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Musical literacy shifts asymmetries in the ventral visual cortex

Florence Bouhali[a,b,c,d,*], Valeria Mongelli[e,f], Laurent Cohen[a,b,c,d,g]

[a] Inserm, U 1127, F-75013 Paris, France
[b] CNRS, UMR 7225, F-75013 Paris, France
[c] Sorbonne Universités, UPMC Univ Paris 06, UMR S 1127, F-75013 Paris, France
[d] Institut du Cerveau et de la Moelle épinière, ICM, F-75013 Paris, France
[e] Neurobiology of Language Department, Max Planck Institute for Psycholinguistics, Nijmegen, Netherlands
[f] Department of Psychology, University of Amsterdam, Netherlands
[g] AP-HP, Hôpital de la Pitié Salpêtrière, Féderation de Neurologie, F-75013, Paris, France

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ABSTRACT

The acquisition of literacy has a profound impact on the functional specialization and lateralization of the visual cortex. Due to the overall lateralization of the language network, specialization for printed words develops in the left occipitotemporal cortex, allegedly inducing a secondary shift of visual face processing to the right, in literate as compared to illiterate subjects. Applying the same logic to the acquisition of high-level musical literacy, we predicted that, in musicians as compared to non-musicians, occipitotemporal activations should show a leftward shift for music reading, and an additional rightward push for face perception. To test these predictions, professional musicians and non-musicians viewed pictures of musical notation, faces, words, tools and houses in the MRI, and laterality was assessed in the ventral stream combining ROI and voxel-based approaches. The results supported both predictions, and allowed to locate the leftward shift to the inferior temporal gyrus and the rightward shift to the fusiform cortex. Moreover, these laterality shifts generalized to categories other than music and faces. Finally, correlation measures across subjects did not support a causal link between the leftward and rightward shifts. Thus the acquisition of an additional perceptual expertise extensively modifies the laterality pattern in the visual system.

Introduction

The ventral visual stream hosts a set of regions preferentially responding to one category of objects more than to others. The Fusiform Face Area (FFA) responds preferentially to faces (Kanwisher et al., 1997), the Visual Word Form Area (VWFA) to strings of letters (Cohen et al., 2000), the Parahippocampal Place Area (PPA) to places and buildings (Epstein and Kanwisher, 1998), etc. Such category-selective areas vary in their distribution across the two hemispheres. Some of the homologous regions show similar profiles of object selectivity, as for instance the left- and right-hemispheric versions of the PPA. Yet, the overall symmetry of the ventral stream is broken for two major category-specific regions, the VWFA and the FFA, which show strong lateralization biases to the left (Cohen et al., 2002) and to the right (Rossion et al., 2012; Yovel et al., 2008), respectively. A rightward bias for faces exists already in 4-to-6-month-old infants (Heering and de Rossion, 2015), long before the acquisition of literacy (Le Grand et al., 2003). It has been suggested that an additional rightward push of face processing results from the later acquisition of literacy, possibly as a consequence of competition of the FFA with the newly developed left-hemispheric VWFA (Behrmann and Plaut, 2015; Dehaene et al., 2010, 2015). In the present study, we assess the impact on functional lateralization in the ventral stream of expertise for music reading, a form of perceptual expertise in many respects comparable to word reading.

The main cause of the asymmetry of visual regions is thought to be the asymmetry of distant networks to which they provide an input (Cai et al., 2008; Mahon and Caramazza, 2011; Pinel and Dehaene, 2010). This hypothesis has been mostly documented in the case of reading. Indeed, the VWFA collateralizes with language areas, particularly Broca's area and the posterior superior temporal sulcus (pSTS) (Cai et al., 2010, 2008; Pinel and Dehaene, 2010; Pinel et al., 2015; Van der Haegen et al., 2012). A similar process may be at play for the lateralization of the FFA, as a set of remote regions specifically activated during face processing are also right-lateralized (Rossion et al., 2012). In addition to this driving factor, the lateralization of ventral visual regions may be modulated by interactions among them, possibly involving competition for cortical space. Supporting evidence

* Correspondence to: Institut du Cerveau et de la Moelle épinière, Hôpital Pitié-Salpêtrière, 47 boulevard de l'Hôpital, CS 21414, 75646 Paris Cedex 13, France.
E-mail address: florence.bouhali@gmail.com (F. Bouhali).

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Table 1
Demographic information on the group of controls and professional musicians. Means and standard deviations are given for numerical variables. The third column indicates statistical difference between groups (using a chi-square test for the first row, and Wilcoxon rank sum tests for the others). In addition, there were no statistical differences between the ages when musicians learnt to read words and music (Wilcoxon signed rank test V=50.5, p=0.12), or between the ages when they started to practice and read music (V=54, p=0.95).

	Controls	Musicians	Group comparison
Number of women / men	9 / 11	10 / 10	χ^2 = 0.10, p = 0.75
Age (years)	30.9 (± 10.8)	32.8 (± 10.4)	W = 159.5, p = 0.28
Years of education	14.7 (± 1.8)	15.7 (± 1.9)	W = 134.5, p = 0.07
Age when learning to read words	5.2 (± 0.9)	4.9 (± 1.3)	W = 222, p = 0.54
Age when learning to read music		5.9 (± 2.9)	
Age when learning to play music		5.9 (± 2.2)	
Years of music practice		26.2 (± 9.6)	
Main instrument played		Violin (6), Piano / Keyboard (5), Oboe (3), Cello (3), Trumpet (1), Clarinet (1), Viola (1)	

comes from Dundas and colleagues who showed that left-hemifield preference for faces, an index of right-hemispheric dominance, emerges from childhood to adulthood, and is positively correlated with reading competence. This behavioral finding was paralleled by a right shift of the N170 potential evoked by faces. The link between lateralization for faces and words was further supported by the correlation observed in children between the N170 for faces over the RH and for words over the LH (Dundas et al., 2013, 2014). Congruent evidence also comes from the comparison of literate and illiterate adults. Illiterates fail to show the typical right-lateralization of the FFA (Dehaene et al., 2010), and reading proficiency correlates positively with the activation level in the right FFA, while it is negatively correlated with the activation to faces in the left VWFA (Dehaene et al., 2010, 2015). In addition, left handers lack on average both the left-lateralization of the VWFA (Van der Haegen et al., 2012) and the right-lateralization of the FFA (Bukowski et al., 2013) supporting the existence of a link between those two features. In left-handers, all face-selective areas other than the FFA show the same right-lateralization as in right-handers, suggesting that the atypical lateralization of the FFA might result from reduced competition with the VWFA within the visual cortex (Dundas et al., 2015). Finally, dyslexic children show both an hypoactivation of the VWFA in the left and of the FFA in the right hemisphere, as compared to normal readers (Monzalvo et al., 2012).

In exploring the impact that the acquisition of musical literacy may have on functional lateralization in the ventral visual cortex, we will consider the contribution of the two factors we just discussed, namely the lateralization of distant cortical networks, and the interaction between specialized ventral areas. More specifically, we derived two predictions from the above overview.

First, in the same way as the lateralization of distant language areas drive that of the VWFA in literate subjects, ventral activations to music stimuli should be biased by functional lateralization in distant regions involved in music expertise. Although the traditional view of an overall left-lateralization of expert musical abilities may be an oversimplification (Bever and Chiarello, 1974), various aspects of musical expertise do recruit predominantly left-hemispheric networks, unlike music processing in non-experts. This is the case for musical reading by professional musicians, which, compared to other visual stimuli and to musically naïve subjects, activates a left predominant fronto-parietal network (Mongelli et al., 2017). Accordingly, impairments of music reading results exclusively from left-hemispheric lesions (Hébert and Cuddy, 2006). A leftward asymmetry also prevails with auditory (Habibi et al., 2013; Matsui et al., 2013; Ono et al., 2011) and motor (Bangert et al., 2006; Pa and Hickok, 2008) components of musical expertise. Our first prediction was therefore that ventral activations to music stimuli should be left-lateralized in musicians, and more so than in musically naïve subjects.

Second, would the tuning of the visual cortex to music reading modify the lateralization of other category-selective regions, in the same way as the development of the VWFA shifts face-related activations to the right? Mongelli et al. (2017) showed that group-level activations for music and words in the occipitotemporal cortex were largely overlapping. However, individual analyses revealed that activations for music peaked significantly posterior and lateral to activations for words, and had a larger volume in musicians than in controls. Thus, category-selective activations to music being close to activations to words, we predicted that they may interact similarly with neighboring areas. Specifically, our second prediction was that music reading should team up with word reading, resulting in a stronger right-hemispheric shift of face processing in professional musicians as compared to controls.

To assess these predictions, we studied the lateralization pattern of ventral activations in professional musicians and musically naïve controls, as they viewed five different categories of visual objects (words, faces, musical scores, houses, and tools). Changes in asymmetry were assessed both by using a laterality index over a ventral occipitotemporal region of interest (ROI), and by deriving asymmetry maps in order to preserve spatial resolution.

Material and methods

Participants

Twenty-one adult musicians (12 men) and 23 musically naïve controls (13 men) took part in the experiment. Both groups were matched in gender and age. All participants were right-handed according to the Edinburgh inventory (Oldfield, 1971). Musicians were either professional musicians or masters' students at one of the most prestigious music schools in France (CNSM, *Conservatoire de Musique et de Danse de Paris*). They varied in their type of musical practice, but they all started learning to read both words and music around the age of 5/6 years old (words: 4.9, music: 5.9, V=50.5, p > 0.1). One musician and three controls were found to be right lateralized for language (see below), and were excluded from further analyses, resulting in a final cohort of 20 musicians and 20 controls. Table 1 provides detailed information on the final cohort.

Stimuli

We used five categories of black and white pictures: faces, tools, houses, pairs of words, music scores (Fig. 1A). Each category contained 38 pictures. All stimuli were black line drawings on a white background. Faces, houses and tools were derived from highly contrasted gray-level photographs matched for size and overall luminance. Faces (17 females, 21 men) were front or slightly lateral views of non-famous people. Houses comprised outside pictures of houses and buildings. Tools were common hand-held household objects (e.g. knife, hair-dryer) presented in a normal orientation. The faces, tools, and houses images used here were used in previous studies in order to map category selectivity in the occipitotemporal cortex (Dehaene et al., 2010; Gaillard et al., 2006; Pegado et al., 2014; Pinel et al., 2015; Thirion et al., 2007). Music notation corresponded to one bar of