ranges of information. These bar codes could therefore also convey the diagnostic cues to face identity.

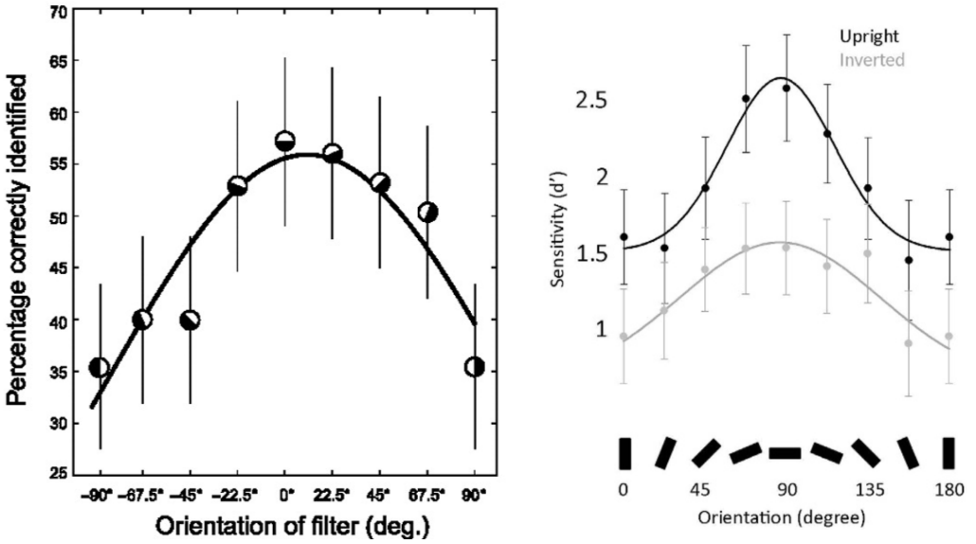
Based on these findings, we propose that the vertical arrangement of horizontal range of the face conveys the face diagnostic information, that is, face natural statistics, both at the basic-level face categorization and face identity categorization. If this is indeed the case, faces presented with their horizontal range only would need to share the same properties as face recognition described in the previous sections, while faces presented with other oriented information would not. To validate this hypothesis, basic-level face categorization and face identity categorization of faces only carrying their horizontal should yield better accuracy, possibly close to full spectrum images, compared to other orientation ranges. Facial horizontal range should also enable face identity recognition tolerant to noise, distortion or variable viewpoint, yet its advantage should be disrupted by inversion and negation, which seem to be the case, as described by Dakin & Watt, (2009) using the bar code (Fig 1.3b).



<u>Figure 1.3.</u> a. From Watt (1994) A face and its orientation filtered blobs output at coarse (top) and fine (bottom) spatial frequencies along the horizontal (left) and vertical (right) ranges. **b.** From Dakin & Watt (2009) Faces in full spectrum with their horizontally filtered output, and corresponding bar code through diverse image transformations. The bar code is proposed as an explanation of why face identity recognition is resistant to noise and distortion but not to inversion and contrast negation

Even before Dakin & Watt (2009) talked about the face bar code, two studies demonstrated the importance of the vertical arrangement of the face. They demonstrated that inversion disrupted vertical distances between features (eye-mouth distance) to a larger extent than horizontal distances (inter-eye distance; Goffaux & Rossion, 2007). Going back to (Fig 1.3a), we can see that horizontal distance is measured inside the same horizontal blob. Thus, changing this distance would not affect the bar code at all. On the contrary vertical distance (e.g. between eyes and mouth) is measured along the face vertical elongation axis. Changing vertical distance therefore affects the bar code by increasing or decreasing the width of the blobs in question. If inversion disrupts the face bar code, perception of distance between the different horizontal blobs would be more affected than relations inside the same horizontal band. Which was the case in this experiment. These results have been replicated with fMRI, showing that the brain region involved in whole face processing was more affected by inversion when vertical relations were changed (Goffaux et al., 2009), again pointing at the bar code as a potential carrier of face diagnostic cues. This is further supported by the work of Ramon (2015) who found a stronger reliance on vertical relation in familiar face identity recognition.

Later studies have been conducted by restricting the access to face-images to one orientation band only, and compared recognition performance between orientations. Studies comparing only horizontal and vertical orientation found greater recognition accuracy when participants had access to the horizontal range compared to vertical (Goffaux & Dakin, 2010; Pachai et al., 2017). Similarly, studies comparing horizontal, vertical and oblique orientations found that identity recognition accuracy peaks when the available range is horizontal and decreases towards its minimum, reached with the vertical range of face information, as a Gaussian centered on the horizontal (Fig 1.4; Dakin & Watt, 2009; Goffaux & Greenwood, 2016; Pachai et al., 2013). There is therefore an advantage for the horizontal range over other orientation ranges in face identity categorization, which is said to be tuned to the horizontal information.



<u>Figure 1.4.</u> <u>Left</u>. Figure taken from Dakin & Watt (2009). <u>Right</u>. Figure taken from Goffaux & Greenwood (2016). We can see that both experiments yielded highly similar results, with a strong advantage for the horizontal in face recognition. On the left, in light grey, we also see the loss of advantage of the horizontal range with inversion.

Several studies also demonstrate the face specificity of the horizontal tuning. The horizontal tuning of face recognition is disrupted by inversion (Goffaux et al., 2015; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2017) and the sole absence of the horizontal range cancels the face inversion effect (Jacques et al., 2014). Such interaction of orientation content and inversion was not found for non-face objects or scenes (Goffaux & Dakin, 2010; Jacques et al., 2014); although a horizontal advantage was found for car discrimination. Although face images contain most of their energy in the horizontal range (Goffaux & Greenwood, 2016a), the fact that the horizontal advantage is disrupted by inversion demonstrates that it is not solely due to the orientation itself but that there is something more to this horizontal advantage. Other arguments in favor of the involvement of face specialized mechanisms in face horizontal information processing was brought by Goffaux & Dakin (2010), who showed that identity adaptation was only measured when faces displayed horizontal information but not in its absence. The horizontal range was also shown to enable better face identity generalization across viewpoints compared to the vertical range. Unsurprisingly, the horizontal advantage is stronger for familiar faces (Pachai et al., 2017), and for people with better identity recognition (Duncan et al., 2019; Pachai et al., 2013). Finally a stronger activation of the FFA was recorded for faces containing the horizontal range compared to obliques and the vertical range and activity pattern in the right FFA and OFA for upright and inverted faces could only be differentiated for horizontally filtered faces (Goffaux et al., 2015).

To summarize, the horizontal tuning appears to drive face specialized processing. We therefore hypothesize that the horizontal range of face information carries the diagnostic cues enabling the fast and efficient processing of faces at the basic and identity categorization levels. This thesis work aimed at defining more precisely the horizontal range of face information and to gather further evidence of the link between the face's horizontal range of and face categorization from basic to finer levels.

4.1 Thesis Outline

In this thesis, we chose to study the face's horizontal range as diagnostic information for face categorization. Face processing has been extensively studied, and some key elements of face categorization research have been summarized in this introduction. In a lot of these studies, key information and processes where studied in isolation (e.g., features, or their configuration, or shading information…). Here by proposing to study the oriented content of the face, we chose a more ecological segmentation process as, like Watt explained in his paper (1994) is follows the visual system's functioning. Yet, the horizontal range of face information seem to convey at least some of the face diagnostic information like the features and their configuration, as well as contrast distribution. This extended focus on the face horizontal information in the following chapters therefore aims at a more comprehensive study of face categorization diagnostic cues.

The first step in studying the horizontal tuning of face recognition is to determine whether this orientation is linked to the face itself or whether the horizontal orientation is reflected in the retinotopy of the observer. In other words, is the face identity recognition advantage due to the information contained in the horizontal range of the face, or is it due to upright faces projecting a strong horizontal signal on the retina. The question especially arises knowing that early visual areas, like V1, demonstrate orientation selectivity (Hubel & Wiesel, 1962; Priebe, 2016) and therefore the ability to discriminate between orientations. Huynh & Balas (2014), by rotating faces 90° and showing the advantage of horizontal in emotion categorization over vertical information persisted, concluded that the horizontal range seemed linked to the face itself. Similarly, studies demonstrating a disruption of the horizontal preference with inversion indicate a low probability that this preference would solely rely on retinotopy. Indeed, with a 180° rotation, inversion keeps the horizontal and the vertical axis of both the face and the observer's retina aligned. If the horizontal tuning was only due to retinotopy, it should only be disrupted when the face's horizontal and the retina's horizontal are misaligned. To this date, this question has not been studied more extensively. In Chapter 2, by comparing the orientation tuning of filtered faces, presented rotated (tilted), we will resolve this question and further characterize the reference frame.

As we saw in the introduction, face natural statistics seem to encompass both configural and surface and shading information. The processing of which are disrupted by picture plane inversion and contrast negation, respectively. To determine whether the horizontal range indeed conveys configural and surface and shading information, in Chapter 3, we compared the horizontal tuning of upright, inverted and contrast negated faces. Although the effect of inversion on the horizontal advantage in face recognition has been thoroughly investigated (Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Jacques et al., 2014; Pachai et al., 2017), it is not the case for contrast negation. Furthermore, comparing the effect of both manipulations will also give insight as to how the horizontal range conveys both types of identity information. If there is no relationship between the effects then the horizontal range would convey configural and surface and shading information separately. However, if the effects are linked it would favor the hypothesis that the horizontal range conveys these types of face identity information as part of a whole, embedded as the natural face statistics face.

The advantage of the horizontal range in upright face recognition could simply translate that this orientation range is the most informative about identity. It contains the face features (eyes, eyebrows, nose, mouth) and was also found to be more advantageous for car discrimination. However, with the finding that the horizontal range, more than the vertical, helped matching the different views of face identity (Fig 1.5; Goffaux & Dakin, 2010), Chapter 4 will examine whether the horizontal range could bind together the different views of a face to create a tolerant internal identity representation. Chapter 4 will explore this hypothesis by comparing the orientation tuning of face identity recognition under different viewpoints, as well as the orientation tuning of two models exploring the pixelwise informativity of the horizontal cues as well as their stability across views.

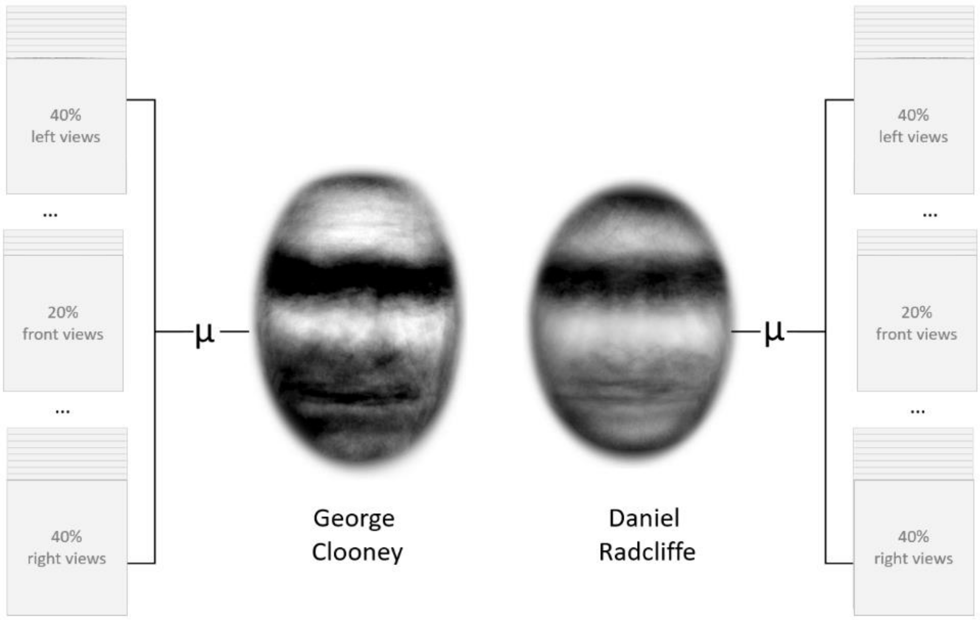


Figure 1.5. Images made from averages of two male actors, George Clooney (left) and Daniel Radcliffe (right) with pictures taken at different viewpoints. Although identity recognition from these images is complicated, distinctive elements from each actor can still be perceived, blended in a strongly contrasted horizontal signal. Furthermore, this signal also conveys natural face contrast and configuration. Based on these average images, the horizontal range appears as a good candidate to convey individual identity as well as faces natural statistics.

Finally, if the horizontal range indeed conveys the face natural statistics, this range should enable better basic-level face categorization than the other ranges of information. So far, a possible horizontal advantage in face detection has not been studied, although a preferential response was found in

FFA and OFA for horizontally-filtered images (Goffaux et al., 2016). In our last chapter, we will compare basic-level face categorization of faces filtered in different orientations. Basic-level categorization will be measured both implicitly, using a Fast-Periodic Visual Stimulation EEG paradigm, and explicitly in a behavioral detection task.

4.2 The FameSet

Chapters 2, 3 and 4 study face identity categorization. As seen in the previous parts of this introduction, familiar and unfamiliar face identity categorization are different processes. With familiar faces, face-specialized mechanisms are recruited and the horizontal advantage is greater compared to unfamiliar faces. We therefore decided to use familiar faces to investigate the horizontal range as a gateway to face-specialized mechanisms for genuine identity categorization. Although in Chapter 4, participants were familiarized with identities that would then become familiar during the test, in Chapter 2 and 3, we chose to use faces that were naturally familiar to participants. The easiest way to find identities familiar to most participants was to use famous identities. Our use of famous actors also had other advantages: we chose more natural images, with natural pose variations therefore tapping into tolerant recognition mechanisms at stake during everyday life; making the task easier to participants, especially for the Chapter 3 in which images are filtered and presented either inverted or contrast negated; and not having to familiarize our participants with the identity before the experiment.

To this aim, we create our FameSet. we selected 21 British or American white male actors and found 10 pictures for each, using a previously made image set the *FaceScrub* (Ng & Winkler, 2014), completed with a google image search for free to use images. Pictures were then rotated to align the eyes with the horizontal, resized and cropped to have faces of roughly the same size. To determine which of these actors were indeed familiar to and recognized on most pictures by most of our participants, we ran a selection pilot. A total of 237 subjects entered the pilot. They were presented with a third of the images (between 3 and 4 images of each actor randomly selected among the 10). After each image was presented on screen for 500ms, their task was to select the corresponding name among 5 possibilities. Based on the results we eliminated 3 actors that were too poorly recognized (when participants responded “I don’t know” more than 40% of the time on average), resulting in a total of 18 actors, and selected the 4 best recognized images per actor based on participants aggregated responses. The selected images can be seen in Fig 1.6.

In Chapter 2 and 3 experiments, participants started with a task similar to the pilot to select 10 out of the 18 pre-selected actors they recognized best to ensure they were indeed familiar with the identities of the stimuli. To select an actor, participants had to be able to recognize at least 3 out of the 4 pictures. Once the 10 actors were selected, three images were used in the actual experiment while the last one was used during reminders of the identities present in the experiment. The selection of this image was made by averaging the four images per actor and measuring the correlation between the mean image and each of the four images. The images with the highest correlation, i.e. the most representative of the identity, was selected. The three remaining images were randomly assigned to *same* or *different* pairs of identity for the tests. Finally, to insure our participants were identity matching and not image matching, the images in a *same* pair were always two different images of the actor.

Figure 1.6. The four pictures of each of the 18 actors embedded in an isoluminant oval outline, designed based on the average of all the selected images. The 18 actors are (from top left to bottom right corner Ben Affleck, Ben Stiller, Brad Pitt, Daniel Craig, Daniel Radcliffe, Elijah Wood, George Clooney, Hugh Jackman, Justin Timberlake, Keanu Reeves, Leonardo DiCaprio, Matt Damon, Orlando Bloom, Patrick Dempsey, Robert Downey Jr., Robert Pattinson, Ryan Gosling, Ryan Reynolds.

4.3 Filtering

There are several ways to restrict the face information in terms of orientation. The image can be kept intact and oriented noise can be superimposed (Goffaux & Dakin, 2010; Pachai et al., 2013), or be phase randomized at specific orientations (Jacques et al., 2014). Both these manipulations prevent the access to one orientation while letting other orientation visible: oriented horizontal noise hides the horizontal range of the image. Orientation filtering, another manipulation, works the other way around: only the information contained in one orientation band, i.e. the spatial variations of the image along one band of orientation, is displayed while the rest is filtered out. In all our experiments we used orientation filtering.

To filter our images in orientation, images are greyscaled, equalized in luminance and root mean square (RMS, i.e. the standard deviation of pixel values of an image) contrast and padded, to avoid any border effects. Images are then fast Fourier transformed (FFT) into the frequency domain. The FFT output is then multiplied with orientation filters. These filters are centered around one orientation, and let through spatial variations along this orientation, and level out spatial variations of the rest of the image. Because the filters used are Gaussian, the passed information includes energy variations along the center orientation and neighboring orientations. The extent of the latter depends on the filter's standard deviation. A very sharp Gaussian filter with a very small standard deviation will only let through the information of a narrow orientation band, with a slight gaussian attenuation. As the filter's standard deviation increases, it will be more permissive and the final image will include more information around the orientation band, and a stronger attenuation (Fig.1.7). The resulting images are then transformed back to the spatial domain, cropped to their original size and equalized in luminance and RMS contrast.

In this thesis when we describe filter orientation, they always refer to the orientation relative to the image. A vertical filter follows the elongation axis of the face while a horizontal filter follows its transverse. The orientation of a filter is the orientation let through by the filter. With a horizontal filter, for instance, the images spatial variations along the horizontal (and close to horizontal, following the standard deviation) range are preserved while the rest is level out. In all our chapters we describe a horizontally filtered image as containing only horizontal information. It is however important to note that although we restrict the information to only one orientation, it does not mean that there is no other oriented information. For instance, as the result of the horizontal filter is an alignment of horizontal blobs along the elongation axis of the face, horizontally filtered images also have vertical information. When we talk about orientation information, we refer to the pixels preserved from the original image.

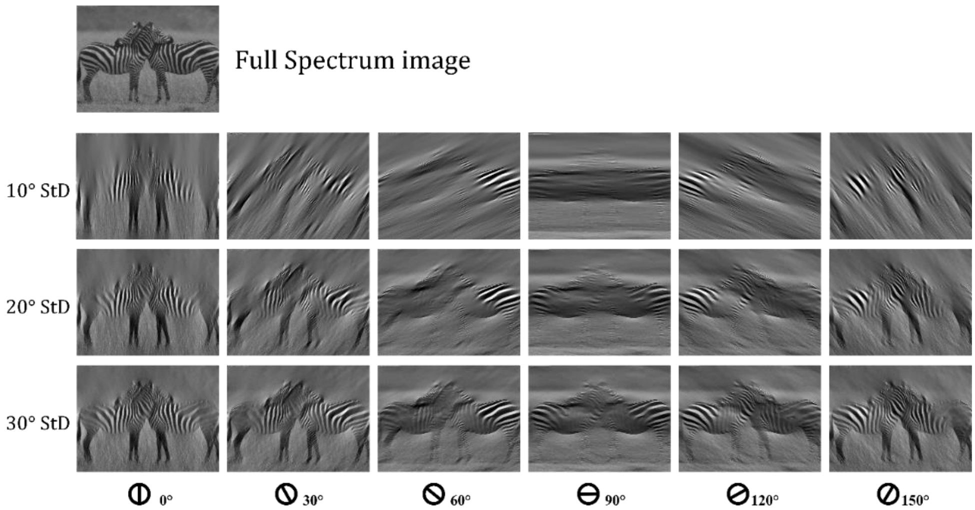


Figure 1.7. Full spectrum image and its orientation filtered version. Gaussian filters with different standard deviations were used: 10° for the top row, 20° for the middle row and 30° for the bottom row. The zebras' stripes give a good understanding of how the filter works. We can also see that the greater the standard deviation the more permissive it is and the more overlap between filters there is.

4.4 Gaussian modeling

In Chapters 2, 3 and 4, we compared the orientation tuning through different experimental manipulations: different angles of rotation, inversion, negation and viewpoint variations. To have a representation of the orientation tuning, we plotted the unbiased recognition performance (sensitivity *d'*) for each orientation filter. In the case of the orientation tuning, as seen in Figure 1.4, it looks like a gaussian centered on the horizontal range (90°). The question is how to compare the orientation tuning profiles between conditions and address the possible variation.

As all our conditions yielded a Gaussian orientation tuning centered on the horizontal, like in Figure 1.4, we modelled the different orientations tuning following a Gaussian, using the method described in Goffaux & Greenwood (2016). The gaussian formula is the following:

$$d' \sim Base\ Amplitude + Peak\ Amplitude * e^{\frac{(Orientation\ filter - Peak\ Location)^2}{2 Standard\ Deviation^2}}$$

with base amplitude the lowest sensitivity value, peak amplitude the difference between the highest and lowest sensitivity, peak location the orientation filter at which highest sensitivity is obtained and finally the standard deviation, the sharpness of the tuning (see Fig 1.8).

To fit this model, we ran Bayesian non-linear mixed models in each Chapter. Using this formula to approximate our data to a Gaussian helped refine the horizontal tuning comparison between condition, by comparing it along the 4 parameters illustrated in Figure 1.8 separately. Indeed, after the model was fit to our data, we could extract our four parameters estimations from the model, and use them as dependent variables. The use of a Bayesian mixed model also enabled us to set our participants as a random effect, to model the general trend while considering individual variations. This model uses each participant's data as priors, to determine individuality, while avoiding outliers. This enabled us to compare parameters between subjects, as in Chapter 3 for instance, where we compared each parameter estimate for each participant between the studied inversion and negation effects, to determine they were correlated or not.

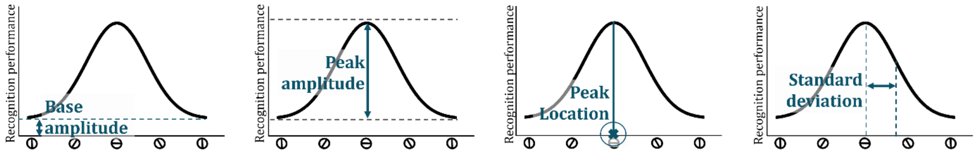


Figure 1.8. Graphical explanation of the Gaussian formula, with each parameter separately represented. Base amplitude and peak amplitude are measured in the same units as the performance (of the effect in the case of Chapter 3) while peak location and standard deviation are measured in degrees (°) of orientation filter.

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Chapter 2: Dissociating retina- and face-centered reference frames of human face recognition.

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Abstract

Face identity recognition is a core and challenging function of the human brain, predominantly driven by horizontally-oriented facial cues. The reference frame of the (horizontal) information driving human face identification is still largely elusive. Therefore, a core characteristic of human face identity recognition remains undefined.

The reference frame of the horizontal information driving face identification may be centered either on the observer's retina (i.e. retina centered reference frame), or the face stimulus (i.e. face-centered reference frame). To disentangle these alternatives, 42 young adults performed identity recognition using famous face stimuli that were filtered to restrict orientation content to narrow bands centered on 0° to 150°, in 30°-steps, and presented either upright, rotated by ±45° or by ±90° away from upright. Such experimental design enabled straightforward predictions about the contribution of retina- and face-centered reference frames as these would result in very different orientation tuning profiles. Indeed, a horizontal face identity information defined along retinal coordinates implies that the peak of identification performance shifts away from horizontal (90°) as a function of rotation angle (peak shift from 90° to 135° for a +45° rotation). In contrast, if the horizontal cues to identity are best defined in a reference frame centered on the face, identity recognition performance should stay tuned to the horizontal irrespective of rotation angle.

Across all rotation angles, we found that recognition performance peaked in the horizontal range of the face stimulus. These results indicate that it is the horizontal information as defined within the reference frame of the face image and not as it falls on observer's retina, which drives human face-specialized identity recognition.

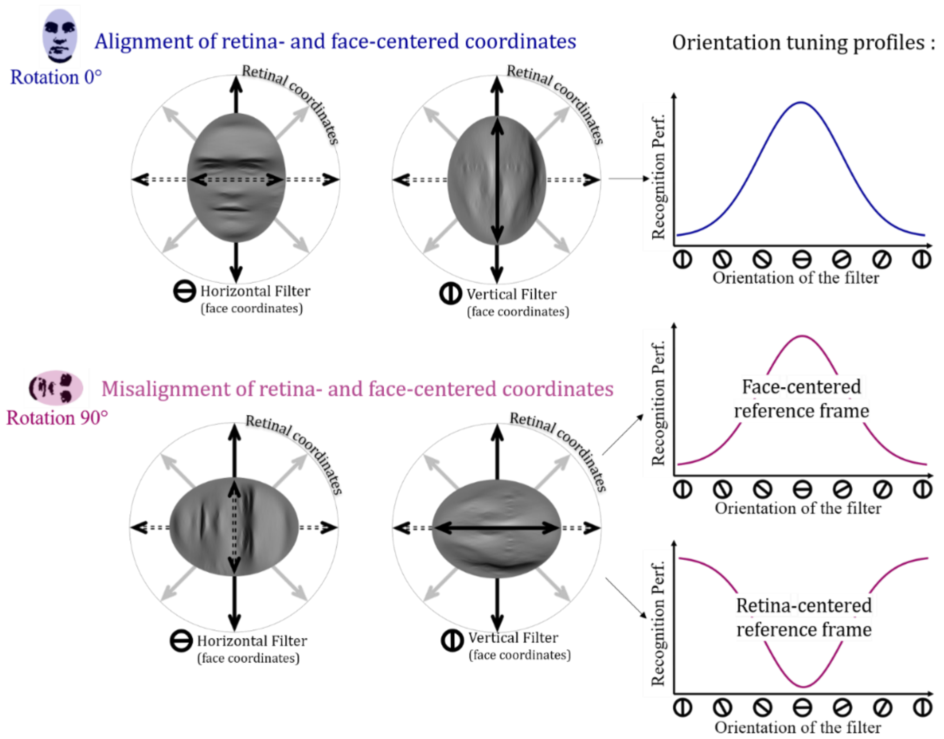
Introduction

Faces are ubiquitous in the visual environment of humans and their processing is a pillar of human social communication (Holler, 2025). The human brain has developed visual mechanisms specialized for the perception of the rich and complex social cues conveyed by faces (e.g., gaze direction, age, identity, emotional expression, etc). In particular, visual mechanisms for identity recognition have consistently been shown to be selectively tuned to the horizontally-structured input of the face stimulus. For example, when humans are asked to recognize the identity of face images filtered to restrict content to a narrow band of orientations, recognition performance typically draws a Gaussian, peaking in the horizontal range, and reaching its minimum for vertically-filtered faces. This horizontal tuning of face processing is robust, as it has been found using diverse image manipulations such as orientation filtering (Dakin & Watt, 2009; Dumont et al., 2024; Duncan et al., 2017a, 2019; Goffaux et al., 2015, 2016; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016), noise masking (Goffaux & Dakin, 2010; Pachai et al., 2013, 2017), and phase randomization (Jacques et al., 2014) as well as across various cognitive tasks such as face identity recognition (Dakin & Watt, 2009; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2017), face detection (Balas et al., 2015) emotional expression recognition (B. Balas et al., 2015; Duncan et al., 2017b; Huynh & Balas, 2014; Yu et al., 2018).

Altogether, this past evidence suggests that the specialization and efficiency of face identity processing by the human brain relies on orientation-dependent visual mechanisms and, more specifically, resides in the selective processing of horizontally-oriented face cues. Yet, this characterization of the visual information supporting the essential function of face identity recognition is missing one key insight: its reference frame. It is elusive whether the horizontal information driving human face identification is best defined in egocentric coordinates, namely with respect to the observer's retina, or in the allocentric coordinates of the human face stimulus, with respect to its vertical axis of elongation. Indeed, past investigations of the horizontal tuning of face recognition conflated retina and face-centered reference frames as they have typically presented face stimuli upright (or inverted) to observers sitting in front of the computer screen head-straight (See Fig 2.1 top).

A retina-centered reference frame implies that the horizontal face identity information is determined in early retinotopic visual areas like V1. However, a purely retinotopic code is unlikely (Duncan et al., 2019; Jacobs et al., 2020). Indeed, face identity recognition recruits a vast network of high-level regions in the ventral visual pathway and beyond, which are only broadly tuned to retinal position (Henderson et al., 2023; Poltoratski et al., 2021). Past electrophysiological and neuroimaging findings additionally indicate that the human face perception preferentially relies on horizontal information from around 170ms post stimulus in high-level face-specialized regions (Goffaux et al., 2016; Jacques et al., 2014). Furthermore, the horizontal tuning of human face recognition is disrupted, if not eliminated, by face inversion in the image plane and contrast negation (Dumont et al., 2024 for inversion and negation; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2017 for inversion alone), i.e., manipulations which severely disrupt face identity recognition despite maintaining the alignment of face- and retina-centered reference frames. Altogether, this evidence indicates that the reliance on face horizontal information predominantly arises in high-level mechanisms tuned to the statistical properties of the *upright* human face and is not primarily driven by retinotopic mechanisms. Yet, a systematic investigation of the respective contribution of retina- and face-centered frames of reference is timely in order to quantify the retinotopic influences on the specialized and horizontally-tuned mechanisms recruited during face identity recognition.

The present study investigated the contribution of retina- and face-centered reference frames to face identity recognition. To do so, we filtered face images in the orientation domain and presented these images rotated in space to upright-sitting-observers. In these conditions, upright (0° rotation) face images had both cardinal axes aligned with those of the observer retina's while rotating the face image (by 45° or 90°) misaligned image and retina axes proportionally to rotation angle. By comparing the orientation tuning profile of identity recognition performance of orientation-filtered faces at different rotation angles, we were able to determine the reference frame(s) contributing to the horizontal information advantage for face recognition. If the reference frame is strictly face-centered, we expect identical orientation tuning profiles for rotated and upright faces with recognition performance remaining tuned to the horizontal range, no matter the rotation angle of the face stimulus. A strict retinotopic reference frame instead implies a shift of the orientation tuning peak equal to the face rotation angle. For instance, with faces rotated by 45°, recognition performance would be highest for faces filtered with a filter centered on 135° (i.e., 90° (horizontal filter) + 45° (rotation) = 135°; Fig 2.1 bottom). However, considering the evidence reviewed above, a more nuanced pattern where the peak of the tuning curve deviates only slightly from the horizontal according to rotation angle seems more plausible. The amount of deviation would enable quantifying the extent of the retinal contribution to face identity recognition.



<u>Figure 2.1.</u> Left. In upright faces (0° rotation), the orientation-filtered stimulus content is aligned across the face- and retina-centered reference frames. Rotating the face stimulus away from upright misaligns the face- and retina-centered frames of reference. **Right.** Predictions of the orientation tuning profile of face recognition are presented, in the case of a strictly face-centered reference frame top) and in the case of a strictly retina-centered reference frame.

Material and Methods

Our goal was to characterize the coordinate system of the (horizontal) information driving human face recognition. To this end, we filtered faces in orientation from 0° to 150° in steps of 30° (in face-centered coordinates; 0°

being vertical and 90° horizontal). These images were then presented either upright or rotated by 45° and 90° (counter) clockwise, relative to the observer. Not exceeding a 90° rotation ensured the engagement of face-specialized mechanisms in all conditions (e.g., Carbon et al., 2007; Stürzel & Spillmann, 2000).

Participants

A total of 46 participants were recruited via ads on Facebook groups from 02/11/23 to 10/05/24. A total of 42, nine males, two non-binary participants, aged 25.38 ± 3.7 completed the experiment, divided into two groups, one for each rotation side: 17 for clockwise and 25 for counter clockwise. Before the start of the experiment participants gave their written informed consent, based on a short descriptive of the study and its goal. They were informed that they could withdraw their consent at any time. The experiments lasted for 3 sessions of approximately 1h, participants were compensated 10 euros per session. At the end of their last session participants had the opportunity to ask any question they wished.

All participants had normal or corrected to normal vision (FrACT scores < 0 for all enrolled participants), as well as normal face recognition abilities (Benton recognition task scores = 48.56 ± 2.86). The experimental protocol was approved by local ethical committee (Psychological Sciences Research Institute, UCLouvain).

Stimuli

We used orientation-filtered images of famous actors' faces were presented upright, rotated by 45° or 90° degrees (counter)clockwise. We used the FameSet image set as in Dumont et al., (2024). The set consists of greyscale images of famous male actors, selected through an online piloting phase on Pavlovia (Open Science Tools, Nottingham, UK), to ensure recognition from the greatest numbers of participants (see Dumont et al. (2024) paper Supporting information S1). The image set was composed of a total of 72 full front (or close to full front) pictures, 4 images for each identity, deprived of any distinctive accessory (such a glasses, tattoos or piercings). All actors were white American or English males. Images were greyscaled and rotated to align the eyes with the horizontal meridian when necessary. Images were centered around the face using the chin and forehead as reference and resized to 302 x 339 pixels. Pixel values were normalized to vary between 0 and 1. We set each image mean luminance to 0.5, and RMS contrast to 0.1, all the while insuring a clipping proportion (proportion of pixel below zero or above 1) under 3%. Images were symmetrically padded to thrice their size to avoid border effect during filtering. Images were fast Fourier Transformed, and their amplitude spectra were multiplied with wrapped Gaussian filters designed to restrict image energy to narrow orientation bands. The center of the Gaussian filters ranged from 0° – horizontal – to 150° in steps of 30°, with a standard deviation of 20° (see Fig 2.2). Compared to our previous study (Dumont et al., 2024), the filter's standard deviation was reduced (from 25° to 20°) to avoid the ceiling performance described by Dumont et al (2024) for upright images. After the inverse Fourier Transform, the mean luminance and RMS contrast of all filtered images was again equalized to match 0.5 and 0.1. An aperture designed to broadly match the contours of the average of the face images was alpha-blended with each filtered and full spectrum image. Finally, and as in Dumont et al. 2024, pink noise masks (1/f) were designed to match the mean luminance and RMS contrast values of the face images. MatlabR2014a and Python3.11 were used for image processing.

All of the stimuli (faces images and masks) were displayed on an isoluminant uniform grey background ([127.5, 127.5, 127.5] in RGB).

Procedure

Before starting the experiment, participants selected actors whose faces were familiar to them (See Supplementary Information). The actor selection process consisted of each of the 72 images (4 images for each of the 18 identities) presented in the middle of the screen for 500ms, followed by 5 actors names (the name of the actor just presented and 4 other names, randomly selected among the 17 remaining actors). Participants had to click on the name of the actor that was just presented or on the “I don’t know” button. An actor was only considered familiar if the participant recognized him in at least 3 out of the 4 images. Each participant had to recognize and select 10 actors to move on to the main experiment.

The main experimental task consisted in a delayed face identity matching task, similar to the one used in Dumont et al., (2024). A trial started with a white fixation point lasting randomly between 750ms to 1350ms, followed by a face image for 200ms, a mask during 200ms and the second face image during 200ms, all displayed at screen center. Participants had to press the letter “S” for same identity and “L” for different identity on the keyboard placed in front of them. Whether the pair similarity was “same” or “different” identities, the displayed images were different, ensuring the measurement of identity recognition and not image matching in the case of “same” identity. Answers were recorded from stimulus onset and up to 4000ms after stimulus offset. Once a keypress was recorded, the fixation point turned to green for a right answer and red for a wrong answer, then back to white, after which a new trial began.

Trials were blocked per rotation condition (either upright, at 45° or at 90°). Each block was made of 14 trials, two for each filter condition (including full spectrum). Each block was followed by a three-second break, after which a tone indicated the start of the new block. Blocks were grouped by three, one for each rotation condition, in a randomized order. After each block triplet, the accuracy score, calculated over the last block triplet, appeared as well as the block number. This screen lasted for at least 10 seconds and required participants to press the “space” bar to continue the experiment.

Before the main experiment, participants were trained to the task (42 trials), first with- full spectrum upright and rotated images (rotation angle at 45° or 90°; clockwise for 17 participants, counter clockwise for the 25 others), and next with upright and rotated full spectrum as well as orientation-filtered. In order to move to the main experiment, accuracy had to be of at least 80% for full-spectrum trials and 75% for orientation-filtered trials.

The main experiment consisted of a total of 90 blocks (30 blocks per rotation condition), giving a total of 1260 trials, 30 trials per condition combination: three rotation angles (0°, 45°, 90°) as each participant only saw rotations on one side, either clockwise or counterclockwise, seven filters (full spectrum, 0°, 30°, 60°, 90°, 120°, 150°), and two levels of pair similarity (same/different).

Stimuli were presented on a Viewpixx monitor (VPixx Technologies Inc., Saint-Bruno, Canada) with a 1920 × 1080 pixels resolution and a 70Hz refresh rate. Participants used a head-and-chin-rest to maintain head position and a viewing distance of 60 cm. Face images presented at this distance subtended a visual angle of 9° by 10.4°, which simulates conversational distance; the masks had a diameter of 11°. The experiment lasted for three hours split into three one-hour sessions. We used Psychopy2021.2.3 to code and run the experiment.

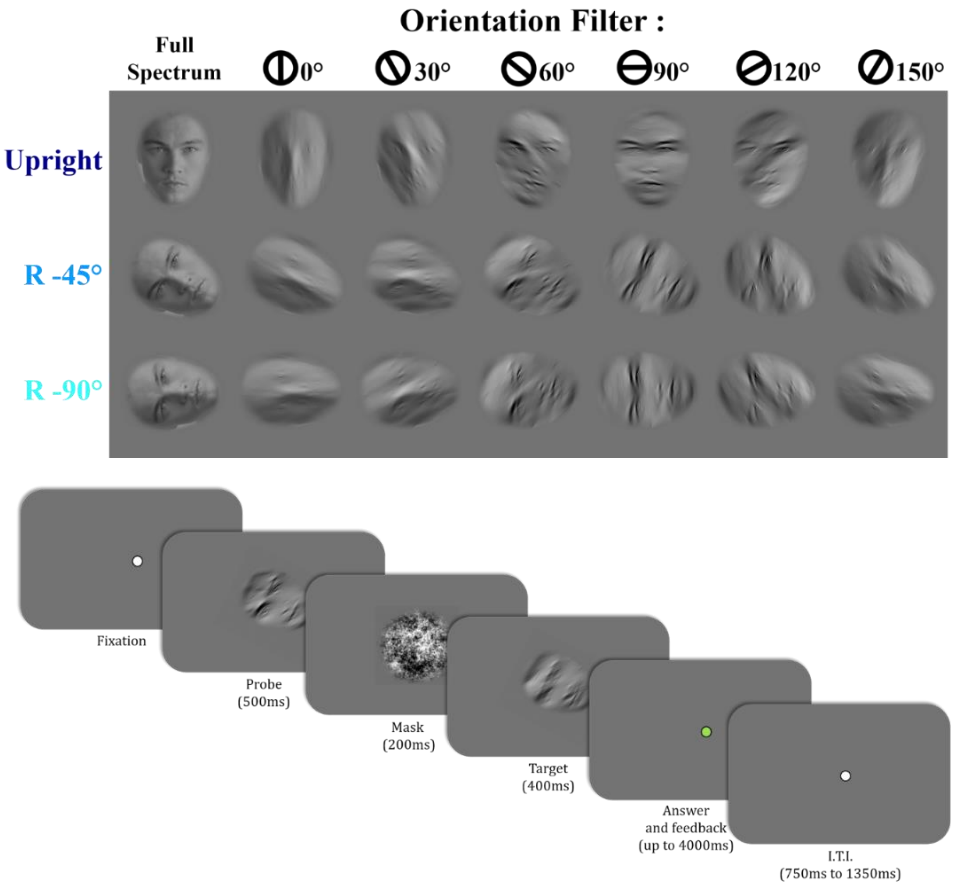


Figure 2.2. **Top**. Illustration of all experimental conditions (filter x counter-clockwise rotation angle) with one of the images of Leonardo DiCaprio. Images are filtered from 0° to 150° in steps of 30°. The filter standard deviation is 20°. The clockwise 45° and 90° rotations are not represented. **Bottom**. Example trial. Here the condition is 120° filter and -45° rotation. It is a *same* trial, using two different images of the same identity, here, Daniel Radcliffe. Trials are blocked. Each block is made of 14 trials, two for each condition combination (filter x rotation angle). Blocks are separated by at least 3 second breaks.

Data analysis

To determine the reference frame of the horizontal cues to face identity, we compared the orientation tuning of recognition performance across stimulus rotation angles. Our analyses are similar to Dumont et al., (2024).

For each participant, we analyzed response accuracy and latency. First, we removed all participants who, did not managed to complete the experiment in 3 sessions or withdrew, had not completed the full experiment; this brought the final number of participants from 46 to 42. We checked that all participants scored above chance level in all conditions. Finally, to exclude outlier response, we 10log transformed the response time (Log_{10}(RT))), calculated its mean and standard deviation (sd) for each subject and kept only the trials which Log_{10}(RT) were included in [mean – 2.5*sd, mean + 2.5*sd], resulting in a removal of 2% of the trials overall.

We analyzed sensitivity d' to control for potential response bias (for accuracy analysis, see Supplementary Information S1). For d' calculation, we designated *same* answers for same identity as ***hits***, *same* answers for different identity as ***false alarms***, *different* answers for different identity as ***correct rejections*** and *different* answers for same identity as ***misses***. Hit and false alarm rates were corrected following Hautus (1995). To increase intersubject comparison across conditions and facilitate data modelling the resulting d' values were normalized (*normd')* with a z transform using the grand (i.e. across conditions and subjects) mean and standard deviation. Finally, we duplicated the 0°-filter *normd'* to make the 180°-filter to represent an orientation tuning profile centered on the horizontal.

First, we investigated the effect of stimulus rotation angle on identity recognition irrespective of orientation filter using a Bayesian General Linear Mixed Model (GLMM) on *nomd'* with subjects as a random effect and with *brms* automatic priors. The model followed this formula:

normd' ~ Rotation Angle + (Rotation Angle | Subject)

Second, we examined the orientation tuning profile of identity recognition across face rotations. Performance as a function of the orientation filter followed a Gaussian distribution in each rotation angle. To compare the orientation of face recognition tuning across rotation angles, we modelled each tuning curve with a Bayesian non-linear, Gaussian, model. The Gaussian formula is the same as used in Dumont et al. (2024) and Goffaux & Greenwood (2016):

$$Normd' \sim Base\ Amplitude + Peak\ Amplitude * e^{\frac{(Orientation\ filter - Peak\ Location)^2}{2Standard\ Deviation^2}}$$

Peak location is the orientation filter at which recognition performance is best; standard deviation measures the sharpness of the performance's orientation tuning around the peak location; base amplitude is the minimum performance; and peak amplitude indicates the difference between minimum and maximum (i.e., peak) performance. The estimated parameters were compared between rotation angles using their 89% credible intervals (CrI) to test for a "significant" difference.

With all 4 parameters estimated defined along these linear regressions:

Peak Location ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

Standard Deviation ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

Base Amplitude ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

Peak Amplitude ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

For each of these regression models, prior distributions were defined for intercept (i.e. 1), slope (i.e. the effect of Rotation Angle), and random effect of Subjects. Priors for the intercepts of the linear regression models were normal distributions, whose means were chosen based on theoretical expectations and previous results. For example, the prior for Standard deviation was set at 50°, halfway between previous results from our team (Dumont et al., 2024; Goffaux & Greenwood, 2016). Priors for slopes of the linear regression models were also normal distributions centered on 0 (i.e., the most probable *a priori* was that there would be no difference between the tuning curves of each rotation angle). Precise values of the standard deviations of prior normal distributions were chosen in a compromise between allowing Monte Carlo Markov chains (MCMC) to converge and keeping priors as broad, thus uninformative, as possible, to not influence the model toward a specific estimation. Since the model had to fit five Gaussians compared to two, which complicated the convergence of MCMC, the priors used here were slightly more limited than in (Dumont et al., 2024). Finally, priors for random effects were exponential distributions (i.e. positive values only, to specify that there cannot be less than zero variance between subjects; see Table 2.1 for details about the prior distributions used in the model).

Table 2.1. Priors of Bayesian non-linear Gaussian models. Normal prior distributions were set on parameters of linear regressions (intercept and slope) and exponential distributions were set on parameters estimating random effects.

Parameter of non-linear Gaussian model	**Peak Location**	**Standard Deviation**	**Peak Amplitude**	**Base Amplitude**
Prior for Intercept	normal(90, 5)	normal(50, 10)	normal(1.5, 1)	normal(-1.5, 1)
Prior for slope (effect of Stimulus Type)	normal(0, 5)	normal(0, 10)	normal(0, 1)	normal(0, 1)
Prior for random effects	exponential(0.1)	exponential(0.1)	exponential(0.1)	exponential(0.1)

All models were fitted with four MCMC with 12,000 iterations each (4,000 warm up, resulting in 32,000 iterations after warmup). The fit of each model was evaluated with convergence of MCMC chains thanks to diagnostic values such as the number of divergent chains post warmup, Rhat statistics, effective sample size and number of divergent chains.

For sake of comprehensibility, it is important to remind the reader that, in Bayesian mixed-effects analysis, "population-level" includes all participants (fixed effects), and "group-level" is used to describe the sub-categories of the multilevel analysis (random effects), here the participant level.

The analysis was done using R 4.2.2. We used the *brms* package (Bürkner, 2017, 2018) to fit all Bayesian models. Data and analysis codes can be found at: https://osf.io/zyv7b/?view_only=9dd0672a866748e5b2d489b9ec625db0.

Results

As expected, overall recognition performance (*normd'*) was best for upright images and decreased progressively as a function of stimulus rotation angle (see Fig 2.3). Sensitivity to identity was best for upright faces. The 89% Credible Intervals reported in Table 2.2 show a significant difference between upright (i.e., 0° rotation) and all other rotation angles, as well as between the 45° and -45° rotations and the rest of the rotation angles. The clockwise or counter-clockwise direction of rotation did not influence *normd'*.

Besides these influences of stimulus rotation on overall recognition performance, the orientation tuning profile of identity recognition performance at all rotation angles described a Gaussian peaking at 90° and decreasing as the orientation filter neared the vertical (Fig 2.4 Top; see Supplementary S1 for analyses of accuracy). The Gaussian models we obtained with the Bayesian non-linear mixed modelling confirmed these observations (Fig 2.4 Bottom).

Table 2.2. GLMM means and 89% Credible Intervals (CrI) of normd' for each rotation angle.

Rotation Angle	Mean	CI_low	CI_high
0°	.40	.30	.52
-45°	.01	-.07	.20
45°	.06	-.05	.30
-90°	-.7	-.69	-.43
90°	-.7	-.69	-.32

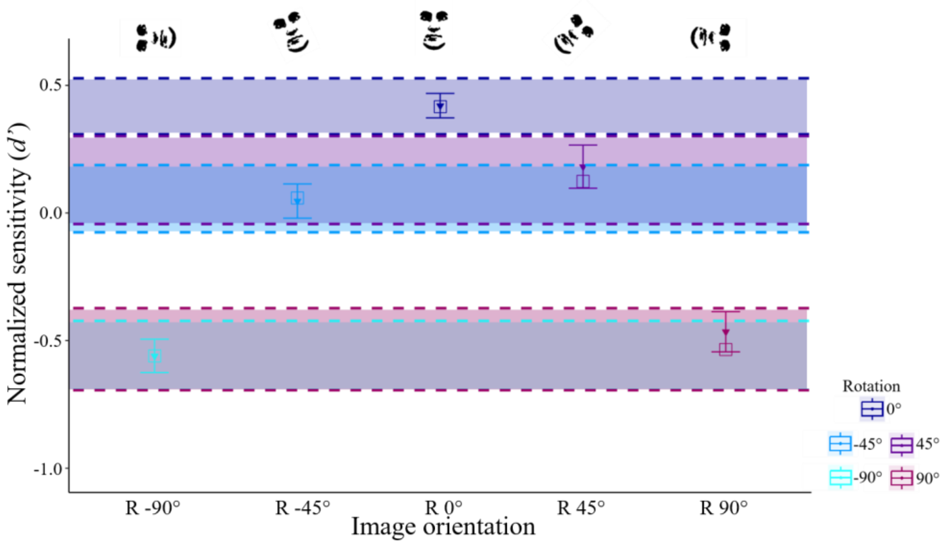
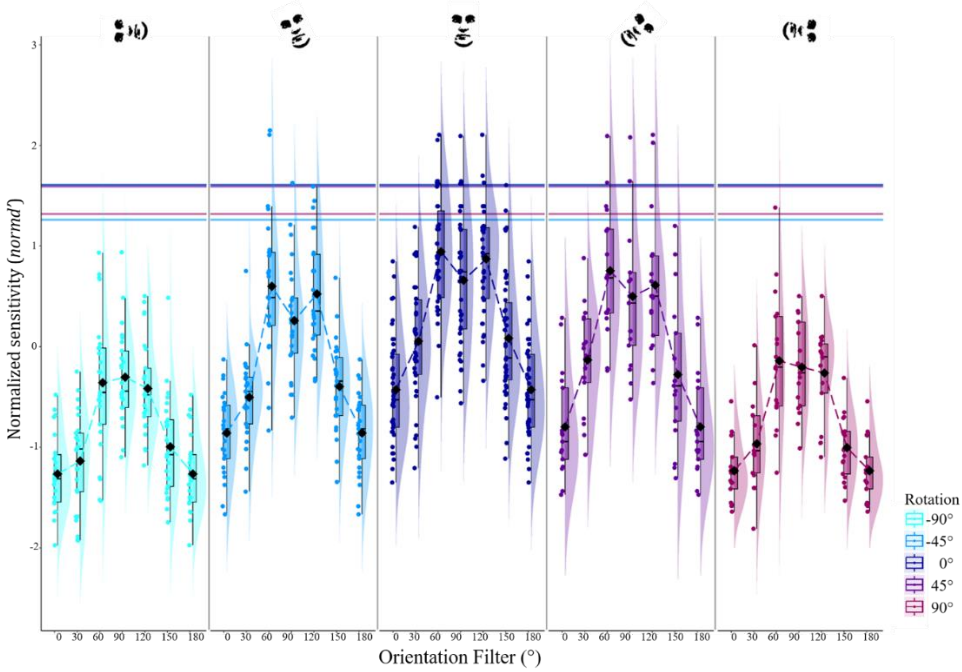


Figure 2.3. Predictions from the Bayesian GLMM comparison of the rotation condition. The non-overlapping 89% credible intervals (CrI) of model predictions indicate a substantive difference between each rotation angle. Triangles and error bars represent the means and standard errors. Squares are the model predicted means, and the shaded regions represent the 89% CrI.

A. Normalized sensitivity (*normd'*)



B. Gaussian model predictions

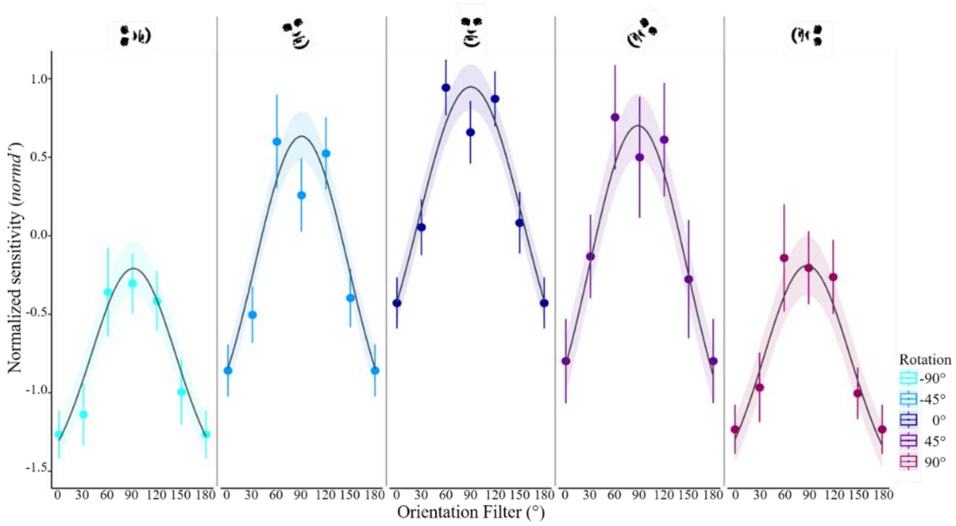
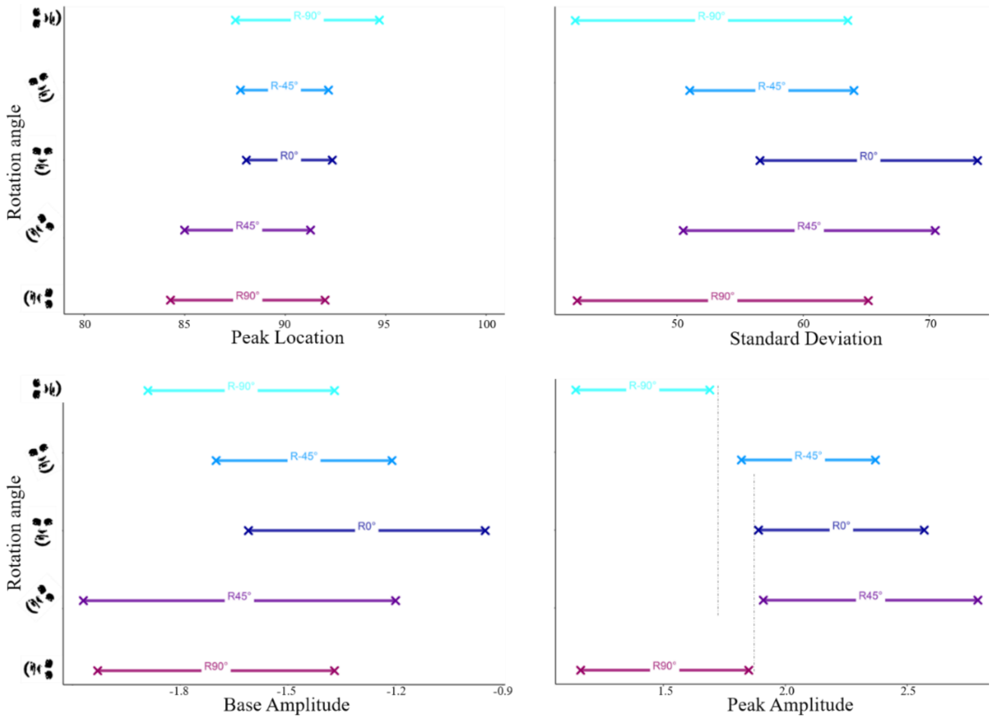


Figure 2.4. **A**. Group-level normalized sensitivity (*normd'*) for identity recognition as a function of orientation filters and stimulus rotation. The black diamonds represent the mean performance for each condition and the boxplots represent the 25%, 50% (median) and 75% quantiles. Each point is

one participant's recognition performance for an Orientation filter and Stimulus rotation. The half violins represent data distribution in each condition. The straight lines on top are the normd' for full-spectrum images for each stimulus rotation. **B.** Bayesian non-linear Gaussian mixed model predictions of normd'. for each rotation condition. Dots represent population-level mean recognition sensitivity and error bars are 95% confidence intervals (CI). The model mean posterior predictions for each Stimulus rotation are drawn in black (line) and the 89% credible intervals (CrI) of predictions are represented as the faded ribbons. Normalized sensitivity peaked in the horizontal range and decreased towards the vertical orientation at all stimulus rotation angles.

To compare the orientation tuning of face recognition across stimulus rotation angles, we analyzed the posterior parameters estimates from the Gaussian model (see Fig 2.5). Peak location estimates did not differ across rotation angles. The 89% CI were all tightly centered on the 90° filter and overlapped in-between rotation angles. Indeed, they ranged from CrI = [84.29, 91.98] for 90° rotation to [87.52, 94.68] for -90° rotation (see Table 2.2). The stability of peak location against face rotation indicates that face recognition performance is tuned to the horizontal range as defined in the face image. Tuning sharpness (standard deviation parameter) varied slightly, yet not significantly, indicating a tendency for the horizontal tuning of face recognition to be broader for upright than rotated faces. Base amplitude estimates seemed to progressively increase, although not significantly (i.e., better recognition for vertically-filtered faces) as rotation angle approached 0°. Finally, peak amplitude estimates 89% CrI were significantly larger for upright faces (0°-rotation, upright: CrI = [1.87, 2.53]), and moderately rotated faces (45° rotation: CrI = [1.88, 2.73]; -45° rotation: CrI = [1.77, 2.45]) compared to the most extreme rotation angles (90° rotation: CrI = [1.14, 1.83], -90° rotation: CrI = [1.24, 1.76]). However peak amplitude at 90° rotation was not significantly different -45° rotation.

Altogether, while these results indicate that rotating faces away from upright does not influence the preferred (horizontal) orientation of face identity recognition, performance in the horizontal range selectively decreased at extreme rotations.



<u>Figure 2.5.</u> 89% Credible Intervals (CrI) of the Bayesian Gaussian model posterior parameter estimates across stimulus rotation angles. The only significant difference is found for the peak amplitude estimate, where the amplitude for the orientation tuning of face recognition is significantly lower for 90° and -90° rotations than for other rotation angles (dashed grey lines).

Table 2.2. Gaussian parameter estimates mean, median and 89% credible intervals (CrI) for each face rotation angle.

	Peak Location (°)				**Standard Deviation(°)**			
	CI_low	CI_high	Mean	Median	CI_low	CI_high	Mean	Median
T 0°	88.05	92.41	90.19	90.20	55.86	72.92	64.52	64.30
T -45°	87.67	93.00	90.36	90.37	48.06	63.45	55.83	55.72
T 45°	84.72	91.17	88.08	88.10	50.04	69.80	60.04	59.68
T -90°	87.60	92.95	90.26	90.27	49.03	66.25	57.67	57.42
T 90°	84.35	92.06	88.20	88.20	41.03	63.63	52.89	52.36
	Base Amplitude				**Peak Amplitude**			
	CI_low	CI_high	Mean	Median	CI_low	CI_high	Mean	Median
T 0°	-1.58	-0.94	-1.25	-1.23	1.87	2.53	2.20	2.18
T -45°	-1.93	-1.49	-1.71	-1.70	1.24	1.76	1.49	1.49
T 45°	-2.00	-1.18	-1.60	-1.58	1.88	2.73	2.31	2.29
T -90°	-1.79	-1.15	-1.48	-1.46	1.77	2.45	2.11	2.11
T 90°	-2.00	-1.35	-1.68	-1.65	1.14	1.83	1.49	1.48

	Peak Location (°)				Standard Deviation(°)			
	Mean	Median	CrI_low	CrI_high	Mean	Median	CrI_low	CrI_high
T 0°	90.19	90.20	88.05	92.41	64.52	64.30	55.86	72.92
T -45°	90.26	90.27	87.60	92.95	57.67	57.42	49.03	66.25
T 45°	88.08	88.10	84.72	91.17	60.04	59.68	50.04	69.80
T -90°	90.36	90.37	87.67	93.00	55.83	55.72	48.06	63.45
T 90°	88.20	88.20	84.35	92.06	52.89	52.36	41.03	63.63
	Base Amplitude				**Peak Amplitude**			
	Mean	Median	CrI_low	CrI_high	Mean	Median	CrI_low	CrI_high
T 0°	-1.25	-1.23	-1.58	-0.94	2.20	2.18	1.87	2.53
T -45°	-1.48	-1.46	-1.79	-1.15	2.11	2.11	1.77	2.45
T 45°	-1.60	-1.58	-2.00	-1.18	2.31	2.29	1.88	2.73
T -90°	-1.71	-1.70	-1.93	-1.49	1.49	1.49	1.24	1.76
T 90°	-1.68	-1.65	-2.00	-1.35	1.49	1.48	1.14	1.83

Discussion

In order to dissociate the contribution of retina- and face-centered reference frames to the horizontal information driving face identity recognition, this experiment compared the orientation tuning profile of identity recognition performance with orientation-filtered faces, rotated at different angles. Overall human sensitivity to face identity was best for upright faces and decreased as a function of face rotation angle. This drop of recognition with rotation angle was also found in previous studies (Jacques & Rossion, 2007; Rossion, 2008; see Rossion & Boremanse, 2008 for review).

In contrast to this overall downward shift in recognition sensitivity, the relative orientation tuning profile was largely stable with comparable peak location, base amplitude and standard deviation across rotation angles. In other words, identity recognition kept tuned to the horizontal range with comparable sharpness and comparable floor performance in the vertical range. Importantly, identity recognition performance invariably peaked in the horizontal range (see also Huynh & Balas, (2014) for face emotion recognition). Yet, peak amplitude, i.e., the recognition advantage of horizontal over vertical information, was significantly smaller for 90° and -90° than for 45°, 0° and -45° rotation angles. This indicates that the overall drop of sensitivity with stimulus rotation found here and in past studies (e.g., Jacques & Rossion, 2007; Rossion, 2008; see Rossion & Boremanse, 2008) is due to the impaired processing of horizontal face cues. Our findings agree with past evidence that the face information suffering most from inversion lies in the horizontal range (Dumont et al., 2024; Goffaux & Greenwood, 2016; Pachai et al., 2017).

The stability of the horizontal preference for identity recognition across face rotations (up to ±90°) confirms that the horizontal information is best defined in a face-centered reference frame. The orientation tuning of face recognition thus reflects the diagnosticity of the information oriented orthogonally to the vertical elongation axis of the human face, irrespective of its orientation when imprinting the observer’s retina. The functional importance of the horizontal face information is thus linked to the natural statistics of the upright human face more than to its retinotopic projection (see Dakin and Watt, 2009).

While our results demonstrate its non-retinotopic, high-level and face-centered nature, they do not exclude the possibility that the horizontal tuning of face identity recognition emerges based on functional interactions across visual processing levels, including the primary visual cortex (V1) (de-Wit et al., 2012; Goffaux et al., 2016). The observation of a selective reduction of sensitivity to identity cues in the horizontal range with stimulus rotation may still suggest some retinotopic influence on the encoding of face identity information although we believe that a high-level account is most likely (see below). Orientation selectivity is a core functional property of V1 and past evidence suggests this function is not limited to the early and static orientation filtering of visual input; instead V1 orientation-selective encoding is a dynamic and protracted process (Ringach et al., 1997, 2002, 2003) operating under the top-down influence of internal representations (e.g., Goffaux et al., 2016; Kok et al., 2012), unconstrained by retinotopy (de-Wit et al., 2012; Hsieh et al., 2010; Williams et al., 2008).

Our study focused on disentangling the retino- and face-centered coordinate systems of face identity information and discarded another fundamental reference frame: the one relative to the space in which the stimulus is viewed and/or to the directional pull of gravity, i.e. the environmental reference frame. Few studies rotated both the observer and the stimulus to address whether human face perception operates in an environmental coordinate system. Findings are mixed (Davidenko & Flusberg, 2012; de Schonen et al., 1998; Lobmaier & Mast, 2007; Troje, 2003). If the horizontal tuning of face identity recognition operates in line with environmental coordinates, we would expect it to be stronger when faces are upright with respect to the environment alone (e.g., when the observer is rotated by 90° but the stimulus is projected upright on the screen) than with respect to the observer alone (e.g. when both observer and stimulus are rotated by 90°). However, since past evidence for the environmental influence on human face perception is scarce and small (Davidenko & Flusberg, 2012), we think that it is unlikely to account for our results.

Although identity recognition peaked in the horizontal range irrespective of face rotation, the magnitude of the horizontal advantage over vertical (i.e., peak amplitude) decreased for extreme ±90° rotations. It is unlikely that such reduction in horizontal peak amplitude resulted from a floor effect in the vertical range preventing the downward shifting of the psychometric curve. Indeed, accuracy in the vertical range was well above chance level for ± 90° rotations (See Supplementary S1). Past studies have shown that face identity recognition drops abruptly at ±90° of rotation (Edmonds & Lewis, 2007; Jacques & Rossion, 2007; McKone, 2004; McKone et al., 2001). Our subjects' performance on full spectrum images also demonstrated this decrease in performance around ±90° (Supplementary S3). Such recognition deficit at ±90° of rotation with full spectrum faces has been attributed to the disruption of specialized holistic processing (Bozana Meinhardt-Injac, Malte Persike, Günter Meinhardt, 2013; Jiang et al., 2011; Rossion, 2008; Rossion & Boremanse, 2008; Schwaninger & Mast, 2005), namely the perceptual integration of local facial features into a global representation of face identity (Farah et al., 1995; Rossion, 2008). Our past work indicates that the holistic processing of faces is mainly driven by horizontal face cues (Goffaux & Dakin, 2010). Therefore, we believe that the reduced horizontal peak amplitude of face identity recognition at ±90° observed here results at least in part from the disruption of face-specialized holistic processing. The drop in performance with 90° rotation may in addition reflect an even more fundamental contribution of the horizontal range to face perception namely the carriage of the shape and surface natural statistics of the upright human face, which are by definition disrupted by picture-plane rotation (Dakin & Watt, 2009; Dumont et al., 2024; Goffaux et al., 2016; Goffaux & Greenwood, 2016; Jacques et al., 2014).

To summarize, our results demonstrate that human face identification stays horizontally-tuned irrespective of face rotation therefore suggesting that the horizontal cues to face identity are defined in a face-centered reference frame. This agrees with the notion that the horizontally-driven visual mechanisms supporting face-specialized identity recognition are tuned to the natural statistics of the upright face.

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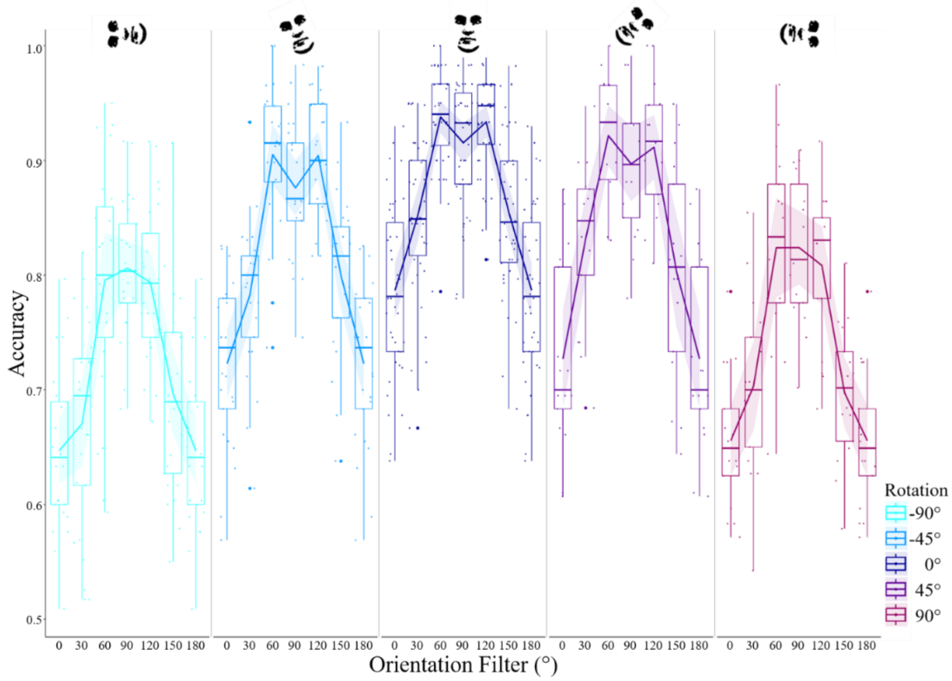
Supplementary Information

S1. Accuracy analysis

The accuracy analysis gives very similar results as the *normd'* analysis. There is a preference for the horizontal or close to horizontal ranges of information for each rotation angle.



<u>Figure 2.S1.</u> Averaged response accuracy (proportion correct) data for each Orientation filter in each Stimulus type condition. The lines link mean accuracy values across orientation filters, boxplots represent the 25%, 50% (median) and 75% quantiles. Each point is one participant's recognition performance for an Orientation filter and Stimulus type. There is a symmetry between clockwise and counterclockwise rotation angles.

S2. Individual sensitivity *normd’*

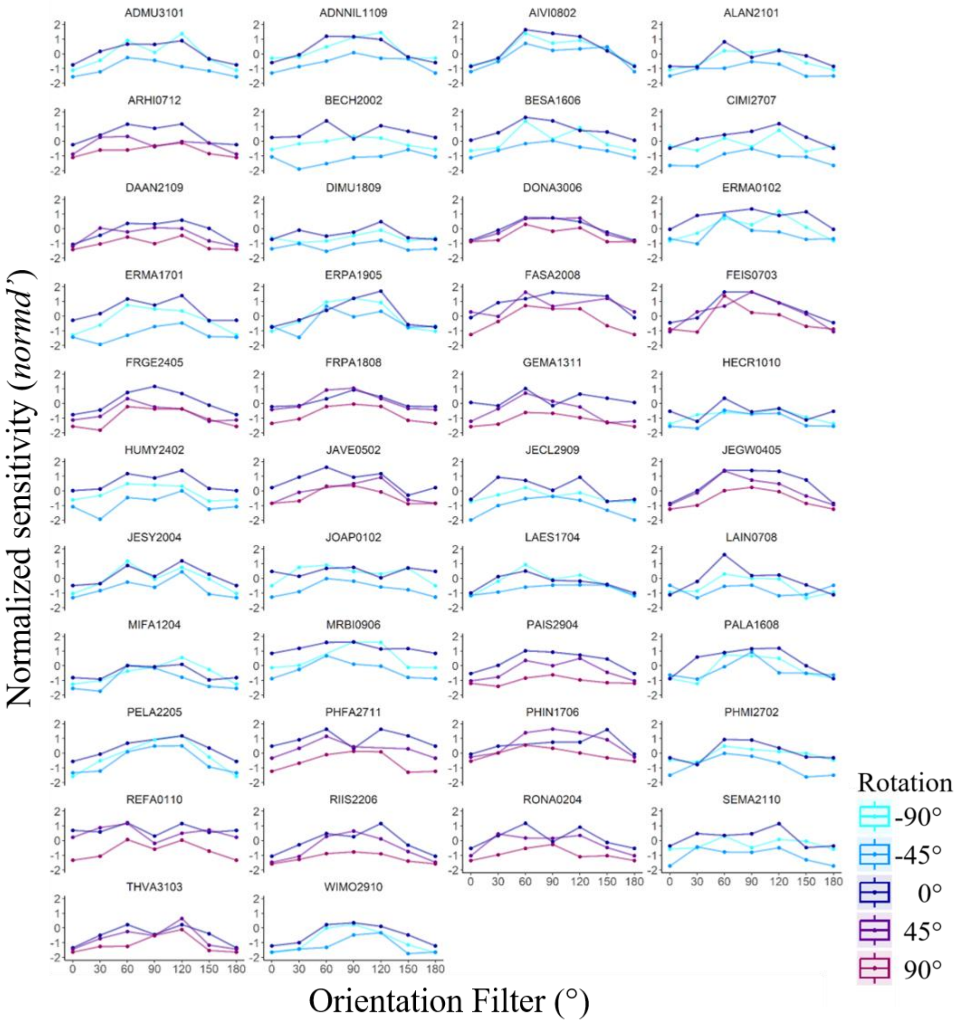


Figure 2.S2. Individual sensitivity (*normd’*) for each subject.

S3. Comparison of the recognition performance for non-filtered images

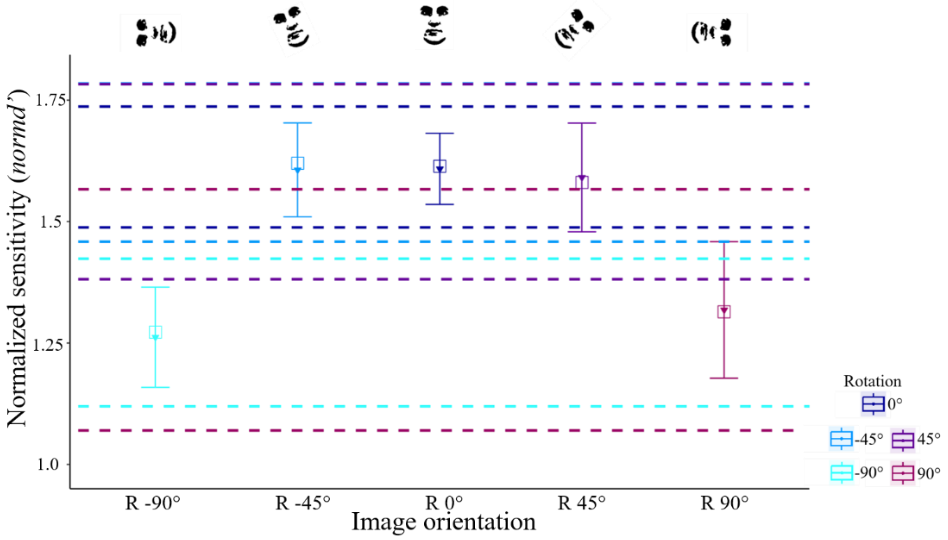


Figure 2.S3. Predictions from the Bayesian GLMM comparison of the rotation condition. The non-overlapping 89% credible intervals (CrI) of model predictions indicate a substantive difference between each rotation angle. Triangles and error bars represent the means and standard errors. Squares are the model predicted means, and the shaded regions represent the 89% CrI.

Chapter 3: Horizontal face information is the main gateway to the shape and surface cues to familiar face identity.

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Abstract

Humans preferentially rely on horizontal cues when recognizing face identity. The reasons for this preference are largely elusive. Past research has proposed the existence of two main sources of face identity information: shape and surface reflectance. The access to surface and shape is disrupted by picture-plane inversion while contrast negation selectively impedes access to surface cues. Our objective was to characterize the shape versus surface nature of the face information conveyed by the horizontal range. To do this, we tracked the effects of inversion and negation in the orientation domain.

Participants performed an identity recognition task using orientation-filtered (0° to 150°, 30° steps) pictures of familiar male actors presented either in a natural upright position and contrast polarity, inverted, or negated. We modelled the inversion and negation effects across orientations with a Gaussian function using a Bayesian nonlinear mixed-effects modelling approach. The effects of inversion and negation showed strikingly similar orientation tuning profiles, both peaking in the horizontal range, with a comparable tuning strength. These results suggest that the horizontal preference of human face recognition is due to this range yielding privileged access to shape and surface cues, i.e. the two main sources of face identity information.

Introduction

Among the myriad of essential social cues conveyed by the human face (e.g., age, emotion, familiarity…; (Jack & Schyns, 2017), identity plays a crucial role in human social organization (e.g., cooperation, kin recognition). The ability to recognize identity in a species is supported by the presence of distinctive identity signals (Tibbetts & Dale, 2007). The study of Sheehan & Nachman (2014) suggests that human social evolution maximized the human face phenotypic and genetic diversity. For instance, this is shown by a larger variation of length and distance among facial features than among non-facial features (i.e. someone with big hands is more likely to have big fingers, but someone with a big nose in not more likely to have big eyes or mouth).

The important function of human face identification relies on specialized visual mechanisms and brain regions (e.g., V. Bruce & Young, 1986; Farah, 1996; Kanwisher & Yovel, 2006; Sergent, Signoret, et al., 1992). Humans reach very high identification performance especially in the case of naturally familiar faces, which can be recognized even with bad quality images or videos and drastic changes in appearance (Burton, 2013; Sinha et al., 2006). Such tolerance of familiar face recognition is impressive as variability in the appearance of the same face across pictures taken under different conditions (illumination, viewpoint, expression, camera) often exceeds variability between pictures of different identities taken under the same conditions (Adini et al., 1997; Burton, 2013; Jenkins et al., 2011). The visual mechanisms and information allowing the tolerance of familiar face identification are not yet well understood and are extensively researched in vision sciences (DiCarlo & Cox, 2007; Hole et al., 2002; Jenkins & Burton, 2011; Johnston & Edmonds, 2009).

Recent evidence showed that the information that drives human face identity recognition is optimally conveyed by an orientation range centered around the horizontal axis. Dakin & Watt (2009) filtered familiar face images in the Fourier domain to only keep the information contained in a narrow orientation band. They found that identity recognition performance describes a bell-shaped curve peaking in the horizontal range and reaching its minimum in the vertical range. Such horizontal tuning of face identity recognition has been documented in several studies, and replicates across various methodologies, e.g. orientation filtering (Dakin & Watt, 2009; Goffaux et al., 2015, 2016; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016), oriented noise masking (Goffaux & Dakin, 2010; Pachai et al., 2013) and oriented phase randomization (Jacques et al., 2014). It is present from three months of age on (de Heering & Maurer, 2013) and develops over lifespan (Balas et al., 2015; Goffaux et al., 2015; Obermeyer et al., 2012). The perception of face emotional expressions has also been found to be horizontally-tuned (Huynh & Balas, 2014; Yu et al., 2018). This horizontal tuning is correlated to face recognition performance in participants exhibiting normal recognition skills (Duncan et al., 2019; Little & Susilo, 2023; Pachai et al., 2013) and is stronger for the recognition of familiar faces (Pachai et al., 2017), suggesting a link between horizontal tuning and genuine and specialized face identity recognition.

This link between horizontal tuning and face-specialized identity processing is further supported by evidence that the former is disrupted by picture-plane inversion (Goffaux et al., 2016; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Jacques et al., 2014; Pachai et al., 2013). Inversion, while largely preserving image content, greatly disrupts face recognition. Faces shown upside-down are harder to recognize than faces shown in a canonical upright position, and this decrease in recognition performance affects faces disproportionately more than other mono-oriented objects or scenes (Albonico et al., 2018; Epstein et al., 2006; Robbins & McKone, 2007; Rossion, 2008; Valentine, 1988; Yin, 1969). Similarly to inversion, another image manipulation known to affect the recognition of faces more than other objects is contrast-polarity reversal (referred to as negation in this paper; Galper, 1970; Nederhouser et al., 2007).

The disproportionate effects of inversion and negation indicate the existence of visual mechanisms tuned to the natural statistics of the human face. Indeed, over evolution and lifespan, the human visual system presumably builds an internal representation of how faces appear in everyday life, i.e., usually in upright position, lit from above (Hong Liu et al., 1999) and depicting characteristic contrast relationships (i.e., an alternation of light and dark, with facial features relatively darker than surrounding skin; Gilad et al., 2009; Liu-Shuang et al., 2022; Ohayon et al., 2012). The typical vertical contrast alternation of the human face is thought to be conveyed by the horizontal range of the face image (Dakin & Watt, 2009; Goffaux & Rossion, 2007). Such natural statistics are reversed in space and polarity in inverted and negated faces, respectively, which likely explains the drastic influence of these manipulations on face recognition (Dakin & Watt, 2009). Past evidence showed that inversion strongly weakens the horizontal tuning of human face identity recognition, with a reduction in the amplitude of the horizontal peak and a doubling in bandwidth (Goffaux & Greenwood, 2016). However, whether and how the polarity reversal of the face contrast alternance caused by negation influences the orientation tuning profile of human face identification remains elusive.

While inversion and negation both alter horizontal face structure, they do so in very distinct ways. Indeed, while inversion flips the edge and shape properties of the face upside-down, negation reverses luminance gradient polarity but preserves edge and shape information. Past behavioral (Bruce & Langton, 1994; Hole et al., 1999; Kemp et al., 1990) and neural (Itier & Taylor, 2002; Liu-Shuang et al., 2015) evidence further indicates that they disrupt distinct aspects of face processing. Inversion is commonly thought to disrupt the so-called holistic processing (i.e. perceiving the face as a whole; Farah, 1996; Rossion, 2008, 2009) of face shape properties (Bozana Meinhardt-Injac, Malte Persike, Günter Meinhardt, 2013; Jiang et al., 2011; Rossion, 2009). On the other hand, negation has been proposed to disrupt the access to face surface cues such as pigmentation (Bruce & Langton, 1994; Russell et al., 2006; Vuong et al., 2005), and shape-from-shading cues (Bruce & Langton, 1994; Kemp et al., 1996; Liu et al., 2000). Although some recent studies found little to no effect of negation on holistic processing (Hole et al., 1999; Taubert & Alais, 2011), others reported that disruption of surface cues with negation could also result in a disruption of holistic processing (Sormaz et al., 2013). Overall, while some studies indicate some functional overlap between these effects, inversion and negation are generally thought to disrupt relatively distinct aspects of face information: shape and surface, respectively.

Our study characterizes the orientation profile of inversion and negation effects on human face recognition in order to infer the shape versus surface nature of the information contained in the horizontal range of the face stimulus. We used familiar face stimuli to tap into genuine and specific face recognition mechanisms (Burton, 2013; Pachai et al., 2017). We measured the difference between the orientation tuning profile for natural faces (faces in natural upright orientation and contrast polarity) and that for (i) inverted faces and (ii) negated faces in the same participants. A difference in the horizontal tuning profile of the inversion and negation effects would indirectly point to a differential contribution of this orientation range to shape and surface processing. Alternatively, finding that inversion and negation similarly modulate recognition orientation profile would indicate that the horizontal range conveys either the information driving shape and surface cue processing of the face image, or a more fundamental aspect of the natural statistics of the upright face coming in play prior to the presumed functional dissociation of shape and surface cue processing.

Material and methods

Subjects

40 healthy young adults were recruited (from 15/06/22 to 12/12/22) for the experiment. Only 21 of them, eight males, aged 23.6 (± 4.5) years old, recognized the requested number of celebrities and completed the experiment in exchange for (i) course credits (1 credit per hour of testing) for participants recruited via a psychology course, or (ii) monetary compensation (10 euros per hour of testing) for participants recruited through a Facebook ad. All participants gave their written, informed consent, based on a short explanation of the protocol before starting the experiment. At the end of the experiment (usually after three sessions) participants received detailed information regarding the experiment and had the opportunity to ask any question they might have had during a debriefing. Visual acuity was tested with the Landolt C test of the $FrACT_{10}$ v1.0 (Bach, 1996) and all logMAR

scores indicated normal or corrected to normal vision (logMAR<0). Face perception abilities were measured with a computerized Benton Facial Recognition Task (Rossion & Michel, 2018) and all scores indicated normal face perception (score = 46.6 ± 3.6). The experimental protocol was approved by local ethical committee (Psychological Sciences Research Institute, UCLouvain).

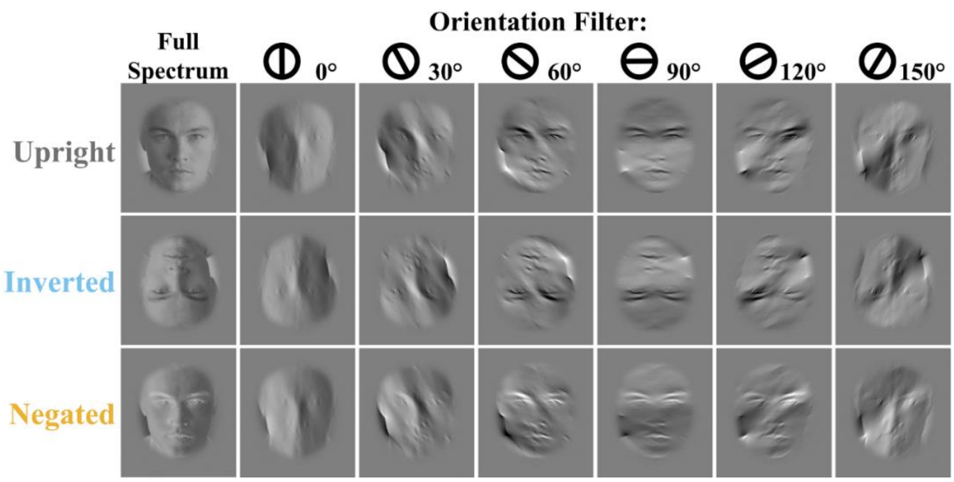
Stimuli

In order to compare the influence of inversion and negation on the horizontal tuning of face identity recognition, we measured participants' identification performance with upright-positive (i.e., 'natural'), inverted, and contrast-negated stimuli that were either full-spectrum, or orientation-filtered in Fourier domain.

Stimuli consisted of greyscale, 302 x 309 pixels, full front or close to full front, faces images of contemporary white American or British famous male actors (18 actors, four pictures each) selected from the Facescrub dataset (Ng & Winkler, 2014) and a Google search for free to use images. Images were carefully selected to exclude any distinctive accessory (glasses, hat, …) and to have a neutral or close-to-neutral facial expression. Eighteen celebrities were selected from a larger set of actor images with an online pilot running on Pavlovia (Open Science Tools, Nottingham, UK) to ensure that they were recognized by most participants. We only kept the four best recognized images for each recognized actor (see Supporting Information S1), resulting in a total of 72 images.

Images were converted to greyscale and rotated to align the eyes with the horizontal meridian. We then cropped and resized each one using forehead and chin as points of reference to match face size across all images. The resulting images were padded with 100 pixels that were mirroring the face image, to prevent border artefacts during filtering. Next, images were normalized to obtain a mean luminance and root-mean square (RMS) contrast of 0 and 1 respectively and fast Fourier transformed, with the amplitude spectra multiplied with six wrapped Gaussian filters centered on 0° to 150° in steps of 30°, where 0° is vertical and 90° horizontal (Dakin & Watt, 2009; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016). The Gaussian filters' standard deviation was set at 25° to approximately match the standard deviation of the horizontal tuning of the identity recognition performance in upright unfamiliar faces previously documented by Goffaux & Greenwood (2016) and were close to those used by Dakin and Watt (2009; 23°). This broad bandwidth resulted in some overlap between adjacent orientation ranges but was chosen to ensure that recognition was possible even in the most difficult condition (i.e. inverted and 0° filter). The proportion of clipped pixels in an image (i.e., pixels with an intensity below 0 or above 1, on a [0,1] scale) was below 3%. Mean luminance and RMS contrast of all images were set to the mean luminance and RMS contrast of the image set (0.5 and 0.12 respectively). A grey elliptical aperture was created to match the shape of an average image of all the faces in the set, and blend with the background of the experiment. It was blended with each image (filtered and non-filtered), after RMS equalization, to cover most of the background, hair and the neck (Fig 3.1). Gaussian white noise masks were also designed with 1/f noise, and global luminance and RMS contrast set to match those of the face images. We used Matlab R2014a for these image processing steps.

In the experiment, images were displayed naturally, inverted or negated. Inverted images were presented using a 180° clockwise rotation on Psychopy. Negated images were made prior to the experiment, using Matlab by reversing contrast values, after filtering, luminance and contrast equalization but before the elliptical aperture was blended with the picture.



<u>Figure 3.1.</u> Example of the stimulus conditions. Each column represents the orientation-filter condition starting by non-filtered images and going in steps of 30° from 0° to 150° from left to right. Each row represents the stimulus type (natural, inverted, negated).

Procedure

Participants did the experiment on a VIEWpixx monitor (VPixx Technologies Inc., Saint-Bruno, Canada) with a 1920 × 1080 pixels resolution and a 70Hz refresh rate. They used a head-and-chin-rest to support their head and maintain a viewing distance of 60 cm. Face images presented at this distance subtended a visual angle of 9° by 10.4°, which simulates an observer distance ideal for holistic processing (McKone, 2009); masks had a diameter of 11°. The experiment lasted for three one-hour sessions. We used Psychopy2021.2.3 to code and run the experiment.

During a prescreening phase, each participant selected 10 actors that they were familiar with (see Supporting Information S1 for details). To do so, participants performed a 5-alternative forced choice identity recognition task with upright full spectrum images (four images for each of the 18 actor identities as selected based on the online pilot ran with a different participant sample; see Stimuli). Each image appeared on the center of the screen for 500ms followed by the names of five actors: the name of the actor corresponding to the image and four other names, randomly taken out of the 17 remaining names. Participants were instructed to select the name corresponding to face identity. An actor's identity was selected only if at least three out of the four images were recognized. Once 10 familiar identities were selected, the four images of each identity were displayed again on the monitor for five seconds. With this procedure, the selection of actors was different for each participant and adapted to their knowledge of the identities, thus ensuring a recognition performance rooted into natural familiarity during the main experiment (Burton, 2013). In the next training, and main experimental trials, three out of the four images per actor were used as stimuli. The remaining images were presented in-between blocks, to remind participants of unmodified selected identities without exposing them with actual stimulus.

Participants performed an identity face-matching task (Fig 3.2). A trial started with a white fixation dot on a grey background. The first face image (probe) was presented during 500ms followed by a mask presented for 200ms and a second face image (target) for 400ms. Participants had to decide whether faces in the just-seen-pair depicted the same identity or different identities with a keypress ('S' for same identity or 'L' for different identity). Participants had up to 4400ms to respond from target onset. After target offset, the fixation dot turned black. When an answer was recorded, the fixation dot briefly turned green for a correct answer and red for an incorrect one. The following trial started after a random duration interval (ranging from 750 to 1350ms). Identity was matching in 50% of the trials. Pairs of each trial were composed after the prescreening phase for each participant (30 pairs for *same* and 30 pairs for *different* trials), and replicated across conditions. Importantly, in the case of *same* trials, both images were always two different images of the same identity, ensuring participants were recognizing identity and not merely matching images. Both images of a trial were presented under same stimulus type and orientation-filter condition. During the piloting phase of this study, we noticed difficulties for participants to reach above chance accuracy when conditions were fully randomized. We thus decided to block stimulus type to facilitate task performance.

As our task involved recognition of face images with orientation filtering, coupled with either inversion or negation, participants first started with a training phase. They were familiarized with the task with increasing levels of difficulty, to ensure they would reach stable and sufficient performance before gathering data. The training phase was divided in three steps of increasing difficulty. In the first training step, participants did the face identity matching task with natural, full spectrum face images. Once participants reached an accuracy > 80%, training went on to the second step. In the second step, face images were either natural, inverted or (contrast-)negated and full spectrum, and presented per Stimulus type in 14-trial blocks. Blocks were grouped by three, one for each Stimulus type, and scores were calculated over these groups of three blocks. Inside each group of blocks, the order of blocks (i.e., of Stimulus type) was set randomly. Once participants achieved a mean score > 75%, training went on to the third training step which was exactly the same as the second, except that within each block (natural, inverted or negated), stimuli were presented both filtered in orientations and full spectrum (i.e., two trials of each of the six orientations, from 0° to 150°, and two full spectrum trials). To pass this last part of training participants needed to reach a mean score of at least 75% (calculated over three-blocks groups with the three Stimulus type conditions), twice in a row. This ensured participants had good comprehension of the task and were able to score well above chance level (50%) before starting the testing phase.

The main experiment consisted of 90 blocks (30 blocks per Stimulus type). Each block was composed of 14 trials: two trials of each orientation filter plus two full spectrum trials. This resulted in a total of 60 trials per condition (i.e., combination of each Stimulus type and Orientation filter), 420 trials per Stimulus type, and 1260 trials overall. With 30 images (three per preselected identities), three Stimulus type (i.e., natural, inverted, negated) and seven Orientation Filter (i.e., 0° to 150° in steps of 30° and full spectrum) conditions, there was a total of

630 images, each repeated four times (twice in *same* trials twice in *different* trials) throughout the experiment.

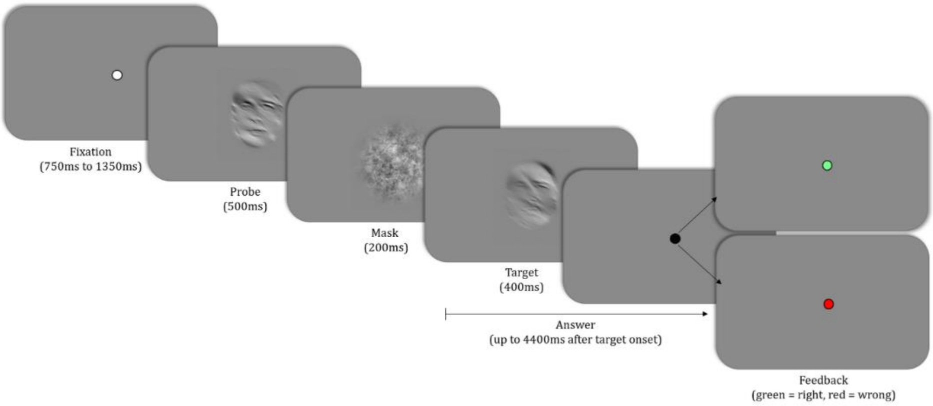


Figure 3.2. Example *same* trial sequence of the main experiment. Each trial starts with a fixation of random duration (between 750ms to 1350ms). A probe face is then presented for 500ms, followed by a 200ms mask and a target face for 400ms. Participants can answer from target onset and up to 4000ms after target offset by pressing either 'S' for same identity or 'L' for different identity. The fixation dot briefly turns green after a correct answer and red after an error.

Stimulus type was blocked while Orientation filter varied randomly within blocks. Blocks were presented three by three, one per Stimulus type, in a randomized order, with a short break in-between (of a minimum duration of five seconds) and a light tone indicating the beginning of a new block. Longer breaks (of at least 30 seconds) happened every three blocks. Longer breaks started with a score informing participants on their performance over the last three blocks and the number of remaining blocks; and ended with the (non-filtered) picture of each selected actor that was not used during the experimental trials, along with their name.

Data Analysis

Through the comparison of inversion and negation effects on the Orientation filter dependence of identity recognition performance, the purpose of this study was to understand the extent to which the horizontal tuning of face identification reflects its contribution to the processing of shape versus surface cues.

During the experiment accuracy was recorded for each participant. All participants scored above chance level. We calculated the mean response time and standard deviation of each participant and considered outlier every answer with a response time faster than *mean − 2.5*sd* or slower than *mean + 2.5*sd,* which resulted in a loss of 3.3% of all answers.

From accuracy data, we computed a sensitivity index (*d'*) to assess participants' performance in bias-free manner (accuracy was also analyzed and produced very similar results – this analysis can be found in Supporting Information S6). We computed a *d'* for each combination of Stimulus type and Orientation filter (with a *same* answer in the presence of same identity considered as a *hit*, a *different* answer in the presence of different identities considered as a *correct rejection*, a *same* answer in the presence of different identities considered as a *false alarm,* and a *different answer* in the presence of the same identity considered as an *omission*). Following the log-linear correction (Hautus, 1995), we added 0.5 to the hits and false-alarm counts, and calculated the *d'* value for each subject in each condition and filter. The normalization of dependent variables is common practice when using complex hierarchical models, as it facilitates model convergence (Stan Development Team, 2023). Sensitivity was thus normalized with a Z transform using this formula:

$$normd'(x) = \frac{d'(x) - \text{mean}\,(d'(x))}{\text{sd}\,(d'(x))}$$

where, for a given combination of Orientation filter and Stimulus type *x*, *normd'* is the normalized *d'* output, *d'* is the non-normalized sensitivity value, mean(*d'*) is the group-level mean *d'*, and sd(*d'*) is the group-level standard deviation of *d'*.

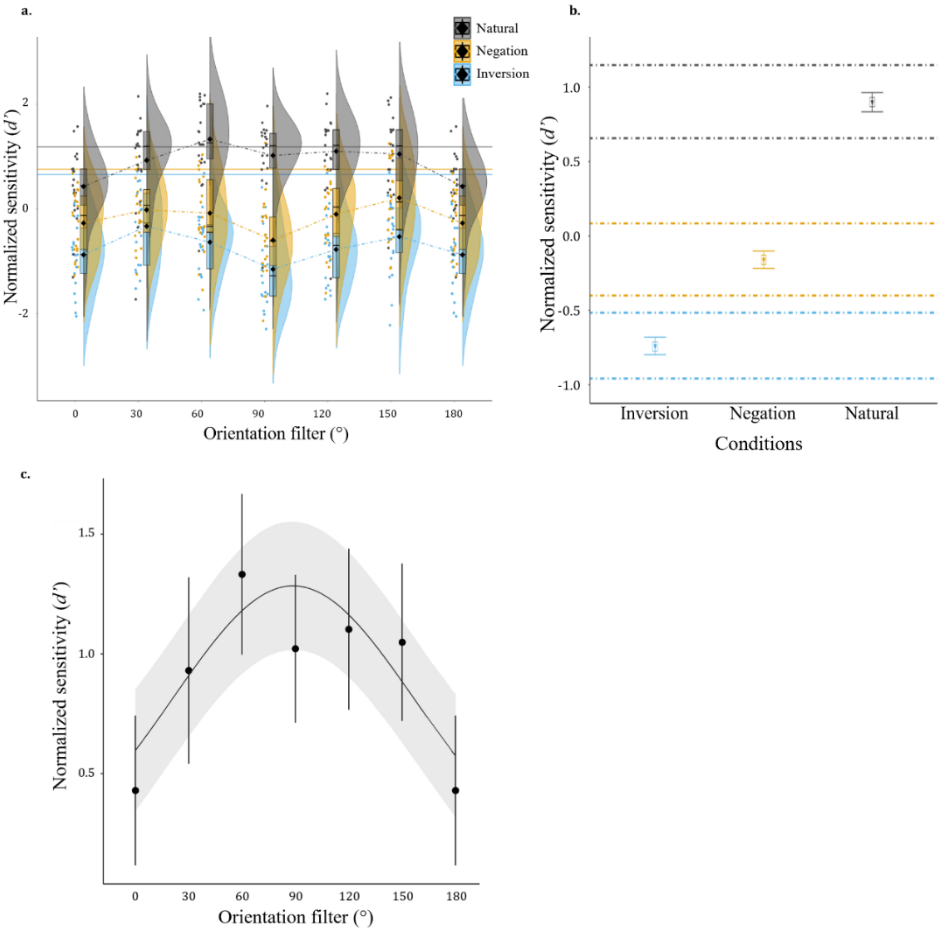
Performance at the 0° filter was duplicated to have circular filter values from 0° to 180°.

First, to ensure participants scored higher for natural stimulus type, which we use as baseline to calculate inversion and negation effects, average performance (across Orientation filters, excluding the full spectrum trials) in each stimulus type condition was compared to the others using a Bayesian general linear mixed model (GLMM), using participants as a random effect, to consider inter-subject variability in the performance estimations for each condition, with this equation:

normd' ~ Stimulus type + (Stimulus type | Subject)

We ran the model with default *brms* priors with four Markov chain Monte Carlo (MCMC) with 6,000 iterations each (2,000 warm up, resulting in 16,000 iterations after warmup), and evaluated the convergence of the chains with diagnostic values such as number of divergent chains post warmup, Rhat statistics and effective sample size.

As expected, the GLMM indicated that participants performed better in natural condition than in inverted and negated conditions (Fig 3.3).



<u>Figure 3.3.</u> a. Group-level normalized sensitivity (*normd'*) for identity recognition as a function of Orientation filters. The black diamonds represent the mean performance for each condition and the boxplots represent the 25%, 50% (median) and 75% quantiles. Each point is one participant's recognition performance for an Orientation filter and Stimulus type. The half violins represent the distribution of the data for each condition. The full lines represent the full spectrum performance for each condition. **b. Predictions from the Bayesian general linear mixed model comparison of Stimulus type.** The non-overlapping 89% credible intervals (CrI) of model predictions indicate a substantive performance difference between each stimulus type. The triangles and error bars represent the group mean and standard error of the data in each condition. The square is the mean in each condition given by the model prediction, and the doted lines are the 89% CrI. **c.**

Population-level averaged recognition performance for natural images and Bayesian Gaussian mixed model predictions. The dots are the population-level averaged normalized sensitivity with the 95% CrI in error bars. The model mean posterior prediction is drawn in black (line) and the 89% CrI of the predictions are represented as the faded ribbons.

Recognition performance for natural face images described a broad Gaussian centered around 90° and was modelled using a Bayesian Gaussian mixed model (Fig 3.3). The model is similar as the one used by Goffaux & Greenwood (2016) and described in the next section. Results of this analysis are reported and interpreted in Supporting Information S4.

Next, the magnitude of the inversion and negation effects was calculated in each subject and for each Orientation filter by a subtraction method:

$$Inversion\,effect = \text{Natural}\,normd' - \text{Inversion}\,normd'$$

$$Negation\,effect = \text{Natural}\,normd' - \text{Negated}\,normd'$$

As can be seen on Figure 3.4, the magnitude of inversion and negation effects as a function of the Orientation filter described a bell-shaped curve peaking around 90° (horizontal range) and decreasing towards 0° and 180° (vertical range). We used a Bayesian non-linear mixed model to fit a Gaussian function to our data. This enabled the comparison of the effects of inversion and negation along the four parameters of the Gaussian tuning function: (i) Peak Location, in degrees: orientation at which the estimated effect is highest; (ii) Standard Deviation: sharpness of the effect’s tuning around the peak orientation; (iii) Peak Amplitude: difference between the effect at its highest (i.e., at the estimated peak orientation) and at its lowest; and (iv) Base Amplitude: minimum size of the effect (i.e., at the orientation where effect estimate is the lowest). The mixed dimension of the model allowed to consider the inter-subject variability during the parameters estimation by setting it as a random effect. The inversion and negation effects were fitted with the following Gaussian equation (Goffaux & Greenwood, 2016):

$$d'effect \sim Base\ Amplitude + Peak\ Amplitude * e^{\frac{(Orientation\ filter - Peak\ Location)^2}{2Standard\ Deviation^2}}$$

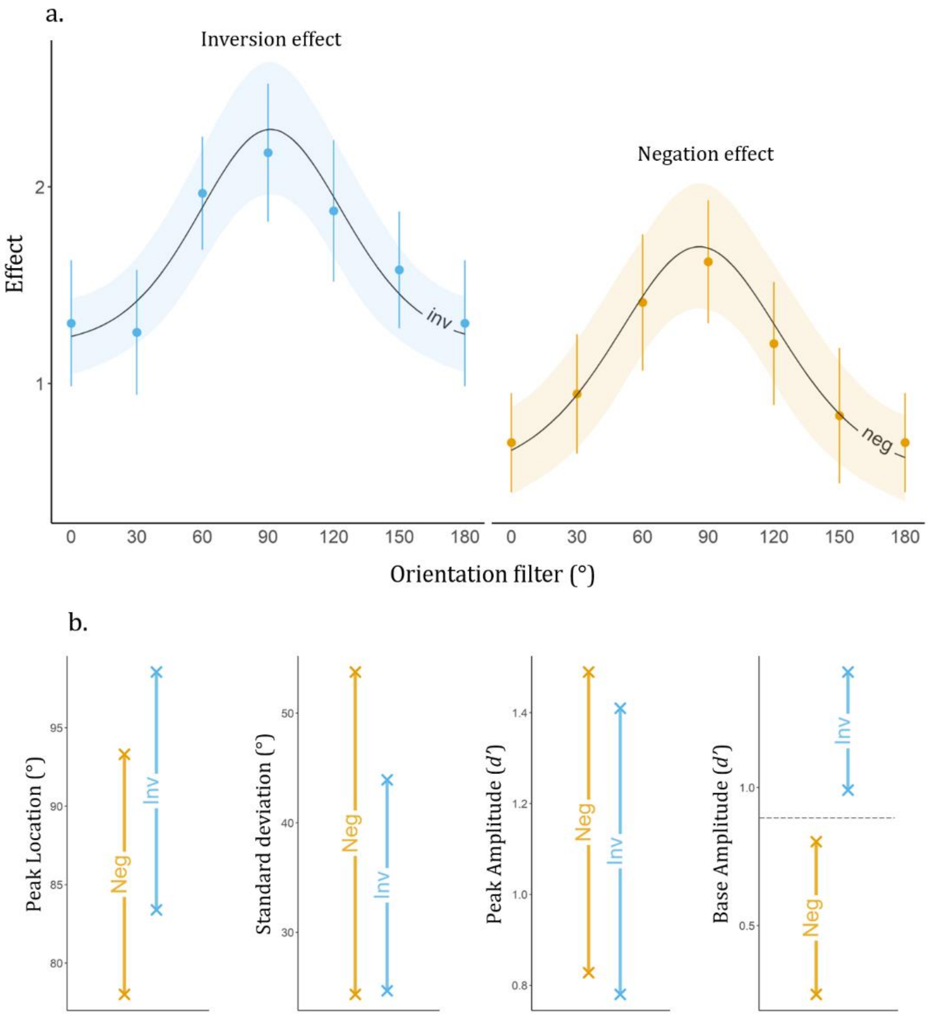
We estimated the four Gaussian parameters (see Fig 3.4b) with the following linear regression models:

Peak Location ~ 1 + Stimulus type + (1 + Stimulus type | Subject)

Standard Deviation ~ 1 + Stimulus type + (1 + Stimulus type | Subject)

Base Amplitude ~ 1 + Stimulus type + (1 + Stimulus type | Subject)

Peak Amplitude ~ 1 + Stimulus type + (1 + Stimulus type | Subject)



<u>Figure 3.4</u>. a.Population-level averaged inversion and negation effects and Bayesian non-linear mixed model predictions as a function of Orientation filter. On the y axis, inversion and negation effects are calculated at the individual level by subtracting performance (*normd'*) in the Inverted and Negated condition from performance in the Natural stimulus type condition. The dots are population-level mean effects of inversion (blue) and negation (yellow), with the 95% confidence interval in the error bars. The model mean posterior predictions for each Stimulus type are drawn in black (line) and the 89% credible intervals (CrI) of predictions are represented as the faded ribbons. Both Gaussians peaked in the horizontal range and decreased towards the vertical orientation. This shows that inversion and negation effects on identity recognition both culminate in the horizontal range. **b. 89% CrI of the four Gaussian parameters posterior predictions distribution.** A difference is significant when the CrI of the parameters of the inversion effect (blue) and negation effect (yellow) do not overlap. The CrI of Peak Location, Standard Deviation and Peak Amplitude of inversion and negation effect overlapped, indicating highly similar model estimates for both effects. However, there was a significant difference in the estimates of the base amplitude for inversion and negation effects, with a higher CrI for the inversion effect, indicating that the effect of inversion was overall larger that the effect of negation.

For each of these regression models, prior distributions were defined for intercept (i.e. 1), slope (i.e. the effect of Stimulus type), and random effect of Subjects. Priors for the intercepts of the linear regression models were normal distributions, whose means were chosen based on theoretical expectations. For example, the prior for Peak Location intercept was a normal distribution centered on 90°, as we expected the effects of inversion and negation to peak for horizontally oriented filters. Priors for slopes of the linear regression models were also normal distributions, whose means were 0 (i.e., the most probable *a priori* was that there would be no difference between inversion and negation effects). Precise values of the standard deviations of prior normal distributions were chosen in a compromise between allowing MCMC chains to converge and keeping priors as broad, thus uninformative, as possible, to not influence the model toward a specific estimation. Finally, priors for random effects were exponential distributions (i.e. positive values only, to specify that there cannot be less than zero variance between subjects; see Table 3.1 for details about the prior distributions used in the model).

Table 3.1. Priors of Bayesian non-linear Gaussian models.

Parameter of non-linear Gaussian model	Peak Location	Standard Deviation	Peak Amplitude	Base Amplitude
Prior for Intercept	normal(90, 20)	normal(35, 20)	normal(1.5, 1)	normal(1.5, 1)
Prior for slope (effect of Stimulus Type)	normal(0, 20)	normal(0, 30)	normal(0, 1.5)	normal(0, 1.5)
Prior for random effects	exponential(0.1)	exponential(0.1)	exponential(0.1)	exponential(0.05)

Normal prior distributions were set on parameters of linear regressions (intercept and slope) and exponential distributions were set on parameters estimating random effects.

The model was fitted with four MCMC with 6,000 iterations each (2,000 warm up, resulting in 16,000 iterations after warmup). The fit of the model was evaluated with convergence of MCMC chains thanks to diagnostic values such as the number of divergent chains post warmup, Rhat statistics, effective sample size and number of divergent chains. The estimated parameters were compared between inversion and negation effects using their 89% credible intervals (CrI) to test for a "significant" difference.

Since the parameter estimates of the effects of inversion and negation were strikingly similar, we explored whether the two effects were functionally linked at the individual level. We ran Pearson correlations between the individual parameters estimates of the inversion and the negation effects for each of the four Gaussian parameters. These results would give us insight on whether inversion and negation disrupt face identification in a similar way.

In Bayesian mixed-effects analysis, “population-level” includes all participants (fixed effects), and “group-level” is used to describe the sub-categories of the multilevel analysis (random effects), here the group-level represents each participant.

The analysis was done using R 4.2.2. We used the *brms* package (Bürkner, 2017, 2018) to fit all Bayesian models. All data and analysis codes can be found at
https://www.openicpsr.org/openicpsr/project/208541/version/V1/view

Results

At a descriptive level, normalized *d'* was higher across all orientations for natural than negated faces, and higher for negated than inverted faces (see Fig 3.3a and Supporting Fig 3.S.1 in Supporting Information S2).

Bayesian GLMM comparison of Stimulus type showed significant differences in recognition performance between Stimulus type conditions: the 89% CrI of GLMM predictions of the mean performance of the three conditions do not overlap (Inverted CrI = [-.958; -.516], Negated CrI = [-.4; .084], Natural CrI = [.657; 1.148]; see Fig 3.3b**)**.

Population-level inversion and negation effects as a function of Orientation filter and their Gaussian model are shown in Figure 3.4a. Inversion and negation effects both showed a Gaussian tuning profile centered on the horizontal range (see Table 3.2 and Fig 3.4). Indeed, while inversion and negation disrupted identity recognition across all orientations, both effects peaked in the horizontal range (mean and CrI Peak Location in degrees; inversion: m = 91.52, CrI = [83.40; 98.56]; negation: m = 85.99, CrI = [78.01; 93.31]). The amplitude of the horizontal peak was comparable across inversion and negation effects (mean and CrI Peak Amplitude in *d'effect*; inversion: m = 1.11, CrI = [.78; 1.41]; negation: m = 1.18, CrI = [.83; 1.49]). The Standard Deviation of the Gaussian tuning functions was also similar across effects (mean and CrI in degrees; inversion: m = 34.06, CrI = [24.66; 43.92]; negation: m = 39.39, CrI = [24.34; 53.77]). The only difference was found at the level of the Base Amplitude of the Gaussian functions relating inversion and negation effects to Orientation filter (mean and CrI in *d'effect*; inversion: m = 1.20 CrI = [.99; 1.42], negation m = .53, CrI = [.25; .80]). The fact that the base amplitude was larger for inversion than negation (and that this was the only difference between the two effects) shows that inversion impaired recognition performance overall more than negation.

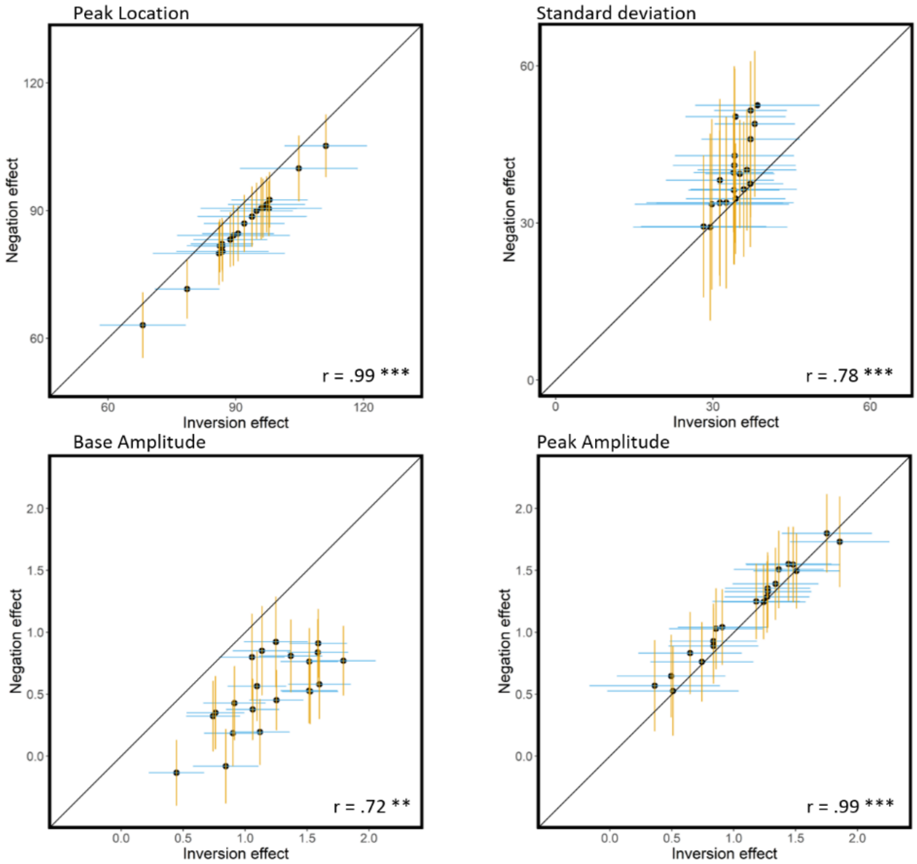
Table 3.2. Summary of population-level parameter estimates of the Gaussian mixed model.

	Inversion Effect				Negation Effect			
Parameter	**Median**	**Mean**	**CrI lower**	**CrI upper**	**Median**	**Mean**	**CrI lower**	**CrI upper**
Peak Location	91.53	91.52	83.40	98.56	85.92	85.99	78.01	93.31
Standard Deviation	33.99	34.06	24.66	43.92	38.54	39.39	24.34	53.77
Base Amplitude	1.20	1.20	.99	1.42	.54	.53	.25	.80
Peak Amplitude	1.10	1.11	.78	1.41	1.18	1.18	.83	1.49

The 89% CrI of the Base Amplitude parameter on inversion and negation effects do not overlap indicating a significant difference between the two conditions.

Comparison of population-level model parameter estimates between inversion and negation effects highlights their similar tuning to face orientation content (Fig 3.5). To examine whether the similarity in the Gaussian parameters reflects a functional relationship between inversion and negation effects at the individual subject level, we ran correlation analyses on the group (i.e., participant)-level Gaussian parameters' posterior predictions. Correlations between inversion and negation effects were very high for all four Gaussian model parameters' (all $r \geq .72$, all $p < .001$). Stronger correlations were found for Peak location ($r = .99$, $p < .0001$, CI = [.99; 1]) and Peak amplitude ($r = .99$, $p < .0001$, CI = [.97; .99]) parameter estimates than for Base amplitude ($r = .72$, $p < .001$, CI = [.42; .88]) and Standard deviation ($r = .78$,

$p <.0001$, CI = [.53; .91]; Fig 3.5) parameter estimates. Supplementary analyses (Supporting Information S3 and S7) indicate that the strong functional dependence of the Gaussian tuning parameters of inversion and negation effects described here is due neither to the use of the upright-positive condition as a common comparison condition (i.e., the correlations were similar when computed while controlling for the variance due to the upright-positive condition; see Supporting Information S3), nor to the use of a smooth Gaussian model to fit the data (i.e., results replicate with a Linear Mixed Model; see Supporting Information S7).



<u>Figure 3.5.</u> Scatter plot of the four group (i.e., participant)-level Gaussian-model parameter estimates of inversion and negation effects with standard deviation for each group-level parameter estimates as error bars; in blue for inversion and in yellow for negation. The four Gaussian parameters group-level estimates are highly correlated between inversion and negation effects, the Pearson correlation coefficients are indicated for each parameter. We find a strong correlation between the Gaussian parameters of the inversion and negation orientation tuning profiles, yet several differences can be observed graphically. While peak location and amplitude are very similar across inversion and negation effects (close to diagonal), the base amplitude individual estimate was largest for the inversion effect in all participants, indicating that the decrease in overall recognition performance was consistently more drastic for inversion than negation.

Most group-level estimates of Standard deviation were located above the diagonal, in favor of the negation effect section, indicating a narrower horizontal tuning for inversion than negation. Pearson correlation coefficients are written for each of the four parameters with *** for $p < .0001$, and ** for $p < .001$. Using partial correlations controlling for the Natural condition we found no evidence that these high correlations were driven by the use of the Natural condition to calculate the effects (see Supporting Information S3).

Discussion

Past evidence showed that the horizontally-oriented cues of the face stimulus enable better identity recognition accuracy than facial cues in other orientation ranges. Yet, the nature of the information contained in the horizontal range remained elusive. Face identity recognition is thought to rely on two main and separable sources of information: shape and surface (Bozana Meinhardt-Injac, Malte Persike, Günter Meinhardt, 2013; Jiang et al., 2009, 2011). The drastic recognition impairments caused by inversion and negation have been attributed to the disrupted processing of shape and surface cues, respectively (Bruce & Langton, 1994; Freire et al., 2000; Liu et al., 2000; Maurer et al., 2002; Vuong et al., 2005). Here, we exploited the relative functional selectivity of these effects to characterize the shape versus surface nature of the cues carried by the horizontal range of the face image. Participants identified face images filtered to preserve a narrow orientation band selectively and presented in natural (i.e., upright and in natural contrast polarity), inverted or negated conditions. We estimated the orientation tuning profile of the impairments caused by inversion and negation on face identification performance. As expected, inversion and negation both drastically impaired face identification performance compared to when faces were shown in natural viewing conditions (i.e., upright and in normal positive contrast). Overall, the impairment caused by inversion was stronger than negation. However, the orientation profile of the two effects was strikingly similar: both effects peaked in the horizontal range with similar strength and sharpness. Both effects decreased as the orientation neared vertical. The similar peak location and peak amplitude (which is the difference of effect between its highest, i.e., in the horizontal range, and its lowest, i.e., in the vertical range) indicate that inversion and negation both mostly disrupted access to the horizontally-oriented content of the face stimulus. As inversion and negation prevent the face-specialized processing of shape and surface cues, respectively, these results indicate that the horizontal preference of human face recognition is due to this range yielding a privileged access both to face shape and surface, i.e., two main sources of face identity information.

In line with past evidence, identity recognition in natural viewing condition was tuned to the horizontal range (Supporting Information S4; Dakin & Watt, 2009; Goffaux et al., 2015; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016), although compared to the reported results, the horizontal tuning we measured here was broader. Goffaux &

Greenwood (2016) found that the bandwidth of the horizontal tuning was influenced by the availability of external facial features such as facial outline cues to perform face recognition. Namely, the horizontal tuning was significantly broader when face outline was available. Our stimulus set contained much larger and more natural outline variations than in this previous study, which could explain the relative broadening of the horizontal tuning. Using familiar faces, as in the present study, Dakin and Watt (2009) also seemed to have found a relatively broadly tuned recognition performance (as they do not report it, this assumption is based on their figure). Finally, to ensure participants performed above chance level in negated and inverted trials, we set the orientation filters to have a broader standard deviation than used in other studies (25° compared to e.g. 15° in Goffaux & Greenwood, 2016). This orientation filter breadth resulted in some overlap in the oriented energy across adjacent orientation ranges. This may to some extent explain the shallower horizontal tuning in the Natural condition and why recognition performance was close to ceiling in the horizontal and adjacent oblique orientations, (See Supporting Information S4).

To investigate their orientation tuning profile, we submitted the effects of inversion and contrast negation on face identification to a Bayesian non-linear Gaussian mixed model. This analysis showed that both effects peaked in the horizontal range and followed a strikingly similar orientation tuning profile. Our finding of the disruption of horizontal tuning of face identification with inversion effect is in line with previous studies comparing the orientation tuning of upright and inverted faces (Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2013). The disruption of the horizontal tuning with negation we measured however constitutes new knowledge regarding the orientation tuning of face identification.

The only difference between the inversion and negation effects was at the level of the base amplitude of the orientation tuning profile. Combined with the fact that the peak amplitude was as large for inversion as it was for negation, we conclude that inversion impaired recognition performance more strongly than negation overall (i.e., across orientations, see Fig 3.4a). Studies about contrast negation showed that the presence of pigmentation cues (e.g., skin texture) in the face stimulus increases the strength of the negation effect (Russell et al., 2006; Vuong et al., 2005). Orientation filtering may have reduced the availability of pigmentation cues, and therefore reduced the impact of negation overall. The weaker effect of negation compared to inversion may also indicate that inversion disrupts face perception at an earlier processing stage than negation (Hole et al., 1999; Itier & Taylor, 2002). Indeed, compared to negation which flips the polarity while preserving the shape and retinotopic location of the contrast variations making up the face stimulus, inversion drastically changes the latter, and may impact visual processing as soon as V1 (see Goffaux et al., 2016 for supportive evidence); such earlier impact may result in an overall stronger impact on behavioral performance of inversion compared to negation.

Through the demonstration of the additivity and functional selectivity of the behavioral and neural effects, past research showed that inversion and negation affect face processing differently (Bruce & Langton, 1994; Hole et al., 1999; Itier & Taylor, 2002; Kemp et al., 1990; Liu-Shuang et al., 2015). This view is suggested by the fact that we have found no evidence for an association between the two effects with full-spectrum faces in our data (see Supporting Information S5). Altogether, our findings indicate that despite inversion and negation showing some functional independence in full-spectrum viewing conditions, they affect access to face-oriented content in a similar way. Previous work has demonstrated that the specialized holistic processing of the face stimulus is affected by inversion and, to a lesser extent, by negation (Farah, 1996; Hole et al., 1999; Jiang et al., 2011; Rossion, 2008, 2009; Sormaz et al., 2013), the horizontal advantage over other orientations may therefore arise from the essential nature of the horizontal shape and surface cues to allow holistic face processing.

Another plausible account to the similar orientation tuning properties observed across inversion and negation effects is that the horizontal range of face information carries a more primitive source of information yielding common entry point to the functionally separate shape and surface cue processing. The horizontal structure of a human face has indeed been proposed to convey the natural statistical properties of the face stimulus. These natural statistics are described as an alternance of light and dark horizontal bands along the vertical axis of the face image, from forehead to chin (see Figure 1 of Liu-Shuang et al., 2022, the appearance of which is drastically distorted by inversion and negation (Dakin & Watt, 2009; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016). As a matter of fact, the horizontal range of face information was shown to drive the human behavioral and neural responses to faces at more generic levels of categorization than the fine-grained level of identity recognition tested here. A preference for the horizontal was indeed found in infants and children in face categorization (Balas et al., 2015; de Heering et al., 2016). Emotion categorization has also been shown to rely on the horizontal range of face information (Balas et al., 2015; Duncan et al., 2017; Huynh & Balas, 2014; Yu et al., 2018). At the neural level, Jacques et al. (2014) showed that the face horizontal tuning appears as early as the activation of face specialized-processing (in the N170 time window), in other words as early as face detection. Furthermore, Goffaux et al. (2016) showed a preferential activation of face-preferring brain areas such as the Fusiform Face Area and the Occipital Face area to upright faces containing horizonal information. In both cases the neural preference for the horizontal was disrupted with inversion.

A recent unpublished study of our lab suggests that the horizontal range not only conveys the statistical regularities of the human face category, but that it also carries stable identity cues that are optimal for viewpoint-tolerant recognition of identity (see also (Goffaux & Dakin, 2010). Supporting the crucial contribution of horizontal information to fine-grained identity recognition, horizontal tuning is positively correlated to the face identification performance (Duncan et al., 2019; Little & Susilo, 2023; Pachai et al., 2013) and the horizontal tuning is stronger for the recognition of familiar than unfamiliar faces (Pachai et al., 2017). Past and present evidence therefore indicates that the horizontal advantage may actively operate at various processing stages leading from early detection to fine-grained identification. Future studies need to investigate the orientation profile of human face processing at different processing stages to uncover the potential shifts in the orientation dependence of the neural representation of faces over the course of their processing by the human brain (see Jacobs et al., 2020 for such an approach).

To conclude, we have shown that the disruption of human face identity recognition by inversion and negation follows the orientation preference of face identity recognition: it is horizontally tuned. Although inversion and negation presumably disrupt distinct sources of face information, their orientation tuning profiles are highly similar and correlated. These results suggest that the horizontal tuning of face identification is due to this range conveying the two main sources of information driving the specialized processing of face identity: shape and surface.

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Supporting information

S1. Image selection pre-test

For the image selection pilot, 237 subjects, mean age = 25.3 ± 4.3 were recruited via social media and gave their informed written consent to do the task (no compensation was given but participants could enroll in a lottery to win 10 euros every 10 participants). We had 10 pictures for each of the 21 male actors we selected (210 images in total). Participants viewed a total of 70 randomly selected images (between three and four per actor). Each image was presented on a grey background for 500ms. Participants then had to click on the name of the actor among five names or click on 'I don't know'. After analysis, three actors were taken out of the set as more than half of the answers for their pictures were 'I don't know'. For the remaining 18 actors, the four best recognized images were selected. Three to be used during the trials of the experiment. The last image was kept to remind the different identities to the participants during the breaks, without exposing them to the experimental stimuli. To ensure the image was the most representative of all 4 images we calculated the correlation between each of the 4 images and a mean image of the actor made from all of his pictures on Matlab R2014a, and took the one with the highest score. The 18 selected actors are Ben Affleck, Ben Stiller, Brad Pitt, Daniel Craig, Daniel Radcliffe, Elijah Wood, George Clooney, Hugh Jackman, Justin Timberlake, Keanu Reeves, Leonardo DiCaprio, Matt Damon, Orlando Bloom, Patrick Dempsey, Robert Downey Jr., Robert Pattinson, Ryan Gosling, Ryan Reynolds

S2. Individual orientation tuning for each Stimulus type

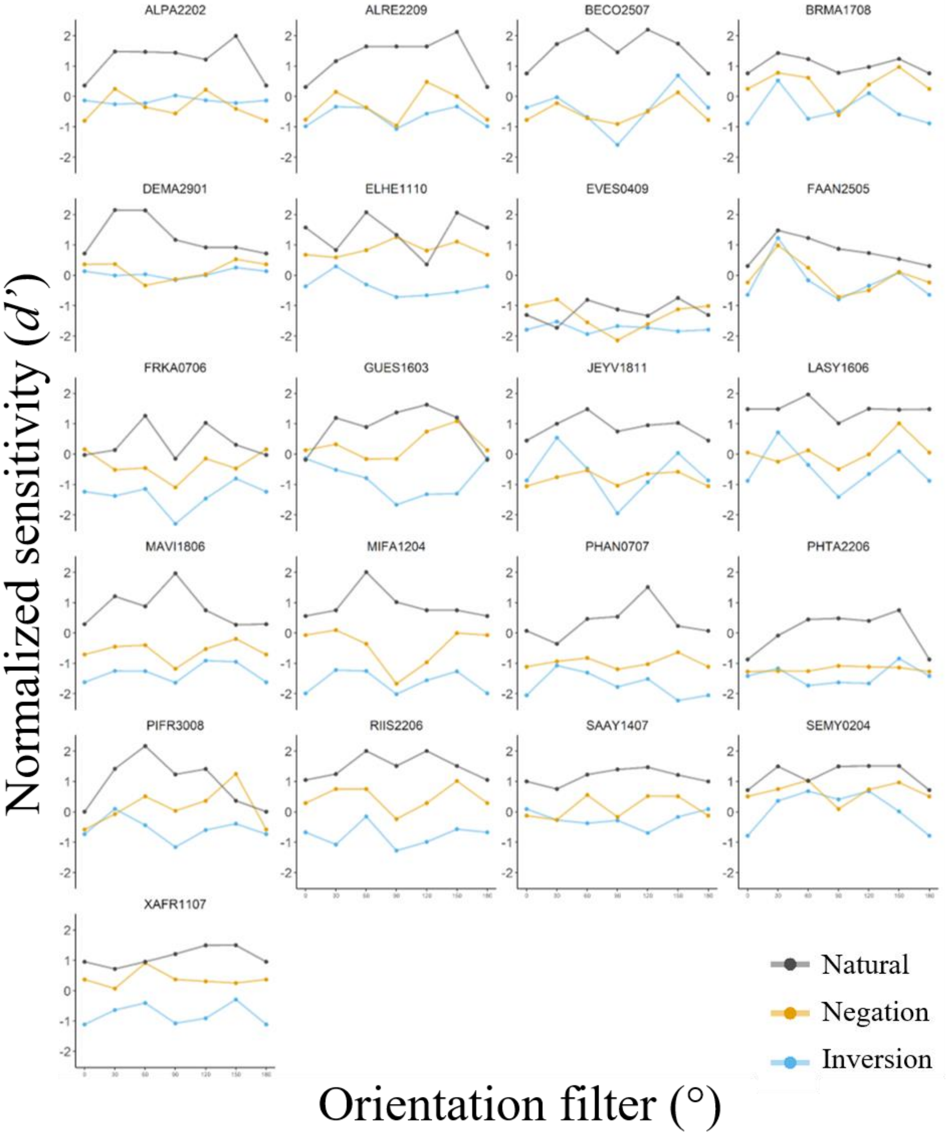


Figure 3.S1. Recognition performance (*normd'*) as a function of the Orientation filter for each Stimulus type (grey: Natural faces; yellow: Negated faces; blue: Inverted faces) and each participant.

S3. Partialling out the contribution of the performance in the Natural face condition to correlations between inversion and negation effects

The correlations between the Gaussian parameter estimates of the inversion and the negation effects were high and significant. Because we obtained the effects by subtracting the sensitivity under Inverted or Negated conditions from the sensitivity for Natural images, at each orientation filter, the Natural condition is common to both effect and could explain the correlation between inversion and negation (DeGutis et al., 2013). To determine whether it is the case or not, we ran partial Pearson correlations between the inversion and negation effects parameter estimates while using the parameter estimates of the model of the Natural condition (Supplementary 4) as controlling variables. If the shared variance of the orientation tuning profile of the inversion and negation effects reflect the use of sensitivity in the Natural condition as a common reference, the coefficient of the partial correlations should drop compared to the correlations reported in the main text.

Results of these partial Pearson correlations showed similar correlations (in terms of value, significance and confidence interval, see Table 3.S.1) between the effects of inversion and negation when controlling for the Natural condition or not. This was the case for the Standard deviation estimate ($r = .79$, $p < .0001$), the Peak amplitude estimate ($r = .99$, $p < .0001$), the Peak location estimate ($r = .99$, $p < .0001$) and the Base amplitude estimate ($r = .6$, $p < .01$). These results show that the use of the Natural condition to compute the effects of inversion and negation does not explain the high correlations we measured between the effects of inversion and negation on those parameters.

Table 3.S1. Pearson correlations values, p-values and 95% confidence interval between the parameter estimates of the inversion and negation effect as reported in the manuscript (left) and partial correlation using the parameter estimates of the Natural condition.

Parameter Estimate	Cor	Pvalue	CI Low	CI High	Par. Cor.	Pvalue	CI Low	CI High
Base Amplitude	.7192	p < .001	[.4170	.8782]	.5996	p = .005	[.2265	.8192]
Peak Amplitude	.9863	p < .001	[.9657	.9945]	.9783	p < .001	[.9462	.9913]
Standard Deviation	.7815	p < .001	[.5279	.9072]	.7891	p < .001	[.5320	.9106]
Peak Location	.9967	p < .001	[.9917	.9987]	.9871	p < .001	[.9677	.9948]

S.4 - Orientation tuning profile for the recognition of faces in the Natural condition

To compare the orientation tuning of face recognition obtained in the Natural condition to the results obtained in previous studies, we modelled normalized sensitivity (*normd'*) obtained in this experimental condition with a Gaussian model. We used the exact same formula and settings as the one used to model the inversion and negation effects (see Methods – Data Analysis). Namely, we ran the model with default *brms* priors with four Markov chain Monte Carlo (MCMC) with 6,000 iterations each (3,000 warm up, resulting in 12,000 iterations after warmup), and evaluated the fit with diagnostic values such as the number of divergent chains post warmup, the Rhat statistics and the effective sample size the convergence of the chains. Model and data are shown in Figure 3.S.2, the parameters estimated by the model are reported in Table 3.S2.

In brief, recognition performance peaked in the horizontal range (Peak location estimated at 88.8°) in line with previous studies (e.g., Goffaux & Greenwood, 2016). However, the tuning was shallower than in previous work, with a mean standard deviation estimate at 70.1°. We noticed that the highest performance was obtained in the close-to-horizontal oblique orientation filters (60° and 120°) with an advantage in the left oblique range relative to the right oblique. Previous studies, like Dakin and Watt (2009) or Goffaux and Greenwood (2016), also found a slight asymmetry of the orientation tuning in favor of one of the left oblique filtering condition . When looking at our individual data (Supplementary 2), some participants show similar asymmetry in favor of one or the other oblique condition. This asymmetry may result from an adaptation to natural face statistics. Indeed, despite the human face anatomical symmetry, its appearance in everyday life is not. Non-frontal pose, illumination direction typically from above, and tilts relative to the observer may tune the face-selective visual system to one oblique orientation more than to the other, symmetrical one. The fact that we used ‘ambient’ images of celebrities, i.e., images of faces shot under a variety of poses and illumination directions, may have amplified this asymmetry in the recognition performance.

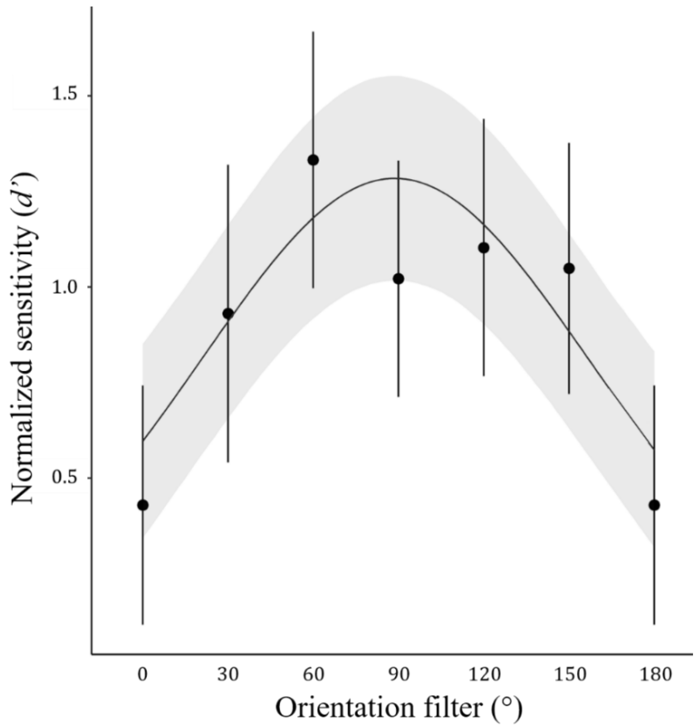


Figure 3.S2. Population-level averaged recognition performance in the Natural face condition and Bayesian Gaussian mixed model predictions. The dots are the population-level averaged normalized sensitivity with the 95% confidence interval in error bars. The mean of the model posterior predictions is drawn in black (line) and the 89% credible intervals of the predictions are represented as faded ribbons.

Table 3.S2. Credible interval (CrI), median and mean estimates of the four parameters of the Bayesian Gaussian model of the recognition performance in the Natural face condition.

Parameter	CrI_low	CrI_high	Median	Mean
Peak Location	81.32	96.18	88.82	88.76
Standard Deviation	52.68	87.9	69.78	70.09
Base Amplitude	-0.45	0.51	0.04	0.02
Peak Amplitude	0.8	1.71	1.24	1.27

S.5 - Comparison of the inversion and negation effects for full spectrum faces and orientation-filtered faces

Inversion and negation presumably disrupt distinct aspects of face processing, yet we found that their orientation tuning profiles were highly correlated. We investigated whether the high similarity in orientation tuning is due to these effects being highly correlated in full spectrum conditions, which would question their supposed relative functional independence (as reported in previous studies, e.g., (V. Bruce & Langton, 1994a; Hole et al., 1999; Itier & Taylor, 2004; Kemp et al., 1990; Liu-Shuang et al., 2015b)).

To this aim, we first analyzed the correlation between inversion and negation effects for full spectrum images. The correlation of the full spectrum inversion and negation *d' effects* was moderate and non-significant using a frequentist correlation method ($r = .43$, $p = 0.051$, CI = [-.001, .727]), as well as when using a Bayesian correlation analysis ($r = .33$; CI = [-.03, .63]; and BF = 2.11). As a comparison, we computed the same correlation between the inversion and negation *d' effects* averaged across orientations ($r=.61$, $p<.001$, CI = [.495, .701]). However, these results need to be interpreted cautiously as the lack of significance might be due to a lack of statistical power; indeed, compared to other correlation analyses reported in this work, the number of trials on which the present analysis relies is quite small (6 times lower in the full spectrum condition than in all filtered conditions combined).

Yet, these results suggest that while their shared orientation tuning profile inversion and negation effects seem decorrelated in full spectrum viewing conditions.

Furthermore, as we measured a stronger inversion effect compared to the negation effect for filtered images, we wanted to measure whether this difference was found for full spectrum images as well. To this aim, we first compared the recognition performance for full spectrum in inverted *vs* negated faces, using a Bayesian general linear mixed model (GLMM), using the participants as a random effect to consider the inter-subject variability in the estimations, with this equation:

sensitivity (*d'*) ~ Stimulus type + (Stimulus type | Subject)

We ran the model with default *brms* priors with 4 Markov chain Monte Carlo (MCMC) with 6,000 iterations each (2,000 warm up, resulting in 16,000 iterations after warmup), and evaluated the fit with diagnostic values such as the number of divergent chains post warmup, the Rhat statistics and the effective sample size the convergence of the chains.

We found no difference in recognition performance between inverted and negated full spectrum faces: Inversion (mean = .72 , CrI = [.37, 1.06]) , Negation (mean = .58 , CrI = [.22, .93]) (see Fig. 3.S.3). In other words, we did not replicate the difference in effect magnitude between inversion and negation that we found with orientation-filtered images.

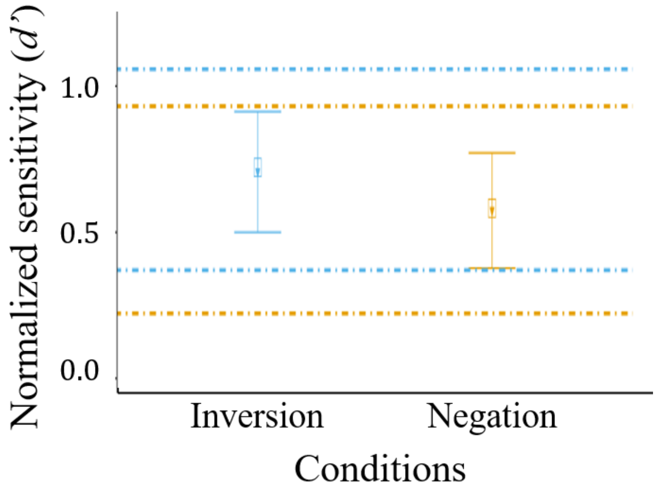
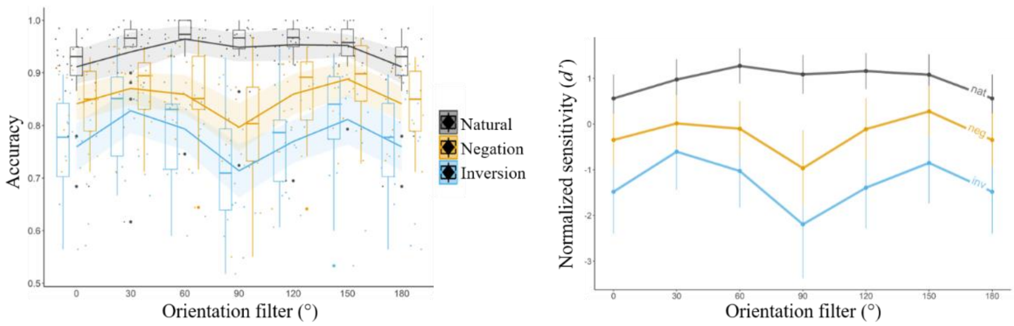


Figure 3.S3. Predictions from the GLMM of the recognition performance for full spectrum inverted and negated faces. The overlapping 89% CrI of model predictions and the similar values indicate that both Stimulus types gave similar recognition performance when the images were full spectrum. The triangles and error bars represent the mean and standard error of the performance in each condition from real data. The square is the mean in each condition given by the model prediction, and the doted lines are the 89% CrI.

S.6 – Accuracy analysis

Although sensitivity (*d'*) analysis is the most adapted to our data, we have repeated our analysis on accuracy (proportion correct) to have a better appreciation of the data. Data was processed as described in the manuscript in the Material and Methods>Data Analysis section. Mean accuracy in the Natural condition was close to ceiling (.94 ± 0.02; Figure 3.S.4). The mean accuracy for the Inverted and Negated conditions was well above chance level (Inverted = .78 ± 0.03; Negated = .85 ± 0.03), which was also the case for every filter condition (see Figure 3.S.4 and Table 3.S3 below).



<u>Figure 3.S4.</u> Left: Averaged accuracy (proportion correct) data for each Orientation filter in each Stimulus type condition. The lines link mean accuracy values across orientation filters, boxplots represent the 25%, 50% (median) and 75% quantiles. Each point is one participant's recognition performance for an Orientation filter and Stimulus type. **Right**: Group-level normalized accuracy for each Orientation filter in each Stimulus type condition (mean and 95% CI).

<u>Table 3.S3.</u> Accuracy (proportion correct) in each experimental condition averaged across participants.

Cond	All	Filt. only	FS	0°	30°	60°	90°	120°	150°
natural	.94	.94	.97	.91	.94	.96	.95	.95	.95
negated	.86	.85	.94	.84	.87	.86	.80	.86	.89
inverted	.80	.78	.94	.76	.83	.79	.71	.77	.81

There were significant differences in recognition performance between Stimulus type conditions. On average, (normalized) accuracy was better for natural than inverted and negated faces, and for negated than inverted faces (see average accuracy and normalized accuracy data in the Figure 3.S.4; Natural CrI = [.64; 1.35]; Inverted CrI = [-1.8; -.57]; Negated CrI = [-.64; .35]). Inversion and negation effects on accuracy were bell-shaped as found with sensitivity d', peaking around 90° (horizontal filter), and could be modelled with the same Gaussian model than the *d'* data. Parameter estimates of this model are reported in Table 3.S4.

<u>Table 3.S4</u>. Summary of the population-level parameter estimates of the Gaussian mixed model run on normalized accuracy data (dependent variable is normACC effect; i.e. difference in normalized accuracy between the natural and inverted conditions and between the natural and negated conditions). The 89% credible interval (CrI) of the Base Amplitude parameter on inversion and negation effects do not overlap indicating a significant difference between the two conditions.

	Inversion Effect				**Negation Effect**			
Parameter	**Med.**	**Mean**	**CrI lower**	**CrI upper**	**Med.**	**Mean**	**CrI lower**	**CrI upper**
Peak Location	93.74	93.7	89.60	97.8	89.86	89.88	84.02	95.74
Standard Deviation	28.3	28.4	22.05	34.11	27.41	27.56	18.98	35.91
Base Amplitude	1.71	1.71	1.38	2.02	.81	.81	.53	1.1
Peak Amplitude	1.24	1.24	.81	1.66	1.09	1.1	.74	1.45

The correlation analyses on the group (i.e. participant)-level Gaussian parameters' posterior predictions indicated that the inversion and negation effects were functionally related at the individual participant level, although the correlations were more moderate than those obtained with *d'* (Peak location r = .85, p <.0001; Peak amplitude r = .80, p <.0001; Standard deviation r = .98, p <.0001; Base amplitude r = .57, p <.01; see also scatterplots in the Figure 3.S5).

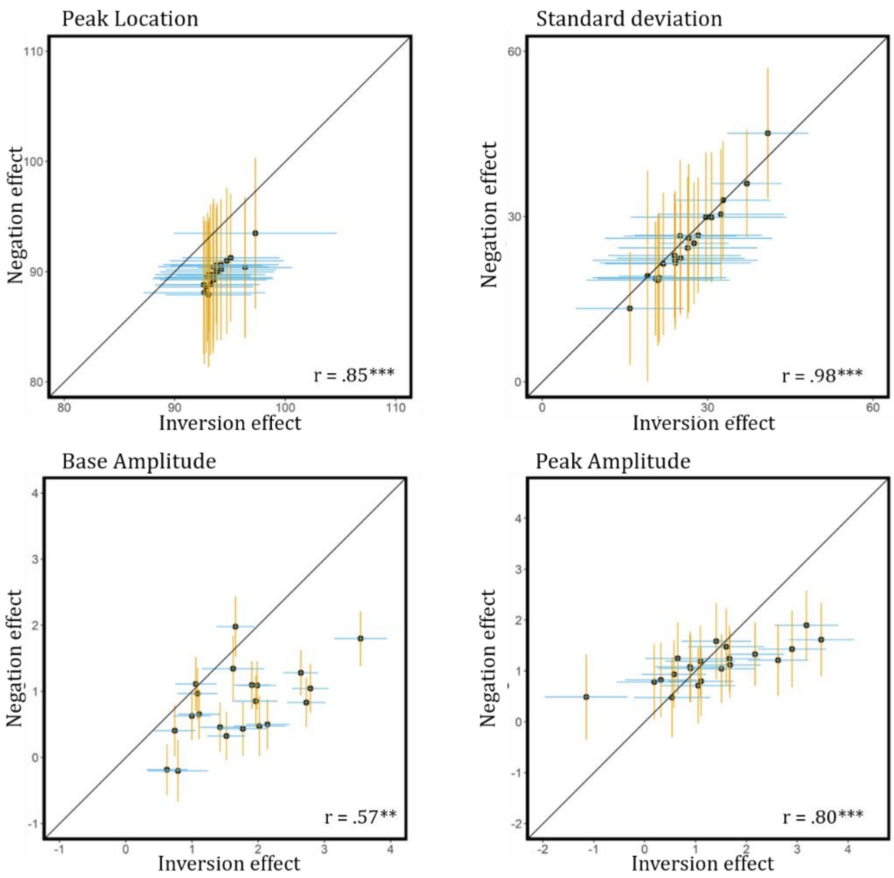


Figure 3.S5. Correlation between the group (i.e. participant)-level Gaussian parameters' posterior predictions – from the Bayesian gaussian mixed-model run on normalized accuracy data. The error bars are the standard deviation for each group-level parameter estimate; in blue for inversion and in yellow for negation.

S.7 – Linear Mixed Modelling of Normalized sensitivity

Here we consider the possibility that the Gaussian fitting used in our main analyses may have acted as a lowpass filter of the inversion and negation effect orientation tuning profiles. Fitting the data with a Gaussian as we did may have attenuated finer differences across orientations, therefore inflating the similarity of the orientation profiles of the inversion and negation effects. We believe this unlikely accounts for the similar orientation tuning profile found for the inversion and negation effects. Indeed, the diagnostic values showed that our model made a good prediction of the data: no post warmup divergent chain, all Rhat < 1.01, all Effective sample size > 450 (see also posterior predictive check graph in Figure 3.S6). Moreover, when fitting a simple linear mixed model to the data (without the Gaussian fit) to test the interaction between Stimulus type and Orientation filter, we find significant main effects of Stimulus type ($F(1,260) = 73.67$, $p < .001$) and Orientation filter ($F(6,260) = 16.18$, $p < .001$) but no interaction effect between the two factors ($F(6,260) = 0.57$, $p = .75$). These results agree with our finding from our Gaussian model that both inversion and negation effects are similarly disruptive across orientations.

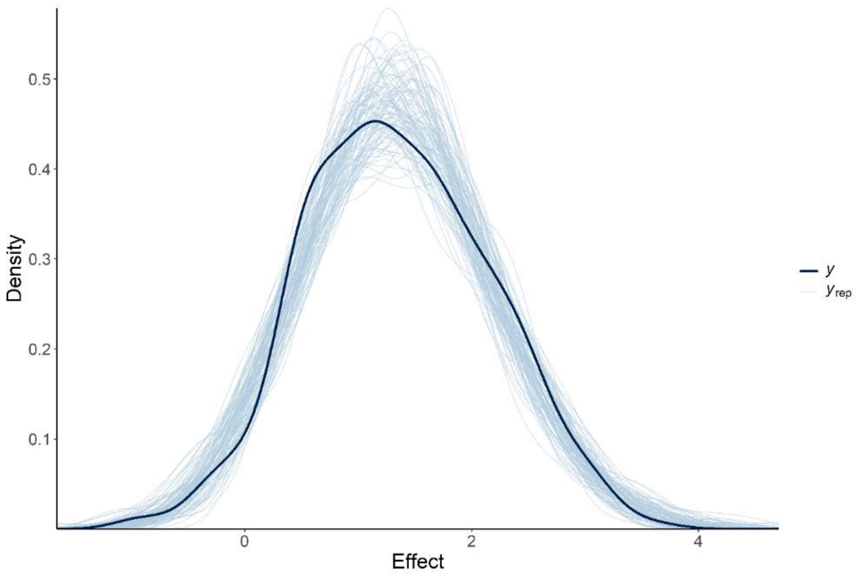


Figure 3.S.6. Posterior predictive check. The model predictions (thin light blue lines, N=100) follow the same distribution than our data (thick dark blue line), demonstrating our model has satisfactory predictive capabilities.

Chapter 4: the view tolerance of human identity recognition depends on horizontal face information.

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Abstract

How we recognise objects and people despite their physical appearance can change dramatically across encounters is a central yet unresolved question in vision science. In particular, the visual information that supports the human ability to recognize face identity across views is unknown. Past research suggests horizontally oriented face information plays a key role. We tested this hypothesis by characterizing the orientation of the visual information physically available in the face stimulus to support view-tolerant face recognition and how human observers make use of it.

Human observers performed an old/new identity recognition task with face stimuli presented under different viewpoints, achieved by rotating the faces in yaw (from full-frontal to profile) and filtered to preserve contrast in selective orientation ranges. Human performance remained tuned to the horizontal range of face information irrespective of yaw.

We used a model observer approach to define the information physically available in the stimulus for matching face identity within each viewpoint (view-selective model observer) or across different viewpoints (view-tolerant model observer). The view-selective model indicated that face identity is carried by orientation ranges shifting from horizontal in frontal views to vertical in profile views. In contrast, the view-tolerant model showed that the horizontal range provides the most stable identity cues across views. The horizontally-tuned orientation profile of human recognition performance was predicted by the high diagnosticity of horizontal information in frontal views and the stability of the horizontal identity cues across views.

Our findings indicate that the invariant representation of a face, gradually learned through repeated exposure to its natural appearance

statistics, relies primarily on horizontal facial information. By identifying the spatial information supporting view-tolerant face recognition in humans, the present work yields concrete, data-driven constraints for the refinement of visual recognition models.

Introduction

The way in which we recognize objects and people is a central but as yet unresolved question in vision sciences. Our understanding of visual perception is still limited by our ability to account for how we recognize objects and people despite the sometimes radically different images they project onto the retinae, due to varying lighting, distance, depth rotation, etc (DiCarlo & Cox, 2007). We experience faces under a broad range of depth rotations mainly along the x axis, i.e., from left to right profile (i.e., yaw; Favelle & Palmisano, 2012) due to biomechanical constrains favoring x-axis head rotations and the vantage point on our conspecifics' faces also varying more along the x than the y axis (i.e., when moving around people). While rotating in depth, a given face projects retinal images that are more dissimilar than the ones that different faces under the same viewpoint would project (Adini et al., 1997; Burton et al., 2016; Hill et al., 1997). Yet humans generally have no difficulty in recognizing a familiar face across views, which implies the joint ability to differentiate its identity from others and to generalize it from one view to another, i.e., with tolerance to variations (Ritchie & Burton, 2017).

The tolerance of face identity recognition culminates when faces are familiar to the observer (e.g., Favelle & Palmisano, 2018; Hancock et al., 2000; Hill et al., 1997; Jeffery et al., 2006; Johnston & Edmonds, 2009; Jones et al., 2017; Liu, 2002; Newell et al., 1999; O'Toole et al., 1998, 1999; Troje & Bülthoff, 1996), suggesting that a core determinant of tolerant recognition is the repeated exposure to the natural statistics of a person's face (e.g., to the variability of a person appearance across different views; Tian & Grill-Spector, 2015a; Troje & Bülthoff, 1996; Van Meel & Op de Beeck, 2018; Wallis & Bülthoff, 2001). Such statistical learning is assumed to be the main unsupervised learning route for tolerant face/object recognition in humans and animals (DiCarlo & Cox, 2007b; Fiser & Aslin, 2002; Hauser et al., 2001; Huber et al., 2023; Li & DiCarlo, 2008, 2010, 2012; Tian & Grill-Spector, 2015b). Since exposure to the natural variations of a given person is typically prolonged (several seconds), it has been proposed that temporal contiguity contributes to the generation of a multi-view representation of identity. The importance of temporal contiguity in identity recognition is supported by findings that human observers tend to confound identities if learnt in the same temporal sequence of views (Li & DiCarlo, 2010; Miyashita, 1993; Pitts & McCulloch, 1947; Van Meel & Op De Beeck, 2018; Wallis et al., 2009; Wallis & Bülthoff, 1999). Other findings suggest that temporal contiguity is not necessary and that the important contributing factor is the number of learnt views, be them seen randomly or in sequence (T. Liu, 2007; Tian & Grill-Spector, 2015b). Yet, since the different views of a given person are usually seen in temporal contiguity in natural viewing, it seems likely that temporal contiguity contributes to statistical learning of face identity.

While some attention has been devoted to the contribution of temporal contiguity in view-tolerant recognition, the *spatial* aspects of the natural statistics supporting view-tolerant face identity recognition are still largely elusive. Face appearance results from the complex interaction between extrinsic viewing conditions and the intrinsic 3D shape and reflectance properties of the face (determined e.g., by viewpoint and lighting; Favelle et al., 2017; Hill & Bruce, 1996; Liu et al., 2000). A study by Hill et al. (1997) suggested that shape is the primary determinant of view-tolerant recognition, and that surface cues such as reflectance and texture contribute less. Burton and colleagues (Burton et al., 2005; Burton, 2013) suggested that as exposure to multiple appearances of a person increases, the accidental, irrelevant variations would be progressively whitened (i.e., averaged out) and reveal the stable cues to identity. Figure 4.1 simulates such averaging using the pictures of a given identity taken from drastically variable poses, as experienced in natural viewing. It can be seen that additionally to the whitening of accidental properties, the resulting average contains a strong horizontal structure; namely it results in the emergence of the so-called (horizontal) bar code of the face (Dakin & Watt, 2009). We, as others, proposed that the horizontal content of the face stimulus may drive the visual mechanisms engaged for the view-tolerant recognition of face identity (Caldara & Seghier, 2009; Dakin & Watt, 2009; Gilad-Gutnick et al., 2018; Goffaux, 2008; Goffaux & Dakin, 2010). Several lines of empirical evidence indicate that the horizontally-oriented face information conveys optimal cues to identity. First, the visual mechanisms specialized for the identity recognition of faces' frontal view were found to rely preferentially on the horizontal structure of the face image, indicating a better sensitivity to identity in the horizontal range of face information (e.g., Balas et al., 2015; Dumont et al., 2024; Goffaux, 2019; Goffaux & Dakin, 2010; Pachai et al., 2013, 2018). The horizontal dependence of face identity recognition has also been shown to predict face identification accuracy at the individual observer level (Duncan et al., 2019; M. V. Pachai et al., 2013). Furthermore, there is indirect evidence that horizontal face information may optimally drive the tolerance of face identity recognition. For example, while the horizontal dependence manifests from three months of age (De Heering et al., 2016), it strengthens over the lifespan as individuals accumulate experience with the natural statistics of face appearance (Goffaux et al., 2015). Moreover, and considering that the recognition of familiar faces differs from unfamiliar face recognition by its stronger tolerance to retinal variations due to e.g., a change in view (Bruce et al., 1999; Burton et al., 1999, 2010; Hill & Bruce, 1996; Megreya & Burton, 2006; O'Toole et al., 1998; Ramon, 2015b), the finding by Pachai and colleagues that the recognition of a face from ¾ to full-frontal view increasingly relies on horizontal information as a function of familiarity supports the notion that not only the accuracy but also the tolerance of identity recognition most crucially depends on horizontal face cues (Pachai et al., 2017; see also Ramon, 2015a). In one of the Goffaux and Dakin (2010)'s experiments, the matching of unfamiliar faces from frontal to ¾ view was more largely disrupted by horizontal than vertical noise masking. Yet, whether this effect reflects view-tolerant recognition or whether it is primarily due to the encoding of the frontal view probe is unclear. The important question of whether the horizontal range of face information is a privileged informational avenue for view-tolerant identity recognition is therefore still unanswered.

The present study aims at directly investigating the hypothesis that the tolerance of human face identity recognition is supported by the horizontal range of face information. We familiarized a sample of human observers with the multiple views of a set of face identities. In an old-new recognition task involving face stimuli presented in various views, we demonstrated that humans stay broadly tuned to the horizontal range of face information irrespective of yaw, with a stronger tuning observed for frontal views. We used a model observer approach to define the information physically available in the stimulus for the matching of face identity within a given viewpoint and across different viewpoints. A model observer is a basic image processing algorithm that cross-correlates a target image with probe images at the pixel level, and selects the probe with the highest correlation, i.e., the most likely match. Combined with orientation filtering, this method provides a formal way to describe how the information most useful for matching identity is distributed in the orientation domain of the face image (e.g., Collin et al., 2014 for a similar approach in the spatial frequency domain).

We tested two model observers on the same multiple views of face identities as used in the human old-new recognition task: a *view-selective* model observer, which matched identities within the same view (e.g., matching a profile view of identity A with profile views of all identities), and a *view-tolerant* model observer, which matched identities across different views (e.g., matching a profile view of identity A with the other views of all identities). This approach revealed a substantial difference in the orientation distribution of view-specific and view-tolerant information. The view-selective model indicated that, at the image level, face identity is conveyed by a broad view-dependent spectrum of orientations: identity cues were distributed

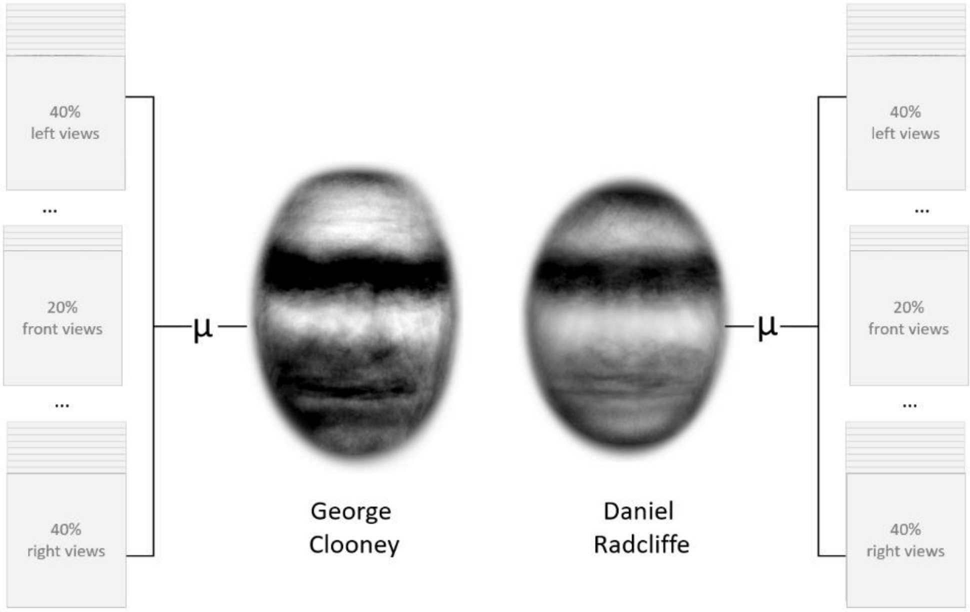


Figure 4.1. Graphic illustration of the horizontal smearing occurring when averaging multiple views of a face. The tolerance of human face identity recognition to drastic appearance variations caused by varying lighting, viewpoint, facial expression, etc. has been proposed to emerge thanks to an averaging mechanism that would progressively whiten these accidental variations and preserve the stable identity cues to identity. Past illustrations (Burton, 2013) used varying lighting and expressions but moderate pose variations. Here we show that when pose varies from left to right profile, averaging results in horizontally smeared face cues suggesting that across encounters with a face, cues at most orientations except horizontal are whitened. As the observer learns the natural statistics of a person's face, it seems plausible that they increasingly rely on horizontal cues for identity recognition (see Pachai et al., 2017 for supporting evidence). Images of two celebrities (George Clooney and Daniel Radcliffe) were sampled from the internet and sorted into three view categories: frontal, left-, and right-averted. In order to illustrate the horizontal smearing due to view variations, the averages were made of 40% left-averted, 40% right-averted, and 20% frontal views. The luminance and RMS contrast of the averaged faces were set to a luminance of .5 and contrast of .4. Using this procedure, one can appreciate the emergence of the so-called bar code, namely the vertical arrangement of horizontally-oriented cues typical of the face at basic and individual levels of categorization (Dakin & Watt, 2009).

in the horizontal range at frontal views (in line with Pachai et al., 2013) but shifted to the vertical range as the face turned to profile. In contrast, the view-tolerant model indicated that the horizontal structure of the face stimulus provides the most useful cues for matching identity across yaws. Partial correlations between model and human observer performance suggest that the horizontal tuning of human face identity recognition is due to the high diagnosticity of horizontal information at frontal view and the stability of the horizontal identity cues across views.

Methods

Subjects

Twenty-two healthy young adults took part in this experiment in exchange for monetary compensation (8 euros per hour of testing). They were 14 females and 8 males, aged 23.5 (± 3.4) on average (4 were left-handed), recruited via Facebook advertisement. They received a written description of the experiment protocol and gave their written informed consent. Participants had normal vision as verified by a Landolt C acuity test (conducted using FRACT; Bach, 1996). Participants wore optical corrections when necessary. The experimental protocol was approved by the local ethical committee (Psychological Sciences Research Institute, UCLouvain).

Stimuli

We selected 30 face identities (15 male, 15 female) from the 3D laser-scanned face database of the Max-Planck Institute for Biological Cybernetics (Tuebingen, Germany; Troje & Bülthoff, 1996). Faces were viewed under seven different viewpoints ranging from -75° to +75° in steps of 25° (see Figure 4.2). We first converted all images into grayscales and resized them so that all faces subtended a height of 210 pixels. All images were padded into 400x400 pixels gray canvas and alpha-blended with a view-specific aperture designed to cover the hair and neck of the average of all face images at a given viewpoint (using Adobe Photoshop).

Next, images were normalized to obtain a mean luminance of 0 and root-mean square (RMS) contrast of 1 and submitted to a fast two-dimensional Fourier transform to manipulate orientation content. Since manipulations in the Fourier domain apply to the whole image, they encompass both the face and background pixels. When the image of a face on a plain background is filtered in the Fourier orientation domain, energy belonging to the face therefore smears to the background and vice-versa, resulting in an oriented halo. To minimize this smearing, we applied an iterative phase-scrambling procedure (as in Canoluk et al., 2023; Petras et al., 2019; Roux-Sibilon et al., 2023; Schuurmans et al., 2023), which consists in iteratively phase-scrambling the image, pasting the original face pixels, and phase-scrambling again (50 iterations). By making the power spectra of the face and background pixels more comparable, this procedure minimizes smearing during orientation filtering. The amplitude spectra of the resulting images were then multiplied with wrapped Gaussian filters (standard deviation of 20°) centered on orientations ranging from 0° (vertical) to 157.5° in steps of 22.5°. After inverse-Fourier transform, the filtered images were combined with the view-specific aperture.

In all images, the luminance and RMS contrast of the face pixels were fixed to 0.55 and 0.15, respectively, and background pixels were uniformly set to 0.55. The percentage of clipped pixel values (below 0 or above 1) per image did not exceed 3%. We used custom-written scripts in Matlab 2014a (Mathworks Inc, Natick, MA) for stimulus preparation.

Stimuli were displayed against a grey background (0.55 luminance across RGB channels) at a viewing distance of 57 cm on a Viewpixx monitor (VPixx Technologies Inc., Saint-Bruno, Canada) with a resolution of 1920 x 1080 pixels and a 70Hz refresh rate using PsychToolbox (Brainard, 1997). With this display, face area subtended 5° (width) by 8° (height) of visual angle (approximately corresponding to conversational distance). At the start of the experiment lighting was switched off and the testing area of the lab was closed off separately with light-draining black curtains.

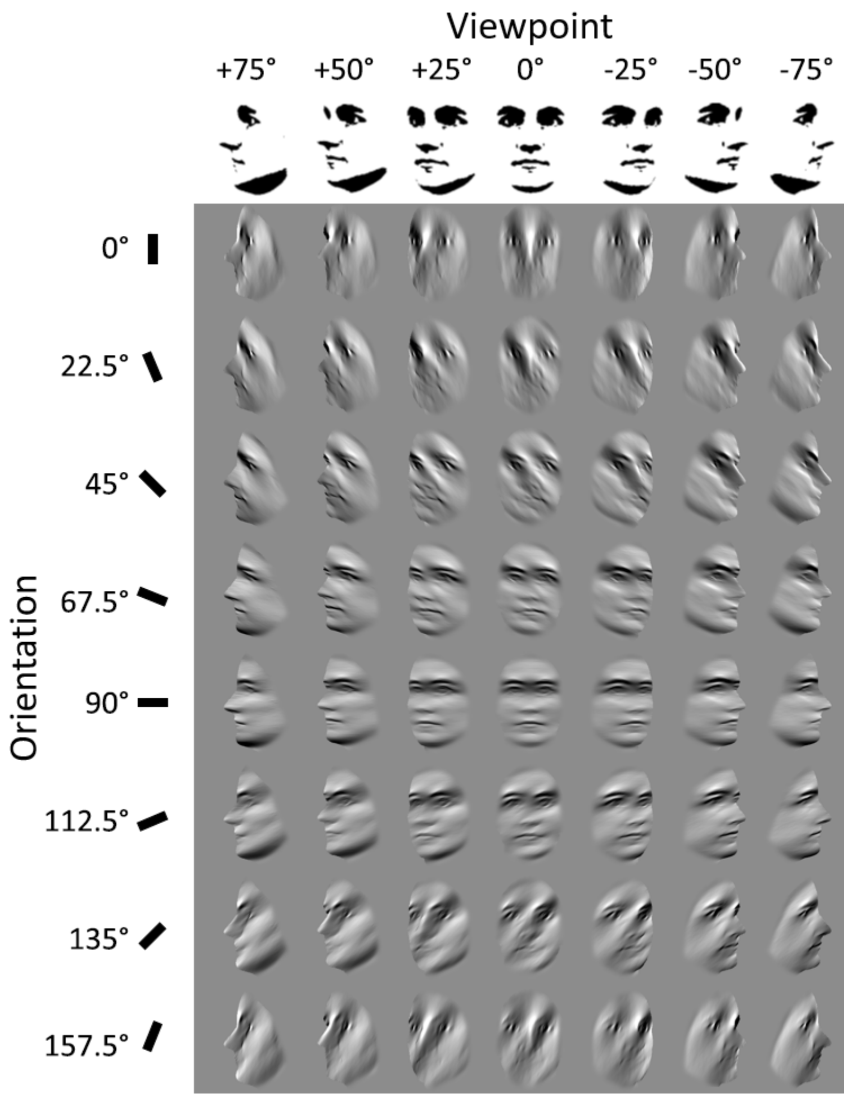


Figure 4.2. Stimulus conditions. Columns. Each identity was viewed from seven different viewpoints ranging from +75° to -75° in steps of 25°. Rows. All images were filtered in the Fourier domain to preserve only a selective range of orientation, from 0° (vertical) to 157.5° in steps of 22.5°.

Procedure

Face identification performance was measured with an old/new recognition task. Faces were presented one by one at screen center and participants were instructed to determine for each of them whether it was a face with which they had been a priori familiarized (‘old’ face) or not (‘new’ face). They answered using a button box by pressing ‘1’ for ‘old’ and ‘2’ for ‘new’. Out of the 30 face identities used in the main experiment, participants were familiarized with 5 female and 5 male faces. The familiar identities were randomly sampled from the stimulus set on the first visit of the participant and were kept identical throughout the experiment.

In the initial session, we familiarized each participant with their selection of to-be-learnt ‘old’ faces, presented in their full spectrum version. To engage participants in the face learning procedure, they were asked to remember a face–name pairing, although during the main experiment they were only asked to judge whether the face was seen during familiarization (‘old’) or new (i.e., incidental learning method as in Liu and Chaudhuri, 2002). Each identity was first shown centrally rotating from left profile (+75°) to right profile (-75°) pseudo-dynamically along with its assigned first name on top of the screen (400ms per frame). The various views of the given face (from +75° to -75° in steps of 25°, i.e. seven views) were then presented one by one for 400ms. After each identity presentation, a recap screen appeared with all the faces learned in previous trials, clustered by identity and shown under the various viewpoints side by side. All learnt identities were randomly presented one-by-one in the second familiarization phase, each under one of the seven viewpoints. The face appeared in isolation for 1000ms. Then the name associated with the face was added and both name and face were shown together for another 2000ms.

Participants were then evaluated on their ability to name the learnt so-called ‘old’ faces at various viewpoints (+75° to -75°, in steps of 25°). A trial started with a 500ms fixation, then the stimulus was presented at screen center along with the name options (the five names of the ‘old’ faces of the same gender of the shown face), numbered from 1 to 5, at the top of the screen until participant response (maximum of 3000ms). Participants responded by pressing on the corresponding key (1 to 5). The fixation turned green in case of a correct response. When incorrect, the fixation turned red. In both cases, the correct name appeared along with feedback. Feedback lasted for 500ms. Familiarization and test were looped until naming accuracy reached 80 %.

The main experiment was divided into 32 runs of 40 trials. A run started with recap screens for all learned identities under the seven viewpoints (from +75° to -75° in 25° steps) along with their associated name. In each main experiment trial, a face stimulus was presented centrally at a specified viewpoint and orientation range (from 0° to 157.5° in 22.5° steps). Viewpoint and orientation range varied randomly from one trial to the other. A trial started with a 1s fixation, next the face stimulus appeared until response or for 3s maximum. At the end of a run, participants received feedback on their average accuracy. To avoid inducing a response bias, there were as many 'old' as 'new' trials, making the 10 'old' faces twice as frequent as the 20 'new' ones, which were each presented only once per condition. There were 40 trials per condition and a total of 1280 trials.

Participants first practiced the main experimental task on 20 randomly selected trials with full spectrum stimuli. If they reached 80% accuracy, they could start the main experiment with the filtered stimuli. If practice accuracy was lower than 80%, participants were invited to run the familiarization (learning and test) again. Whenever accuracy in an experiment run dropped below 55% correct, and every third run regardless of performance, participants were presented with the recap screens again. All through the experiment, they were encouraged to respond as accurately and rapidly as possible.

The total experiment lasted for 1.5 hours on average, split into three testing sessions.

Human data analysis

To prevent outlier responses from contaminating the results, we applied a log10 transformation on response latencies at the trial level and excluded trials with latencies at more than 2.5 times the standard deviation above and below the individual mean, in each participant. This procedure resulted in the exclusion of 1.81% of the trials on average.

In order to estimate the orientation dependence of human sensitivity to identity across views, we derived individual *d'* at each viewpoint and orientation. To do so, we determined hit and false alarm rates (Tanner & Birdsall, 1958) from the 'old'/'new' response in each participant, at each orientation and for each viewpoint. Following the log-linear rule (Hautus, 1995), we added a 0.5 correction to both before calculating the z scores. Performance at the 0° filter was duplicated to have circular filter values from 0° to 180°. As expected from previous studies (Dumont et al., 2024; Goffaux & Greenwood, 2016; M. V. Pachai et al., 2018), the d' plotted as a function of orientation in the frontal view condition (yaw = 0°) depicted a bell-shaped function centred on horizontal orientation (i.e., 90°; see Figure 4.3A, central panel). At the other viewpoints, d' followed a very similar shape, with maximum sensitivity roughly centred on horizontal orientation. Therefore, human sensitivity data could be fitted using a simple Gaussian model. The Gaussian model is defined as:

$$f(orientation) = BaseAmplitude + \ PeakAmplitude * \ \mathrm{e}(-\frac{(orientation - PeakLocation)^2}{2StandardDeviation^2})$$

with $orientation$ being the orientation of the filter, ranging from 0 to 180°. The model estimates four free parameters. The $Peak\,Location$ is the orientation on which the gaussian curve is centred. The $Standard\ Deviation$ is the width of the Gaussian curve (i.e., strength of the tuning). The $Base\ Amplitude$ is the height of the gaussian curve base (i.e., the minimum sensitivity, typically found near vertical orientations). $Peak\,Amplitude$ refers to the height of the Gaussian curve relative to its baseline — that is, it reflects the advantage of horizontal over vertical orientations.

We used the package *brms* (Bürkner, 2018) in R to implement this model in the Bayesian framework, using a multilevel modelling approach (Dumont et al., 2024; Moors et al., 2020; Nalborczyk et al., 2019). The four parameters $Peak\,Location$, $Standard\,Deviation$, $Base\,Amplitude$, and

$Peak\ Amplitude$ were conjointly estimated by linear predictor terms which included an intercept and the effect of Viewpoint. We also estimated a subject-level intercept of $Standard\ Deviation$ and $Base\ Amplitude$ as random effects, to allow the shape of the gaussian to vary across participants. This multilevel structure provides a more accurate estimation of population-level parameters by accounting for subject variability. The prior distributions of the different parameters of the model were specified based on a compromise between (1) using knowledge from previous research (e.g., we used a normal distribution centred on horizontal orientation – 90° – for $Peak\ Location$, in line with the well-established horizontal tuning of face identification), (2) keeping unbiased uncertainty when previous research was not informative (e.g., for the effect of Viewpoint on the different parameters), and (3) allowing the convergence of the model. The details of the prior distributions can be found in Supplementary Table 4.1. We ran four Markov Chain Monte-Carlo simulations, with 20,000 iterations including 3,000 warm-up iterations.

Model diagnostics of the model were checked and indicated a good convergence: The potential scale reduction factor (R-hat) was of 1.00 for all parameters, the Bulk Effective Sample Size (ESS) was superior to 10.000 for all but four parameters (Intercept of the Base Amplitude: Bulk ESS = 5504; Intercept of the Peak Amplitude: Bulk ESS = 8494; Subject-level random effect of the Standard Deviation: Bulk ESS = 5965; Subject-level random effect of the Base Amplitude: Bulk ESS = 6308), and the Tail ESS was superior to 10.000 for all but one parameters (Subject-level random effect of the Standard Deviation: Bulk ESS = 5321).

Table 4.1. Posterior mean and 95% credible interval for each parameter of the Gaussian model, at each viewpoint.

Parameter	Viewpoint	Estimate (posterior mean)	95% credible interval – lower bound	95% credible interval – upper bound
Peak Location	-75 (left profile)	99.5	90.02	108.98
	-50	94.4	86.98	101.87
	-25	90.62	83.58	97.73
	0 (full front view)	90.99	88.22	93.78
	25	91.98	85.00	99.01
	50	88.19	80.82	95.51
	75 (right profile)	80.24	70.73	89.76
Standard Deviation	-75 (left profile)	40.37	27.40	54.4
	-50	46.51	34.51	59.29
	-25	47.2	35.75	59.07
	0 (full front view)	44.94	40.55	49.41
	25	51.36	40.04	63.14
	50	50.02	38.18	62.23
	75 (right profile)	45.06	32.5	58.12
Base Amplitude	-75 (left profile)	0.81	0.29	1.31
	-50	0.44	-0.16	0.99
	-25	0.11	-0.49	0.66
	0 (full front view)	0.07	-0.2	0.34
	25	-0.09	-0.72	0.5
	50	0.27	-0.34	0.84
	75 (right profile)	0.65	0.11	1.16
Peak Amplitude	-75 (left profile)	1.01	0.47	1.58
	-50	1.68	1.10	2.30
	-25	1.87	1.29	2.48
	0 (full front view)	1.72	1.49	1.97
	25	2.07	1.45	2.72
	50	1.81	1.22	2.45
	75 (right profile)	1.12	0.56	1.71

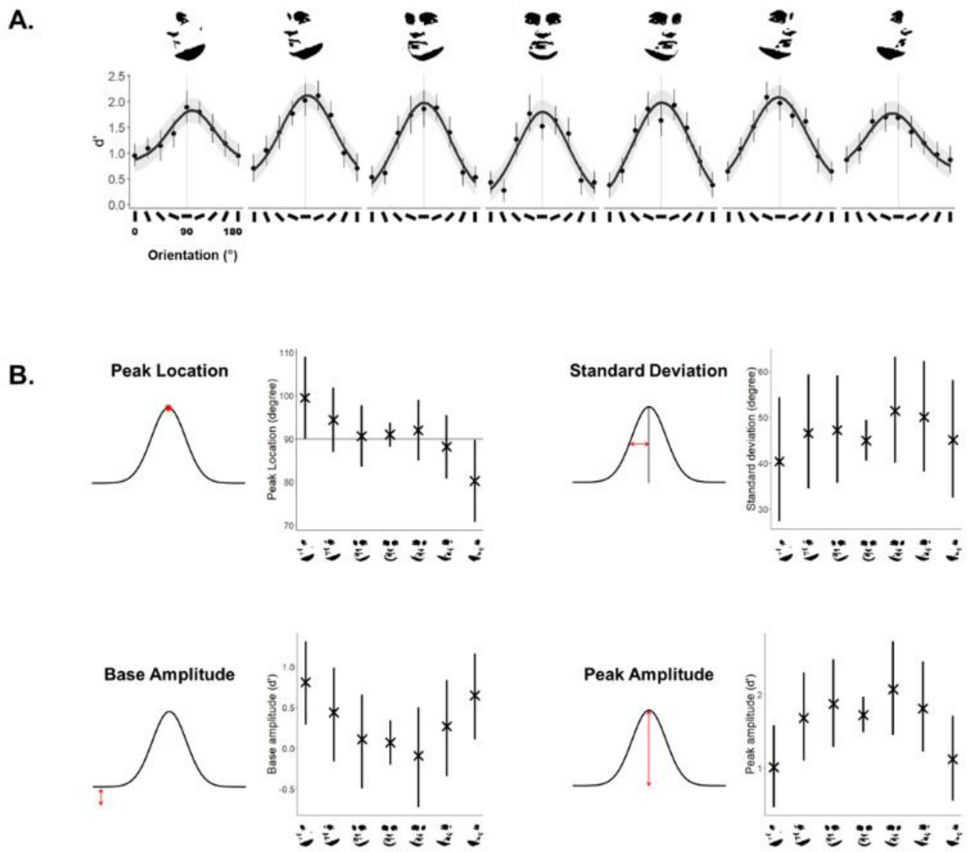


Figure 4.3. **A.** Sensitivity of human observers to facial identity (*d'*) as a function of the orientation filter (0° to 180° in 22.5° steps) and face viewpoint (yaw: +75° to -75° in 25° steps). Dots and error bars represent mean *d'* values and 95% confidence intervals across participants. Solid lines and shaded areas indicate the mean posterior predictions and 95% credible intervals from the Gaussian Bayesian multilevel model. **B.** Population-level mean parameters of the Gaussian Bayesian Multilevel model, plotted with 95% credible intervals as a function of face viewpoint. The 95% credible intervals reflect the uncertainty of the model and can be interpreted as follows: there is a 95% chance that the value of the population parameter lies within this interval.

Image analysis

We investigated how the distribution of energy across orientations in the experimental stimuli varied as a function of viewpoint. The amplitude and phase spectra for the image of each full spectrum face were obtained by means of a two-dimensional fast Fourier Transform and multiplied with wrapped Gaussian filters, with peak orientations centred on orientation values from 0° to 157.5° in steps of 22.5° (20° standard deviation; as in Goffaux & Greenwood, 2016) and with peak spatial frequencies ranging from 1 to 200 cycles per image in 20 logarithmic steps. Amplitude values within each spatial frequency and orientation bin were squared and summed, then averaged across spatial frequencies per orientation bin.

Note that because the Fourier transform represents image energy in a discrete manner, energy at the lowest spatial frequency components can only be reliably sampled at the main cardinal and oblique ranges (i.e., 0°, 45°, 90°, 135°) especially when very narrow orientation filters are used (Hansen & Essock, 2004). However, because orientation filters were broad and we interpret relative differences, and not absolute values, of energy distribution across viewpoints, the influence of this issue is minimal. We obtained one mean energy value per orientation band by averaging across identities.

We found that while face images contained most of their energy in the horizontal range, irrespective of viewpoint (Figure 4.3), the amplitude of the horizontal energy peak decreased as the face viewpoint moved away from frontal. For profile views, there was a plateau covering the horizontal plus the adjacent left and right oblique orientations for the left- and right-pointing profile views, respectively. In comparison, vertical energy was lower than any other range regardless of viewpoint. These findings replicate past evidence that most of the energy in a face image is contained in a range centred over the horizontal angle (Goffaux, 2019a; Goffaux & Greenwood, 2016; Keil, 2009).

Yet the distribution of image energy as a function of orientation does not provide any insight about its potential usefulness for face identity recognition; we addressed this using model observers.

Model observers

To systematically quantify the orientation profile of the stimulus information physically available (1) to identify faces seen under a fixed viewpoint and (2) to match face identities across viewpoints (requesting tolerance to change in views), we designed two different model observers: a view-selective model observer and a view-tolerant model observer, respectively. By characterizing the orientation profile of the information available to recognize face identity in a view-selective and -tolerant manner, this approach enables emitting formal, stimulus-driven hypotheses on the information as used by humans (Collin et al., 2014; M. V. Pachai et al., 2013). Namely, it allows addressing the extent to which human view-tolerant identity recognition relies on the orientation range that is the most informative for the view at stake, or the one most stable across views.

Model observers performed the task on the same 10 “old” faces and 20 “new” faces as randomly selected for the human observers; we ran 22 view-selective and 22 view-tolerant model observers to match the number of tested human subjects. We presented each of the 30 faces once per condition. In each trial, the models computed the pixelwise similarity based on the calculation of a cross-correlation between a target image (either from the ‘old’ or ‘new’ set) and each of the possible exemplars of the same gender (i.e., probes) filtered at the same orientation as the target image. The probe face with the highest correlation (i.e., the more similar) to the target image was selected as the model response (winner-take-all scheme). Depending on the correspondence between the ”winner” probe and the actual target, the responses of the model observer were categorized as hit or false alarm, allowing for the computation of a sensitivity d’ in each orientation and viewpoint condition along a procedure like the one used to compute human performance.

In both model types, target and probes were of the same orientation range (see Collin et al., 2014; Näsänen, 1999 for a similar method applied to the spatial frequency domain). Targets and probes in the view-selective model observer stemmed from a fixed viewpoint whereas the view-tolerant model observer matched target and probe separated by more than one viewpoint step to force tolerance to viewpoint in this model performance (e.g., a face at +025 of yaw was matched to faces at +075, -025, -050, and -075). Since profile views stood at the viewpoint continuum extrema, one extra viewpoint was available for comparison. We therefore decided to drop the mirror profile view to match the number of comparisons across profile and non-profile viewpoints. Performance of the view-tolerant model was averaged across comparison viewpoints.

In a pilot phase, we measured the overall identification performance of each model. In the view-selective model, we had to decrease signal-to-noise ratio (SNR) of the target and probe images to .125 (face RMS contrast: .01; noise RMS contrast: .08) to avoid ceiling effects and keep overall performance close to human levels. Sensitivity *d’* of the view-tolerant model was much lower than human sensitivity, even without noise. The view-tolerant model therefore processed fully visible stimuli (SNR of 1). This decreased sensitivity in the view-tolerant compared to the view-selective model is expected as none of the probes exactly matched the target at the pixel level due to viewpoint differences. In contrast to humans who rely on internally stored representations to match identity across views, the model observer lacks such internal representations and entirely relies on (inefficient) pixelwise comparisons.

The main objective of running these model observers is to interpret human orientation sensitivity profiles considering the available information in the stimulus; following this reasoning, model observer performance is only interesting when compared to human performance. Therefore, we investigated which model observer best predicted the orientation dependence profile of human face recognition using partial Pearson correlation analyses. We controlled for the variance in image energy across orientations and viewpoints, in all partial correlation analyses to exclude the possibility that view-selective/tolerant model performance is a mere epiphenomenon of absolute oriented energy. The Fisher-Z transform of perfect correlations leading to infinite values, we replaced all -1 and 1 partial correlation coefficients to -.99 and .99, respectively, before applying Fisher Z-transformation and computing 95% confidence intervals (see Table 4.1). We (partial) correlated the orientation profiles of human and each model observer at each viewpoint separately (eight orientation vectors). For each specific viewpoint, the orientation sensitivity profile of each human observer was correlated to the average orientation sensitivity profile of either model observer, while controlling for the variance explained by (1) the average orientation sensitivity profile of the alternate model observer and (2) the average profile of orientation energy. The variability in human individual orientation profiles was taken as an estimate of the maximally achievable data-model correlation. We computed the cross-correlation between each human individual orientation sensitivity profile and the average sensitivity profile of the remaining participants. The maximally achievable correlation was the mean of these individual-to-group correlations.

Results

Human observers

Upon visual inspection, group-averaged d' plotted as a function of orientation depicted a bell-shaped function roughly centred on horizontal orientation in the frontal view condition as in the other Viewpoint conditions (Figure 4.3A). The fitting confirmed that sensitivity to identity shows a roughly similar Gaussian orientation tuning profile across viewpoints (see bell-shaped curves on Figure 4.3A).

The relative stability of the human orientation sensitivity profile was corroborated by the stable and significantly positive correlations of the orientation tuning profile across viewpoints (rs> .67, ps < .05; Figure 4.4).

Despite human sensitivity for face identity always being best around horizontal orientations and worse around vertical ones, there were notable fluctuations in the orientation sensitivity profile across viewpoints. To better grasp these variations, we plotted the population-level estimates of the four parameters of the Gaussian curve as a function of viewpoint in Figure 4.3B. Population-level estimates and 95% credible intervals can also be found in Table 4.2.

$Peak\ Location$ is estimated to lie close to 90° (grey horizontal line in Figure 4.3B) in all viewpoints except at the two profile views where peak location shifts toward adjacent obliques orientations (yaw = -75/75; see Figure 4.3A). Specifically, peak human sensitivity tended to shift towards left and right oblique for the most extreme leftward and rightward deviations in viewpoint, respectively. $Peak\ amplitude$, which corresponds to the difference in sensitivity between the vertical and horizontal ranges, is relatively stable across all viewpoints except for the two profile views where it is lower. $Base\ amplitude$, reflecting sensitivity in the vertical range, is highest for the two profile views and progressively decreases towards the full-frontal view. This pattern suggests that vertically-oriented face content is more diagnostic for profile than for other viewpoints. The variation of $Standard\ Deviation$ across viewpoints can hardly be interpreted because of the high uncertainty of the estimations; the 95% credible intervals of the $Standard\ Deviation$ for the different viewpoints mostly overlap.

Table 4.2. Mean and 95% confidence interval of the (Fisher Z-transformed) partial correlation coefficients between human and each model orientation d' profiles while controlling for the variance in image energy and alternate model.

Model	Viewpoint-specific		Viewpoint-tolerant	
	mean	95% ci	mean	95% ci
+075	0.06	[-0.09 0.2]	0.49	[0.30 0.67]
+050	0.04	[-0.10 0.18]	0.5	[0.34 0.66]
+025	0.56	[0.42 0.71]	0.3	[0.17 0.42]
000	0.79	[0.62 0.97]	0.19	[0.09 0.30]
-025	0.36	[0.18 0.54]	0.34	[0.17 0.51]
-050	0.1	[-0.06 0.25]	0.59	[0.45 0.72]
-075	-0.05	[-0.17 0.08]	0.56	[0.35 0.77]

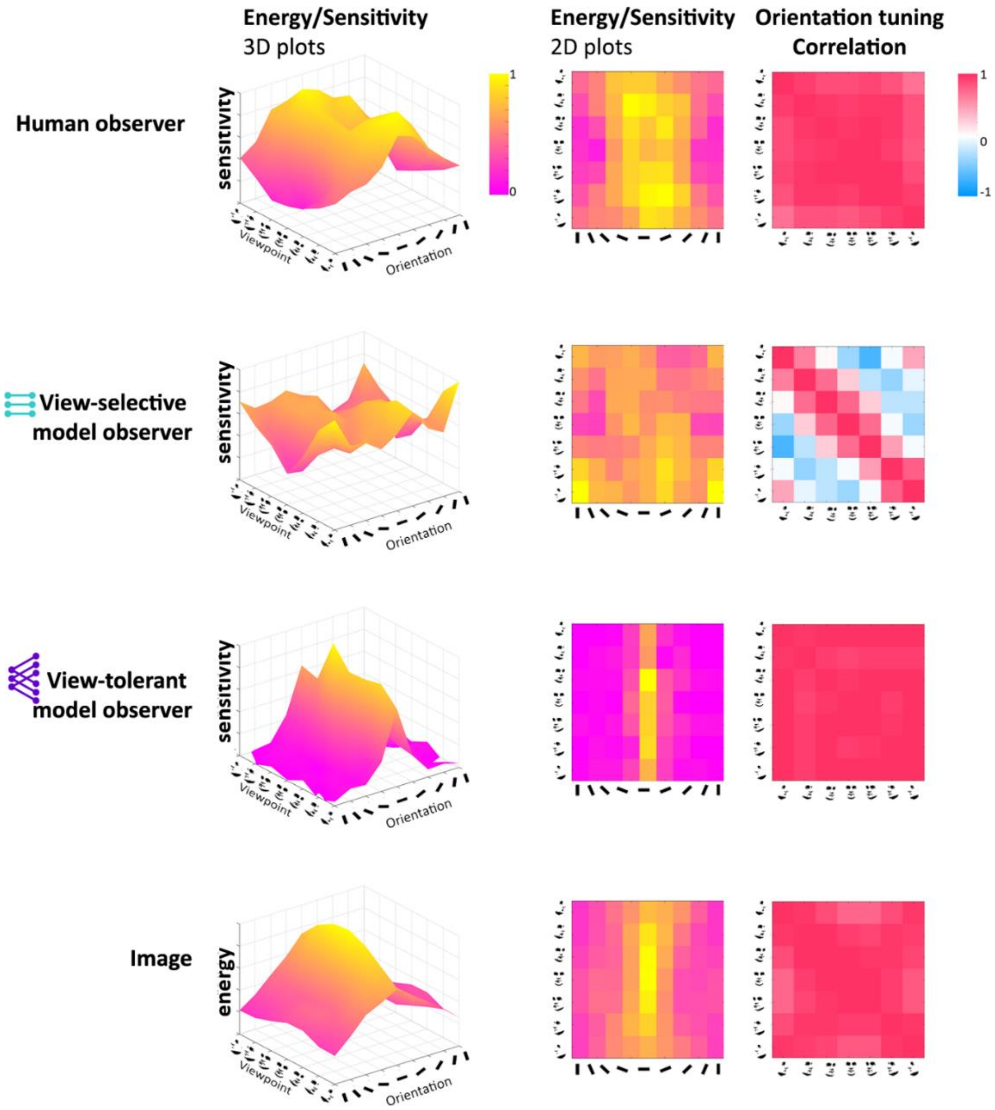
View-selective model observer

The performance of the model observer matching faces at specific viewpoints indicates that the most diagnostic orientation range varies as a function of viewpoint (Figure 4.4).

Within the frontal view, optimal cues to identity are conveyed by orientations close to the horizontal angle (between 90° and 112.5°). The striking similarity of the orientation tuning profile of the view-selective model observer with the human performance indicates that at frontal view, the human visual system makes an efficient use of the information as made available in the stimulus. The peak of model performance shifted to the left and right oblique orientations closest to horizontal angle (67.5° and 112.5°) for leftward and rightward deviations in viewpoint, respectively. Additionally, the view-selective model observer increasingly relied on vertical cues as the face is turned towards its profile, in line with human performance.

We found only (significant) weakly positive correlations of the orientation sensitivity profiles across adjacent viewpoints (e.g., +075 and +050) confirming the orientation tuning variations across views (Figure 4.4).

Except for the frontal view, the orientation tuning of the view-selective model observer differs from human orientation profiles, which kept tuned to horizontal and adjacent oblique ranges irrespective of viewpoint.



<u>Figure 4.4.</u> Sensitivity (i.e., performance at the recognition task) of human and model observers and image energy across viewpoints and orientations. *Left column*. 3D surf plots of the normalized energy/sensitivy across orientation and viewpoints. *Middle column*. Matrix representations of the normalized energy/sensitivity across orientation and viewpoints. *Right column*. Matrix representations of the Pearson correlation (non Fisher-z transformed) of the normalized orientation distributions of energy/sensitivity across viewpoints.

View-tolerant model observer

The model observer matching face identity across viewpoints performed in a drastically different way from the view-selective model observer. Recognition performance peaked sharply in horizontal angles and dropped abruptly at other ranges (Figure 4.4). Such orientation profile was relatively stable across viewpoints as shown by the homogeneous matrix of large positive and significant Pearson correlation coefficients for sensitivity profiles across viewpoints ($rs > .88$, $ps < .002$).

Such horizontal tuning was sharper than the one observed for humans with a much more severe drop of sensitivity in the vertical orientation range. The horizontal tuning of human performance is much shallower even at frontal view. It shows a similar dip in sensitivity for the vertical range but the latter however tends to reduce when moving away from the frontal view, which does not happen for the view-tolerant model observer that keeps sharply horizontally-tuned.

Human Versus Model observers

What model observer best predicts the orientation tuning profile of human face recognition? Is it the view-selective model taking advantage of the identity cues that are optimal for the viewpoint at stake, or the view-tolerant model the performance of which performance relies on the identity cues most stable across viewpoints? To address this question directly, human orientation *d'* profiles were correlated at the individual level with each model orientation *d'* profile, when partialling out the variance explained by the alternate model and image energy. We submitted the so-obtained individual

Fisher-Z transformed partial correlation coefficients to a repeated-measure ANOVA with Model and Viewpoint as within-subject factors.

These partial correlations showed that the orientation tuning profiles of human and view-selective model observers correlated strongly for frontal and near-frontal views, approaching the maximally achievable correlation. However, partial correlations dropped steeply as the views deviated further from frontal (Figure 4.5; Table 4.2). The correlation of orientation tuning profiles between human and view-tolerant model observers was lower overall but significant across all viewpoints.

The repeated-measure ANOVA confirmed that the human-model correlation of orientation sensitivity profiles differed depending on Model ($F(1,21)= 5.21$, $p = .033$, $\eta^2= .017$) and Viewpoint ($F(3.85,80.9)= 11.064$, $p< .001$, $\eta^2= .11$). The interaction between Model and Viewpoint was also significant ($F(4.2,88.35)= 13.035$, $p< .001$, $\eta^2= .23$).

We explored the impact of viewpoint on human-model correlation for the view-selective and view-tolerant models separately using a repeated-measure ANOVA with Viewpoint as a within-subject factor. For the view-selective model, this analysis revealed a robust effect of Viewpoint on the human-model partial correlation ($F(3.86,80.99)= 22.795$, $p< .001$, $\eta^2= .52$). For the view-tolerant model, the effect of Viewpoint on the human-model partial correlation was not significant ($F(6,126)= 1.2$, $p= .32$, $\eta^2= .054$). This confirms the relatively stable human-model partial correlation coefficients across viewpoints observed for the view-tolerant model and the fluctuant profile of human-model partial correlation coefficients for the view-specific model (peaking at frontal views and decreasing as moving toward profile views).

Furthermore, at each viewpoint, we examined which model observer best correlated with human orientation sensitivity profile (using Holm-corrected post-hoc tests on Fisher Z-transformed partial correlation coefficients; Table 4.3). The view-tolerant model predicted a significantly larger portion of the variance in human orientation sensitivity profile at +/-050 and +/-075 viewpoints, this difference was marginal for the +050 viewpoint. It is only for the identification of frontal views of faces that the view-selective model correlated best with human data. Correlations were of similar strength for the +075, +025, -025 (and +050) viewpoints (Table 4.3).

Table 4.3. Difference of the human-model correlation coefficients between viewpoint-selective and view-tolerant model observers. Positive t values indicate a stronger correlation with the viewpoint-selective model and negative t values stronger correlation with the view-tolerant model.

		95% CI for Mean Difference			
View	Mean Difference	Lower	Upper	t	p Holm
+075	-0.47	-0.86	-0.07	-4.20	0.002
+050	-0.43	-0.82	-0.03	-3.82	0.01
+025	0.23	-0.16	0.63	2.08	1
+000	0.69	0.30	1.09	6.21	< .001
-025	0.03	-0.37	0.42	0.23	1
-050	-0.61	-1.00	-0.21	-5.44	< .001
-075	-0.78	-1.18	-0.39	-7.02	< .001

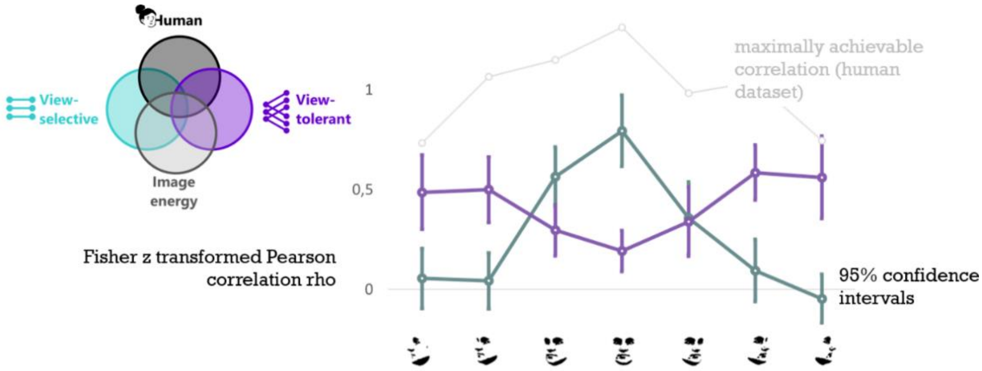


Figure 4.5. Fisher-z transformed Pearson partial correlation of the orientation sensitivity profiles between humans and each model, while controlling for the alternate model and image energy. Error bars show the 95% confidence intervals. The fade grey line depicts the maximally achievable correlation for the separate viewpoint conditions in the human dataset (see Methods for details).

Is model observers' performance predicted by horizontal energy predominance?

In the above correlation analyses, we controlled the variance in image energy to yield a clean measure of the functional link between human and model observer performance. Here, we explore the possibility that the horizontal reliance of either model observer performance scales with the energy predominance of this orientation range in the stimulus image.

To analyze the influence of horizontal predominance on the model's performance, we computed for each image the horizontal minus vertical difference in terms of energy and model observer sensitivity. For each identity and at each viewpoint, energy and model sensitivity difference values were submitted to a Pearson correlation. We found a positive modest correlation between view-selective model observer and image energy (Pearson $r = .24$, $p < .0005$). There was no similar correlation for the view-tolerant model

(Pearson rho = .025, p = .72) despite energy and view-tolerant model performance similarly peaked in the horizontal range across viewpoints.

What this analysis shows is that, in a given face, the stronger the predominance in horizontal energy (relative to the vertical energy), the more diagnostic the horizontally-oriented identity cues for view-selective recognition. However, horizontal energy predominance in a given face does not account for this range carrying the most stable cues across viewpoints.

This image-level analysis did not include human data since human sensitivity necessarily aggregates performance across trials. However, it would likely show a similar detachment from horizontal energy predominance as the view-tolerant model. Namely, humans are expected to rely on horizontal cues to match faces across views no matter the amount of horizontal energy predominance in the face at stake (e.g., George Clooney versus Brad Pitt).

Discussion

Tolerant face identity recognition is defined as the ability to extract idiosyncratic face cues despite the large variability in any given face appearance (e.g., Burton et al., 2016; Kramer et al., 2018). The spatial information supporting the tolerance of visual recognition is a central and debated topic in the field of the visual and computational neurosciences (e.g, Andrews et al., 2023; DiCarlo & Cox, 2007a). By showing that the information supporting tolerance in face identity recognition is image-computable, i.e. that it can be objectively defined in the orientation domain of the face image, the present work makes a decisive advance on this question. Our finding that view-tolerant face identity recognition is driven by the horizontal range of face information yields concrete, image-driven constraints for the development of theoretical models of visual recognition.

Human participants performed an old/new identity recognition task on face stimuli presented under a variable view (from left to right profile) and filtered to contain a restricted range of oriented content (from 0° to 157.5° in steps of 22.5°; see Figure 4.2). For each view, recognition performance followed a Gaussian profile with a peak in the horizontal range and declining progressively when shifting towards the vertical range (Figure 4.3). Yet, while identity recognition stayed broadly tuned to the horizontal range irrespective of the vantage view, there were moderate but notable fluctuations in the tuning profiles. First, the peak location of the Gaussian tuning profile slightly and gradually shifted away from horizontal towards right and left adjacent obliques as the face turned to left or right profile. Second, the base amplitude of the Gaussian increased drastically towards profile views. The U-shaped profile of base amplitude as a function of viewpoint shows the increasing contribution of vertically oriented information as the face moves away from the frontal view (see Figure 4.3B). In other words, the horizontal advantage of human identity recognition is largest at full-frontal views and attenuates for non-frontal views due to the increased contribution of vertical (and close-to-vertical) orientations. In other words, while human identity recognition stays tuned to the horizontal range irrespective viewpoints, it tends to increasingly rely on non-horizontal orientations as the face shifts to profile.

As the vantage point of a face shifts away from frontal view, morphological features related to the 3D structure of the face become more apparent (e.g., nose and cheek protuberances, jaw line, nose bridge, eyebrow head…; see e.g., Stephan & Caine, 2007 for evidence that the nose gains in informativeness from frontal to profile view). Our finding that non-horizontal ranges, particularly vertical, gain importance in non-frontal views suggests that these orientations may facilitate access to such features.

In contrast, other sources of information are lost when shifting towards profile views, such as the bilateral symmetric organization of the face as well as the 2D shape of features and their configuration along the x axis (e.g., size of eyebrows, interocular distance; Royer et al., 2016; Troje & Bülthoff, 1996). In a way, it is surprising that this shift in accessible information did not manifest in a substantial variation of the peak location of the orientation tuning profile. Instead, the relatively stable preference for horizontal information across views suggests that it is not solely due to this range facilitating access to the 2D properties and bilateral symmetry (Dakin & Watt, 2009), features that are most available in frontal views. Our recent work (Dumont et al., 2024) showed that the inversion and negation effects on identity recognition, presumed to reflect a disrupted access to 2D shape and surface cues, respectively (for shape: Jiang et al., 2011; Meinhardt-Injac et al., 2013; Rossion, 2009; for surface: Bruce & Langton, 1994; Kemp et al., 1996; C. H. Liu et al., 2000; Russell et al., 2006; Vuong et al., 2005), are strongest in the horizontal range. This supports the notion that the contribution of the horizontal face information to identification goes beyond the carriage of 2D shape cues. Alternatively, the stable horizontal tuning may be due to identity recognition relying mostly on the eye region irrespective of view. Despite the eye appearance being strongly affected by changes in view, the identity information extracted from the eye region is the most diagnostic across views (Stephan & Caine, 2007; but see Royer et al., 2016 for conflicting results) and stays best defined in the horizontal range.

Using a model observer approach, we investigated how the human observer makes use of the identity cues physically available in the image across orientations and views. It is indeed important to compare the human tuning profile to a pixel-based quantification of the information that is available in the stimulus in order to characterize more formally the human sampling specificities potentially at stake when recognizing face identity. We designed two model observers to measure the information available in the stimulus to “recognize” (i.e., cross-correlate) face identity within and across views and disentangle stimulus information available for view-selective and view-tolerant recognition, respectively.

Let’s first summarize the findings related to the view-selective model observer. It showed that identity cues most diagnostic to discriminate face identity in a view-specific manner is highly variable across views (Figure 4.4). The view-selective model observer was horizontally-tuned for frontal views of faces, in a manner strikingly similar to the human performance profile. This suggests that human observers make a close-to-optimal use of the orientation information in face images when identifying frontal face views. Akin to human recognition, the view-selective model progressively increased its reliance on vertically-oriented cues when the face moved from frontal to profile. However, for the view-selective model – and in contrast to human performance – this came to the expense of the horizontal tuning, which vanished completely. What these findings suggest is that the robustness of the horizontal tuning of face identity recognition at frontal view is due to this range conveying the optimal cues to identity in these specific conditions. However, they also show that the horizontal range loses its view-specific informativeness in non-frontal views; namely, differences in face identity at non-frontal views are predominantly carried by non-horizontal ranges of information. Therefore, view-specific informativeness cannot account for the generalization of the horizontal tuning profile of human identity recognition across views. In other words, the reason human recognition remains tuned to the horizontal range from frontal to profile views cannot be that this range provides optimal identity cues at each view.

In contrast to the view-selective model observer, the view-tolerant model observer kept sharply tuned to the horizontal range irrespective of view (Figure 4.4). The horizontal range resulted in the highest cross-correlation among the different views of a given face indicating that this range yields the identity cues that are the most stable across views, those that enable binding different face views into a unique representation of identity (Burton, 2013). This physical property of the face image likely explains why human identity recognition keeps horizontally-tuned across views (see Goffaux & Dakin, 2010 for a similar suggestion based on empirical evidence in a viewpoint-generalization identity matching task).

For a direct comparison of human and model performance, we quantified the variance shared between each model observer and human orientation tuning profile while controlling for image energy and the alternate model (Figure 4.5). These analyses confirmed that the view-selective model best predicted the orientation tuning of human identity recognition at frontal and close-to-frontal views, that are typically experienced during so-called face-to-face conversations, but not at profile and close-to-profile views. In contrast, the variance explained by the view-tolerant model was relatively stable across viewpoints. The particularly strong horizontal tuning of human identity recognition is thus likely due to the visual system extracting a representation that simultaneously prioritizes the orientation range conveying the cues that are the richest at frontal view and the most stable across views.

The horizontal tuning of human face recognition was found to be relatively broad across views, compared with the sharp tuning of the view-tolerant model observer. This tuning breadth may serve to retain information of the complex manifold of a given face appearance variability across views. Indeed, each face identity has its own specific way to vary across expression, illumination, view, etc. Such idiosyncratic within-person variability was proposed to drive familiar face identity recognition as much as the stable (horizontal) identity information (e.g., Burton et al., 2016; Ritchie & Burton, 2017). Moreover, accidental properties such as head and gaze orientation carry important cues for the regulation of social interactions. Our past evidence shows that the fine discrimination of gaze direction is best supported in the vertical range (Goffaux, 2019). The vertical range also likely carries most of the information about the head direction. Thus, the broad horizontal tuning of identity recognition by humans may allow for the integration of such accidental properties of a face with the (more) stable identity (Or & Wilson, 2010). For functional social interactions, it may be necessary to retain the dynamic and variable signals emitted by a face as much as its invariant aspects, and this would entail a relatively broad tuning to orientation.

Effect of lighting are even more disruptive than view changes (Adini et al., 1997; Braje et al., 1998; S. Favelle et al., 2017; Hill & Bruce, 1996; A. Johnston et al., 2013; Tarr et al., 1998, 2008). Image representations that emphasized the horizontal features were found to be less sensitive to changes in the direction of illumination (Adini et al., 1997). Future research should test whether tolerance of human face identity recognition to lighting is also supported by the horizontal range.

To conclude, this study demonstrates that the horizontal range carries the richest identity cues in frontal views, and the most stable across views. The orientation tuning profile of human identity recognition aligns with this combination of high diagnostic value in frontal views and cross-view stability. Taken together, this body of evidence suggests that the invariant representation of a given face, gradually learned through repeated exposure to its natural appearance statistics, relies heavily on horizontal facial information (Figure 4.1; Burton et al., 2016; Dakin & Watt, 2009; Ritchie & Burton, 2017).

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Supporting information

Supplementary Table 4.1. Prior distributions of the four parameters of the Gaussian Bayesian multilevel model.

	Peak Location	Standard Deviation	Peak Amplitude	Base Amplitude
Prior for Intercept	**normal(90, 3)**	**normal(40, 3)**	**normal(2.32, 1.5)**	**normal(2.32, 1.5)**
Prior for the slope (effect of Viewpoint)	Viewpoints -50, -25, 25, 50: **normal(0, 5)** Viewpoints -75, 75: **normal(0, 10)**	**normal(0, 5)**	**normal(0, 1)**	**normal(0, 1)**
Prior for random effects	*NA*	**exponential(0.1)**	*NA*	**exponential(0.1)**

Chapter 5: Neural signatures of human face categorization are broadly tuned to horizontal information

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Abstract

Face identity recognition preferentially relies on the horizontal range of face information. The horizontal range has been proposed to convey the richest and most stable cues to face identity. The extent to which the horizontal range carries the natural statistics of the human face at coarser, basic-level, category levels is however elusive. We therefore investigated the orientation tuning of face basic-level categorization using a fast-periodic visual stimulation (FPVS) EEG paradigm. This paradigm enables to measure face categorization among various other categories, as well as face generalization across a large pool of face exemplars. Thirty-two subjects viewed sequences of highly variable images from different categories (e.g., animals, plants, objects) displayed at a periodicity rate of 6Hz (i.e., 6 images per second) and with oddball face images inserted every 5 images (i.e., 1.2Hz), while performing an orthogonal task. In a sequence, stimuli were either full-spectrum or filtered to retain information in selective orientation ranges (from 0° to 135° in steps of 45°). Brain response synchronization to periodic stimuli enabled us to measure the general neural response to the base visual stimulation rate (i.e., 6Hz and harmonics) and the face categorization response at the oddball periodicity rate of 1.2Hz (and harmonics). Additionally, 26 subjects participated in a behavioral experiment with the same images and periodicity as in the EEG experiment and were explicitly instructed to respond any time they saw a face.

In the EEG experiment, the general visual response was similar across orientation filters. The categorization response was significantly weaker for vertically filtered images than other orientation ranges. There was no significant difference between horizontally filtered images and obliquely filtered images or non-filtered images. In the behavioral experiment, face

categorization response was faster and more accurate for horizontal and oblique compared to vertical orientation filters. There was no difference between horizontal and oblique filters. Although surprising, the absence of orientation effect between horizontal and oblique filters on both the implicit and explicit response is potentially due to the large overlap of the orientation filters used here. Our finding that the horizontal and close to horizontal orientations facilitate face categorization demonstrates that this range of information carries the visual properties that contribute to the categorization of faces in the wild. They also suggest that the horizontal advantage characterizes human face categorization in a large range of granularity: from the coarse basic-level image parsing to the fine-grained individuation.

Introduction

Identity recognition has been shown to be tuned to the horizontal range of face information (Dakin & Watt, 2009; Dumont et al., 2024; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2013, 2017). This horizontal advantage of face identity recognition has been linked to face specialized mechanisms. Indeed, the better recognition with the horizontal range is found in faces but not in scenes (Goffaux & Dakin, 2010). The horizontal range, more than the vertical one seem to carry diagnostic cues to face adaptation, and identity generalization to other viewpoints (Goffaux & Dakin, 2010, Roux-Sibilon et al., under review). Inversion and contrast negation, that severely disrupt face processing from basic-level categorization (Garrido et al., 2008; Lewis & Edmonds, 2003; Liu-Shuang et al., 2015, 2022) to identity categorization (Bruce & Langton, 1994; Galper, 1970; Gilad et al., 2009; Hochberg & Galper, 1967; Nederhouser et al., 2007; Yin, 1969), by obstructing shape (Bozana Meinhardt-Injac, Malte Persike, Günter Meinhardt, 2013; Jiang et al., 2011; Rossion, 2009) and surface and shading information (Bruce & Langton, 1994; Kemp et al., 1996; Liu et al., 2000; Russell et al., 2006; Vuong et al., 2005), respectively, had a stronger effect in the horizontal range, thus demonstrating that face specialized mechanisms are driven by this range of facial information (Dumont et al., 2024; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Jacques et al., 2014; Pachai et al., 2013). In an event-related potential (ERP) study, Jacques et al. (2014) showed that a neural inversion effect measured around 170 ms post-stimulus onset on occipitotemporal electrodes, i.e., the N170, was delayed and reduced when access to the horizontal range of the face stimulus was disrupted due to narrow band-oriented phase randomization. In an fMRI study, Goffaux et al. (2016) found that activation in the fusiform face area and the occipital face area elicited by upright and inverted face images could only be dissociated based on horizontal information. That the strength of the behavioral and neural face inversion effects selectively depends on the horizontal range of information, demonstrates that this orientation drives face specialized mechanisms.

Although past literature indeed supports the link between a horizontal advantage and face processes, the orientation tuning has so far mainly been tested with identity recognition. To further establish the link between the horizontal advantage and face mechanisms, face processes other than face identity recognition need to be tested for orientation preference. In this study, we take an interest in basic-level face categorization. Humans are highly efficient and fast at detecting and categorizing faces. Humans can saccade towards face faster than any other category, as soon as 100ms after presentation (Crouzet et al., 2010), whether the face was designated as a target or not (Cerf et al., 2009). Using fast periodic visual stimulation (FPVS) coupled with electroencephalography (EEG), studies have shown neural face categorization responses elicited by face images masked by previous and following stimuli presented in a stream of images displayed for only a few milliseconds (Liu-Shuang et al., 2022; Retter et al., 2020; Rossion et al., 2015). The advantage of the EEG-FVPS paradigm is that it enables implicit measurements, ridding the experiment of effects of decision and motor response, as presented in Liu-Shuang et al. (2014), in the context of a face identity discrimination task. For face categorization, the oddball paradigm consists in presenting images at a base frequency for example, 6Hz, (i.e., 6 images per second). Thanks to the synchronization of the steady-state evoked potentials to the stimulation periodicity (Norcia et al., 2015), a general response to the visual stimulation should be observed at 6Hz in the medial occipital region. At a smaller frequency for example 1.2Hz (every 5 images), face images (the oddballs) are presented (see Fig 5.1). If faces are categorized as such, a response should also be observed at 1.2Hz, in the ventral occipital-temporal cortex (Jonas et al., 2016). Another advantage of this FPVS paradigm is that if a face categorization response is measured, its amplitude is proportional to the amount of categorized faces (Retter et al., 2020) which enables fine comparison between conditions. We used this FPVS oddball paradigm, to measure and compare the implicit categorization of face images filtered in different orientations. We used images previously used in similar experiments (Liu-Shuang et al., 2022; Quek et al., 2018; Quek & Rossion, 2017). Neither the faces nor the objects were segmented from their background, and they were not necessary at the center of images. With these various images, from many categories, faces had to be differentiated from a large variety of non-face categories Furthermore, the face images used were widely different from one another. People of all ages, genders, with or without hair, hats or glasses are presented. The pictures were also taken from different viewpoints and angles, with different lighting and background. Presenting so many different exemplars of the single face category, such stimulus enabled generalization of categorization (Rossion et al., 2015), therefore allowing ecological categorization measures.

In a second experiment, to measure a potential influence of the horizontal range on behavioral face categorization, we compared the explicit face categorization of different orientation filtered images. The main difference between implicit and explicit categorization stimulus was the face periodicity. In this explicit face categorization experiment, participants view non-face images at a rate of 6Hz but face images appear randomly, not periodically. However, the images set used in both experiments was the same.

Measuring and comparing the implicit and explicit face categorization of images filtered in orientation, will enable to test the hypothesis that the horizontal range conveys important information for face basic-level categorization, and thus that the horizontal advantage is found from basic-liven to identity categorization. An absence of difference of face categorization response between filter orientation would indicate that the horizontal range only yields an advantage during face processes higher than categorization. A significant difference in response categorization for horizontally filtered images and other orientations however would confirm this hypothesis that the advantage for the horizontal appears at coarser stages of face processing. It would also confirm the hypothesis, that the horizontal range of the face may convey faces natural statistics (Dumont et al., 2024; Goffaux & Greenwood, 2016), therefore enabling better face categorization than other orientation ranges.

Material and Methods

Experiment 1. EEG-FPVS experiment

Participants.

A total of 32 right-handed subjects (7 males) aged 21.03 ± 3.86 years old completed the experiment. All participants were Bachelor students from our faculty (Faculty of psychology, UCLouvain). They received course credit as compensation for their participation. They had normal or correct to normal vision as tested with the Landolt C on the FrACT$_{10}$ v1.0 (Bach, 1996) with all participants having negative logMAR values (-0.178 ± 0.07). They scored highly (mean score = 45.50 ± 3.48) on a computerized version of the Benton task (Rossion & Michel, 2018), indicating normal face recognition abilities. All participants gave their written informed consent in accordance with the local ethics committee (Psychological Sciences Research Institute, UCLouvain).

Stimuli.

Images consisted of 312 greyscale images (256x256 pixels), 112 faces and 200 of non-face objects (plants, buildings, animal, as in e.g. Liu-Shuang et al. (2022)). Faces and non-face objects appeared in their natural surroundings at variable image locations and under variable lighting and viewpoint. To avoid border effects during filtering, images were padded to three times their original size by mirroring the images using the borders as symmetry axes. Image pixels were next normalized resulting in a global luminance and root mean square (RMS) contrast of 0 and 1, respectively. Images were then Fast Fourier transformed and multiplied by a wrapped Gaussian filter centered on orientations from 0° to 135° in steps of 45°, with a standard deviation of 28°.

This standard deviation is larger than in most past studies. This was chosen to ascertain that the long sequences of highly variable images were still perceived as meaningful. Images were then transformed back into the spatial domain, cropped to their original size and equalized in luminance and RMS contrast to 0.40 and 0.12 respectively, with no image exceeding 3% of clipping. Finally, a 12x12 pixel fixation purple dot was added to all image centers (Fig 5.1a). Images were displayed on an isoluminant grey background, on a BenQ XL2420T monitor, with a refresh rate of 120Hz and a resolution of 1920x1020, placed 100cm from the participants, resulting in 4.04°x4.04° images with a 0.18° fixation point.

Procedure.

Participants performed the experiment in a dark, quiet room. They were presented with 64-sec sequences of highly variable face and non-face images. In a sequence, non-face images were displayed at a 6Hz rate (6 per second) with a face image (i.e., the deviant or oddball category) presented every five images (i.e., at a rate of 6Hz/5=1.2Hz; seeFig 5.1b). Based on previous studies based on a similar paradigm (e.g., Retter et al., 2020; Rossion et al., 2015), we expected to measure a robust EEG, so-called base, response at 6Hz (and harmonics) reflecting the general brain response to the visual stimulation and a neural response at oddball frequency, 1.2Hz, and harmonics reflecting the neural face categorization response.

There were 5 sequences per orientation filtering condition (full spectrum, 0°, 45°, 90°, 135°) adding up to a total of 25 sequences, presented in a randomized order. Each sequence was flanked by 2sec face-in and fade-out. The contrast was progressively increased from 0% to 100% during fade-in and similarly decreased during fade-out to prevent eye-movement or blink do to the sudden on- and offset (Rossion et al., 2015). During each sequence, a total of 384 images, of which either 76 or 77 (76.8) were face images. For each image was displayed a sine-wave modulated contrast between 80% to 100%. Image size varied randomly between 90% and 110% of their original size, in 5% steps, resulting in five possible image sizes, to prevent image adaptation effects. To ensure participants kept their attention on the stimulation sequences, a 4.45° green circle appeared on screen center around the images. During the sequence, participants had to press the space bar anytime the circle randomly changed color (from light-green to orange). Each sequence had between eight and nine color changes, with a minimum of 800ms between changes and each color change lasting for 300ms (Liu-Shuang et al., 2022). In-between sequences, participants were free to take breaks as long as they wanted. Before starting the experiment, participants were familiarized with the sequences and their task during three example sequences (one with full spectrum images and two with filtered images).

The experiment was created and displayed using Experiment Manager, running of JavaScript (Java SE Version 8, Oracle Corporation, USA).

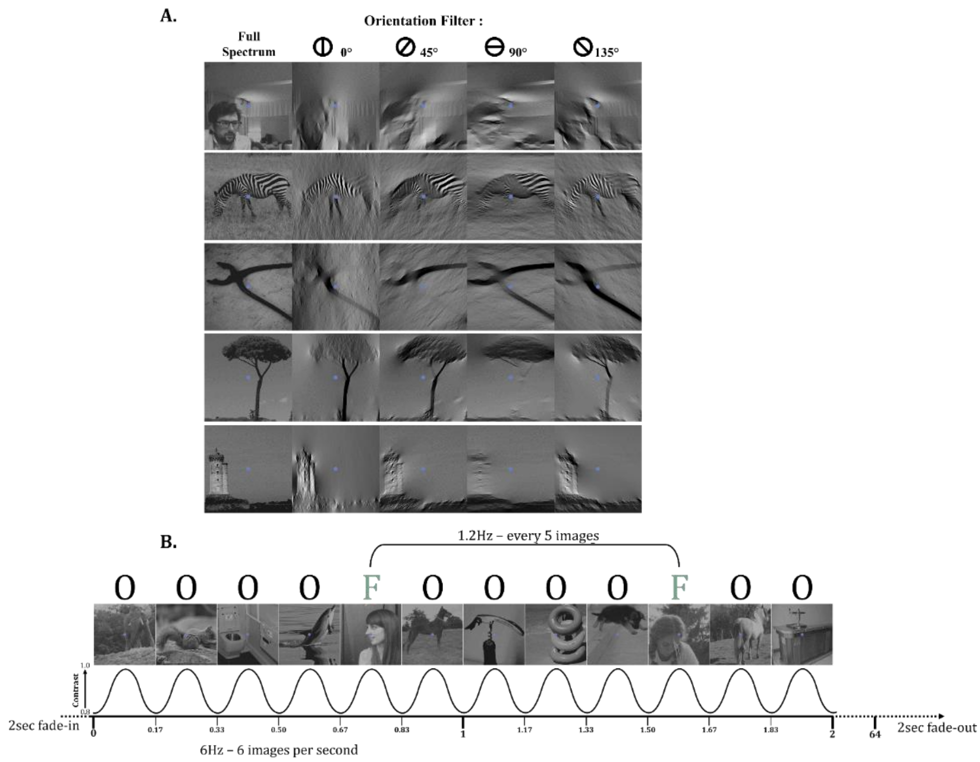


Figure 5.1. **Top**. Example images of the different categories (faces and non-face categories) in full spectrum and filtered condition, from 0° to 135° in steps of 45° with a standard deviation of 28°. **Bottom.** Example sequence with full spectrum images. Sequences were 64sec long with 2sec fade-in and fade-out.

EEG acquisition.

Scalp EEG was recorded with a Biosemi Active II system (Biosemi, Amsterdam, The Netherlands), with 64 electrodes positioned according to the 10-20 system, and four extra electrodes in the occipital region: I1, I2, PO9 and PO10, as well as two electrodes placed below and next to the left eye to record eye movements. Brain activity was sampled at a rate of 2048Hz. EEG signal analysis was done using Letswave6 (https://github.com/NOCIONS/letswave6), and Matlab R2023a (The Mathworks).

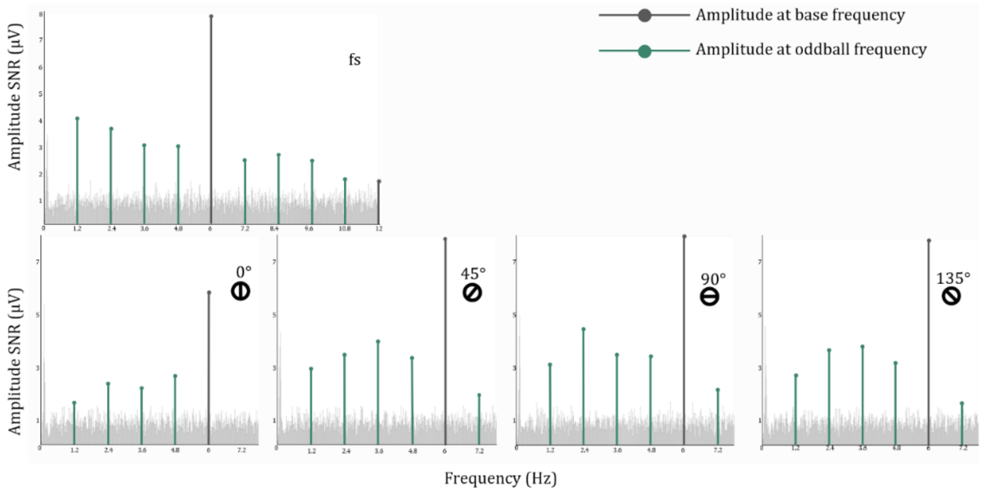
Data analysis

Preprocessing.

A 0.05Hz – 100Hz bandpass filter was applied to the signal and the DC component (50Hz and 100Hz) was filtered out. To make data processing easier and faster, the signal was downsampled from 2048Hz to 256Hz and a first segmentation was made with 70sec segments starting 2sec before fade-in (2 + 2 + 64 + 2). Seventeen participants showed an average blink rate superior to 0.2 blinks/sec. Their eye movements were corrected using the ICA matrix and removing from signal the segment best reflecting the eye movement, based on electrode location and signal shape. Channels with abnormal signal variations over 5 epochs or more were interpolated using the 3 neighboring channels. On average, 2.57% of the channels had to be interpolated (equivalent to 1.75 channel per subject). The grand average over all channels was used as a reference. Finally, the signal was segmented again, this time according to frequency: segment size was calculated to have the most complete cycles based on the 1.2Hz rate: 16213 bins, resulting in 63.33sec segments, starting after fade-in.

Frequency-domain analysis

Segments were fast Fourier transformed to obtain brain amplitude over a normalized frequency range of 0Hz – 128Hz with a high resolution (1/63.33 = 0.057Hz) enabling observation of the signal at the precise frequencies of interest. Epochs were then averaged for each condition and each participant separately. For illustrative purposes, signal was baseline-corrected by dividing by the 10 neighboring bins, excluding direct neighbors, and averaged across participants for each condition (see Fig 5.2). For data analysis, instead of baseline-correction after FFT and average, chunks of signal centered on the frequencies of interest (1.2Hz and 6Hz) and harmonics were summed. The aggregation was made over 20 chunks for the base response (harmonics from 6Hz to 120Hz) and over 12 chunks for the categorization response (harmonics from 1.2Hz to 16.8Hz, excluding 6Hz and 12Hz). This signal was then baseline-corrected by subtracting the 10 neighboring bins, excluding direct neighbors (Rossion et al., 2015), and averaged across participants for each condition. Z scores were computed for each condition at each frequency of interest (base with harmonics; oddball with harmonics) to determine significant signal amplitudes (Retter et al., 2020) and the response at 0° has been replicated at 180° for illustrative purposes.



<u>Figure 5.2.</u> Frequency domain characterization of the neural response. Grand averaged of divided-baseline corrected amplitude of responses at the frequencies of interest and harmonics at occipito-temporal channel (PO10). Base response (i.e., the general visual response) in grey and the oddball response (i.e. the face categorization response) in green. On top response amplitude for full spectrum images and below response amplitude for filtered images

<u>Regions of interest</u>

To determine regions of interest (ROIs), we selected for each participant the four electrodes with the strongest Zscore aggregated amplitude in full spectrum condition at 6Hz and harmonics for the general visual ROI, and at 1.2Hz for the face categorization ROI. The most selected electrodes are O1, O2, Oz, PO8 for the base response, and P10, PO10, P7, PO9 for the face categorization response (all individual ROIs are reported in Supplementary Information S.1.). Unless indicated otherwise we used the average of these selected electrodes relative to the general visual or face categorization response in our data analysis.

To investigate the lateralization of face categorization response (Liu-Shuang et al., 2022; Retter & Rossion, 2016), we selected at the group level four channels on each side, symmetrical between left and right, based on the Zscore of aggregated amplitude at 1.2Hz and harmonics for non-filtered images. This group-level, symmetrical channels selection ensured objective analysis of the lateralization of the categorization response, and prevented differences due to selection of different channels on each side. These lateralized ROI are P10, PO10, PO8, P8 and P9, PO9, P7, PO7 in the right and the left hemisphere, respectively.

Response amplitude comparisons

We first used the Z scored response amplitudes to determine whether individual ROI base and oddball responses in each filter was significant or not. We considered a Zscore > 2.32 as significant at the group level (Retter et al., 2020). To determine the effect of filter orientation, we ran repeated measure ANOVAs on the baseline-subtracted summed amplitudes for the general visual response and the face categorization response separately. Tukey post-hoc were then run to further analyze the ANOVA outputs. Finally, to compute the difference between orientation filters, we ran two-tailed paired t-test between each possible orientation filter pairs, resulting in a total of ten comparison. For the paired t-test the alpha was Bonferroni corrected for multiple comparisons: $\alpha = .05 / 10 = .005$.

Experiment 2. Behavioral experiment

Participants

A behavioral experiment was conducted offline in a different group of participants to measure the explicit face categorization behavior as a function of the orientation filter. A total of 26 right-handed subjects (2 males) aged 20.27 ± 1.46 years old completed the experiment 2. All participants were Bachelor students from our faculty (Faculty of psychology, UCLouvain). They were compensated with course credit. They had normal or correct to normal vision as tested with the Landolt C on the $FrACT_{10}$ v1.0 (Bach, 1996) with all participants having negative logMAR values (-0.186 ± 0.07). All participants scored highly (mean score = 46.27 ± 3.55) on a computerized version of the Benton task (Rossion & Michel, 2018), indicating normal face recognition abilities. All participants gave their written informed consent in accordance with the local ethics committee (Psychological Sciences Research Institute, UCLouvain).

Procedure

The procedure is based on the behavioral experiment described in (Retter et al., 2020). Participants viewed the same stimuli as in (EEG) experiment 1. Sequences lasted for 30 seconds with a total of 30 sequences (6 per condition). Images followed the same overall frequency of 6Hz as in the EEG experiment, however face images appeared randomly along the sequence. There were 5 to 7 face images in 5 of the 6 sequences per condition and 0 in one sequence, resulting in a mean 30.11 face occurrences per condition. Participants were tasked with pressing the space bar as fast as possible when a face was detected. Between each sequence, the number of face images presented in the previous sequence was displayed as well as the number of remaining sequences. Before starting the experiment, participants were familiarized with the task with 5 sequences, one per filter condition.

Data Analysis

To compare the explicit face categorization between filter conditions we measured the response time and accuracy of face categorization of participants. We ran a repeated measure ANOVA to determine the presence of a significant effect of filter orientation, with follow-up Tukey post hoc test in case of significance. Finally, to compare the effect of filter orientation we ran two-tailed paired t-test with a repeated measure Bonferroni correction ($\alpha = .05 / 10 = .005$).

Data analysis was done using RStudio 2024.09.1 running with R 4.4.2. EEG recordings can be transferred upon request, data and codes for Experiments 1 and 2 can be found here :
https://osf.io/3zpfr/?view_only=597d61f466b447f08427711d838000ee.

Results

Experiment 1 results

The general visual response was significant in full spectrum and in all orientation filtering conditions showing the brain synchronization to the base stimulation frequency of 6Hz (and harmonics). The oddball face categorization response to full spectrum and orientation-filtered images showed weaker yet significant responses (Fig 5.3). Visual analysis of the Z scores shows a bell-shaped curve for the face categorization response, resembling those observed for face recognition in function of the orientation.

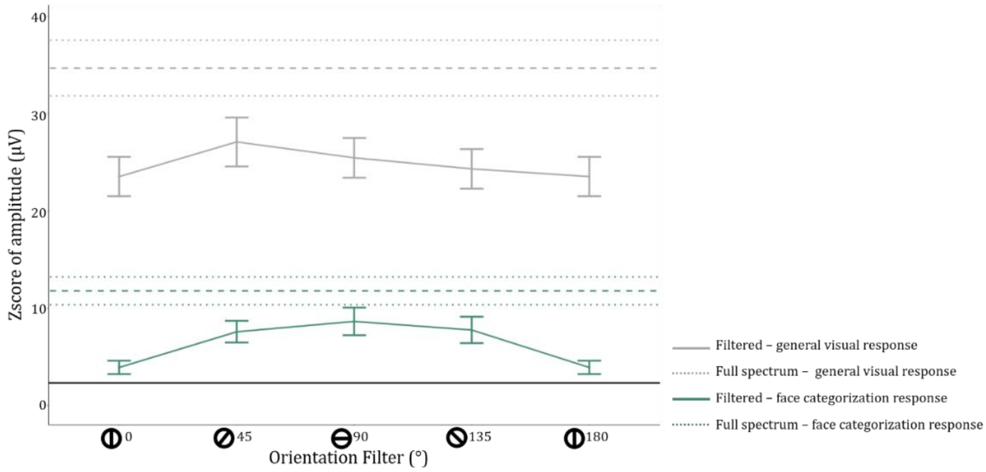
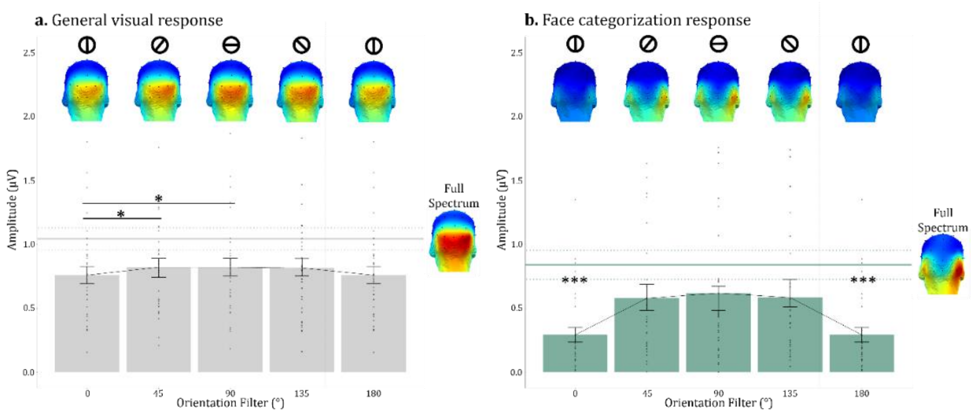


Figure 5.3. Z score of the summed amplitudes (sum of the amplitude at the frequency of interest and harmonics) for the general visual response in grey and the face categorization response (response to face images) in green. The dotted lines represent the Z score for non-filtered images. The black line represents the significance cut-off at 2.32: Z scores above that line are considered as a significant brain response. Errors bars represent standard error.

Analysis of the general visual response amplitude with a repeated measure ANOVA showed an effect of orientation filter ($F(3) = 3.67$, pvalue $< .05$). Tukey post-hoc tests demonstrated that the amplitude of the general visual response differed significantly between 0° and 45° and 90° orientation filters (Fig 5.4). Paired t-test comparing the general visual response between orientation filters and full spectrum images two-by-two did however not demonstrate any significant effect of orientation filters (Fig 5.5). The same analysis on the face categorization response amplitude revealed a strongly significant effect of orientation filter ($F(3) = 22.89$, pvalue $< .0001$). Post-hoc analysis revealed a significant difference between vertically filtered images and all the other orientation filter conditions (Fig 5.4). A paired sample t-test was performed to compare face categorization response between filter orientations. There was no significant difference in face categorization response amplitude between 45°, 90° and 135°.



<u>Figure 5.4</u>. **Left: general visual response** <u>Top</u>. Scalp topography of the group-averaged baseline-subtracted summed amplitude. The base response is occipital and medial. There is little difference across orientation filters, except for vertically-filtered images eliciting a weaker activation than other orientation ranges and full spectrum images. <u>Bottom</u>. Baseline-subtracted summed amplitude for all participants. **Right: face categorization response.** <u>Top</u>. Scalp topography of the group-averaged baseline-subtracted summed amplitude. The response peaks at occipitotemporal electrodes and is right lateralized. Face categorization response amplitude is strongest in full spectrum condition. It increases gradually from vertical to horizontal filter. <u>Bottom</u>. Group-averaged baseline-subtracted summed amplitude. Significant differences are shown with asterisks. Error bars represent the standard error.

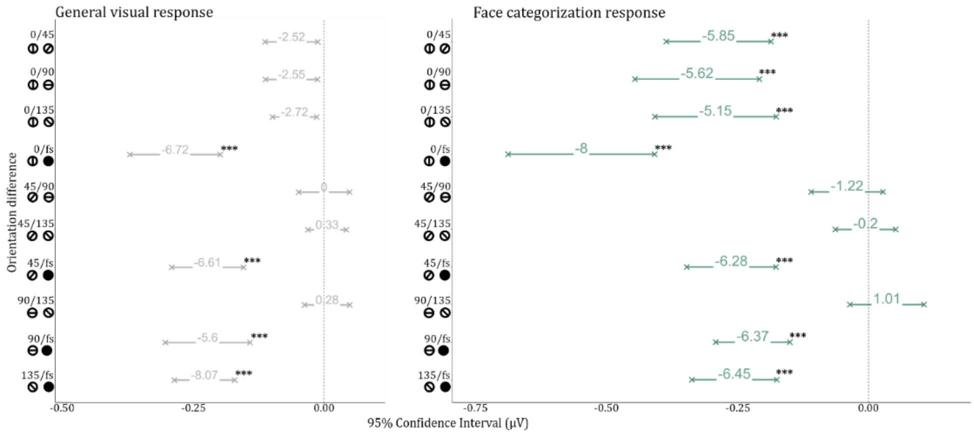


Figure 5.5. 95% confidence interval of the paired t-test run between the baseline corrected summed amplitude with different orientation filters and full-spectrum images with the respective t(31) value of the difference between each orientation. Results for paired t-test between orientations for the base response are on the left, and for the face categorization response on the right. Significance is indicated with asterisks.

Visual analysis of brain topography (Fig.5.4b) indicates that the occipito-temporal face categorization response is right-lateralized. To investigate this further, we compared the face categorization response measured for each orientation filter in lateralized group-level ROIs with a two-way repeated measure ANOVA. This analysis revealed an effect of orientation filter ($F(3) = 19.11$, pvalue $< .0001$) but no effect of ROI ($F(1) = 1.76$, pvalue $= .19$) and no interaction between filter and ROI ($F(3) = 1.83$, pvalue $= .15$). Although the ANOVA showed no significant lateralization, based on previously reported results (Liu-Shuang et al., 2022) and our data (Fig. 5.4b and Fig. 5.6), we decided to run further analysis and ran a paired t-test. We found a moderate but significant difference between the face categorization response in the left ROI (M = .37, SD = .37) and the right ROI (M = .46, SD = .49); $t(123) = 2.5183$, pvalue $< .05$.

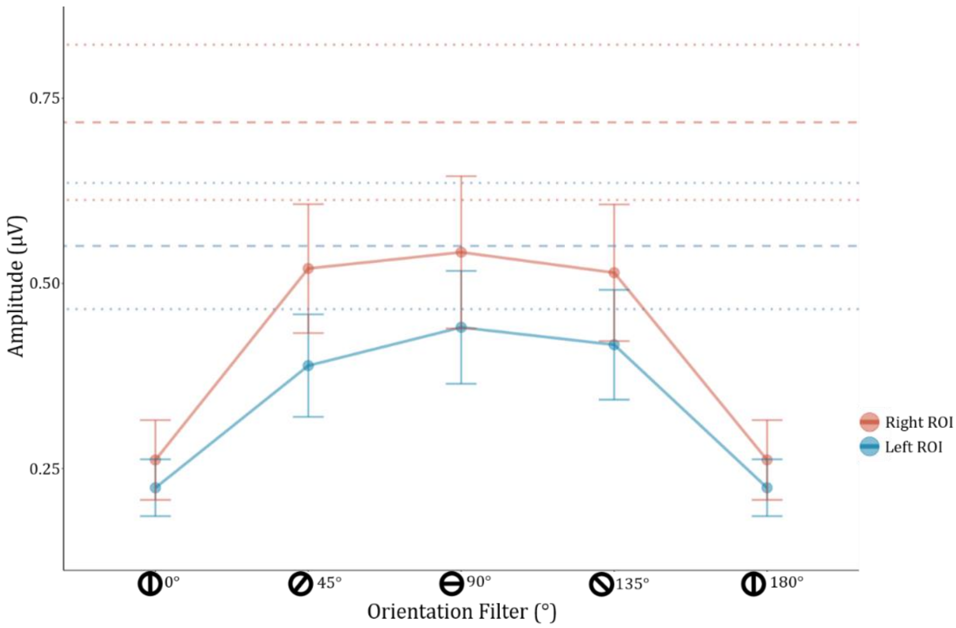
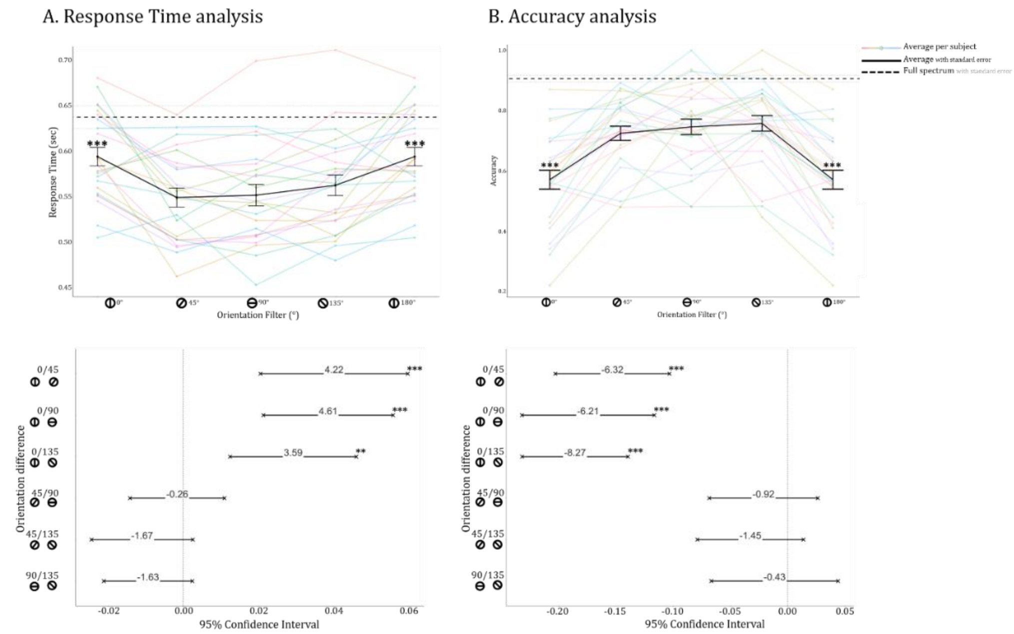


Figure 5.6: Amplitude of face categorization response for each orientation filter in the right ROI (P10-PO10-P8-PO8) in red, and the left ROI (P9-PO9-P7-PO7) in blue. Average values and standard errors are drawn. Dotted lines represent average of for full spectrum images.

Experiment 2 results

Behavioral data was analyzed in terms of response time and accuracy. We ran a repeated measure ANOVA to compare the effect of orientation filter on response time and found a significant effect ($F(3) = 12.26$, pvalue $< .0001$). A Tukey post-hoc analysis demonstrated a significant difference between the response time of face categorization of images filtered at 0° and those of images filtered at 45°, 90° and 135° (see Fig 5.7.A.Top). Paired sample t-test were performed to compare face categorization response between filter orientations and full spectrum images, results are reported in Figure 5.7.A.Bottom.



<u>Figure 5.7: Left. Response Time.</u> <u>Top</u>. Response time for each filter orientation. Individual responses are shown in light color and their mean in black. Response time for non-filtered images is shown as the dotes line. <u>Bottom.</u> 95% confidence interval of the paired t-test run between the different orientation filters and full-spectrum images. The value t(25) of the difference between each orientation is written. **<u>Right. Accuracy</u>**. <u>Top</u> Face categorization accuracy for each filter orientation. Accuracy of 1 means that participants detected all the images presented in the sequences, an accuracy of .5 mean that participants only detected half of the face-images in the sequences. Individual responses are shown in light color and their mean in black. Accuracy for non-filtered images is shown as the dotes line. <u>Bottom.</u> 95% confidence interval of the paired t-test run between the different orientation filters and full-spectrum images. The value t(25) of the difference between each orientation is written. Significance is indicated with asterisks.

We ran a similar analysis with face categorization accuracy. The repeated measure ANOVA showed a significant effect of orientation filter on categorization accuracy ($F(3) = 24.75$, $pvalue < .0001$). A Tukey post-hoc analysis demonstrated a significant difference between the accuracy of face categorization of images filtered at 0° and those of images filtered at 45°, 90° and 135° (see Fig 5.7.B.Top). Paired sample t-test were performed to compare face categorization response between filter orientations and full spectrum images, results are reported in Figure 5.7.B.Bottom.

Discussion

In order to determine whether the advantage of the horizontal range documented for face identity recognition generalizes to the coarser abstraction level of face basic-level categorization, we investigated the orientation tuning profile of EEG neural signatures of face categorization. We used the EEG FPVS oddball paradigm with a wide diversity of face and non-face natural images filtered to preserve limited ranges of orientation. This approach enabled to quantify neural signatures of the genuine categorization of faces (Retter et al., 2020) among many other categories, as well as face generalization amongst the many different face exemplars.

Analysis of the response to base images, thought to reflect the general brain response to the stimulus sequence, showed that our experimental design elicited high amplitude responses synchronized with the stimulus frequency. Non-filtered images elicited a stronger general response than filtered images. There was only a slight effect of filter orientation, found non-significant with t-test, enabling us to conclude that differences measured between filter orientations for the oddball response is related to categorization and not solely to earlier visual processes.

The neural face categorization response was weaker for vertically filtered images compared to orientation filter and full spectrum (non-filtered) images. Since there were no other significant difference across orientations, our results support a disadvantage for the vertical range for face categorization rather than a tuning to the horizontal range.

To further examine the potential advantage of the horizontal range in face categorization, we characterized the orientation tuning profile of explicit face categorization behavior. In terms of response time, participants were significantly faster for images filtered at 45°, 90° and 135° compared to 0°. In terms of accuracy, participants where better at categorizing faces filtered at 45°, 90° and 135° compared to 0°. Further analysis of false alarms demonstrated that this increased accuracy in these ranges was not due to more key presses in these sequences (See Supplementary Information S.2.). As in the first experiment, our result support, if not a selective advantage, a broad horizontal tuning of face categorization and a disadvantage of the vertical range. The similarity of the orientation tuning profiles of behavioral and EEG face categorization support past evidence that the neural face categorization response is proportional to the number of faces categorized as such in the sequence (Retter et al., 2020). The fact that the broad horizontal tuning of face categorization replicates across different groups of subjects indicates the robustness of this effect.

At first glance, it may seem surprising that the amplitude of face categorization response plateaued from left to right obliques instead of showing a peak at the horizontal range, as shown in face identity recognition studies. However, we do not think that the absence of a clear horizontal peak is due to the coarser level of face categorization investigated here. Instead, we believe that the comparable amplitude of the oddball response across horizontal and oblique ranges is due to our stimulus design. Past studies with orientation filtered stimuli typically presented (only) face stimuli one-by-one and in pairs. This makes the visual input more predictable and likely more resistant to the degradation caused by orientation filtering than in the present study. We thus chose a large standard deviation for our orientation filter to simplify the visual stimulus. Due to the large (28°) standard deviation of the orientation filters, there was a substantial overlap in the information passed through our orientation filters. As a consequence, the 45° and 135°-filtered images still contained large amounts of horizontal information. Past evidence for horizontal tuning of recognition performance relied on the use of sharper filters (Dakin & Watt, 2009; Goffaux et al., 2016; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016). Similarly to what we observe here, in a previous experiment with images filtered from 0° to 150° in steps of 30° with a 28° standard deviation, we observed a very broad horizontal tuning, with a similar plateau between recognition performance at 60°, 90° and 120°, using Gaussian filters with a 25° standard deviation (Dumont et al., 2024). Pachai et al. (2017) demonstrated that the advantage of the horizontal over the vertical range in unfamiliar face recognition reached its maximum with sharp-edges orientation filters with a bandwidth at 90°, which we could grossly approximate to a Gaussian filter with a standard deviation of at least 45°. They did however not compare performance between horizontal and oblique orientations, which could have confirmed or not the fact that with a standard deviation as large as ours gave the same advantage to images filtered in oblique orientations. To further explore this hypothesis, we plan on running similar experiments with faces filtered with smaller standard deviations (e.g. 14° and 22°) to see how the categorization response as a function of orientation filter evolves. If with a smaller standard deviation, the advantage become more specific to the horizontal range, this would validate our hypothesis. However, if the results remain identical, this would indicate that the orientation advantage found at the coarse level of face categorization is less sharply tuned to the horizontal than fine-grained identity recognition.

These results suggest that the advantage of the horizontal range, is found across face categorization levels, from basic-level categorization to fine face identity recognition. These results support the hypothesis that the horizontal range of face information carries faces natural statistics, which enable better face categorization. Whether the breadth of such horizontal advantage is a function of categorization level deserves further investigation. To challenge these hypotheses further, comparing face identity recognition and face categorization is necessary. As the FPVS oddball paradigm can also be used to measure identity recognition (Liu-Shuang et al., 2014; Xu et al., 2017; Yan et al., 2022), it would be interesting to test participants with face identity discrimination sequences and with face categorization sequences, using identical parameters and to compare the orientation tuning of both responses. This comparison would shed light on whether the horizontal advantage is the same for categorization and identity recognition, or whether it differently affects both processes.

To summarize determine whether the horizontal advantage was only found at fine face processing levels such as identification, or whether coarser levels, such as basic-level face categorization were also tuned to the horizontal range of face information, we compared face categorization of orientation filtered images. We found a very broad horizontal tuning with horizontal and neighboring orientation ranges yielding better categorization than the vertical range. These findings support the hypothesis that the horizontal advantage characterizes face specialized mechanisms from coarse basic-level image categorization, albeit in a less specific manner, to identification.

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Supplementary Information

S.1. Regions of Interest for each participant

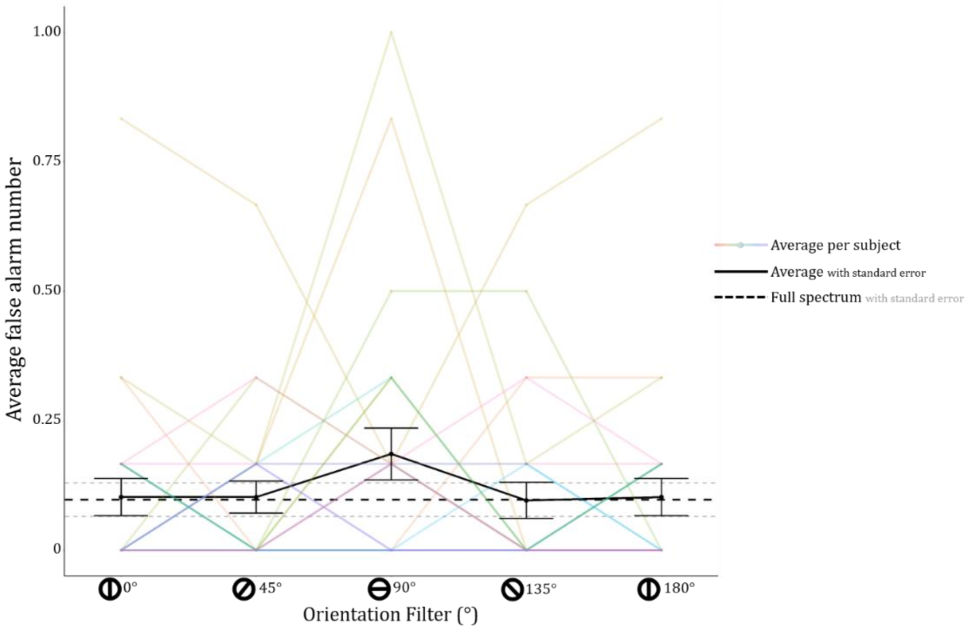
A region of interest was select for each participant based on the Zscore of the aggregated amplitude response. The 4 electrodes with the strongest amplitude at 6Hz and harmonics for full spectrum images were selected for the general visual ROI The 4 electrodes with the strongest amplitude at 1.2Hz and harmonics for full spectrum images were selected for the general visual ROI.

Table 5.S1. ROI selected for each participant for the base response (light grey) and oddball response (dark grey)

Sujet	ROI Base				ROI Odb			
ADVI0407	O2	PO8	O1	Oz	PO8	P9	T8	P7
BEFR2711	O1	PO7	POz	PO3	P10	PO10	P8	PO7
CHMA0501	O1	PO7	PO3	PO9	P9	P7	P5	P3
DAAN0411	Oz	PO7	PO3	PO4	P8	P9	PO10	Cz
DAFE1803	PO7	Oz	O1	O2	PO10	P10	PO8	P8
DASY0201	I1	PO8	PO7	Iz	PO9	P10	I1	POz
DIDA0106	I2	Oz	PO10	Iz	P10	P4	CP2	PO10
DOAU1506	O2	O1	Oz	PO3	P7	P9	PO9	P10
DOJO2601	O2	PO8	Oz	PO4	P10	P8	TP8	PO10
EIE29121	O1	Oz	PO8	O2	P8	TP8	PO9	P7
ERAN1001	PO8	O1	Oz	O2	P5	P10	FC6	CP2
ETAN2712	PO10	P10	PO8	P8	P8	TP8	P10	PO10
FRDO2407	P3	O1	PO3	PO10	PO10	P10	I2	P8
GAGE2702	I2	O2	I1	Iz	PO9	P7	PO10	O1
GUGA1401	I1	PO9	O1	P9	P10	P9	PO10	PO7
HANA1909	PO9	PO7	PO3	O1	Pz	PO10	P2	CP2
JEGE2505	O2	Oz	Iz	PO4	PO9	PO7	PO10	P9
JELA1710	PO8	PO10	I2	O2	P10	PO10	CP6	TP8
JESA2006	O2	Oz	O1	I1	P9	PO9	I2	P10
JUMA0603	I2	I1	PO10	O1	PO8	O2	C3	P10
KAMA2512	PO4	Oz	PO7	P7	P7	PO8	P10	PO10
KAVA2806	P7	P9	PO7	O1	P7	PO9	I2	PO7
LANA2902	Iz	O2	O1	Cz	P10	FC2	C2	P6
LAST0212	PO8	O2	PO7	P7	P10	PO7	P7	TP8
LUGA2208	PO8	PO10	P8	P10	P9	P7	PO9	I1
MOHA0106	PO8	PO7	O2	O1	I2	PO10	Iz	PO9
NIEV0104	I2	PO10	Iz	PO8	Oz	O2	O1	PO10
PHAU0712	P4	PO4	CP4	P9	TP8	PO10	T8	PO7
PHCH1204	Oz	O2	O1	PO8	PO7	P7	PO10	P10
RACA1404	PO4	POz	Oz	O1	P9	P7	PO9	Iz
STCO2802	I2	I1	Iz	PO8	P10	PO10	P9	PO9
TAAN0507	PO8	O1	O2	Oz	PO8	P10	PO10	P8

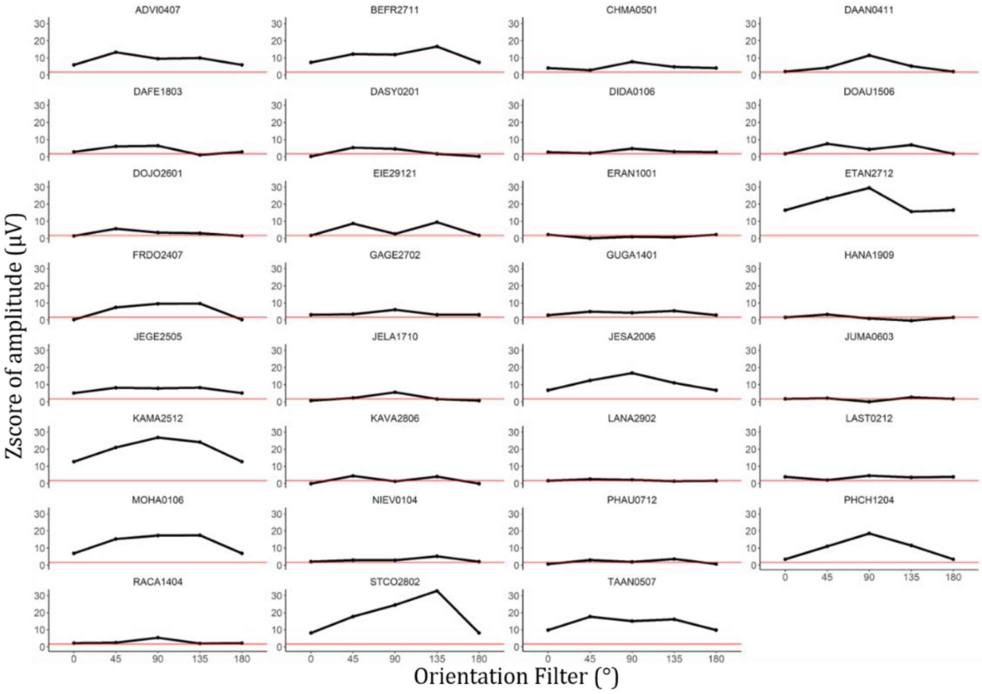
S.2. False Alarms

Analysis of behavioral face categorization showed a significant difference between 0° filter and other orientations. To determine whether the higher number of face categorization responses was due to an increase number of false alarms in these orientations we ran a repeated measure ANOVA was performed to compare the effect orientation filter on false alarms. No significant effect of orientation filter on false alarms was found F = 1.79, pvalue = 0.156.



Supplementary Figure 5.S1. Average number of false alarms at each orientation filter. In colors are shown the individual results and in black full lines the average with standard error. The Dotted lines are the average false alarm number and standard error for full spectrum images.

S.3. Individual Zscore of aggregated amplitude face categorization response.



<u>Supplementary Figure 5.S2.</u> Zscore of the ROI's aggregated amplitude at 1.2Hz and harmonics: the face categorization response. The red line indicates a significant response at $p < .05$, following (Retter et al., 2020).

Chapter 6: General discussion

From the first finding that face identity categorization is tuned to the horizontal range (Dakin & Watt, 2009a), research has confirmed these results and exposed a link between horizontal information and face-specialized processes (Duncan et al., 2019; Goffaux et al., 2016; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Jacques et al., 2014; Pachai et al., 2013, 2017). The present work aimed at better understanding the nature of the advantage conferred by the horizontal range for face identity categorization and thus, its horizontal tuning. Throughout exploration of the privileged horizontal face information in these past chapters, we hypothesized that the horizontal range of the face conveys privileged information enabling efficient recruitment of face specialized mechanisms for categorization both at the basic and identity levels. We studied the reference frame of the horizontal preference, the nature of the information conveyed by the face's horizontal as well as its function in terms of face identity recognition, to finally consider the existence of a potential horizontal advantage for face basic-level categorization.

Summary of findings

Although the horizontal tuning of face identity categorization has been fairly studied, one key insight of this tuning was not explored: its reference frame. Indeed, the horizontal tuning has been almost exclusively explored with the observers' retina and the face stimuli reference frames aligned using upright or inverted images. Before trying to further analyze the horizontal tuning of face identity recognition in detail, it seemed important to determine whether the horizontal preference in face recognition stems from an orientation preference based on the observer's retinotopy or based on face information. In our first experimental chapter, we misaligned the observer's retina-centered and the face-centered reference frames by rotating familiar faces at ±45° and ±90° while observers were sitting upright. Faces were additionally filtered to preserve orientation around 0° (vertical) to 150° in steps of 30°. We compared the profile of orientation tuning of the recognition of these familiar rotated faces. Face rotation caused a significant drop in face recognition performance overall orientation filters, with recognition performance for ±90° faces lower than recognition for ±45° faces, which was lower than for upright faces. However, we found that regardless of the misalignment angle between retina and face centered reference frames, recognition performance peaked when faces contained the horizontal range and declined when shifting towards vertical ranges. Rotation angle only slightly modulated the strength of the horizontal advantage, more specifically the peak amplitude of the Gaussian orientation tuning profile, i.e. the performance difference between horizontal and vertical ranges. The amplitude of the horizontal peak indeed decreased the further away faces were from upright, with a significant difference between ±90° and other rotations angles. Overall, Chapter 2's results demonstrate that although there is a slight influence of retinotopy on the horizontal tuning of face identity, it seems that identity categorization performance is tuned to the face's horizontal range.

As it was shown that it is the facial horizontal range that drives the horizontal advantage of face identity categorization, in Chapter 3, we investigated the nature of the information contained in this range. Past studies on the horizontal tuning had already demonstrated a strong link between inversion and the horizontal information: inversion disrupts the horizontal tuning and the lack of horizontal information decreases the face inversion effect. Another image manipulation, contrast negation, disproportionally disrupts face recognition compared to other objects, like inversion does. Picture plane inversion and contrast negation presumably disrupt separate sources of face information: shape and surface and shading information, respectively. We used these image manipulations to explore the possibility that, in addition to carrying shape cues, as suggested by the detrimental effect of inversion on the horizontal tuning, the horizontal range also carries surface and shading identity cues. We measured the identity recognition of familiar faces, filtered in orientation from 0° to 150° in steps of 30° and presented upright, inverted or contrast negated. We determined the orientation tuning profiles of the inversion and negation effects by subtracting the orientation tuning of inverted and negated faces from the orientation tuning of upright faces. The effect of inversion was overall stronger but both effects followed a strikingly similar orientation tuning profile, peaking in the horizontal range and decreasing as the orientation approached vertical. Inversion and negation thus both mostly disrupt access to the horizontal face information. Comparison of both effects indeed showed high, significant correlations between the Gaussian parameters of the orientation tuning of inversion and contrast negation effects. These results support our hypothesis that the horizontal range conveys both shape and surface and shading information, both diagnostic of identity. The privileged access to face shape and surface cues may explain the advantage of the horizontal range in face identity recognition. Alternatively, and given the highly similar orientation tuning profiles of inversion and negation effects, our results may instead suggest that the horizontal range carries a more primitive source of information than shape and surface and shading: the face natural statistics.

To further analyze the horizontal face information, in chapter 4, we addressed the informativeness of the horizontal cues, as well as the contribution of the horizontal range to view-tolerant face identity recognition, more precisely, whether horizontal information could link different appearances of a given face across views. We measured the orientation tuning profile of face recognition using an old/new task with faces filtered in orientation from 0° to 157.5° in steps of 22.5°, presented under different viewpoints from full front faces (0°) to profile views (±75°), in steps of 25°. Subjects' performance indicated that face identity categorization was tuned to the horizontal for all views. The main difference across views was the increased recognition performance in the vertical range towards profile views, thus decreasing the horizontal advantage over the vertical range. To consider the human tuning to the horizontal across viewpoints under the image content point of view, the orientation tuning of face identity matching was also measured using model observers. A within-view model matched face images within the same viewpoint, thus exploring the informativity of the different orientation bands. An across-view model matched face images across viewpoints thus exploring the stability and view-tolerance of the cues in the orientation ranges. The within-view model observer was tuned to the horizontal for full front faces but not for other views, indicating that the optimal identity cues are conveyed by the horizontal range for full front faces but that towards profile views, other orientation ranges carry more informative identity cues. The view-tolerant model was strictly tuned to the horizontal across all viewpoints, designating the horizontal information as the most stable identity information across all viewpoints. To compare human and model observers, correlations were computed. The highest correlation was obtained between humans and the view-selective model for full front faces. However, at other views, the human/view-selective correlation decreased. Correlation between humans and the view-tolerant model increased from full front views to profiles view, and was stronger than the human/view-selective towards profile view. Comparison between humans and model observers thus indicated that humans' reliance on the horizontal range in face identity recognition is due to its identity diagnostic information for full front faces and to the stability of its information across viewpoints. Taken together, our evidence shows that the horizontal advantage in face identity recognition is due to this range being the most informative for full frontal view, as well as supporting view-tolerant face identity categorization.

In the last experimental chapter, we investigated whether the horizontal tuning, until then only tested at higher categorization levels such as identity and emotion categorization, also transposed to face basic-level categorization. We measured the orientation tuning of implicit categorization, using the FPVS oddball paradigm, with non-face objects presented at the frequency of 6Hz and face images at 1.2Hz (every five images). We used natural images, embedded in their background, filtered in orientation from 0° to 135° in steps of 45°. Using a highly similar behavioral design, we also measured explicit face categorization behavior. With the EEG experiment, we measured a significantly higher amplitude response with the horizontal and neighboring ranges over the vertical one. The orientation tuning was however very broad and described a plateau between 45°, 90° and 135° orientation filters, with no significant differences between the categorization response between these orientations. The behavioral experiment gave almost identical results, with significantly faster responses and higher accuracy for the horizontal and neighboring ranges compared to the vertical range. Based on these results, implicit and explicit face categorization are facilitated by the horizontal and close to horizontal ranges compared to the vertical. Although the orientation tuning did not resemble the Gaussian curve described in identity recognition studies, it thus seems that the horizontal advantage in recognition also translates to basic-level face categorization.

In these four chapters, we demonstrated that the horizontal range of the human face stimulus enables efficient recruitment of face-specialized mechanisms, from coarse basic to fine identity levels of categorization. The horizontal range of the human face conveys shape and surface information to a greater extent than other orientation ranges. The horizontal information is highly informative identity cues at full front views. The horizontal range of facial information was also found to carry identity cues that are the most stable across variable face appearances, thus enabling view-tolerant face identification. Moreover, we found that the advantage of the horizontal range is not confined to face categorization at the fine identity level, as it was also measured in behavioral and neural signatures of face basic-level categorization. Below, we discuss the implications of these findings for current models of visual perception.

A horizontal tuning of face-specialized processes

This work comes within the scope of horizontal tuning research of face identity recognition and furthers the contribution of the facial horizontal range to many aspects of face-specialized mechanisms. First of all, as extensively described in this dissertation, the information that drives human face identity categorization is optimally conveyed by the orientation range centered around the horizontal range (Dakin & Watt, 2009; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2013, 2017). Although the horizontal tuning of face identity recognition in Chapter 3 was broader than in other studies, we found that the horizontal range allowed better face identity categorization than other ranges, thus supporting these past studies. Findings from Chapter 5 demonstrate that this horizontal advantage is also found at coarser, basic-level, levels of face categorization.

Past studies of face identity recognition have demonstrated a strong link between the horizontal advantage and face-specialized mechanisms. For instance, the horizontal tuning is sharper for familiar faces (M. Pachai et al., 2017), known to elicit tolerant face identity recognition (Young & Burton, 2018). In Chapter 2, face rotation decreased the advantage of the horizontal over the vertical, especially for ±90° rotations. Combining our results from Chapters 2 and 3, based on highly similar experimental procedures, the horizontal tuning is strongest and sharpest for upright faces, decreases slightly with ±45° rotation, considerably with ±90° rotation, and is finally completely disrupted with picture plane inversion. As past research had already noted that the holistic processing of faces is mainly driven by horizontal face cues (Goffaux & Dakin, 2010a), taken together our results could also suggest a horizontal tuning of holistic processing. Indeed, our findings echo with past evidence showing that holistic processing is disrupted when the face is rotated by more than 90° and weakest with inverted faces (Edmonds & Lewis, 2007; Rossion, 2008; Rossion & Boremanse, 2008; Schwaninger & Mast, 2005). Picture plane inversion is known to disrupt the holistic processing (Rossion, 2008) as well as the horizontal tuning of face identity-level categorization (Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Jacques et al., 2014; Pachai et al., 2013, Chapter 3).

Using EEG, Jacques et al. (2014) found that the neural face inversion effect measured at the level of the N170, an occipitotemporal event-related potential linked to face-specialized processing (Bentin et al., 1996; Jacques et al., 2007; Jacques & Rossion, 2006; J. Liu et al., 2002), was modulated by horizontal information: without access to horizontal information, the N170 latency was slower, and inversion effect on N170 was decreased by half (Jacques et al., 2014). Furthermore, passive viewing of filtered upright, inverted and scrambled face images with fMRI demonstrated a horizontal tuning of the FFA activity and that the spatial pattern of FFA and OFA response to upright and inverted faces could only be dissociated for horizontally-filtered images (Goffaux et al., 2016). The OFA is an area mostly associated with early face processes and FFA is mostly associated with later processes (Liu et al., 2002; Pitcher et al., 2007, 2011; Sadeh et al., 2010). Together with the results of the horizontal tuning of basic-level face categorization of Chapter 5, these findings suggest that horizontal tuning generalizes across levels of face categorization. As suggested by the high correlation between inversion and contrast negation effects in Chapter 3, the advantage of horizontal range of face information could reflect a more fundamental contribution of the horizontal range to face perception namely the carriage of the shape and surface natural statistics of the upright human face (Dakin & Watt, 2009a; Goffaux et al., 2016; Goffaux & Greenwood, 2016a; Jacques et al., 2014). As natural face statistics encompass elements common to all faces, the facial horizontal range would thus not only carry identity cues, but also cues to face as a category.

A privileged access to diagnostic cues to face category and identity

The process of categorization implies the comparison of an incoming stimulus to internal representations. At a basic-level, it would be comparing a face to a basic face internal representation that would encompass face natural statistics. For identity categorization, the face stimulus is compared to an individual face representation encompassing the individual's natural statistics i.e. the individual's characteristics that remain stable through changes such as lighting, viewpoint, hair.... Dakin & Watt (2009) showed that the human face is characterized by a succession of light and dark horizontal blobs along the face's elongation axis. In the same study, the authors suggest that these light and dark alternating blobs, that they called "bar code" have their structure specifically harmed by inversion and negation. The bar code is however less susceptible to noise and movement, as these manipulations still preserve the order, relative size and polarity of the blobs. Taken together with our results this suggests that the horizontal range conveys faces' natural statistics, diagnostic information to both build a robust face internal representation at the category and at the identity level.

Basic-level face categorization

Basic-level categorization is hypothesized as a comparison between a stimuli and internal representations, enabling its quick process (Bindemann & Lewis, 2013; M. Lewis & and Edmonds, 2005; Prunty et al., 2023). A theory for a face basic-level categorization representation is that it's made out of an average of faces (Prunty et al., 2024), building a representation of the natural statistics of the face category. To test this hypothesis, the authors built face averages with faces taken at random and, using a visual search task with faces embedded in scenes. They demonstrated better face detection performances with average faces than with individual faces. Along this face-average idea, if we look at Figure 1.2a of Chapter 1, the average we made from the faces used in Chapters 2 and 3, we see that the horizontal information of the face is highlighted, while other orientations, mainly the vertical range of information, are faded out. The difference between our average and the one made in (Prunty et al., 2024) was that we used more natural images with variations in viewpoint. As averaging faces across identities should make natural face statistics more salient while toning down individual differences, this image example reinforces the potential role of the horizontal range in the creation of such internal representation. Experimentally, in Chapter 3, we saw that inversion and negation effects while being separable at the behavioral (Bruce & Langton, 1994a; Hole et al., 1999; Kemp et al., 1990) and neural (Itier & Taylor, 2002; Liu-Shuang et al., 2015) levels, similarly disrupted horizontal tuning. The highly similar orientation profiles of inversion and negation effects could be the result of the disruption of not only shape and surface-shading cues to identity, but of a more primitive source of information, namely the natural statistics of the face category. Although so far, no link has been established between face natural statistics cues conveyed by the horizontal range and basic-level face categorization, we have demonstrated that basic-level categorization relies on the horizontal range. In Chapter 5, the implicit and explicit basic-level face categorization of widely different face exemplars more accurate, and faster, is the explicit experiment, with horizontally than vertically filtered images. Basic-level face categorization response of horizontally and obliquely filtered images was even close to non-filtered images, potentially indicating that the horizontal range is enough to elicit basic-level face categorization and would therefore convey diagnostic information of the face as a category.

Face identity categorization

View-tolerant face identity recognition enables identity categorization, despite that various appearances of one's identity are more dissimilar at the image level than the appearances of different identities (Adini et al., 1997a; Jenkins et al., 2011). View-tolerant face identity recognition is more accurate for familiar than unfamiliar faces (Hancock et al., 2000; Hill et al., 1997; Johnston & Edmonds, 2009). To make an unfamiliar face become familiar, there is a need for exposition, to different exemplars of one's face, taken under different viewing conditions, e.g. across hairstyles, emotional expressions, age, viewpoints (Andrews et al., 2015; Etchells et al., 2017; Lander & and Bruce, 2003; Pike et al., 1997; Ritchie & Burton, 2017). Through exposure to this variability in appearance, a tolerant identity representation builds up, linking together various appearances of the identity (S. Andrews et al., 2015; Burton, 2013) and enabling identity categorization across variable appearances.

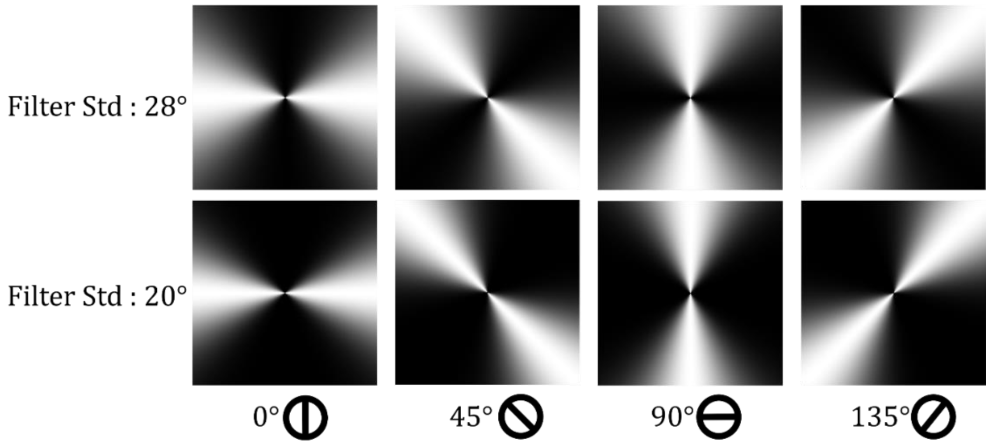
It was previously shown that the presence of surface cues yields increases the view tolerance of identity recognition (Troje & Bülthoff, 1996b). In Chapter 3, our results demonstrated that these surface cues are conveyed by the horizontal range, supporting the hypothesis of the involvement of the horizontal range in view-tolerant identity categorization. Moreover, masking horizontal face information resulted in poorer view tolerance (Goffaux & Dakin, 2010a). Based on our results, we discuss here the possibility that the view-tolerant identity representation is built through information conveyed by the horizontal range. As demonstrated in Chapter 4, using the view-tolerant model observer, the horizontal range carries the most stable information at the image level. This stability explains the human's horizontal tuning to face identity recognition for faces under viewpoints other than the full front view. The view-selective model demonstrated that the horizontal range isn't the most informative at views close to profile. Yet, human identity categorization performance remained tuned to the horizontal at these viewpoints, because of its stability across views. These results support the hypothesis of a view-tolerant face identity internal representation based on horizontal information.

The different profiles of orientation tuning

Through our work, we have made comparisons between experiments possible by using similar experimental designs. In all chapters we used Gaussian orientation filters to reduce information to a narrow range of orientation, and in Chapters 2 and 3, similar experimental paradigms were designed.

Compared to previous studies of orientation tuning of face identity categorization, the orientation tuning of the upright-positive contrast images in Chapter 3 was very broad (see Figure 3.3a in Chapter 3). Although we found that the oblique ranges were sometimes processed better or equally to the horizontal range, previous studies and their resulting orientation tuning indicate that face identity recognition is tuned to the horizontal.

In Chapter 3, the use of inversion and contrast negation already strongly distorted the images, especially for a same/different task with the images only staying on screen for 400ms or 500ms. In a pilot study, we found that the task too difficult and participants were often only at chance level in the most degraded conditions (e.g. vertically-filtered negated faces), unless we increased the standard deviation of the orientation filters. In Chapter 5, as participants passively viewed fast sequences of highly diverse images displayed for less than 160ms, we also used a broader standard deviation to maintain stimulus visibility. Viewing images filtered using a filter with a smaller standard deviation made the experiment too arduous for pilot participants. We believe that the large standard deviation of the Gaussian filters (25° for Chapter 3 and 28° for Chapter 5) used in our studies are responsible for the broader tuning bandwidth: in previous studies using orientation filtering, the standard deviation of the filters ranged from 14° to 23°, with a mean of 18°. For instance, using filters with a standard deviation of 20°, Goffaux & Greenwood, (2016) show that the standard deviation of the horizontal tuning of face identification is 29.9°. In Chapter 2 and 4 also using filters with a 20° standard deviation, the orientation tuning standard deviations were 55.86° and 44.94°, respectively compared to 70.1° in Chapter 3. In Chapter 5, an even greater standard deviation was set for the orientation filters (28°) and the resulting orientation tuning plateaued from 45° to 135° orientation ranges, see Figures 5.3 and 5.4, which supports the hypothesis that filters standard deviation influence the orientation tuning. Of course, because the orientation tuning of basic-level face categorization had not been tested before our experiment, comparison with similar experiments is not possible and future experiments might invalidate this hypothesis. The reason we believe the filter's standard deviation to be responsible for the sharpness of the horizontal tuning is because the more permissive (larger standard deviation) these filters are, the larger the overlap between images filtered at distinct orientations. Of course, it means that there is an overlap between vertically and obliquely filtered images as well. However, since the vertical range of information is not as rich as the horizontal, especially for full front faces, this overlap does not necessarily add any diagnostic information and therefore fails to boost categorization. Looking at Figure 6.1, it is indeed clear that the 28° standard deviation filter results in more overlap in the filtered content than at 20°.



<u>Figure 6.1.</u> Gaussian orientation filters in the Fourier domain. The overlap between orientations is larger for the 28° standard deviation filter (top) than the 20° (bottom).

However, based on the results, of the experiments from Goffaux & Greenwood (2016), Chapters 2 and 4, in which 20° standard deviation filters were used, but still had different orientation tuning standard deviation. There might thus by other elements influencing the sharpness of the horizontal tuning in our experiments. Another possibility would be that face identity processing skills might play a role in the width of the horizontal tuning. This link between horizontal tuning width and face identification performance has already been demonstrated, with a increased horizontal advantage in participants scoring better in identity categorization tasks (Duncan et al., 2019; Pachai et al., 2013). It is thus possible that from one chapter to another, our participants had different identity processing abilities, which could have influenced their tuning. For instance, in Chapters 2 and 3, participants had to recognize and name at 10 out of the 18 actors select in our *FameSet*, to be included in the study, potentially making them better recognitzer than in Chapter 5. This could thus have sharpened the horizontal tuning in these experiments, especially compared to Chapter 5, where there was no such requirements. Looking at the Benton score, subjects in Chapter 2 scored higher than in the other chapters: 48.58 ± 2.86 for Chapter 2; 46.6 ± 3.6 for Chapter3; 45.3 ± 3.48 and 46.27 ± 3.55 for the implicit and explicit experiments of Chapter 5, respectively. To determine whether there were significant differences between the Benton score of participants in the different chapters, we ran a one-way ANOVA (unfortunately, participants did not do the Benton test in Chapter 4, nor in Goffaux & Greenwood (2016)). We found a significant difference ($F(3) = 5.36$, pvalue < 0.01). Post-hoc Tukey analysis revealed a significant difference between the Benton scores of participants in Chapter 2 and Chapter 6 for the implicit experiment and close to significant between Chapter 2 and Chapter 5 for the explicit experiment. Lower face identification abilities in Chapter 5 compared to Chapter 2 might therefore explain the broader horizontal tuning in this study.

Yu & Chung (2011) compared the horizontal tuning of participants with central vision loss, and participants with normal vision. They found that identification performance of participants with central vision loss was more broadly tuned to the horizontal range than that of normally sighted participants. Moreover, the individual horizontal tuning of central participants with central vision loss were highly variable, similar to the individual horizontal tunings obtaines in Chapters 3 and 5 (see Figures 3.S.1 and 5.S.2). We therefore decided to compare FrACT results between our experiments. Interestingly, we obtained highly similar results as with the Benton score: a significant difference in FrAct scores between experiments ($F(3) = 5.13$, pvalue < 0.01). Post-hoc Tukey analysis revealed a significant difference between the Benton scores of participants in Chapter 2 and Chapter 5 for the implicit and explicit experiments. Lower vision acuity in Chapter 5 compared to Chapter 2 might therefore explain the broader horizontal tuning in this study.

Finally, the broader in tuning in Chapter 5 compared to other studies could also be explained by the different images that we used. In Chapter 5, we used natural images amongst which, some face-images with the head tilted (see Fig 6.2), as the aim of these images was to ensure generalization of face categorization across many different exemplars. Therefore, when filtering these tilted images, the horizontal filter was not centered on the face's horizontal. Oblique filters would thus encompass part of the face's horizontal at the expense of orientation specificity. It is therefore important to consider both the advantages and drawbacks of each choice in our procedure, between precision and comfort for the participants, and controlled or ecological stimuli. Similarly, Chapter 4 and Goffaux & Greenwood (2016), in which images were far more controlled than in our other chapters and were strictly upright, showed sharper horizontal tuning than in chapters 2, 3 and 5. crucial identity cues, such as the eyebrows, would appear in obliquely filtered images when face are tilted and thus confer a stronger advantage than expected to oblique orientations. This hypothesis is aligned with the broad orientation tuning profile of identity recognition reported by Dakin & Watt (2009), also using slightly tilted images. It also fits with Chapter 3 results, and the small dip in recognition performance observed in the horizontal compared to oblique orientation. Finally, in Chapter 4, human orientation tuning at profile views show a small symmetrical peak shift towards the oblique orientations which could for instance, reflect the eyebrows orientation at profile views.

Figure 6.2. Example of the images used in Chapter 5. The grey transparent rectangle marks the highest of the two eyes and demonstrates the tilt, as only one eye is inside this horizontal triangle.

Orientation advantage in human face recognition: Why so horizontal?

Through the different chapters of this thesis, we have analyzed the horizontal advantage in human categorization of faces at the identity recognition and basic levels. As summarized in this discussion, we have extended our understanding of the horizontal range of face information and its contribution to face-specialized mechanisms. Chapter by chapter, we have brought elements to answer the question of this thesis. Studying face categorization under the prism of orientation, enabled a global segmentation of faces, compared to isolating features for instance. This method is also interesting because it fits the visual system functioning, specifically, it fits V1's orientation segmentation. It could however also be seen as a disadvantage: as seen in our results, the advantage of the horizontal range seems to be manifold, but because of this comprehensive segmentation, all could be confounded. For instance, could all our results instead be explained by the sole presence of the features in their correct configuration in the horizontal range? The fact the reference frame of horizontal tuning is face-centered, that the horizontal range conveys shape and surface-shading information, informative and stable cues as well as diagnostic basic-level face categorization information could indeed, and are quite possibly, due to the presence of the features in this range. Facial features accounts for the most part of energy in the face image. And our work has demonstrated that image energy does not account for the horizontal preference in face recognition, as seen in Chapter 4. Moreover, human identity recognition is horizontally-tuned even in profile viewing conditions that hinder the saliency of facial feature configuration. This suggests that the orientation advantage is not purely image based, or related to the optimal delivery of facial features. This echoes with previous research on the orientation preference in face processing; one studied gaze processing, which concluded at an advantage of the vertical, not the horizontal range (Goffaux, 2019). Another study investigated the orientation preference in face-specialized areas of the monkey brain, and found one area tuned to the horizontal while the other, with a supposedly different contribution to face processing, was tuned to the vertical range (Taubert et al., 2016). Both experiments demonstrate that the face image does not suffice to produce horizontal tuning. Results from Chapter 2, demonstrating a slight influence of the observer's reference frame also hinted towards such conclusions.

Conclusion

Visual sciences aim towards a deeper understanding of our perception of the world around us and its influence on our behavior. As our perceptual system is shaped by our environment, stimuli and their processing must be studied together to be properly investigated and fully grasped. For instance, face categorization must be studied alongside the face itself. Our goal, during this dissertation was to further understand the face as a stimulus and how its information guides face categorization from the basic to the finer levels. Exploration of the horizontal tuning had already demonstrated the reliance of face-specialized mechanisms on the horizontal facial range. In our work, we expanded our understanding of the face categorization processes relying on the horizontal range and found that face processing is tuned to the horizontal from basic-level categorization to view-invariant identity categorization. These findings further categorized the face’s horizontal range of information as rich in informative stable cues, necessary for basic-level and view-tolerant identity categorization. They also raise the need to determine whether horizontal tuning at basic levels categorization passively transmit to finer categorization processes, or whether it differently affects face categorization across levels.

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