



About turn: How object orientation affects categorisation and mental rotation

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ABSTRACT

High-density ERPs evoked by rotated alphanumeric characters were examined to determine how neural processing is affected by stimulus orientation during letter/digit classifications and during mirror/normal discriminations. The former task typically produces response times that are unaffected by stimulus orientation while the latter is thought to require mental rotation. Sensitivity to orientation was first observed around 100–140 ms and this effect was attributed to differences in low-level features between vertical and oblique orientations. Subsequently, character misorientation amplified the N170, a neural marker of object classification, between 160 and 220 ms. Top-down processing is reflected in the ERPs beginning at 280–320 ms and this time range may reflect binding of ventral and dorsal stream information. In the case of mirror-normal discrimination these top-down processes can lead to mental rotation between 340 and 700 ms. Therefore, although neural processing reflects object orientation, these effects do not translate into increases in reaction-times or impaired accuracy for categorisation, and precede those that do in the mental-rotation task.

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1. Introduction

Many familiar objects are immediately recognisable regardless of their orientation in the world. We can recognise a chair, or a bicycle, or letters of the alphabet independently of how they are oriented relative to one's point of view. Of course, we can also see *how* they are oriented, suggesting that the process of recognition may be differentiated from that of visual perception, at some level at least. Information about orientation and identity of objects is thought to be processed by the dorsal and the ventral pathways, respectively, and the question of how (or when) this information is integrated is central to the “binding” problem. A case in point is what happens when we make decisions about an object's left–right parity (e.g. whether it is normal or mirror-reversed).

These types of decisions require alignment between the object and our own egocentric frame of reference. For example, deciding whether a shoe is the left or the right one requires either physical or *mental* rotation of the shoe into alignment with our feet, or the feet with the shoe. The same holds for any object class that has a well-defined left–right orientation, such as alphanumeric characters, which can be readily recognised as “backward” if they have been mirror-reversed (Cooper & Shepard, 1973; Shepard & Metzler,

1971) – but only if they are presented at upright. Rotated characters require mental rotation to their canonical upright before we can notice if they are normal or backward.

This suggests that object identity must be extracted before information about object orientation can be determined. Although this appears to be a fairly logical conclusion, there is evidence that object recognition can also be affected by changes in stimulus orientation. So, for example, face recognition is worse when faces are inverted (Yin, 1969) and discriminating between objects within a semantic category (subordinate-level decisions) is also affected (while between-category or basic-level decisions are largely unaffected, Hamm & McMullen, 1998). Furthermore, previous experience with objects at a given orientation also seems to enhance recognition, while pre-cuing the upcoming orientation of the stimulus does not result in this benefit (McMullen, Hamm, & Jolicoeur, 1995), suggesting that viewpoint-dependent representations are also stored (Hayward & Tarr, 1997; Jolicoeur, Snow, & Murray, 1987). This has led some authors to suggest that there are multiple routes to object recognition – some based on viewpoint-dependent configuration while others are based on viewpoint-independent feature extraction (Jolicoeur, 1990).

Nevertheless, these object-recognition costs, if they occur, would need to be resolved before mental rotation begins. Furthermore, the evidence that changes in object orientation can affect subordinate-level categorisation (e.g. this is a collie), but not basic-level categorisation (e.g. this is a dog) or superordinate-level categorisation (e.g. this is an animal/quadruped; Hamm & McMullen, 1998) hint that orientation may affect perceptual

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processing of familiar objects in subtle ways, not necessarily evident in behavioural measures, such as reaction times, naming latencies, or accuracy, which reflect combined contribution of multiple, interacting, stages of neural processing. Furthermore, these observations are consistent with the notion that an observer's goal determines whether perception of object orientation will influence their cognition.

Although mental rotation and orientation-dependent object recognition have received considerable attention in the literature, this study attempts to provide a more comprehensive overview of how orientation affects neural processing before and during mental rotation, and to dissociate the effects that can be attributed to mental-rotation task demands from those that result from differences in the orientation of the object. For that reason we compare ERPs evoked by two tasks: a letter-digit discrimination task and a mirror-normal discrimination task with alphanumeric characters. We assume that both tasks require a similar degree of visual processing of letters and digits required for character recognition, but that the mirror-normal task would elicit additional mental rotation processes. Based on results reported by Heil, Rauch, and Hennighausen (1998), we expect that mirror-normal discrimination will elicit linear increases in parietal negativity commonly associated with mental rotation (Heil, 2002; Milivojevic, Hamm, & Corballis, 2009b; Milivojevic, Johnson, Hamm, & Corballis, 2003; Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989) while letter-digit categorisation will not. We aim to extend those results by using a high-density montage which enables us to investigate the effects of orientation on multiple ERP components that may vary in spatial topographies.

We focus the analysis on the time period preceding the time interval thought to be involved in mental rotation in order to examine how orientation affects neural processing independently of mental rotation and at what point in the course of visual processing the effects of orientation become specific to the mental rotation task. The answers may bear on the roles of the ventral stream which underlies perception of identity, and the dorsal stream, which mediates perception of orientation, and reveal how and when the information carried by these streams is integrated. This should provide a temporal window during which the “binding problem” is solved by the brain.

We chose letters and digits as stimuli because they are highly familiar objects that have a clearly defined (and meaningful) left–right orientation. Categorisation of these characters into letters and digits does not appear to be systematically affected by 2D rotation (Corballis & Nagourney, 1978; Corballis, Zbrodoff, Shetzer, & Butler, 1978) while decisions about left–right orientation (i.e. whether they are normal or backward) require rotation back to the canonical upright. Orientation affects both types of tasks, however, when the characters have been mirror-reversed. For categorisation, mirror-reversed characters impose an additional 20 or so milliseconds to classify (Corballis & Nagourney, 1978), while for mirror-normal discrimination, the extra time taken to respond to backward characters is closer to around 200 ms. For mirror-normal discriminations, the reaction-time cost of character reversal is correlated with individuals' mental rotation rates, while that does not seem to be the case for letter-digit categorisation. These results suggest that mirror-reversed characters are “flipped” out of the picture plane following the initial “in-plane” rotation. This additional flip brings them into alignment with their canonical forms in our mental representation, and is used to verify that the character is indeed a backward representation of the one stored in memory (Hamm, Johnson, & Corballis, 2004; Kung & Hamm, 2010).

In terms of in-plane orientation, two types of orientation-related effects are of interest: effects related to mental rotation and effects preceding mental rotation. While mental rotation is expected to induce linear increases in parietal negativity with

larger angular rotation from upright (Milivojevic et al., 2009b), the relationship between orientation and object recognition can be described in terms of a combined linear and quadratic trends. In this sense, modelling the ERP data as linear and quadratic functions may be particularly insightful. Indeed, ERP evidence suggests that such linear–quadratic relationship can also be used to describe effects of orientation on amplitude and latency of the N170 evoked by faces (Jacques & Rossion, 2007) and alphanumeric characters (Milivojevic, Corballis, & Hamm, 2008; Milivojevic, Johnson, et al., 2003). Inversion of faces and scenes further increases activity levels outside of typically face- and scene-responsive areas (Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006; Haxby et al., 1999, 2001), which suggests that visual processing of at least some kinds of rotated familiar shapes requires additional neural resources. Less systematic effects of orientation have also been reported for both the P1 (Boutsen, Humphreys, Praamstra, & Warbrick, 2006; Itier & Taylor, 2004; Taylor, 2002) and the P2 components (Boutsen et al., 2006; Milivojevic, Clapp, Johnson, & Corballis, 2003; Muthukumaraswamy, Johnson, & Hamm, 2003) although it is as yet unknown whether these effects can be described in terms of either linear or quadratic (or combination of linear and quadratic) functions.

Considerably more is known about how mental rotation is carried out by the brain. A large number of neuroimaging studies have identified a network of regions including parietal regions (Alivisatos & Petrides, 1997; Cohen et al., 1996; Harris et al., 2000; Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001; Jordan, Schadow, Wuestenberg, Heinze, & Jäncke, 2004; Jordan, Wuestenberg, Heinze, Peters, & Jäncke, 2002; Koshino, Carpenter, Keller, & Just, 2005; Milivojevic, Hamm, & Corballis, 2009a; Podzbenko, Egan, & Watson, 2002; Richter, Ugurbil, Georgopoulos, & Kim, 1997; Seurinck, Vingerhoets, Vandemaele, Deblaere, & Achtenb, 2005), ventral stream regions such as the inferior temporal gyrus (ITG; Koshino et al., 2005), lateral occipital cortex (Podzbenko et al., 2002) and area MT (Cohen et al., 1996), and higher order premotor regions (Jordan et al., 2001, 2002; Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Podzbenko et al., 2002; Richter et al., 2000) that have been associated with mental rotation tasks. It seems, however, that only areas in dorso-lateral fronto-parietal network are actively involved in mental rotation *per se* (Milivojevic et al., 2009a) while other regions probably subserve other cognitive processes involved in mental-rotation tasks. These processes might include pattern and object recognition, recognition of stimulus orientation, visuospatial working memory and attention, decision making, motor planning and motor output. The extent of the cortical network that has been identified as playing a role in mental-rotation tasks no doubt reflects the synthesis of these cognitive processes.

Nevertheless, the fronto-parietal mental-rotation network is also likely to underlie the ERP correlates of mental rotation (Milivojevic et al., 2009a, 2009b) which are characterised as linear increases in centro-parietal negativity between approximately 400 and 800 ms (Heil, 2002; Milivojevic et al., 2009b; Peronnet & Farah, 1989; Wijers et al., 1989), and which last longer for larger angular departures from upright (Hamm et al., 2004; Milivojevic, Johnson, et al., 2003). As EEG is particularly well suited for analysis of sequential processing stages due to its high temporal resolution, we used it to investigate how orientation, either in the picture plane or as mirror-reversal, affects neural processing associated with object recognition and mental rotation.

2. Methods

2.1. Participants

Eighteen neurologically normal volunteers were recruited from students and faculty at the University of Auckland for approximately 2 h of participation. All had

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