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Predominance of lateral over vertical mirror errors in reading: A case for neuronal recycling and inhibition

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ABSTRACT

We investigated whether lateral mirror errors could be more prevalent than vertical mirror errors (e.g., p/q vs. p/b confusions) because mirror generalization is harder to inhibit for the discrimination of a reversible letter and its lateral than its vertical mirror-image counterpart. Expert adult readers performed a negative priming task in which they determined on the prime whether two letters and on the probe whether two objects facing opposite directions were identical. We found in both experiments longer response times for objects facing opposite lateral orientations preceded by a reversible letter and its lateral mirror-image counterpart (e.g., p/q) than preceded by perceptually matched non-reversible letters (e.g., g/j). No negative priming effect was observed when objects that were vertical (Experiment 1 & 2) or lateral (Experiment 2) mirror images of each other were preceded by a letter and its vertical mirror-image counterpart (e.g. p/b). Finally, we observed longer response times for objects that were lateral mirror images of each other after lateral than after vertical reversible letters. These results suggest that lateral mirror errors are more prevalent than vertical ones because mirror generalization might be stronger and thus more difficult to inhibit in the context of the former than the latter.

1. Introduction

The accurate recognition of written symbols is a key step of reading (Carreiras, Armstrong, Perea, & Frost, 2014). Unfortunately, as a skill that developed a few thousand years ago, reading is far too recent in regard to evolution for humans to possess an innate brain network that specializes in recognizing written symbols (Dehaene, 2004). Reading can nevertheless be acquired via intense training. Learning to read modifies the brain to such a degree that an area specialized in the visual recognition of letters and words emerges in readers (Cohen et al., 2000; Petersen, Fox, Posner, Mintun, & Raichle, 1988). This area, referred to as the visual word form area (VWFA), is the product of a specific type of neuroplasticity called neuronal recycling (Dehaene, 2004). According to the neuronal recycling hypothesis, learning to read involves the recycling of an already existing neuronal network whose initial function is close to reading and which is sufficiently plastic to specialize for a new type of stimuli. Indeed, the VWFA can be systematically localized in readers in the language-dominant occipitotemporal cortex (Jobard, Crivello, & Tzourio-Mazoyer, 2003) at the junction of visual areas specialized in the visual processing of faces, animals and objects (Hasson, Harel, Levy, & Malach, 2003). A consequence of neuronal recycling is that reading inherits the functional properties of the recycled neuronal networks (Dehaene, 2004).

A notable property of these visual areas is mirror invariance or mirror generalization (hereafter referred to as MG, Lachmann, 2002). MG is presumably an adaptive process that enables animals to quickly recognize a predator, a prey, or a mate independently of its lateral or vertical orientation (Bornstein, Gross, & Wolf, 1978). It is arguably an innate property of the neurons of the ventrolateral occipitotemporal cortex because it exists in animals such as the octopus (Sutherland, 1960), the pigeon (Todrin & Blough, 1983), the rhesus macaque (Rollenhagen & Olson, 2000), as well as in human adults (Dehaene et al., 2010) and in infants as young as three months old (Bornstein et al., 1978). Although MG is an advantageous property for the visual recognition of non-verbal stimuli such as faces, animals or objects, it is deleterious for reading, most notably when one attempts to learn an alphabet compris-

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ing reversible symbols that have existing lateral or vertical mirror-image counterparts, such as b/d or b/p in the Latin alphabet.

Lateral mirror errors are confusions of a reversible letter and its lateral mirror-image counterpart, such as b for d or p for q. They are the direct and deleterious consequences of the inheritance of the MG process by the VWFA (Dehaene, 2004; for alternative theories based on hemispheric symmetry, see Lachmann, 2002; Orton, 1925). These errors are frequent during reading acquisition in childhood (Davidson, 1935). They do not disappear spontaneously but rather after intense training to read (Fernandes, Leite, & Kolinsky, 2016) at an age directly related to the grade at which school-aged children learn to read (Rudel & Teuber, 1963; Serpell, 1971). Furthermore, adult analphabets (Dehaene, Cohen, Morais, & Kolinsky, 2015; Pegado et al., 2014) or literate adults in the Tamil alphabet that contains no laterally reversible symbol tend to consider that 'b' and 'd' are the same symbols (Pederson, 2003). Some authors have argued that overcoming lateral mirror errors in reading is supported by "unlearning" MG specifically for letters (Dehaene, Cohen, Sigman, & Vinckier, 2005). Indeed, the discrimination process of lateral mirror images of written stimuli appears to be different from the discrimination process of lateral mirror images of faces, animals or objects. Literate patients with right temporoparietal (Priftis, Rusconi, Umiltà, & Zorzi, 2003) and bilateral occipitoparietal lesions (Davidoff & Warrington, 2001; Vinckier et al., 2006) correctly discriminate lateral mirror images of letters, words or pseudo-words, but are unable to discriminate lateral mirror-images of faces, animals or objects. Thus, authors have argued that the "unlearning" of MG for written symbols is intrinsic to the visual ventral stream, whereas additional information is needed from the visual dorsal stream to process the lateral orientation of faces, animals or objects (for studies demonstrating a double dissociation between recognition and orientation in the ventral and dorsal streams see Turnbull, 1997; Warrington & Davido, 2000, respectively). Two negative priming studies recently demonstrated in expert readers (adults, Borst, Ahr, Roell, & Houdé, 2015) and in novice readers (7 to 10-year-old children, Ahr, Houdé, & Borst, 2016) that "unlearning" MG in the ventrolateral occipitotemporal cortex might be rooted in part in learning to inhibit MG when discriminating a reversible letters and its lateral mirror image counterpart (i.e., b/d, and p/q in the Latin alphabet). In both studies, participants needed more time to determine that two animals (i.e., a category of stimuli that elicits activation in areas of the ventrolateral occipitotemporal cortex also activated by letters, see Hasson et al., 2003) facing opposite lateral orientations were identical (a context that requires the activation of MG) when preceded by a reversible letter and its lateral mirror-image counterpart (e.g., p/q, a context that requires to inhibit MG) than by non-reversible letters that matched the ascending/descending feature of the reversible letters (e.g., g/j, a context that requires neither the activation nor the inhibition of MG).

In addition to lateral mirror errors, readers also commit vertical mirror errors, which are confusions of a reversible letter and its vertical mirror-image counterpart such as b for p or d for q, more than other types of errors (Davidson, 1935). Vertical mirror errors are less prevalent than lateral mirror errors: they are less frequent in novice readers (Davidson, 1935) and disappear earlier (Cairns & Steward, 1970). Animals (Rollenhagen & Olson, 2000; Sutherland, 1960; Todrin & Blough, 1983) and three-month-old babies (Bornstein et al., 1978) confound both lateral and vertical mirror-images of letter-like shapes, but do so with the former to a greater extent than the latter.

Whether the mechanism triggering vertical mirror errors is exactly similar to the one triggering lateral mirror errors remains uncertain. It has been suggested that the mechanism might be the same (i.e., MG) but that it might be more strongly activated for lateral than vertical mirror images (Bornstein et al., 1978) because visual non-verbal stimuli such as faces, animals or objects are more often observed in different lateral (left vs. right) than in different vertical (upright vs. upside-down) orientations. Single neuron recording in the inferotemporal cortex in macaques (homologous to the occipitotemporal cortex in humans) confirmed that most IT neurons respond equally to the presentation of lateral or vertical mirror images, but more often for the former than the latter (Rollenhagen & Olson, 2000). Thus, MG might be more strongly or more spontaneously activated in the context of the discrimination of a reversible letter and its lateral than its vertical mirror-image counterpart because lateral MG is more frequently required in our visual environment than vertical MG.

In the present study, we investigated whether lateral mirror errors in reading might be more prevalent than vertical ones because MG might be stronger and thus harder to inhibit when discriminating a reversible letter and its lateral mirror-image counterpart than when discriminating a reversible letter and its vertical mirror-image counterpart. To do so, we designed a negative priming paradigm adapted from a study by Borst et al. (2015). The negative priming paradigm is based on the rationale that a representation or a process is more difficult to activate if it was previously inhibited (Houdé & Borst, 2014; Tipper, 1985). In Experiment 1, expert adult readers performed a negative priming discrimination task in which pairs of letters were displayed on the primes and line drawings of objects (a category of stimuli that elicits its activation in areas of the ventrolateral occipitotemporal cortex partially overlapping with the VWFA, see Hasson et al., 2003) were displayed on the probes.

We reasoned that if MG is stronger and thus more difficult to inhibit when discriminating a reversible letter and its lateral mirror-image counterpart (e.g., p/q) than when discriminating a reversible letter and its vertical mirror-image counterpart (e.g., p/b) due to the greater occurrence of lateral than vertical MG in our visual environment, participants should be less efficient in discriminating a reversible letter and its lateral than its vertical mirror-image counterparts on the primes. Moreover, participants should require more time (or commit more errors) to determine that two objects that are lateral mirror-images of each other are identical on the probes (a context that requires the activation of MG) when preceded by a reversible letter and its lateral mirror-image counterpart (e.g., p/q, a context that requires to inhibit MG) than when preceded by non-reversible letters that matched the ascending/descending feature of the reversible letters (e.g., g/j, a context that requires neither the activation nor the inhibition of MG) (i.e., a typical negative priming effect). By contrast, a smaller or no negative priming effect on response times (RTs) or accuracy rates should be found between probes preceded by a reversible letter and its vertical mirror-image counterpart (e.g., p/b) and probes preceded by perceptually matched non-reversible letters (e.g., g/t).

2. Experiment 1

2.1. Method

2.1.1. Participants

Forty-eight right-handed voluntary students were recruited at Paris Descartes University (France); this university served as a diverse population. All had normal or corrected-to-normal vision and gave free and informed written consent. Two participants left before the end of the test and were excluded from the analyses. The analyses were thus restricted to 46 participants (36 females and 10 males, average age of 21.5 ± 1.9 years). The study was carried out in accordance with the national and international norms that govern the use of human research participants.