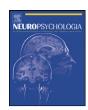
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Developmental prosopagnosia and super-recognition: No special role for surface reflectance processing

Richard Russell^{a,*}, Garga Chatterjee^b, Ken Nakayama^b

- ^a Gettysburg College, Department of Psychology, Gettysburg College, 300 North Washington Street, Gettysburg, PA 17325, USA
- ^b Harvard University, USA

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ABSTRACT

Face recognition by normal subjects depends in roughly equal proportions on shape and surface reflectance cues, while object recognition depends predominantly on shape cues. It is possible that developmental prosopagnosics are deficient not in their ability to recognize faces per se, but rather in their ability to use reflectance cues. Similarly, super-recognizers' exceptional ability with face recognition may be a result of superior surface reflectance perception and memory. We tested this possibility by administering tests of face perception and face recognition in which only shape or reflectance cues are available to developmental prosopagnosics, super-recognizers, and control subjects. Face recognition ability and the relative use of shape and pigmentation were unrelated in all the tests. Subjects who were better at using shape or reflectance cues were also better at using the other type of cue. These results do not support the proposal that variation in surface reflectance perception ability is the underlying cause of variation in face recognition ability. Instead, these findings support the idea that face recognition ability is related to neural circuits using representations that integrate shape and pigmentation information.

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1. Introduction

Recognizing conspecifics is of critical importance to social species such as humans, and is foundational for social behavior and social cognition. Though there are many sources of information about the identity of another person, including voice, clothing, patterns of gait, and context (e.g. I expect to see my dentist when I go to his office), the primary cue for identifying other people is the face. Given the behavioral importance of face recognition, it is perhaps not surprising that there are entire cortical networks involved in face recognition in humans and other primates (Tsao, Moeller, & Freiwald, 2008). Further evidence for the notion that face recognition is an important and distinct ability is the discovery of neuropsychological cases presenting impaired recognition of faces with otherwise normal visual perception – in some cases with normal or relatively normal visual recognition of other kinds of objects - a condition called prosopagnosia (Farah, Wilson, Drain, & Tanaka, 1995; Henke, Schwinbuerger, Grigo, Klos, & Sommer, 1998).

Until a decade ago, most cases in the literature were of acquired prosopagnosia, where the deficits are a result of trauma, stroke, or other brain damage. During the past decade there have been numerous reports of people with very poor face recognition

ability where the deficits cannot be tied to specific brain damage, a condition called developmental prosopagnosia (sometimes called congenital prosopagnosia or hereditary prosopagnosia) (Behrmann & Avidan, 2005; Duchaine & Nakayama, 2005). The discovery of many cases of developmental prosopagnosia is part of a larger discovery that the common range of face recognition ability is much wider than previously assumed. On the low end of face recognition ability lie the developmental prosopagnosics who have been estimated to comprise around 2% of the general population (Kennerknecht et al., 2006). On the other end of the face recognition spectrum are super-recognizers (Russell, Duchaine, & Nakayama, 2009), who are far better than average at recognizing faces. Superrecognizers have been proposed to represent the high end of a unitary distribution of ability with developmental prosopagnosia at the low end, which would mean that both groups are quantitatively rather than qualitatively different from average (Russell et al., 2009). Aside from the knowledge that face recognition ability is highly heritable (Wilmer et al., 2010; Zhu et al., 2010), little is known about the specific causes of the range of ability.

Prosopagnosia, and now super-recognition, have been a focus of research in part because of the debate over whether face recognition is separable from the recognition of other classes of object, a debate which is itself part of a larger question in cognitive neuroscience about modularity – whether the brain is organized along domain-specific or domain-general lines. According to the domain-specific account, the mind is divided according to the content of the information processed, while in the domain-general account,

^{*} Corresponding author. Tel.: +1 717 337 6175. E-mail address: rrussell@gettysburg.edu (R. Russell).

the mind is divided according to the kinds of processes it carries out (Kanwisher, 2000; Tarr & Gauthier, 2000). This debate has played out with respect to prosopagnosia with researchers debating whether the deficits seen in prosopagnosia are truly specific to the domain of faces or are instead specific to the process of expert recognition. Some researchers have argued that prosopagnosia is a deficit specific to the recognition of faces (Duchaine & Nakayama, 2005), while others have argued that prosopagnosia is a deficit not in face recognition per se, but rather in the recognition of any object class for which the observer has expertise (Gauthier, Behrmann, & Tarr, 1999). In this latter account all normal adults could be considered face experts, and some are also experts at recognizing other classes of stimuli, such as birds, dogs, or cars.

However, there is also a third possibility for why developmental prosopagnosics have face recognition deficits. Rather than being a deficit in face specific processes or expert specific processes, developmental prosopagnosia could be due to a deficit in a visual competency that is more relevant for recognizing faces than for recognizing other kinds of objects. In such an account, developmental prosopagnosia results not from abnormal development of face-specific neural circuits or expertise-specific neural circuits, but rather from abnormal development of a perceptual ability that is useful only or mostly for recognizing faces. An analogous situation has been found in auditory perception with a disorder that affects a specific component of high level perception and recognition – congenital amusia.

Congenital amusia is marked by impairments in music memory and recognition, as well as singing, and appears specific to the domain of music, without impairment to language comprehension (Zatorre, Belin, & Penhune, 2002). Like prosopagnosia, amusia has been a focus for speculation about the modularity of cognition (Peretz & Coltheart, 2003). While the most apparent deficit in this disorder is the inability to perceive music, it is now known that amusia is caused by severe deficiencies in the perception of changes in pitch (Ayotte, Peretz, & Hyde, 2002; Peretz et al., 2002). The specificity of the disorder is not caused by damage to neural circuits specific for music. Instead it is a result of music perception and production being the only cognitive function that requires fine discrimination of pitch. While pitch plays a role in language (especially tonal languages such as Mandarin Chinese), the meaningful pitch variations are coarse compared to those of music, and can be comprehended by people with amusia. Thus, the origin of the disorder appears to be acoustic and music-relevant, not musicspecific (Peretz, 2008; Peretz & Hyde, 2003). Prosopagnosia may similarly have origins that are perceptual and face-relevant, but not face-specific. For this to be the case, the impaired perceptual ability would need to be one that is required much more for the recognition of faces than for the recognition of other object classes.

The appearance of any three-dimensional object can be explained in terms of three variables: the shape of the object, the way that the surface of the object reflects and transmits light, and the illumination of the object. Considering the face as an object, we can explain the difference in appearance between two faces under the same conditions of illumination as arising from differences in their shape and differences in their surface reflectance properties. The reflectance properties of facial skin are quite complex, with a great deal of sub-surface scattering of light (Debevec et al., 2000). Here we also use the term 'pigmentation' interchangeably with 'reflectance' to refer to all of the reflectance properties of the face, including the proportion of incident light that the surface reflects, the proportion of light it reflects as a function of wavelength, surface and sub-surface scattering of light, as well as variation across the surface of these properties (i.e. color and visual texture are included in our definition, among other properties). Work from several laboratories using a variety of methods has evaluated the use of shape and pigmentation information for face recognition, arriving at the general conclusion that the two kinds of cues are about equally useful for face recognition by normal observers (Caharel, Jiang, Blanz, & Rossion, 2009; Jiang, Blanz, & O'Toole, 2006; O'Toole, Vetter, & Blanz, 1999; Russell & Sinha, 2007; Russell, Sinha, Biederman, & Nederhouser, 2006; Russell, Biederman, Nederhouser, & Sinha, 2007; Siemionow & Agaoglu, 2006).

While the literature supports the idea that shape and reflectance are equally useful for recognizing faces, the situation with most other classes of objects is different. Most basic level categories of objects are recognized predominantly on the basis of shape cues (Biederman & Ju, 1988; Tanaka, Weiskopf, & Williams, 2001; Ullman, 1996). This is not to say that reflectance properties are irrelevant for recognizing objects, but rather that shape is clearly more important than surface reflectance properties. Thus one way that recognition of faces differs from recognition of most other classes of objects is in the utility of surface reflectance properties. Reflectance properties are much more important for recognizing faces than recognizing other kinds of objects.

The equivalent importance of shape and pigmentation for face recognition but greater importance of shape for recognition of most other objects is consistent with recent neuroimaging work (Cant et al., 2009; Cant & Goodale, 2007; Cant & Goodale, 2011) showing a gradient in ventral cortex between regions involved in perception of shape and regions involved in perception of texture (reflectance). Specifically, lateral occipital complex (LO), a cortical region involved in object recognition (Malach et al., 1995), lies at the end of the gradient dominated by shape, while the collateral sulcus (CoS) and parahippocampal place area (PPA) (Epstein & Kanwisher, 1998) lie at the end dominated by surface properties. The fusiform face area (FFA), a cortical region involved in the perception of faces (Kanwisher, McDermott, & Chun, 1997), sits midway between the shape and reflectance ends of the gradient and is sensitive to both shape and surface properties.

Developmental prosopagnosics are generally more impaired at recognizing faces than recognizing other classes of objects. While developmental prosopagnosics report difficulties with face recognition in their day to day lives, few report difficulties recognizing other kinds of objects. Indeed, it is possible for the same individual to have extreme face recognition impairments but be perfectly normal at recognizing other objects in standardized tests – i.e. to have "pure" prosopagnosia (Duchaine, Dingle, Butterworth, & Nakayama, 2004), though a recent study with a large number of developmental prosopagnosics found that most are impaired at recognizing other object classes (Chatterjee, Russell, & Nakayama, 2009). However, even in that study, the developmental prosopagnosics were more impaired with faces than with the other object classes.

Given that recognition of faces requires the ability to perceive and remember surface reflectance properties more than does recognition of other kinds of objects, and that prosopagnosics are much worse at recognizing faces than other kinds of objects, it is possible that prosopagnosia is a deficit of reflectance (pigmentation) perception. In other words, developmental prosopagnosia could be a selective deficit not of face recognition but rather of perception and memory for surface reflectance properties. Similarly, super-recognizers may simply be exceptionally good at perceiving reflectance properties. Here we describe efforts to test the idea that variation in the ability to perceive and remember facial pigmentation causes variation in face recognition ability. Unless pigmentation perception is completely irrelevant for face recognition, it should be related to some extent with face recognition ability. The critical question is whether pigmentation perception is more strongly related to face recognition than is the other perceptual component of recognition – shape perception.

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