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List of Abbreviations

AC-PC line = Plane defined by Anterior Commissure-to-Posterior Commissure line
BA = Broadmann Area
BOLD = Blood Oxygenation Level Dependent
dIPS = dorsal intraparietal sulcus
dIPSa = dorsoanterior Intraparietal Sulcus
dIPSm = dorsomedial Intraparietal Sulcus
DLPFC = Dorsolateral prefrontal cortex
EEG = Electroencephalography
EPI = Echo Planar Imaging
ERP = Event-Related Potentials
FDR = False discovery rate
FFG = Fusiform Gyrus
fMRI = functional Magnetic Resonance Imaging
FOV = Field of View
FWE = Family wise error
FWHM = Full Width at Half Maximum
GDS = Global Dissimilarity Score
GFP = Global Field Power
GLM = General Linear Model
IFG = Inferior Frontal Gyrus
IPL = Inferior Parietal Lobule
IPS = Intraparietal Sulcus
ITG = Inferior temporal gyrus
LOC = Lateral-occipital complex
LP = Late Parietal
LQ = Laterality Quotient
MEG = Magnetoencephalography
MNI = Montreal Neurological Institute
MOG = Middle occipital gyrus
N1 = First negative deflection in a VEP complex, around 150 ms
P1 = First positive deflection in a VEP complex, around 100 ms
P2 = Second positive deflection in a VEP complex, around 200 ms
PET = Positron Emission Tomography
PPC = Posterior parietal cortex
pre-SMA = Supplementary Pre-Motor Area
RT = Reaction Time
SMA = Supplementary Motor Area
SMG = supramarginal gyrus
SPL = Superior Parietal Lobule
SPM = Statistical Parametric Mapping
TE = Echo Time
TMS = Transcranial Magnetic Stimulation
TR = Time to Repetition
VEP = Visual-Evoked Potentials
vIPS = ventral Intraparietal Sulcus

List of Conference Abstracts

Some of the material in this thesis was presented at the following conferences:

Milivojevic, B., Corballis, M.C. & Hamm, J.P., 2006, “Parametric fMRI study of the effects of stimulus orientation on alphanumeric categorisation and mental rotation”, Organisation for Human Brain Mapping, Florence, Italy.

Milivojevic, B., Corballis, M.C. & Hamm, J.P., 2006, “Effects of stimulus orientation on semantic categorisation and mental rotation”, Federation of European Physiological Societies Meeting, Budapest, Hungary.

Milivojevic, B., & Corballis, M.C., 2005, “Semantic Categorisation and Mental Rotation of Misorientated Letters and Numbers”, Australasian Winter Conference on Brain Research, Queenstown, New Zealand.

Chapter 1: General Introduction

This thesis is concerned with the effect of angular orientation on the way we process visual information. Many familiar objects are immediately recognizable regardless of their orientations in the world. We can recognise a chair, or a bicycle, or letters of the alphabet regardless 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. In some cases, though, recognition is affected by changes in orientation, and perceptual experience may also vary in subtle ways unrelated to the perception of orientation itself. The question of how and when changes in spatial orientation of objects affect the perception and recognition has received considerable attention in the literature, some of which will be reviewed in this chapter.

More specifically, this thesis is concerned with the effect angular orientation has on neural processing underlying visual perception, object recognition, and mental rotation. The development of neuroimaging tools over the past two decades has allowed for neural mechanisms accompanying these perceptual and cognitive processes to be investigated. The contribution of neuroimaging towards answering the question of how we process visual information is two-fold. Firstly, techniques based on monitoring electrophysiological changes associated with cognitive or perceptual task-demands, such as electroencephalography (EEG) and more recently magnetoencephalography (MEG), have been used to investigate the relative timing of cognitive and perceptual processes. Secondly, techniques based on monitoring blood-flow or blood-oxygenation levels associated with cognitive or perceptual task-demands, such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI), have been used to derive precise information regarding anatomical localisation of cortical regions involved in mental operations of interest. The present thesis aims to investigate the cortical underpinnings – using fMRI – and the sequence of perceptual and cognitive processing stages – using EEG – associated with the visual perception, shape recognition, and mental rotation of misoriented alphanumeric characters.

As an introduction to the topic, this literature review will start by outlining the types of perceptual changes that are associated with changes in orientation of an image. Subsequently, it will detail the circumstances in which recognition mechanisms fail as a consequence of changes in spatial orientation of objects and discuss the theoretical frameworks related to orientation-dependence in object recognition. Finally, an overview of the current understanding of functional organisation of the visual system in reference to orientation dependence in object recognition and mental rotation will be provided.

Perceptual effects of angular orientation

It is useful at this stage to make a distinction between effects of orientation on perceptual processing, and processes involved in shape recognition (Corballis, 1988). Stimulus orientation can have notable effects on perceptual processing, as evident from the *oblique effect*, discussed below. Also, perceptual experience may change due to changes in stimulus orientation, as illustrated by the *inversion effect*, also discussed below – a change that may or may not result in poorer shape recognition. Finally, in some circumstances, changes in orientation can affect shape recognition.

The oblique effect

The *oblique effect* refers to a type of perceptual disruption that can be attributed to orientation. The observation is that visual discrimination is often better for stimuli presented at vertical and horizontal orientations than for stimuli presented at any of the intermediate orientations (Appelle, 1972). This seems to be the case for a variety of measures such as contrast sensitivity, visual acuity (Saarinen & Levi, 1995), orientation discrimination

(Buchanan-Smith & Heeley, 1993), perception of right angles (Goldmeier, 1937), and detection and resolution of gratings (Appelle, 1972; Arakawa *et al*., 2000).

The oblique effect is thought to originate in the primary visual cortex due to proportionately fewer neurons showing response-selectivity to oblique than to cardinal (horizontal and vertical) orientations (B. Li, Peterson, & Freeman, 2003). However, preference for stimuli at cardinal orientations has also been observed in higher-order visual areas in the middle temporal (Xu, Collins, Khaytin, Kaas, & Casagrande, 2006) and inferior temporal (Vogels & Orban, 1994) cortices.

Although more commonly investigated with simple visual stimuli such as lines and sinusoidal gratings, the oblique effect has been demonstrated more recently with simple 2D shapes. W. Li and Westheimer (1997) showed that perceived orientation of simple symmetrical visual shapes, such as ellipses or the letter 'X', corresponds to the principal axis of elongation. Additionally, the estimates of orientation of these shapes exhibit an oblique effect similar to that for line segments, whereby orientation judgements were faster and more accurate when the shape was presented at either the vertical or horizontal orientations than at oblique orientations. The critical point here is that the orientation of the letter 'X' was based on the principal axis of elongation, rather than the orientation of the constituent oblique lines. W. Li and Westheimer (1997) suggested that the automatic computation of the global shape orientation may be performed by mechanisms closely related to those computing the explicit orientation of a line segment.

Identification of letter orientation is also easier for upright and inverted stimuli than for stimuli presented at oblique orientations (60°, 120°, 240° and 300°) (Corballis, Zbrodoff, Shetzer, & Butler, 1978). Although there is also some evidence that letter-like shape discrimination may be more difficult when the shapes are oriented at oblique (45°) than at cardinal (90° and 180°) orientations (Gibson, Gibson, Pick, & Osser, 1962), the oblique effect is not commonly put in the context of object recognition. In contrast, the influence of stimulus inversion on recognition has been well studied, as will be examined in the following section on the "inversion effect".

The inversion effect

The idea that changing the orientation of an image may radically alter how we perceive it goes back at least to William James (1890):

> "… [A] well-known change is when we look at a landscape with our head upside down. Perception is to a certain extent baffled by this manoeuvre; gradations of distance and other space-determinations are made uncertain; the reproductive or associative processes, in short, decline; and, simultaneously with their diminution, the colors grow richer and more varied, and the contrasts of light and shade more marked. The same thing occurs when we turn a painting bottom upward. We lose much of its meaning, but, to compensate for the loss, we feel more freshly the value of the mere tints and shadings, and become aware of any lack of purely sensible harmony or balance which they may show." (W. James, 1890, p. 81)

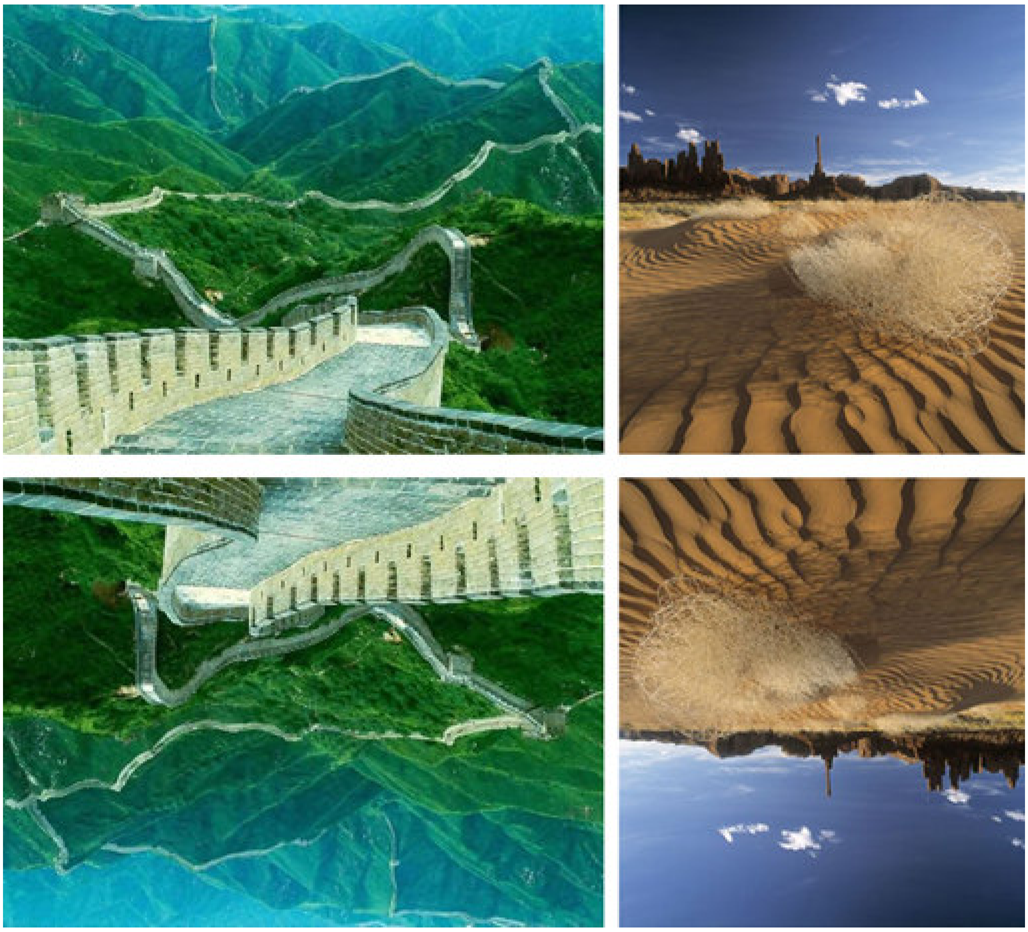

Figure 1.1: Upright and inverted photographs of the Great Wall of China (left) and a desert scene (right).

Therefore, inverting an image, either by turning it upside-down or by viewing it with our head upside down, can change one's perceptual experience (see Figure 1.1). This effect of inversion depends on prior experience with a world that is typically viewed upright. In viewing the upright world, objects farther away appear smaller and colours less bright, but these attributes are distorted when the world is turned upside down, degrading the perception of space. The examples above from William James are instances of what may be termed the *inversion effect*, in which there is loss of perceptual information when images are turned upside down. When looking at the inverted images in Figure 1.1, it is possible, albeit rather difficult, to determine what the images represent by focusing on individual features. What appears to be lost, however, is the spatial configuration of the features, which also carries a considerable amount of information. In some circumstances, an image cannot be successfully recognised at all if the configural information is not available.

The recognition of faces is especially vulnerable to inversion, more so than recognition of other classes of objects (Yin, 1969)[1]. A particularly salient illustration of this effect was demonstrated by Thompson (1980), who inverted the eyes and mouth of a picture of an upright face, causing the face to appear grotesque. Since this was first demonstrated with the face of the former British Prime Minister, Margaret Thatcher, this transformation has come to be known as "thatcherisation." If the distorted face is then rotated 180°, however, it is perceived to be relatively normal (see Figure 1.2), an effect known as the Thatcher Illusion. It is possible to see that the constituent features of the inverted thatcherised face are not in their proper orientation, by detecting that the upper lip, for example, is closer to the chin than the nose, but the grotesque appearance of the face is only seen when the image is upright. This observation also illustrates the point that James (1890) made – the perceptual experience changes when images are viewed upside-down.

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[1] Note though, that in these circumstances a face is still recognised as a face, but that face individuation is impaired.

Figure 1.2. Normal and *thatcherised* versions of Margaret Thatcher's face.

Many authors have attributed the failure to recognise inverted faces to the loss of configural information (e.g. Bruce, Doyle, Dench, & Burton, 1991; Carey, 1992; Farah, Tanaka, & Drain, 1995; Freire, Lee, & Symons, 2000; Tanaka & Farah, 1993). They argued that while the recognition of most objects is primarily feature-based, that is, based on decomposition into constituent parts, face recognition depends more on spatial configuration of the constituent parts. Tanaka and Farah (1993) also noted that the distinction between configural and feature-based processing need not be a strict dichotomy, as both types of representation may exist and be used in different degrees for different classes of objects.

There are other examples of perceptual deficits following stimulus inversion. For example, Reed, Stone, Bozova and Tanaka (2003) reported that discrimination between body postures is faster and more accurate when bodies are presented at canonical upright orientation than when they are inverted. They termed this the *body-inversion effect*. Reed et al. (2003) argued that this effect indicates that recognition of body postures requires configural information which is lost with inversion. Similarly, perception of biological motion, investigated with recorded points of light located on the joints of a moving body, is disrupted when inverted (Jokisch, Daum, Suchan, & Troje, 2005; Troje, 2003).

The effect of inversion on faces and body postures has been taken as evidence that these types of objects are processed via a different route than other object classes. For example, Reed *et al*. (2003) showed that while inversion of bodies results in a comparable effect size as inversion of faces, inversion of houses did not produce an effect of similar magnitude. Scene inversion is frequently investigated using images of houses and inversion effects are not consistently documented – whereby some studies have reported recognition deficits following inversion (Yin, 1969), while others have not (Diamond & Carey, 1986). It is possible, though, that successful recognition of a scene can be accomplished in the absence of configural information, but that configural information is needed for a complete perceptual experience. As illustrated in Figure 1.1, being able to recognise the constituent features of sand and sky can provide sufficient information to deduce that we are viewing a picture of the desert.

Epstein, Higgins, Parker, Aguirre and Cooperman (2006) showed that inversion of faces and scenes elicited increases in reaction times (RTs) in a backward-matching task relative to upright faces and scene, while inversion of common objects did not. The scene-inversion effect was stronger during the first experimental run than in the subsequent three runs, while the face-inversion effect was comparable across all four experimental runs. Both face inversion and scene inversion resulted in increased fMRI activation within the lateral-occipital complex (LOC). The LOC has been associated with extraction of visual features prior to their combination into representations of whole objects (including faces, scenes etc) in the inferior temporal cortex (Malach, Levy, & Hasson, 2002). Epstein *et al*. (2006) speculated that the increase in this area may reflect increased reliance on feature-based matching for faces and scenes. They also suggested that learning to differentiate the scenes over time may, thus, reflect a more flexible processing mechanism which can be based on both featural and configural information.

Changes in orientation and object recognition

Findings reported by Epstein *et al*. (2006) indicate that stimulus inversion results in increased reliance on visual feature extraction. Inversion can affect recognition of some classes of objects, such as faces and bodies. Recognition of these classes of object is thought to depend primarily on configural or holistic processing. Thus, inversion affects configural processing. Recognition of other common objects may depend more exclusively on feature extraction, with little contribution from configural information, and stimulus inversion, in those cases, has little effect on recognition. Even so, changes in the orientation of pictures of common objects can also have an effect on their recognition. When observers are required to simply identify rotated alphanumeric characters (Corballis *et al*., 1978; White, 1980) or naturalistic objects (Jolicoeur, 1985), their RTs do show some variation with angular departure from the upright.

The effect of stimulus misorientation on naming times is relatively transient and diminishes with practice (Jolicoeur, 1985; Jolicoeur, Snow, & Murray, 1987). For example, Jolicoeur *et al*. (1987) asked the participants to name misoriented and upright alphanumeric characters. Each character was presented four times at each orientation in the course of the experiment in two font-types, one familiar and another less familiar. Naming RTs increased linearly from 0° to 120°, but not from 120° to 180°, conforming to an M-shape as a function of angular departure from upright. Jolicoeur *et al.* found that 1) the effects of orientation diminished in the second half of the experiment and 2) that the increase in RTs with misorientation was greater for the less familiar font. These results suggest that exposure to the stimuli within the experiment and outside of the laboratory setting both had an effect on recognition deficits due to stimulus misorientation.

A possibly related phenomenon comes from the study by Corballis *et al*. (1978), in which each participant was given a target letter and instructed to indicate whether the presented character was the target. Corballis et al. found that the RTs to make this decision were a function of stimulus orientation, with linear increases up to 120°, and small decreases between 120° and 180° orientations. This effect was only observed for mirror-reversed characters, which also elicited longer RTs than normal characters overall. Jolicoeur (1990) suggested that repeated presentations at each orientation diminished the effects of orientation on character identification over the course of the experiment. An interesting point is that the effect of practice was greater for normal characters than for mirror-reversed ones. This effect could be related to Jolicoeur *et al.*'s (1987) observation that font novelty affects the magnitude of practice effects on RTs for letter naming, since we have considerably more experience with normal than mirror-reversed characters.

The practice effects observed for object naming or object identification studies have practical implications. In order to avoid the influence of practice, studies investigating the effects of orientation on object recognition need to use each stimulus only once. This can be difficult with a limited set of stimuli consisting of known objects, for example Snodgrass and Vanderwart set (1980), particularly because the familiarity with the objects within the set are not easily controlled. In order to control for stimulus novelty, some authors have developed two- and three-dimensional stimulus sets, typically consisting of line segments or cubes fitted together to form a variety of shapes (Tarr & Pinker, 1989; Tarr & Pinker, 1990; Tarr, Williams, Hayward, & Gauthier, 1998). Using these stimuli Tarr and colleagues have shown that effects of orientation on recognition are dependent on the training view: the RTs increase with angular departure from the closest learned view. Following training and testing blocks, the RTs increase with angular departure from the closest familiar orientation, either an orientation presented during the training phase, or an orientation that the stimuli were previously presented at during a testing phase.

Another factor for orientation effects on object recognition is the level of recognition required for task performance. According to Rosch, Mervis, Gray, Johnson, and Boyes-Braem

(1976) object categories are based on physical and observable properties of the real-world objects and the category labels are arranged hierarchically. The basic-level category is the category at which the physical properties of the object are common to most members of the category – for example, 'dog'. Roch *et al*. (1976) identified two other levels of a hierarchy: superordinate and subordinate levels. Superordinate level involves a more general classification than the basic level – for example animal; while subordinate level involves a more specific classification than the basic level - for example, poodle.

Hamm and McMullen (1998) investigated the effect of recognition level on orientation effects for object identification. They investigated whether effects of orientation on object recognition affect processing before or after access to an internal object representation in long-term memory store. They hypothesised that if orientation-related recognition delays are related to initial delay for access to long-term memory store, than recognition at all levels should be affected to a similar degree. Alternatively if the RT increases are accrued after the long-term memory representation has already been accessed, then identification at the subordinate level would be more affected than basic or superordinate level identification. They found that matching picture of objects with subordinate labels produced larger orientation-dependent effects than matching to basic-level or superordinate-level labels. These results, therefore, support the notion that orientation-related costs follow the access to long-term memory representations.

Effects of recognition level on orientation-dependence are probably related to the observations (e.g. Hayward & Tarr, 1997) that when stimuli vary in subtle ways, either due to small physical differences in features or spatial arrangement of the constituent features, the effects of orientation on identification times are most prominent. This is especially the case with faces, where the features themselves are generally similar across a variety of within-class exemplars (i.e. individuals). Thus, a face is nevertheless recognised as a face irrespective of its orientation, although more subtle qualities may be "hidden" by large rotations in the picture plane. If we go back to the example in Figure 1.1 – we can recognise what is in the picture, such as a wall or sand, but the perceptual experience changes. The full information can only be obtained when familiar views are observed. Corballis (1988) suggested that certain object descriptors may be extracted in an orientation-invariant manner and that these may be sufficient to identify rotated objects to some level but insufficient to distinguish between members within a category.

Mental rotation and object recognition

Some authors have suggested that the 'M'-shaped function reflects a form of normalisation of the input image to a standard orientation, as specified in an orientation-specific mental representation. Due to the linear increase of RTs between 0° and 120°, several authors (Jolicoeur, 1985, 1990; Murray, 1997; Tarr & Pinker, 1989; Tarr & Pinker, 1990) have suggested that the normalisation mechanism is mental rotation – that is, imagined rotation of the object from the orientation at which it is presented to the canonical orientation of the internal representation.

Mental rotation will be discussed in more detail later, but at this stage it may be useful to provide a brief introduction on the topic. Standard mental rotation paradigms involve parity, or handedness, judgements about stimuli at various orientations. The typical finding is that the RTs increase as a function of angular displacement between pairs of stimuli (Shepard & Metzler, 1971) or between a stimulus and its canonical upright position (Cooper & Shepard, 1973, 1975). The RT function for mental-rotation tasks is typically either linear or curve-linear and approximates an inverted V-shape symmetrical around the 180° peak.

In contrast to the RT function for mental-rotation tasks, the slope of the RT function in the case of object recognition tasks is shallower than in studies involving parity judgements, and there is typically a "dip" at 180º, giving rise to an 'M'-shaped function (Jolicoeur, 1985). Jolicoeur (1990) suggested that the dip around the 180° orientation reflects operation of two independent object recognition systems. One of these systems is orientation-dependent and requires transformation to align the input image to a canonical template. The other system depends on orientation-independent descriptions of features and parts. He argued that since upright and inverted stimuli share alignment of the vertical (top-bottom) axis, recognition of individual features or object-parts may be easier at 180° than at orientations at which the top-bottom axis is not aligned with the canonical representation. In this case, orientation-invariant feature extraction mechanism may result in faster object identification than the normalisation to the canonical upright.

An alternative explanation for the dip in RT function around the 180° orientation was offered by Murray (1997). She proposed that inverted stimuli are transformed to upright by a rotation out of the picture plane, and the relatively shorter RTs in response to inverted stimuli can be attributed to faster rotation out of the picture plane, relative to rotation within the picture plane. Although this interpretation is contrary to the original mental-rotation findings which indicated that mental rotation rates are independent of axis of rotation (i.e. in depth or in the picture plane, Shepard & Metzler, 1971), Murray cited results from Metzler and Shepard (1984) and Parsons (1987) who reported that rotations around the axis of elongation of the "torus" shapes were faster, and produces shallower rotation slopes, than rotations within the picture plane. Murray tested whether, in a parity discrimination task, instructing participants to flip the image out of the picture plane (around the horizontal axis) would result in faster RTs than instructing the participants to rotate (spin) the image through the picture plane. She showed that normal-mirror discriminations were faster when the participants were instructed to flip than when they were instructed to rotate the image through the picture plane, even though that flip would have to be followed by another flip across the vertical axis in order to restore the true left-right orientation of the image.

Murray then compared the slopes of RTs in response to mental rotation and object recognition tasks (mirror-normal judgement and identification). The participants were divided into two subgroups based on whether their object naming RTs for stimuli presented at 180° were above or below the average. Participants with the RTs below the mean were assumed to employ a “flipping” strategy, i.e. rotation out of the picture plane, and the participants with RTs above the mean were assumed to employ a “spinning” strategy, i.e. rotation through the picture plane. Murray tested the same participants on a parity-discrimination task where the participants were cued to either “flip” or “spin” stimuli presented at 180° orientation. The resulting object-naming and mirror-normal functions were similar within each group, when using the flipping cued 180° mirror-normal trials for comparison with the “flipping” group and using the spinning cued 180° mirror-normal trials for comparison with the “spinning” group. That is, for both object-naming and mirror-normal trials, the spinning group showed inverted V-shaped RT functions while the flipping group showed M-shaped RT functions. There was, however, a discontinuity in the RT function in the object- naming task that was not evident in the mirror-normal task. For the “spinning” group, it appears that the RTs increased between 0° and 60° and between 120° and 180°, but not between 60° and 120°, which casts some doubt on the idea that the spinning group used a mental-rotation strategy.

Problems with the mental rotation account

This last point aside, Murray’s evidence is fairly convincing, but there are a number of other difficulties with the idea that mental rotation is used for object recognition. First of all, it is logically difficult to understand how an individual may rotate an object to its upright position if they do not know what that object is in the first place. The symmetry of the inverted V-shaped function indicates that rotation is accomplished along the shortest trajectory. This, in turn, implies that object identity, object-orientation, the canonical upright, and direction of required orientation are all known prior to mental rotation.

If object identity is known prior to mental rotation or indeed perception of object orientation, then one would expect RTs for object recognition tasks to be shorter than the RTs for parity judgements or orientation judgements. This is exactly the pattern that has been observed in a number of studies. Naming of alphanumeric characters (Corballis *et al*., 1978) or categorisation as letters or numbers (Corballis & Nagourney, 1978) and naming of simple objects (Jolicoeur, 1985; Murray, 1997) are typically faster than mirror-normal discriminations (Corballis & Nagourney, 1978; Jolicoeur, 1985; Murray, 1997)) or naming of object orientation (Corballis *et al*., 1978), which suggests that object recognition occurs prior to recognition of left-right coordinates, and object-orientation.

Additional evidence against the role of mental rotation in object recognition comes from studies of the effects of rotary motion after-effect. Rotary motion after-effect refers to the observation that a stationary object appears to rotate in the direction opposite to that of a previously viewed rotating disc. In a parity judgement task, Corballis and McLaren (1982) found that if the direction of the motion after-effect is opposite to the direction of mental rotation, the slope on the RT function is increased – indicating that the rate of mental rotation decreased. They also found that if the direction of the motion after-effect is the same as the direction of mental rotation, the slope of the RT function is decreased – indicating that the rate of mental rotation increased. In contrast, the rotary motion after-effect does not affect object recognition (Jolicoeur, Corballis, & Lawson, 1998), suggesting that mental rotation is not involved.

As noted earlier, the effects of orientation on object recognition are particularly prone to practice effects (Jolicoeur, 1985). Jolicoeur (1990) argued that the initial presentations of novel stimuli depend on matching to an internal, orientation-specific, template. If the stimulus is presented at an orientation other than the canonical one, it would, thus, require normalisation to the standard template. Repeated presentations of the same stimuli would result in increased familiarity and may result in orientation-independent recognition involving feature-based processing.

However, as discussed above, it is not entirely clear as to how the normalisation to canonical upright can be performed if one does not know what the object is in the first place. Corballis (1988) argued that misoriented objects can be identified without a normalisation to a canonical upright, but that viewers may then rotate it to the upright as a check on their initial impression. An alternative account was proposed by Hamm and McMullen (1998). They argued that the identification of a misoriented object is determined at the superordinate-level – for example a “quadruped”. This fairly general identification would provide sufficient information required for normalisation – the current orientation and the canonical upright, despite not providing subordinate-level name. Thus, subordinate-level identification may depend on normalisation to upright, *after* superordinate-level identification.

As a final point against the role of mental rotation, brain-imaging studies show that the recognition and mental rotation of rotated objects activate different brain areas, which to some extent follow the distinction between the *ventral* and *dorsal* systems described by Ungerleider and Mishkin (1982). Gauthier *et al.* (2002) showed that mental rotation is dependent on the dorsal stream while orientation-dependent recognition recruits additional areas in the ventral stream, but not the dorsal stream. In contrast, though, Leek, Atherton and Thierry (2007) showed that increases in RTs as a function of stimulus orientation are associated mental-rotation correlates of event-related potentials (ERPs) – an increase in parietal negativity between 400 and 500 ms after stimulus onset, suggesting that orientation-dependent recognition reflects mental rotation to upright. Leek *et al.* (2007) also showed that when recognition could be accomplished by use of distinct features, there was no increase in RTs with changes in orientation *and* no increase in parietal negativity.

The difference in the results from these two studies may be related to the fact that Gauthier *et al.* (2002) used three-dimensional torus shapes, while Leek *et al.* (2007) used two-dimensional shapes. The three-dimensional torus shapes are thought to elicit a piecemeal rotational strategy (Corballis, 1997) while simpler two-dimensional shapes might be rotated in a holistic manner. If this is the case, then it may have been easier for the participants to use feature-based analysis for shape matching in the study by Gauthier *et al.* (2002) and mental-rotation strategy in the study by Leek *et al.* (2007).

Recognition without mental rotation

The evidence reviewed above suggests that mental rotation is unlikely to be the mechanism by which misoriented object recognition is accomplished, although it may serve a role in some circumstances. This section will review two accounts for misoriented object recognition that do not involve mental rotation. I will firstly discuss the view that object recognition is accomplished by matching a stimulus representation to a mental template based on multiple stored views. Subsequently, I will discuss the view that mental representations of objects are object-centred, and thus viewpoint-invariant.

Multiple-views representations

One explanation that does not involve mental rotation for object recognition stipulates that internal object representations are based on stored representations of multiple viewpoints (Schyns, 1998; Tarr, 2003), rather than a single canonical representation, as stipulated by Jolicoeur (1990). In addition to multiple stored views used to represent the object, object representations are also based on known correspondences between the individual views. A familiar object presented at a novel orientation would then be compared to the closest known viewpoint of the object by a process of normalisation (Tarr & Pinker, 1989). Tarr (2003) suggested that the “normalisation” may be view interpolation, rather than mental rotation a as was suggested by Jolicoeur (1985; 1990) and Murray (1997). What is unclear from this theoretical standpoint is how many viewpoints would be stored for any given object or object-class. Nevertheless, this can explain orientation-dependent recognition associated with rotations both in the picture plane and out of the picture plane.

Perrett *et al*. (1998) postulated that the increase in RTs as a function of object orientation can be explained in terms of the rate of accumulation of neural activity of cells selectively responsive to a specific view of a particular object. The number of cells tuned to particular viewpoint would depend on previous experience with the object at that viewpoint. Since we normally encounter objects at upright, more cells would be responsive to the upright views of objects than for other orientations, which seems to be the case (Perrett *et al*., 1998). Activity of a larger cell population would require less time to accumulate a sufficient amount of neural activity then a smaller cell population. Perrett *et al*. (1998) suggested that the RT cost associated with object recognition, stems from increases in the time required to accumulate sufficient neural activity in the inferior temporal cortex. The time required to accumulate sufficient neural activity would be a function of the number of neurons that are selective to a given view of the object. The number of neurons selective to a given object would be a function of visual familiarity with the object at a given viewpoint. Thus, the RTs would be a function of visual familiarity, rather than orientation *per se*.

Since the number of view-specific neurons is a function of exposure to that view, repeated exposure to a particular view of an object would result in plastic changes over time and recruitment of additional neurons for that view-specific configuration of object-specific features. Therefore, the practice effects can be explained in terms of recruitment of additional neurons, which would then result in larger neuronal population which would take less time to accumulate a sufficient amount of neural activity for recognition.

However, Murray, Jolicoeur, McMullen and Ingleton (1993) have shown that practice effects may be independent of training-stimulus orientation. The participants named line drawings of natural objects at various orientations. Following a training block during which each stimulus was presented twice at identical orientation; participants were again presented with the same set of stimuli, where half of the stimuli were presented at the same orientation as during training and the other half of the stimuli were presented at novel orientations. They found that first presentations of the stimuli, during the training phase, resulted in longer RTs for misoriented than for upright objects. Murray et al. (1993) also found that orientation-dependence of the RTs reduced with practice – even if the stimuli was presented at novel orientations. Murray et al.(1993) argued that there is transfer of practice effects to novel orientations, indicating that their results were consistent with the idea that the reduction of orientation-dependence with practice is due to identification of critical features that could aid in object recognition. A method that is only used *after* the misoriented stimuli were recognised using a normalisation strategy.

These results are inconsistent with the explanation offered by Perrett et al. (1998) – that the practice effects reflect recruitment of new neuronal populations for novel orientations. A possibility remains that both of these mechanisms are in place. It is unlikely that a single presentation of an object in a novel orientation would result in plastic changes required for "recruitment of new neurons". Therefore, reduction of orientation effects after a single presentation would not necessarily reflect such plastic changes. In situations in which recognition can be accomplished by feature identification, this may be the more optimal strategy – particularly when dealing with a finite set of relatively simple line-drawings of objects. In more ecologically valid situations though, increased exposure to particular views of objects may lead to development of view-specific stimulus representations, which may – in turn – reflect plastic changes within higher-order visual areas corresponding to increased number of neurons with view-selective firing rates.

Object-centred representations

Another explanation that does not stipulate that mental rotation is involved in object recognition has been proposed by Hummel and Biederman (1992). According to their view, the internal representations of objects are orientation-invariant, and are based on structural descriptions of 3D component features, called geons, and the configural relationships between the geons. The memory representations are thought to depend on object-centred descriptions of the configural arrangement of the constituent parts. The configural relationships between the geons are described in terms of above/below (top-of and bottom-of values) and next-to (side-of values) descriptions, and the individual geons are also specified in terms of attributes for their axes of elongation as horizontal, vertical, or oblique. According to Biederman, this set of descriptors remains largely stable when objects are rotated in depth.

Nevertheless, rotation of an object in the picture plane does result in some disparities between the internal and the input representation in terms of the relationship between the geons and the spatial attributes of individual geons. Inversion would affect only the above/below values, not next-to values or the axes of elongation of individual geons. The largest disparity occurs if an object is rotated by 90° in either the clockwise or counter-clockwise direction because the above/below attributes of the internal representation would be perceived as next-to attributes, and the next-to attributes would be perceived as above/below attributes.

According to Hummel and Biederman (1992) the configural information required for object-recognition is deliberately not coded in terms of left/right information because a switch between the left and right would be commonly observed with large rotations in depth. The left-right coordinates of objects would be coded by viewer-centred representations located in the dorsal visual system (Biederman & Cooper, 1992). This interpretation would also be consistent with the empirical evidence that parity judgements about rotated objects consistently elicit mental rotation.

A point to note here is that Hummel and Biederman (1992) suggest that rotations in the picture plane and rotations in depth are different. The most obvious difference is that the latter results in a loss of visibility of features while the former does not. The loss of visibility of features can occur either through foreshortening of axes or because 3D surfaces would come in and out of the view as the object rotates in depth. Rotations in the picture plane, on the other hand, result in changes of the top-bottom and left-right coordinates between the features *relative* to the observer. The critical point here is that the orientation-invariant internal representations are optimised for commonly observed changes in viewpoint, such as depth rotations.

Orientation-invariant recognition for depth rotations could be accomplished as long as the information regarding the same constituent parts could be extracted. Nevertheless, rotations in depth could elicit orientation dependence if the change in viewpoint results in occlusion of certain object parts. Biederman and Gerhardstein (1993) showed that orientation-invariant recognition could be accomplished with depth rotations of objects with distinctive parts. However, Hayward and Tarr (1997) reported that rotations in depth can also elicit orientation-dependent recognition provided that the objects to be differentiated are composed of a set of similar features. As mentioned earlier, when differences between exemplars of an object class differ in subtle ways, the effects of orientation on object recognition are the most prominent. This observation may relate to the level of recognition category that the object needs to be assigned before a correct identification can be made, as within class exemplars are likely to be more visually similar to each other than to exemplars from other categories.

Orientation-dependent neural processing

So far, I have discussed processes that may explain orientation-dependent behavioural performance. I have briefly discussed how some theories postulate that the internal representations of objects are object-centred (Biederman, 1987) while others postulate that the memory representations of objects are view-dependent, although they differ in the number of viewpoint-dependent representations. Visual processing leading to recognition would have to be viewpoint-dependent, irrespective of whether the representational codes are object-centred and viewpoint-dependent, since rotations of objects either in depth or in the picture plane can result in drastically different retinal images. Orientation specificity of neural processing is observed from primary visual cortex onwards. Neurons responsive to edges show orientation specificity (Hubel & Wiesel, 1959) and, as indicated earlier, larger number of neurons are selectively responsive to cardinal orientations, than to any of the oblique orientations (B. Li et al., 2003).

The orientation sensitivity of edge-detector cells has led Marr (Marr, 1982; Marr & Nishihara, 1978) to develop a computational account of visual processing leading to recognition. According to this account, the visual system extracts information from the edges of the visible object. These edges are then reconstructed into a more complex description of object shape. The following processing stage is deriving a 2½D sketch which provides information regarding the slopes of the edge-defined surfaces of the object. Marr also argued that the 2½D sketch is used to generate three-dimensional object parts referred to as "generalised cylinders", which operate as the building blocks for object-centred three dimensional representations of the shapes. This theoretical framework highlights that, prior to organisation of object-centred descriptions, visual processing is dependent on orientation.

Therefore, as Corballis (1988) noted, it may be necessary to distinguish between perceptual processing and the processes involved in shape recognition itself. If internal representations are object-centred, then only perceptual processing should be orientation-dependent. If, on the other hand, recognition is dependent on generation of sufficient neural activity of object-specific neural populations that consist of both orientation-dependent and orientation-invariant neurons, then neural processing underlying object recognition would always depend at least in part on stimulus orientation (Perrett *et al.*, 1998).

Lawson and Jolicoeur (2003) showed that the M-shaped function which characterises RT to recognise rotated objects also characterises duration thresholds for line drawings briefly presented at varying angular departures from upright. Similar effects of stimulus duration on accuracy rates were observed for identification of alphanumeric characters (Jolicoeur & Landau, 1984). Jolicoeur (1990) suggested that increased processing time may be necessary for misoriented object recognition, because stimulus misorientation may also affect the feature-based recognition route, as suggested by Hummel and Biederman (1992). An alternative explanation is that a smaller number of orientation-specific neurons code for misoriented than for upright objects, and that longer exposure times are needed for the neural activity to reach the critical threshold for recognition. In any case, assessing the neural mechanisms underlying object recognition should reveal orientation-specific response properties and possibly allow differentiation between orientation-specific perceptual processes and those related to recognition itself.

Mirror-image equivalence, parity discrimination and mental rotation

Adult, neurologically unimpaired humans have little difficulty in discriminating objects of opposite parity, as when we need to decide whether a glove would fit the left or the right hand. Although it is rare for objects to be *named* differently depending on parity, an important exception is the naming of the lowercase letters b, d, p, and q. However, children learning to read frequently confuse lower case ‘b’ and ‘d’, and ‘p’ and ‘q’, (e.g. Liberman, Shankweiler, Orlando, Harris, & Bell Berti, 1971) suggesting that, for the purposes of literacy at least, we need to *learn* to discriminate between mirror-image forms of visually presented shapes.

According to Hummel and Biederman (1992), disregarding the left-right information from an internal representation of objects serves to our advantage because a switch between the left and right would be commonly observed with large rotations in depth. Furthermore, as Corballis (1988) pointed out, in the natural world an object can frequently be encountered in either the left or the right profile. That is the profile of any object reverses if we view it from the other side - the same face may be seen in left or right profile, the predator may attack from either side. Thus, it is generally to our advantage to treat mirror images as equivalent.

Neurophysiological evidence provides a mechanism for mirror-image equivalence. Single-cell recordings have shown that viewpoint-dependent cells show decrease in their response rates with stimulus rotation away from the preferred orientation. For example, cells selectively responsive to the profile of the face will show a decrease in the firing rates as the face is rotated away from the profile view, either towards the front view or the back view. However, the cells will be responsive to the left or the right view, and thus depth rotations of 180° elicit the same response properties (Logothetis, Pauls, & Poggio, 1995; Perrett *et al.*, 1998). This property is not observed for all viewpoint-dependent cells and there are some cells that show selectivity to either the left or the right view, but nevertheless the presence of left-right invariant cell populations illustrates the neural mechanism for left-right invariance. These are found in the so-called ventral stream of the visual system, extending from the occipital cortex into the inferior temporal lobe, which is regarded as responsible for shape recognition (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Furthermore, non-human primates with bilateral inferior temporal lesions are considerably better at mirror-image, or parity, discriminations, indicating that mirror-image equivalence can be eliminated when the influence of left-right invariant cell populations is reduced (Perrett *et al.*, 1998).

The dorsal stream, on the other hand, extends from the occipital cortex into the parietal lobe, and is regarded as responsible for the location of objects in space, rather than for shape recognition itself (Ungerleider & Mishkin, 1982).[2] Hummel and Biederman (1992) suggested that it is the dorsal stream, rather than the ventral stream, that encodes the information that allows for mirror-image discrimination. Several neuropsychological case reports have described patients with bilateral posterior lesions who have difficulties

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[2] Goodale and Milner (1992) suggested that the role of the dorsal stream is not for spatial perception but for directing visually guided actions.

discriminating mirror-images, even when they are clearly presented in an array. For example, one patient was unable to choose which image was “the-odd-one-out” when presented with an array of three stimuli, where one was the mirror image of the other two (Priftis, Rusconi, Umiltà, & Zorzi, 2003; Turnbull & McCarthy, 1996).

Warrington and Davidoff (2000) have described a patient with the same impairment in discriminating between mirror-image forms of common objects. Interestingly, this patient’s performance on mirror-image discrimination was only impaired when she was able to identify the object. Her performance was considerably better when she was unable to name the depicted object and she was nearly perfect when she was required to discriminate between mirror-image forms of simple geometrical designs. An MRI scan of the patient showed white matter loss in parieto-occipital areas bilaterally. Warrington and Davidoff (2000) argued that the improved performance on parity discrimination reflected a disconnection between cortical regions in the ventral stream related to object recognition and spatial processing cortical regions in the dorsal stream. Failure to recognise a stimulus would result in purely spatial processing of the available images within the dorsal stream.

However, mirror-image discrimination becomes considerably more difficult if the images are rotated away from each other, or from a canonical upright. For example, it is not immediately obvious whether an upside-down glove is a left or a right one. Determining the handedness, or parity, of a glove may require either physical or imagined rotation – a process known as mental rotation (Shepard & Metzler, 1971) – of the glove into alignment with our hands. Similarly, when disoriented, the lower case b, d, p and q need to be rotated to the upright in order to be disambiguated and named correctly (Corballis & McLaren, 1984).

Cooper and Shepard (1973) devised a simple paradigm to elicit mental rotation, in which they timed the participants as they indicated whether misoriented alphanumeric characters were normal or backward (mirror-reversed). RTs increased monotonically with the angular departure of the characters from upright, consistent with the suggestion that a mental image of the stimulus is rotated in a manner analogous to physical rotation. They also found that the direction of the inferred rotation, clockwise or anticlockwise, had little effect on the slope of the function, thus giving rise to an inverted 'V' function symmetrical around the 180º orientation.

The symmetry of this function implies that mental rotation is performed along the shortest angular trajectory to the upright. This further suggests that participants must have known both the identities and the orientations of the characters prior to the act of mental rotation itself. Logically, one would expect this to be so, since it is otherwise difficult to understand how one could rotate an object to the upright without first knowing its identity, and then knowing its orientation. Corballis *et al*. (1978) found that RT to identify an object was consistently shorter than RT to indicate its orientation. Further empirical support has been provided by DeCaro (DeCaro, 1998; DeCaro & Reeves, 2002). DeCaro used a verbal description-picture matching paradigm, in which a verbal statement described object identity and orientation. A subsequently presented picture either matched the verbal description, or mismatched the verbal description in terms of orientation, object identity, or both the identity and the orientation. DeCaro (DeCaro, 1998; DeCaro & Reeves, 2002) found that orientation mismatches were slower to detect, and less accurate, than identity mismatches, suggesting that object-identity is determined before orientation identification.

Neural mechanisms of mental rotation

Parity-judgement tasks are frequently used to investigate neural mechanisms underlying mental rotation. Neuroimaging studies have identified a network of regions including parietal regions (e.g. Alivisatos & Petrides, 1997; Cohen *et al*., 1996; Harris *et al*., 2000; Koshino, Carpenter, Keller, & Just, 2005; Podzebenko, 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 (Podzebenko *et al.*, 2002) and area MT (Cohen *et al.*, 1996), and higher order pre-motor regions (Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Podzebenko *et al.*, 2002; Richter *et al.*, 2000) that have been associated with parity-discrimination tasks. However, it remains unclear which of these areas reflect the mental rotation process *per se*, and which subserve other cognitive processes associated with parity-judgement 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 parity-judgement tasks no doubt reflects the synthesis of these cognitive processes.

Thus, one might expect that the sequence of processing events leading to parity judgements would be: 1) feature extraction, 2) object recognition, 3) determining the object's orientation, 4) determining which way to rotate to the upright, 5) actual mental rotation to the upright, and 6) parity discrimination. In tasks were a response is required, the following response-related processes would follow parity discrimination: 7) response selection and 8) response execution processes – processes that may also influence RTs.

EEG is particularly well suited for analysis of sequential processing stages due to its excellent temporal resolution. The EEG correlates of mental rotation are also well established. Amplitude modulation of the circa 400–700 ms parietal ERP component during mental rotation of letters was initially described in 1989 by Peronnet and Farah (1989) and Wijers *et al.* (1989) and the basic phenomenon has been extensively replicated since then. Wijers *et al.* (1989) interpreted this amplitude effect as a slow parietal negative wave superimposed upon a temporally- and spatially-coincident, but functionally independent, P300 complex. The amplitude of the slow parietal negativity increases monotonically as a function of the angular disparity of stimuli from the upright position, mirroring the RT results and suggesting that this

ERP component is closely tied to the neurophysiological operations underlying mental rotation. This inference has been strongly validated in a series of experiments by Heil and colleagues, who have systematically elucidated the functional and temporal characteristics of this component (see Heil, 2002 for a review). Taken together, the studies of Heil and colleagues (Bajric, Rösler, Heil, & Hennighausen, 1999; Heil, 2002; Heil, Rauch, & Hennighausen, 1998) provide compelling evidence for the hypothesis that the parietal amplitude modulation is an electrophysiological marker for the mental rotation.

Ventral stream activation in parity-judgement tasks

Activation in the ventral stream is also consistently observed in parity judgement tasks (e.g. Alivisatos & Petrides, 1997; Cohen *et al*., 1996; Ecker, Brammer, David, & Williams, 2006; Koshino *et al*., 2005; Podzebenko *et al*., 2002). The ventral stream activation has been associated with visual processing related to stimulus recognition. In a time-resolved fMRI study, Ecker *et al*. (2006) investigated the time course of Blood-Oxygenation-Level-Dependent (BOLD) activation in response to a parity-judgement task with 3D torus shapes similar to those used by Shepard and Metzler (1971). Ecker et al. (2006) found that the duration of the BOLD activity within the LOC and dorsal extrastriate areas was correlated with stimulus duration, while duration of the BOLD activation within the dorsal parietal and higher order pre-motor areas was correlated with RTs. Ecker *et al*. (2006) concluded that the ventral stream activation can be attributed to visual perception of the stimuli, while the dorsal parietal and prefrontal regions are involved in mental transformation of the images.

Vanrie *et al*. (2002) compared the parity-judgement task with 3D torus shapes with torus-shape matching task. They found that the RTs increased as a function of angular displacement between the two simultaneously presented torus shapes for the parity-judgement task, suggesting that this task elicited mental rotation. The RTs in response to the shape-matching task did not vary as a function of stimulus orientation, indicating that this task did not involve either mental rotation or another form of orientation-dependent recognition mechanism. Neuroimaging findings indicated that both tasks elicited comparable levels of activation in the ventral stream, while only the parity judgement task elicited activation in the dorsal parietal and prefrontal regions.

Using a similar paradigm, Gauthier *et al.* (2002) also compared a parity-judgement task with a torus-shape matching task. However, Gauthier et al. found that both the parity-judgement and the shape-matching task elicited orientation-dependent increases in RTs with angular displacement between the *consecutively* presented stimuli. The difference between the behavioural results reported by Gauthier et al. and Vanrie et al. may be related to differences between simultaneously presented stimuli and consecutively presented stimuli. Alternatively, the differences may be related to the way that the torus shapes differed for the shape-matching task. Vanrie et al. used a distinct feature – an oblique angle between the body and one of the arms of the shape, while Gauthier et al. used a different configuration of "arms". It is possible that the presence of an oblique angle in one shape, and the absence of an oblique angle can be used as a distinct feature, and may preferentially engage orientation-invariant feature-based recognition pattern, while changes in configuration are more difficult to detect.

Neuroimaging results also differed between Gauthier et al. and Vanrie et al. studies. Gauthier et al. found that object-matching task elicited a larger degree of activation in the ventral stream, compared with the parity-judgement task, while the parity-judgement task elicited greater degree of activation in the dorso-parietal regions. Furthermore, ventral-stream activation was orientation dependent only for the shape-matching task, while dorsal-stream activation was orientation dependent only for the parity-judgement task.

A difficulty with these experiments is that they involved matching of shapes that have neither an intrinsic upright, nor any representation in long-term memory. The mechanisms involved in matching may be different from those involved in recognition itself, especially if the shapes to be matched are relatively unfamiliar. Alivisatos and Petrides (1997) showed that parity judgements about upright and rotated letters and digits elicits increases in activation in the ventral stream compared to letter-digit categorisation. There was no difference in the ventral stream activation between parity judgements about upright and rotated stimuli, suggesting that the ventral stream is not involved in mental rotation *per se*.

Mental rotation and the right parietal

It has often been suggested that mental rotation *per se* is predominantly subserved by the right parietal cortex. The evidence for this claim, however, is equivocal. There are *a priori* reasons to suppose that mental rotation may be a right hemisphere function and to suppose that mental rotation is subserved by the posterior-parietal cortex (PPC). These reasons and empirical evidence will be reviewed in the following sections.

Mental rotation and the right hemisphere

Corballis (1997) noted that in many ways mental rotation can be seen as being complementary to language. Similarly to language, mental rotation is a higher-level cognitive process that develops in childhood and involves transformations. However, unlike symbolic and computational transformations used in language, transformations required in mental rotation are non-symbolic and, at least arguably, non-computational; instead mental rotation is a smooth, analogue process similar to physical rotation. Given that language is predominantly left lateralised, one may expect that complementary processes, such as mental rotation, could be subserved by the other, *the right* hemisphere. Furthermore, mental rotation is performed on mental images that are based on holistic representations, rather than lists of features or attributes. Given that the right hemisphere is thought to subserve holistic perceptual mechanisms, while the left is thought to subserve componential or feature based mechanisms (Bradshaw & Nettleton, 1981), one may expect that holistic processes may preferentially recruit right hemisphere functioning.

However, evidence regarding hemispheric dominance of mental rotation is mixed. In a PET study, Harris *et al*. (2000) found selective right parietal increases in activation with increased mental rotation task demands. In contrast, in another PET study Alivisatos and Petrides (1997) found predominantly left-parietal increases and right frontal and subcortical (caudate nucleus) for mental rotation, despite the fact that parity judgements about upright and rotated characters also elicited right parietal activation. Furthermore, a number of other studies have reported bilateral parieto-frontal activation in response to mental rotation (Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Cohen *et al*., 1996; Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001; Just, Carpenter, Maguire, Diwadkar, & McMains, 2001; Podzebenko *et al*., 2002). Similarly, some electrophysiological studies have found that mental-rotation correlates are distributed over the right parietal regions (Bajric *et al*., 1999; Pegna *et al*., 1997; Yoshino, Inoue, & Suzuki, 2000), while others have demonstrated bilateral parietal effects (Heil, 2002; Heil *et al*., 1998).

Neuroimaging evidence does not provide any indication as to whether a cortical region is necessary for successful performance of a task. Rorden and Karnath (2004) noted that it is possible that, in some cases, anatomically-connected cortical regions will show co-activation even if only one of those areas is actively involved in the task. They mentioned that areas that are not directly involved in task-related processing may be activated due to their anatomical connections with regions that are specifically involved in the task. They also noted that bilateral activation is frequently observed because of the strong homotopic neural connections between the two hemispheres. Therefore, it may be more useful to consider neuropsychological or cortical-stimulation evidence in this regard.

Some, but not all, neuropsychological evidence supports the notion that the right hemisphere may be dominant for mental rotation. For example, a split-brain patient, tested by Corballis and Sergent (1989), was unable to perform a parity-judgement task when stimuli were presented to the right visual field, and thus the left hemisphere, but was able to perform the task when stimuli were presented to the left visual field, and thus the right hemisphere. Although the patient's left hemisphere gained some proficiency in later testing, it remained inferior to the right, and may have adopted strategies other than analogue rotation (Corballis, 1997). Additional supporting evidence for right hemisphere dominance was provided by Farah and Hammond (1988). They reported a case of a patient who, following right middle-cerebral artery infarction affecting frontal, temporal and parietal regions, was unable to perform parity judgements about rotated objects. In contrast Mehta and Newcombe (1991) showed that a group of patients with selective *left* parietal damage were impaired on mental rotation tasks.

Cortical-stimulation studies have also yielded inconsistent evidence. Harris and Miniussi (2003) found that transcranial magnetic stimulation (TMS) of the right intraparietal sulcus (IPS) interfered with parity judgements of misoriented alphanumeric characters, while stimulation of the homologous area on the left or midline parietal sites did not affect the rate of mental rotation, supporting the notion that mental rotation is subserved by the right parietal. In another TMS study, Feredoes and Sachdev (2006) found that stimulation to both the left and the right IPS affected the accuracy rates, but not RTs, for parity judgements with 3D torus shapes. The effects on accuracy rates differed following the left and the right stimulation, with impaired performance for rotations up to 120° following right-parietal stimulation, and selective deficits on 180° rotations following left-parietal stimulation. Feredoes and Sachdev (2006) suggested that these effects illustrate right hemispheric involvement in spatial transformations through smaller angles, and use of piecemeal strategies for larger rotations specifically elicited due to the componential nature of the stimuli. Namely, there is some evidence that the Shepard-Metzler figures are rotated in piecemeal fashion (Bethell-Fox & Shepard, 1988; Just & Carpenter, 1985), and it may be this aspect, rather than the rotation component itself, that favours the left hemisphere (Corballis, 1997). More generally, the left hemisphere may be increasingly engaged in spatial performance as the complexity of the task increases (De Renzi, 1978; McGuinness & Bartell, 1982).

However, it is not clear whether TMS stimulation resulted in de-activation of the only area that can perform the necessary transformations. As a part of pre-surgical assessment, Zacks *et al*. (2003) tested a patient on a mental-rotation task while applying direct-cortical stimulation to a portion of the right dorsal IPS. Compared to non-stimulation baseline, the patient exhibited deficits in mental rotation following direct-cortical stimulation. However, following surgical resection of tissue surrounding the stimulated region, the patient's performance on the mental-rotation task was unimpaired. Zacks et al. (2003) suggested that other cortical areas were able to perform mental rotation, but the stimulation of this region interfered with the process by corrupting the information.

Therefore, evidence from both imaging and neuropsychological domains have provided conflicting information regarding hemispheric dominance of mental rotation. Corballis (1997) suggested that one possibility is that both hemispheres are capable of performing mental rotation, but that the "rotation is carried out more quickly and efficiently in the right than in the left hemisphere, so that mental rotation is simply more efficient with less involvement of the left hemisphere" (p. 114). If this is the case, then the results reported by Harris and Miniussi (2003) that TMS stimulation of the right, but not the left, hemisphere, affects the rate of mental rotation could be interpreted as an effect of timing. Firstly, it is important to note that in this experiment the TMS stimulation did not affect accuracy of responses, implying that participants were still able to perform the task. Therefore, it is possible that the increase in mental rotation rate following right IPS stimulation was caused by continued mental rotation by the relatively slower left hemisphere. An alternative may be that mental rotation was disrupted following right-hemisphere stimulation, and that the right hemisphere continued the transformation following recovery from TMS stimulation.

Mental rotation and the parietal cortex

Mental rotation is considered to be a prototypical example of a visuospatial cognitive process (Corballis, 1997). As indicated earlier, according to Ungerleider and Mishkin's (1982) model, the dorsal visual stream, culminating in the PPC subserves visual perception of spatial properties of an image. If this is an accurate interpretation of the functional subdivision within the visual system, then it seems reasonable that mental rotation, which depends on imagined *spatial* transformation of a mental image, would depend on the dorsal visual system, and specifically the PPC.

The involvement of the PPC in parity tasks has been supported by a number of other neuroimaging studies (Cohen et al., 1996; Harris et al., 2000; Jordan et al., 2001; Jordan, Schadow, Wuestenberg, Heinze, & Jäncke, 2004; Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002; Koshino et al., 2005; Lamm et al., 2001; Podzebenko et al., 2002; Richter et al., 1997; Tagaris et al., 1996, 1997; Tagaris et al., 1998), as well as neuropsychological (Ditunno & Mann, 1990; Farah & Hammond, 1988; Mehta & Newcombe, 1991), electrophysiological (Bajric *et al*., 1999; Heil, 2002; Heil *et al*., 1998; Pegna *et al*., 1997; Peronnet & Farah, 1989; Wijers *et al*., 1989; Yoshino *et al*., 2000), TMS stimulation (Feredoes & Sachdev, 2006; Harris & Miniussi, 2003), and direct-cortical stimulation (Zacks *et al*., 2003) studies. Alivisatos and Petrides (1997) also found that inferior parietal lobule (IPL), a portion of the PPC, showed larger activation levels for parity judgements about rotated characters compared with upright characters, thus indicating that these areas are involved in mental rotation *per se*.

There are several issues here. First of all, the PPC is a large area, comprised of superior and inferior parietal lobules (SPL and IPL) which are divided by the IPS. Parity-judgement tasks have been shown to elicit activation in the SPL (e.g. Alivisatos & Petrides, 1997; Cohen et al., 1996; Ng et al., 2001; Tagaris et al., 1997), IPS (e.g. Gauthier *et al*., 2002; Harris *et al*., 2000; Lamm *et al*., 2001; Podzebenko *et al*., 2002; Richter *et al*., 1997) and IPL (e.g. Alivisatos & Petrides, 1997; Ng *et al*., 2001; Tagaris *et al*., 1997). The question is whether at least some of the apparent variation is related to different anatomical labels used for similar regions or may result from differences in task demands. For example, activation within both the SPL and IPL were reported in the studies by Alivisatos and Petrides (1997) and Ng *et al.* (2001). In both cases, the activation was in the vicinity of the intraparietal sulcus, suggesting that it may have been more accurate to refer to this activation as originating from the IPS.

However, although Ng *et al.* (2001) found that the parity-judgement task elicited activation within the IPS, they also found that the activation within the precuneus was correlated with the RTs, possibly suggesting that the mental rotation is dependent on the activation within the precuneus, rather than the IPS. The problem with this interpretation is that the correlation reported was between activation during the parity-judgement task and average RTs across all stimulus orientations. The overall RTs, averaged across all stimulus orientations, would provide information regarding general processing speed as well as speed of rotation. A more sensitive RTs measure for the mental rotation process *per se*, would be the slope of the RT function. The slope of the RT function does not take into account the time taken to process visual information, make a decision, select and then execute the response. Therefore, it is difficult to argue – on the basis of the correlation between overall RTs and precuneus activations – that the precuneus activation reflects mental rotation. The relationship is equally likely to reflect increased reliance on the precuneus for participants who are either poorer at mental rotation *per se*, or other perceptual processes preceding or following mental rotation.

Secondly, activation in areas other than the parietal cortex are frequently found in response to parity judgement tasks, most notably higher-order prefrontal regions (Alivisatos & Petrides, 1997; Carpenter *et al.*, 1999; Cohen *et al.*, 1996; Jordan *et al.*, 2001; Jordan *et al.*, 2004; Jordan *et al.*, 2002; Koshino *et al.*, 2005; Lamm *et al.*, 2001; Podzebenko *et al.*, 2002; Richter *et al.*, 2000), as well as subcortical regions within the basal ganglia (Alivisatos &

Petrides, 1997; Crucian *et al*., 2003; Harris, Harris, & Caine, 2002). Therefore, it seems difficult to argue that mental rotation depends on processing only within the PPC if parity judgements consistently elicit activation within other cortical regions. The next section will review the evidence regarding the role of higher-order pre-motor regions within the pre-frontal cortex.

Mental rotation and the prefrontal cortex

Prefrontal activation is commonly attributed to working memory or attentional demands (Carpenter *et al*., 1999; Cohen *et al*., 1996; Podzebenko *et al*., 2002). However, the temporal characteristics of the BOLD signal are comparable between the higher-order pre-motor areas and PPC. For example, Richter et al. (2000) have shown that the duration of the BOLD signal increases within higher-order pre-motor regions is correlated with RTs, comparable to the effects observed within the PPC (Richter *et al*., 1997). Furthermore, Lamm et al. (2001) have shown that parietal and pre-motor activation follow similar time-course.

It is, nevertheless possible that higher-order pre-motor activation may not reflect mental rotation *per se* despite the correlations with the RTs and PPC activation. Koshino *et al.* (2005) found that increasing stimulus complexity, and thus increasing attentional and working memory load, elicits increases in activation in these areas as a function of angular orientation. Furthermore, frontal lobectomy of either the left or the right prefrontal cortex apparently does not impair mental rotation (Alivisatos, 1992). Therefore, a possibility remains that the prefrontal activation may be a result of prominent anatomical connections between the PPC and the pre-motor areas, given that in some cases anatomically-connected cortical regions will show co-activation even if only one of those areas is actively involved in the task (Rorden & Karnath, 2004).

The present thesis

Of special concern for the present thesis are the shapes of orientation functions associated with mental rotation and object recognition. When plotted against angular departure from the upright, the inverted ‘V’-shaped function associated with mental rotation translates to a linear function, while the ‘M’-shaped function translates to a combination of linear and quadratic functions, because the function is described as linear up until 120°, then dipping at 180°. A quadratic only function would have to “peak” at 90°, while a linear only function would peak at 180°.

While most authors agree that the inverted ‘V’-shaped function for parity judgements reflects mental rotation, there is debate in the literature as to the cognitive mechanisms underlying the ‘M’-shaped function associated with object recognition. A possibility remains that the M-shaped function may arise at the “input” level, prior to access to object information.

The aims of the present thesis are to 1) investigate orientation-dependence of neural processing in a task that requires superordinate-level object recognition, and a task that requires mental rotation; and 2) to differentiate between orientation-dependent neural processing preceding mental rotation and mental rotation itself. To address these issues, I use letter-digit categorisation to assess orientation-dependent neural processing associated with superordinate-level object recognition, and parity discrimination to assess orientation-dependent neural processing associated with mental rotation. Neural processing will be assessed using fMRI and high-density EEG. These two techniques can be used to provide complementary information regarding neural and cognitive processes recruited during the tasks. Functional MRI, with its superior spatial resolution can provide information regarding functional localisation of cognitive operations. EEG, with its superior temporal resolution can provide information regarding the time course of neural events underlying the different stages of processing.

The stimuli used in the thesis are alphanumeric characters. Although these may be considered a special case of objects, not representative of everyday three-dimensional objects, they offer a number of advantages for the study of orientation sensitivity of the basic neural mechanisms involved in object recognition and mental rotation. Firstly, because alphanumeric characters are highly overlearned, there is little effect of orientation on their recognition, so that mental-rotation processes can be easily distinguished from the processes involved in recognition itself. Indeed, parity judgements with alphanumeric characters have already been shown to elicit reliable behavioural and EEG correlates of mental rotation. The studies to be reported here incorporate design features that should permit more precise specification of orientation effects than has been previously reported.

Secondly, because letters and digits form naturally distinct categories, they permit a ready comparison between two dichotomous tasks: A categorisation task in which participants decide whether each character is a letter or a digit, and a parity task in which participants decide whether each character is normal or backward. Previous evidence indicates that the parity task involves mental rotation, while the categorisation task does not. The categorisation task therefore provides a natural control in the identification of neural processes involved in mental rotation, while neural activation common to both tasks indicates processes in common.

Further, alphanumeric characters have a single canonical upright and, unlike most other objects, a defined parity. This makes them ideal for the study of mental rotation, and also for the study of any neural processes that might be affected by angular orientation. For example, although categorization itself might be independent of orientation, earlier processing leading up to categorization might well be affected by rotation away from the canonical upright. And finally, since alphanumeric characters exist in only two dimensions, assessing the effects of orientation can be restricted to rotations in the picture plane, which eliminates any complexities arising from depth rotations.

The aim of Experiment 1 is to use fMRI to locate the areas of activation in response to parity and category tasks, with a preliminary attempt to demarcate them according to the shape of the orientation function. I will be using three angular orientations and systematically varying stimulus orientations between experimental blocks of trials. Linear increases in activity would correspond to mental rotation and should only be observed in the parity task. Quadratic effects could be related to general shape recognition mechanisms and should be observed in both tasks, since both parity and category judgements would require object recognition.

The aim of Experiment 2 is to further differentiate the active areas in terms of their timing. Participants will perform category and parity judgements about upright and misoriented letters and digits while high-density EEG is recorded. Due to its excellent temporal resolution, EEG can be used to assess processing preceding mental rotation, mental rotation and parity discriminations. Linear increases in parietal negativity between 400 and 800 ms are thought to reflect mental rotation, and assessing EEG activation prior to 400 ms can elucidate effects of orientation on perceptual processing.

Experiment 3 is an attempt to examine whether orientation-sensitivity of the visual-evoked potentials (VEPs) is related to lower-level perceptual processing or visual processing associated with object recognition. High-density EEG will be recorded while participants perform category-judgement and colour-judgement tasks in Experiment 3. The colour-judgement task is used because colour discrimination can be accomplished independently of object recognition and empirical evidence indicates that colour judgements do not elicit automatic access to semantic information about objects (Boucart *et al.*, 2000; Pins, Meyer, Foucher, Humphreys, & Boucart, 2004).

Chapter 2: Functional MRI correlates of category and parity judgements about rotated letters and digits[3]

Introduction

In this study, neural activity was monitored using functional MRI while participants performed parity, or normal-backward, judgements and letter-digit category judgements about rotated alphanumeric characters. The typical finding is that parity judgements elicit steady increases in RTs with angular departure from upright (Cooper & Shepard, 1973). This increase in RTs is thought to reflect use of mental-rotation strategy whereby the participants imagine a mental image rotating from the position in which the stimulus was originally presented to the canonical upright orientation of the character. Subsequently, the decision regarding its parity is made by comparing the mental image to a memory representation of the character (Cooper & Shepard, 1973). On the other hand, classification of the characters as letters or digits does not require mental rotation and RTs do not systematically depend on orientation of the stimuli (Corballis & Nagourney, 1978).

Cooper and Shepard (1973) also found that the direction of the inferred rotation, clockwise or anticlockwise, had little effect on the slope of the reaction-time function, thus giving rise to an inverted ‘V’ function symmetrical around the 180º orientation. The symmetry of this function implies that mental rotation is performed along the shortest trajectory to the upright. This further suggests that participants must have known both the identities and the orientations of the characters prior to the act of mental rotation itself. Logically, one would expect this to be so, since it is otherwise difficult to understand how one could rotate an object to the upright without first knowing its identity, and then knowing its orientation.

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[3] Chapter 2 and subsequent experimental chapters (Chapter 3 and Chapter 4) are prepared in publication format. Therefore, slight repetitions will be evident between these chapters and the General Introduction and Discussion - Chapters 1 and 5.

Even when no mental rotation is necessary for parity discrimination, as is the case when stimuli are presented at upright, parity judgements elicit longer RTs than categorisation of alphanumeric characters (Heil, 2002). These results would suggest that parity-discrimination task requires processing steps additional to those required by character classification as letters and digits. Such additional processing steps may be related to orientation discrimination, which is hypothesised to be a distinct processing stage in a mental-rotation task (Cooper & Shepard, 1973). Cooper and Shepard (1973) found that when the participants were given an orientation cue in form of an arrow two seconds before the onset of the stimulus the RTs were approximately 100 ms faster at all stimulus orientations. A similar effect was also observed when the participants were given advance information regarding the identity of the character. These findings illustrate that distinct processing stages during a parity-judgement task can be shortened if the information is available prior to stimulus onset.

Therefore, parity-discrimination task and letter-digit categorisation would share processing stages up to, and including, object recognition. Subsequently, cognitive and response-related processes would diverge for the two tasks. One might expect that the sequence of processing events leading to parity judgements would be: 1) feature extraction; 2) object recognition; 3) determining the object's orientation; 4) determining which way to rotate to the upright; 5) actual mental rotation to the upright; 6) parity discrimination, 7) response mapping and 8) response execution. Meanwhile, the sequence of processing events leading to category judgements would be: 1) feature extraction; 2) object recognition; and 3) category decision, 4) response mapping and 5) response execution.

Object recognition, alphanumeric categorisation and stimulus orientation

Although the RTs in response to alphanumeric categorisation tasks typically do not systematically vary with stimulus orientation, recognition of rotated natural objects often elicits an 'M' shaped RT function. When RTs are plotted against angular departure from upright, this translates into a quadratic function, increasing up to 120° orientation then "dipping" at 180°. There is a possibility that this non-linear function reflects the operation of mechanisms at the input stage, rather than a post-perceptual 'normalisation' mechanism. Lawson and Jolicoeur (2003) showed that the same function also characterised duration thresholds for line drawings briefly presented at varying angular departures from upright. Similar effects of stimulus duration on accuracy rates were observed for identification of alphanumeric characters (Jolicoeur & Landau, 1984).

The design of the present study provides for investigation of orientation-dependence of the BOLD signal related to changes in stimulus orientation. The 'M'-shaped function translates to a combination of linear and quadratic functions, reflecting the increase up to 120° orientation and the "dip" at 180°, whereas mental rotation translates as a linear function. In the present experiment, then, I presented characters at three different angular departures, 30°, 100° and 170°, so that I would be able to assess brain activity for linear and/or quadratic trends as a function of stimulus orientation. If the quadratic function reflects orientation-dependent effects related to recognition itself, then one might expect this function to be task-independent; that is, to occur for both parity judgements and for category judgements. If the linear function reflects mental rotation, then it would depend on the task demands and occur only for the parity task.

Given the importance of the ventral visual stream for object recognition (e.g. Haxby *et al.*, 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Malach *et al.*, 2002), both the category and the parity judgements should elicit activation in the ventral stream. This indeed seems to be the case. A number of neuroimaging studies have shown that alphanumeric categorisation and character identification elicit activation within specific subregions of the left fusiform gyrus (Garrett *et al.*, 2000; K. H. James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Pernet, Celsis, & Démonet, 2005; Pernet *et al.*, 2004; Polk & Farah, 1998), anterior to those elicited by letter strings (K. H.

James *et al*., 2005). Alphanumeric categorisation has also been shown to elicit activation in the precuneus (Pernet *et al*., 2004), insula (Joseph *et al*., 2006; Pernet *et al*., 2004) and dorsolateral prefrontal cortex (DLPFC, Garrett et al., 2000; Joseph et al., 2006; Pernet et al., 2004). The fusiform activation has been related to visual processing, while the insular and prefrontal activation may be related to linguistic processing (Joseph *et al*., 2006) or attentional demands (Garrett *et al*., 2000).

Nevertheless, categorisation of alphanumeric characters elicits lower activation levels than parity-judgements about either upright or rotated characters (Alivisatos & Petrides, 1997). Alivisatos and Petrides (1997) suggested that the increase in ventral stream activation in response to parity discrimination tasks reflected increased visuospatial processing necessary to identify stimuli presented at non-canonical orientations, since only characters presented at the canonical orientation (i.e. upright characters with standard parity) were used for the categorisation task, while upright and rotated normal and mirror-reversed characters were used for the parity judgement task. There is, however, a difficulty with this interpretation. As mentioned above, parity judgements elicit longer RTs even at the upright orientation where no mental rotation is required (Heil, 2002), thus suggesting that parity judgements may place visual processing demands additional to those required for category judgements, not specifically related to identification of misoriented stimuli. In order to test whether the overactivation in the ventral stream is related to misoriented character identification or parity discrimination demands, in the present study normal and mirror-reversed characters were presented singly at various orientations, and participants made both parity judgements and letter-digit category judgements.

Mental rotation

The involvement of the PPC in mental-rotation tasks has been supported by a number of neuropsychological (Farah & Hammond, 1988; Mehta & Newcombe, 1991), neuroimaging (e.g. Alivisatos & Petrides, 1997; Cohen *et al*., 1996; Harris *et al*., 2000; Koshino *et al*., 2005; Podzebenko *et al*., 2002; Richter *et al*., 1997; Seurinck *et al*., 2005), electrophysiological (Bajric *et al*., 1999; Heil, 2002; Heil *et al*., 1998; Milivojevic, Johnson, Hamm, & Corballis, 2003; Pegna *et al*., 1997; Peronnet & Farah, 1989; Wijers *et al*., 1989), TMS ((Feredoes & Sachdev, 2006; Harris & Miniussi, 2003) and direct-cortical stimulation (Zacks *et al*., 2003) studies.

Additionally, activation in the ITG (Koshino *et al*., 2005), lateral-occipital cortex (Podzebenko *et al*., 2002), area MT (Cohen *et al*., 1996), and higher order pre-motor regions (Lamm *et al*., 2001; Podzebenko *et al*., 2002; Richter *et al*., 2000) has been associated with parity-discrimination tasks, although it remains unclear whether these areas reflect mental rotation process *per se*, or other cognitive processes associated with parity-judgement tasks. These processes might include pattern and object recognition, recognition of stimulus orientation, visuospatial working memory and attentional demands, decision making, motor planning and motor output.

The extent of the cortical network that has been identified as playing a role in parity-judgement tasks no doubt reflects the synthesis of these cognitive processes. Nevertheless, increasing evidence suggests that at least the medial and lateral pre-motor cortex may play a role in mental rotation itself. Activation within higher-order pre-motor regions has been reported in a number of mental-rotation studies (Cohen *et al*., 1996; Jordan *et al*., 2001; Koshino *et al*., 2005). In two separate studies Richter and colleagues (Richter *et al*., 2000; Richter *et al*., 1997) showed that the duration of BOLD response increases is correlated with RTs in the parietal (Richter *et al*., 1997) and frontal (Richter *et al*., 2000) areas. Lamm *et al*. (2001) directly compared the time-course of the BOLD signal in the parietal and frontal areas and found that they follow a similar response over time. However, it remains unclear whether the activation within these areas is specifically related to mental rotation, rather than to attention or working memory demands (Carpenter *et al*., 1999; Cohen *et al*., 1996).

On the other hand, the activation in ventral-stream structures has been attributed to visual shape processing. Using torus shapes, Vanrie and colleagues (Vanrie *et al.*, 2002) showed that shape matching to parity matching elicited similar degree of activation in the ventral stream but not the dorsal stream. In contrast, using familiar alphanumeric characters, Alivisatos and Petrides (1997), showed greater activation in both the ventral and dorsal streams to parity judgements than to simple alphanumeric categorisation. In their study, activation in the ventral stream did not appear to be related to mental rotation *per se*, as it did not vary with amount of rotation required (see also Koshino *et al.*, 2005). Alivisatos and Petrides (1997) suggested that processing of misoriented characters, such as mirror-reversal or rotation within the picture plane, requires ventral stream processing additional to that associated with character recognition.

Alivisatos and Petrides (1997) found that, compared with letter-number judgements, parity judgements about upright *or* rotated characters elicited increases in activation in the dorsal stream structures surrounding the intraparietal sulcus (IPS) – the inferior parietal and superior lobules. Within the PPC, only the left IPL showed increases in activation for rotated, compared with upright, characters during the parity judgement task. Alivisatos and Petrides (1997) argued that these results indicate that the IPS is involved in parity discrimination irrespective of whether mental rotation is involved, while the left IPL is involved in mental rotation *per se*.

Alivisatos and Petrides (1997) also found that parity judgements about rotated, but not upright, characters elicited activation in ventrolateral and dorsolateral prefrontal areas, middle frontal areas and caudate nucleus. Alivisatos and Petrides (1997) suggested that the caudate nucleus is also involved in mental rotation *per se*; a conclusion supported by the observation that selective caudal damage can result in mental rotation deficits (Harris *et al.*, 2002). Although the prefrontal regions have been shown to have the same response properties as the caudate nucleus, Alivisatos and Petrides (1997) argued that the prefrontal cortex is not actively involved in mental rotation since Alivisatos (1992) has shown that neither left nor right frontal-lobe resections affect mental rotation. Instead, Alivisatos and Petrides (1997) suggested that the prefrontal activation may reflect executive or working memory demands, an interpretation also proposed by other authors (e.g. Carpenter *et al*., 1999; Cohen *et al*., 1996).

One of the problems with the Alivisatos and Petrides (1997) study is that they used parity judgements with upright stimuli, as the baseline for mental-rotation condition in which participants performed parity judgements about rotated characters. Ilan and Miller (1994) have shown that comparing parity judgements about upright characters with parity judgements about upright and rotated characters violates the assumption of "pure insertion", that is, the assumption that the addition of changes in orientation adds only the mental rotation component to the parity-judgement task. Parity judgements about upright characters were faster when stimuli were presented in a block of trials in which all stimuli were at upright than when stimuli were presented sometimes at upright and sometimes at other orientations. Ilan and Miller termed this effect "rotational uncertainty". They also showed that orientation discrimination, which would not be necessary when stimuli are always presented at upright, cannot explain this reduction in RTs to upright characters between blocks with multiple stimulus orientations, and blocks in which with only upright characters were presented. In a subsequent experiment, Ilan and Miller showed that the "rotational uncertainty" effect was reduced when participants performed a go/no-go version of the same task, suggesting that this effect may be more closely related to response selection, than to perceptual processing preceding mental rotation and response preparation.

Therefore, it is possible that the prefrontal activation reflects additional processes related to response selection, which is made more difficult by the addition of the rotation component to the task (Ilan & Miller, 1994). However, the duration of the increase in the BOLD signal in parity-judgement tasks is tightly correlated with RTs in the parietal (Richter *et al.*, 1997) and frontal (Richter *et al.*, 2000) areas. Furthermore, Lamm et al. (2001) directly compared the time-course of the BOLD signal in the parietal and frontal areas and found that they follow a similar response over time, suggesting that the activation in the parietal and prefrontal regions cannot be easily dissociated. Therefore, the contribution of the prefrontal regions to mental rotation *per se* remains unresolved.

One method for circumventing the issues related to the "assumption of pure insertion" in neuroimaging is to use parametric experimental designs in which the condition of interest is systematically varied between blocks of trials. Previous studies of mental rotation which used parametric block design have assessed the role of mental rotation by varying the proportion of trials requiring mental rotation between blocks. In a PET study, for example, Harris et al. (2000) found that brain activation increased with the proportion of mental-rotation trials only in the posterior portion of the right intraparietal sulcus (IPS). In a similar study using fMRI, Podzebenko *et al.* (2002) also found that brain activation increased with the proportion of mental-rotation trials in the IPS, but the activation was bilateral rather than restricted to the right hemisphere. They also reported bilateral activation in more caudal and anterior portions of the IPS, extrastriate visual areas, lateral pre-motor and supplementary motor areas (SMA), and inferior frontal gyri. However these studies provide no information on the manner in which activation relates to orientation itself.

One would expect that if a cortical region is related to mental rotation itself, the amplitude of the BOLD signal would be correlated with angular departure of the stimuli from upright. Surprisingly few fMRI or PET studies have attempted to correlate activity to the angular rotation of stimuli. The few that did so typically used only two levels of orientation. In those studies, the results regarding the contribution of prefrontal regions are also conflicting; where some studies found modulation in higher-order pre-motor areas (e.g. Alivisatos & Petrides, 1997), while others did not (e.g. Gauthier *et al.*, 2002). One of the difficulties with using only two orientations is that increase from the smaller to the larger orientation does not necessarily indicate continuity of a linear trend because a linear function can be plotted through any two points. To assess whether linear increases in brain activation are correlated with angular departure from upright, at least three orientations need to be used. In the present study, three equidistant stimulus orientations were used: 30º, 100º, and 170º from upright, with an equal number of stimuli rotated clockwise and counterclockwise.

Hemispheric lateralisation of mental rotation

It is often suggested that mental rotation is more dependent on processes in the right than in the left hemisphere (Corballis, 1997). One commissurotomized person, for example, proved initially unable to mentally rotate letters or simple stick figures when they were presented to his right visual field and, thus to the left hemisphere, but was able to do so when they were presented to his left visual field and right hemisphere (Corballis & Sergent, 1989). Although his left hemisphere gained some proficiency in later testing, it remained inferior to the right, and may have adopted strategies other than analogue rotation. In support of this observation, Farah and Hammond (1988) reported that patients exhibit a deficit in mental rotation following right, but not left, parietal damage, and Harris *et al*. (2000), in a PET study, found selective activation in the right parietal lobe during a mental-rotation task.

However, not all studies have shown the right hemisphere to be critical for mental rotation. Mehta and Newcombe (1991) reported that patients with lesions restricted to the left hemisphere show deficits on mental-rotation tasks. Contrary to the evidence of Harris *et al.* (2000), other brain-imaging studies have suggested bilateral parietal involvement rather than exclusive right-hemisphere involvement (e.g. Kosslyn, Digirolamo, Thompson, & Alpert, 1998; Tagaris et al., 1996; Tagaris et al., 1997). These studies, however, used a mental-rotation task similar to that devised by Shepard and Metzler (1971), in which subjects rotate unfamiliar three-dimensional torus shapes, whereas Harris *et al.* (2000) used the simpler Cooper and Shepard (1973) task, in which subjects rotate familiar alphanumeric characters in two-dimensional space. There is some evidence that the Shepard–Metzler figures are rotated in piecemeal fashion (Bethell-Fox & Shepard, 1988; Just & Carpenter, 1985), and it may be this aspect, rather than the rotation component itself, that favours the left hemisphere. More generally, the left hemisphere may be increasingly engaged in spatial performance as the complexity of the task increases (De Renzi, 1978; McGuinness & Bartell, 1982).

This suggests that Cooper and Shepard's (1973) rotated mirror/normal letter discrimination task may be a better measure of pure mental rotation, uncontaminated by piecemeal processing. Yet even this task has failed to yield consistent results in neuroimaging studies. Harris *et al*. (2000) did find right-parietal activation, but Alivisatos and Petrides (1997) found activation in the left inferior and posterio-superior parietal cortices and Tagaris *et al*. (1997) found bilateral activation of parietal areas. Thus, the issue of whether mental rotation processes are lateralised to one hemisphere or the other has not yet been resolved.

Methods

Participants

Fourteen volunteers (six female), ranging in age from 22 to 32 (mean 26.21) were recruited for the purpose of this study and paid NZ$30 per hour for participation. All had normal or corrected-to-normal vision and were right-handed as assessed by Edinburgh Handedness Inventory (Oldfield, 1971), with laterality quotients (LQ) ranging from 60 to 100 (mean = 90.82). The procedures were approved by the University of Auckland Human Participants Ethics Committee, and all participants gave their informed consent to participate in the experiment.

Stimuli

Four letters (P L R F) and four digits (2 4 5 7) printed in bold Arial 72-point font were used as stimuli. They were presented in their normal and mirror reversed form at three clockwise and counterclockwise rotations from upright: 30º, 100º, and 170º. The amount of rotation (30º, 100º, or 170º) was used as a between-block factor; that is, in each block, the characters were only rotated by a single amount, either clockwise or counter-clockwise.

Tasks

The participants performed two tasks, a mirror-normal judgement task (parity task) and a letter-digit judgement task (category task). The participants responded by clicking the mouse with the right hand. In the parity task, the participants were required to press the left mouse button if they judged the character to be normal; and the right mouse button if they judged it to be mirrored. In the category task, the participants were required to press the left mouse button if they judged the character to be a letter, and the right mouse button if they judged the character to be a digit. In both the cases they were instructed to respond as quickly as possible without sacrificing accuracy.

Procedure

Each block of trials was preceded by a 9 s rest block which consisted of a fixation screen for 5 s, followed by an instruction screen for 3 s, and ended by another fixation of 1 s. The instruction screen informed the participants which task they were required to perform next, and reminded the participants which mouse buttons corresponded to which decision. The participants were instructed to perform either a category (letter vs. digit) judgement or a parity (normal vs. backward) judgement about the stimuli that were presented in the subsequent block. The last block of trials in each run was then followed by a fixation only 6-s rest block.

The stimuli were presented for 2 s and followed by a 250-ms inter-stimulus interval, during which a small fixation cross was presented centrally. Each block of trials consisted of eight stimuli, which were controlled for character type (letter or number), character version (normal or backward) and rotational direction (clockwise or anticlockwise). The character identity was randomly selected. Thus, the duration of each experimental block was 18 s. The participants were instructed to make a response while the stimulus was on the screen, and if they failed to make a response during that period to wait for the next stimulus and respond to that. RTs and accuracy were recorded.

The experimental design followed a 2 x 3 factorial model, with two tasks and three stimulus orientations. Each block of trials corresponded to one of the conditions, and each condition was repeated twice during a scanning session. Therefore, each scanning session consisted of 96 trials, with 16 trials for each of the six conditions.

Two sequences of experimental blocks were designed. In both sequences, parity and category tasks alternated until both tasks were completed with stimuli presented at all three orientations, and then the sequence was run in reverse order. One of the sequences began with the parity task, with stimuli presented at the smallest orientation (30º) and the stimulus rotation increased every two blocks. The other sequence began with the category task, with stimuli presented at the largest orientation (170º), and degree of stimulus rotation decreased every two blocks. This method was employed to offset the effects of linear drifts in signal intensity which are inherent in fMRI acquisition.

Each participant performed at least two practice blocks, one for each of the two sequences, before going into the scanner to ensure that they were able to perform the task with high accuracy under the speed limitations. During the fMRI acquisition, the participants performed each sequence twice, resulting in four scanning sessions per subject. Therefore, the experiment consisted of 384 trials in total, with 64 trials for each of the six experimental conditions.

Image acquisition

Images were acquired using a 1.5T Siemens Avanto scanner (Erlangen, Germany). Each scanning session started with an acquisition of at least two T1-weighted structural volumes using 3D MP-RAGE sequence (TR = 11ms; TE = 4.94 ms; flip angle: 15º; FOV: 25.6 x 20.8 cm; matrix size: 256x208; 170 to 176 axial slices, ensuring whole brain coverage, parallel to AC-PC line; slice thickness: 1 mm; interslice gap: 0 mm; resulting in 1x1x1 mm voxels). Following this, a total of 113 volumes, including 2 "dummy" scans which were not recorded and were designed to control for T1 saturation were acquired during each of the 4 functional scanning sessions, resulting in 452 T2*-weighted volumes per subject. The EPI acquisition sequence parameters were as follows: TR = 3000 ms; TE = 50 ms; flip angle = 90º; FOV= 19.2 cm; matrix size: 64x64; with interleaved slice acquisition, starting at the bottom; 30 slices parallel to AC-PC line; slice thickness: 4 mm; 25% gap: resulting in 3x3x5 mm voxels; whole brain coverage of 150 mm.

Image pre-processing

SPM5 software (Wellcome Department of Imaging Neuroscience, London, UK; http THE://www.fil.ion.ucl.ac.uk) was used for image processing and analysis. The first 3 image volumes were discarded to allow for T1 equilibration, and the first volume of the first session was used as a target for coregistration of the first volume of each of the three subsequent sessions. The remaining volumes within each session were then realigned to the first volume of that session and the mean of all volumes across the four sessions was created. The realigned volumes were corrected for slice timing differences and referenced to the middle slice. For each participant, the available T1 volumes were co-registered and averaged. The average T1-weighted structural image was then co-registered to the mean of the functional volumes. Normalisation parameters were estimated using the unified segmentation procedure (Ashburner & Friston, 2005), and used to normalise the structural and functional images to the stereotactic coordinate system defined by the Montreal Neurological Institute (MNI). Finally, the functional volumes were spatially smoothed using an anisotropic Gaussian filter of 9x9x15 mm (3 times the voxel size) at full-width at half-maximum (FWHM).

Results

Behavioural results

In order to maintain a parallel between analysis of behavioural and fMRI data, RTs and accuracy, as percent correct, were analysed with a 2 x 3 repeated measures ANOVA with task and orientation as factors. Huynh-Feldt ε value correction (Huynh & Feldt, 1976) was used to correct for sphericity violations associated with repeated-measures effects. Due to problems with data acquisition, the accuracy measures for two of the participants were excluded from the analysis. The remaining participants had miss rates ranging from 0 to 1.56%. Due to the nature of the BOLD signal response in a block-design presentation, error-trials cannot be removed from the fMRI data. To keep the behavioural and fMRI data-analysis consistent, error RTs were not removed from the RT analysis to determine whether the behavioural measures continued to show the standard effects of orientation. Thus, both correct and incorrect responses were used to calculate the mean RTs for each of the six experimental conditions. Again, to maintain consistency between the analyses of behavioural measures and of fMRI data, RTs and accuracy were calculated within each session separately and then averaged across the four sessions. Figure 2.1 shows RTs and accuracy as a function of stimulus orientation for the two tasks.

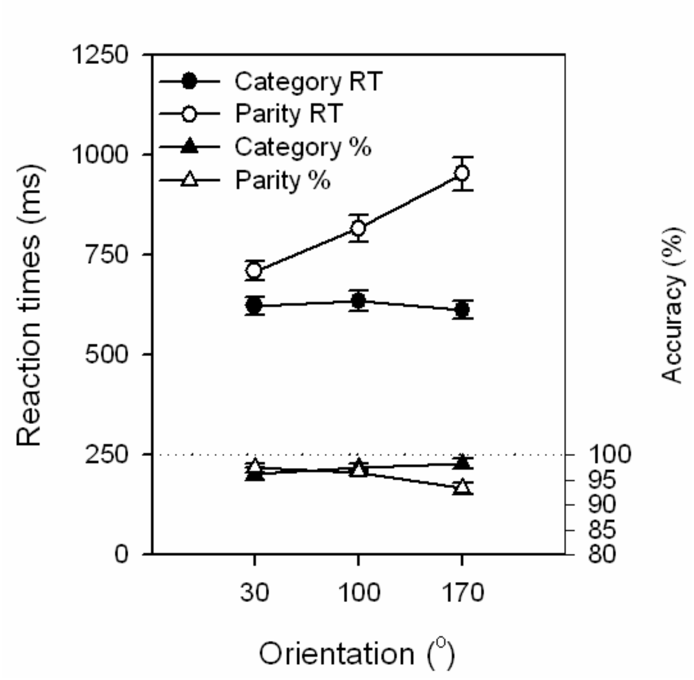


Figure 2.1: Reaction times, in milliseconds, and accuracy, as percent correct, for parity and category tasks as a function of stimulus orientation. RTs are plotted as circles, accuracies as triangles.

Analysis of RTs showed significant main effects of task ($F(1, 13) = 59.52$, $p < 0.001$) and orientation ($F(2, 26) = 71.93$, $p < 0.001$, $\varepsilon = 0.751$), as well as a significant interaction between them ($F(2, 26) = 61.12$, $p < 0.001$, $\varepsilon = 0.965$). Significant differences between tasks were observed at all orientations ($p \leq 0.002$) and ranged between 87.6 ms at 30° to 340.0 ms at 170°. Simple effects of orientation for each task were then examined. The effect of orientation on the parity task was significant ($F(2, 26) = 77.85$, $p < 0.001$, $\varepsilon = 0.700$), and consisted predominantly of a significant linear trend ($F(1, 13) = 90.41$, $p < 0.001$, 99.47% variance explained). The quadratic trend was not significant ($F(1, 13) = 2.83$, $p = 0.117$). The effect of orientation on the category task did not reach significance ($F(2, 26) = 3.474$, $p = 0.055$, $\varepsilon = 0.857$), and neither did the linear ($F(1, 13)= 2.53$, $p = 0.136$) or the quadratic ($F(1, 13)= 3.80$, $p = 0.073$) trend components.

In terms of accuracy, the main effects of task ($F(1, 11) = 2.00$, $p = 0.185$) and stimulus orientation ($F(2, 22) = 1.26$, $p = 0.303$, $\varepsilon = 0.988$) were not significant, but there was a significant interaction between the two factors ($F(2, 22) = 7.98$, $p = 0.006$, $\varepsilon = 0.751$). Significant differences between tasks were observed for 170° orientation only ($p = 0.002$).

Simple effects of orientation for each task were then examined. The effect of orientation on the parity task was significant (F(2, 22) = 4.69, p = 0.026, ε = 0.866), and could be attributed to a linear decrease in response accuracy with increasing angular disparity (F(1, 13) = 5.446, p = 0.040, 90.18% of variance explained). The quadratic trend did not reach significance (F(1, 11) = 2.825, p = 0.177). The effect of stimulus orientation approached significance for the category task (F(2, 22) = 3.426, p = 0.052, ε = 0.973).

In summary, the parity task took longer to execute than the category task, although the task difficulty (as indicated by performance accuracy) was similar. The data also support the notion that the parity task elicited mental rotation, as indicated by the prevalent linear trend apparent in the RTs, while letter-digit categorisation did not.

Imaging results

Functional data analysis was performed using a two-step procedure consisting of a within-subjects GLM time-series regression, and random-effects factorial ANOVA with the resulting parameter estimates as the dependent measure. The time-series analysis was performed with a general-linear model (Friston *et al*., 1995) with the six experimental conditions (two tasks by three orientations) and six movement parameters, three for position and three for rotation, as explanatory variables. The movement parameters were included in the design matrix as potentially confounding nuisance covariates. Each experimental block was modelled as a series of events, and each event was convolved with the canonical hemodynamic response function. The implicit baseline condition, consisting of a fixation and instruction period, was not included in the model. Before estimation, low-frequency noise was removed using a high-pass filter with a cut-off period of 128 s, and serial correlations among scans were removed with an autoregressive moving average 1st order model (AR(1)) implemented in SPM5.

Beta-estimates from GLM time-series analysis for the six experimental conditions were collapsed across the four sessions. In order to assess hemispheric asymmetries, left-right flipped versions of the six resulting contrast images were also created. The resulting 12 contrast images per subject were then imported into a 2x2x3 factorial-design ANOVA, with hemisphere, task and stimulus orientation as factors. Correction for the violation of sphericity resulting from use of repeated measures and possible nonhomogeneity of variance was implemented by SPM5. Model estimation was initially performed with all the available voxels, which numbered 33,625.

Anatomical labels and Brodmann area (BA) labels were derived through Anatomy, an SPM-extension toolbox (Eickhoff, S.; http://www.fz-juelich.de/ime/spm_anatomy_toolbox). Since IPS was considered to be of particular importance for this study, the nomenclature for the anatomical labels for this area were based the paper by Orban et al. (2006).

Descriptive statistics

To visualise which areas showed increased activation in response to any of our six experimental conditions, contrasts showing increases in activation relative to the implicit baseline were calculated. Figure 2.2 illustrates areas of significant (False-discovery rate (FDR) corrected $p < 0.05$) increases in activation elicited by the parity task or the category task in comparison with the implicit baseline. It is evident that the distribution of left-hemispheric responses are similar between the tasks, and include ventral stream regions, dorsal intraparietal sulcus (dIPS), sensory motor cortex, inferior frontal gyrus (IFG), lateral and medial supplementary pre-motor areas (pre-SMA). Increases in activation in the ventral intraparietal sulcus (vIPS) were apparent only in response to the parity task.

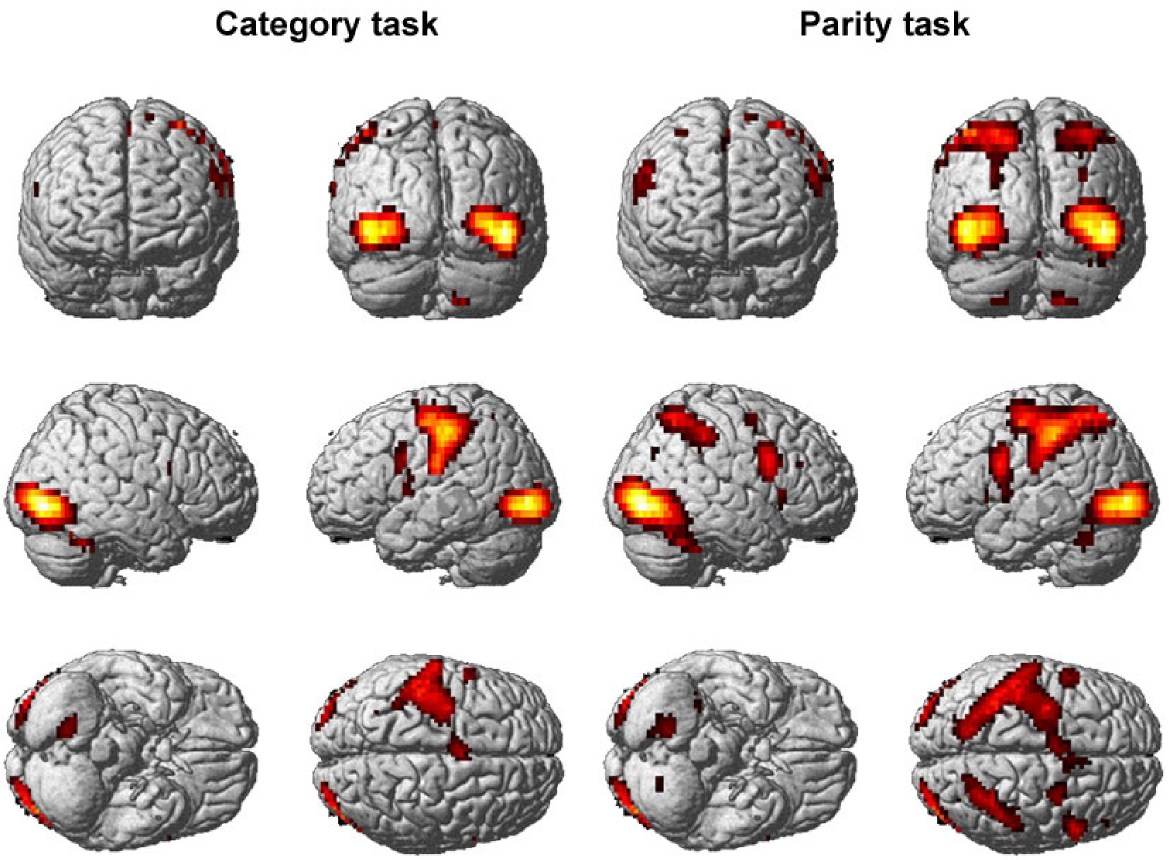


Figure 2.2: Cortical rendering of significant increases (FDR corrected $p < 0.05$) in response to category and parity tasks, compared to the implicit baseline.

The picture is considerably different over the right hemisphere. The parity task produced a more symmetrical pattern of activations between the hemispheres whereas the categorisation task failed to elicit the corresponding changes in the right hemisphere. Specifically there was a lack of activation in the right lateral pre-SMA, dIPS, and IFG in response to the category task. Additionally, the category task elicited right-hemispheric activation in the anterior portion of the ventral stream, with no corresponding activation in the left hemisphere. The parity task elicited bilateral ventral stream activation in the corresponding anterior area.

Masking

Since no prior hypotheses were made regarding de-activation relative to the implicit baseline, any voxels that showed negative estimates were excluded from further analysis. Thus, a mask was created which contained only the voxels which, on average, showed positive estimates within either task, within either hemisphere, collapsed across the three orientations. Furthermore, since both flipped and non-flipped contrasts were included in the analysis, the search was restricted to the “right” hemisphere which now contained both the right (non-flipped) and left (flipped) model estimates. Activation threshold was set at $p < 0.05$, corrected for multiple comparisons using the family-wise error (FWE) correction based on the random-field theorem (Worsley, Poline, Vandal, & Friston, 1995) with 92.1 of resolution elements and smoothness of statistical volume with dimensions of 10.6x10.6x17.3 mm at FWHM.

Hemisphere effects

Figure 2.3 illustrates the spatial distribution and the extent of significant activations associated with the difference between the hemispheres. Parameter estimates for peak activation voxels as a function of task, orientation and hemisphere are also plotted in Figure 2.3 and summary statistics for these voxels are presented in Table 2.1.

Table 2.1: Brain areas showing significant hemispheric differences and cluster extent in mm^3, with MNI-coordinates for the peak activation voxel, and corresponding summary statistics (F- and FWE corrected p-values). Direction of differences is also indicated. Note that a single voxel extent is $45mm^3$.

Label	Location	Brodmann areas	Cluster extent mm3	x y z (mm)	F-value
Left > Right					
1.	Somatosensory cortex	BA 3	21555	42 -21 60	158.84***
2.	lateral SMA	BA 6		30 -21 70	82.7***
8.	SMG	BA 13		51 -24 25	37.12***
5.	vIPS/poIPS	BA 7	990	21 -72 30	31.26**
3.	medial SMA	BA 24	450	6 -6 50	29.05**
4.	Posterior insula	BA 13	360	45 -6 10	28.35**
6.	poIPS/dIPSm	BA 7	450	15 -66 65	27.45**
Right > Left					
10.	Cerebellum	---	3285	18 -51 -20	46.89***
12.	Cerebellum	---	495	12 -63 -50	30.98**
7.	FFG	BA 37	45	39 -45 -20	21.9*

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

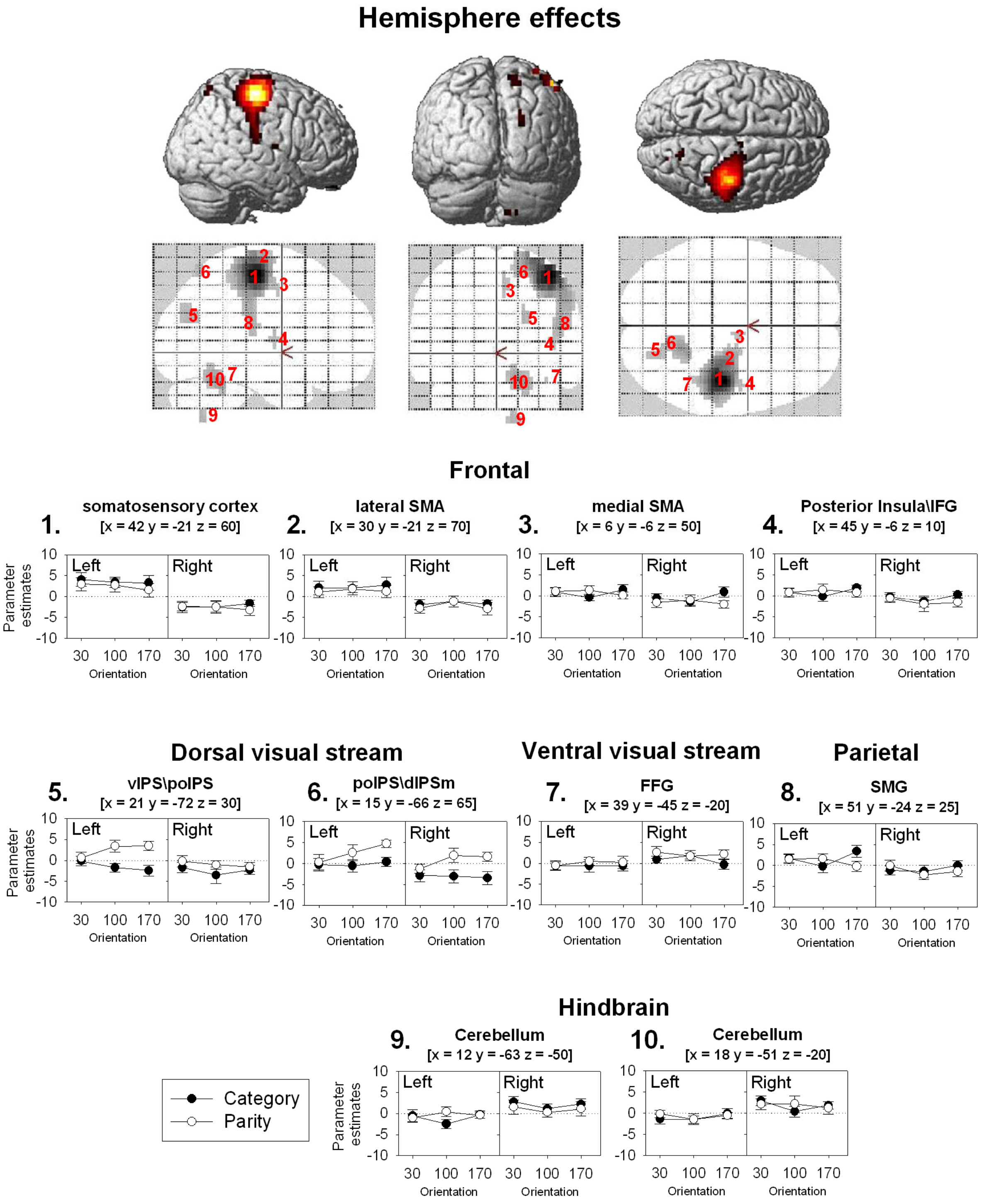


Figure 2.3: Significant differences between the left and the right hemispheres displayed on cortical surface rendering and glass brain SPMs. Peak voxels within the clusters are labelled on the SPMs and corresponding parameter estimates as a function of task, orientation and hemisphere are plotted below. Error bars indicate 95% confidence interval of the mean. Note that activity is shown only in the nominally "right" hemisphere, as explained in the text.

Significantly greater left hemispheric activation was observed over the sensory-motor cortex, SMA, cerebellum, vIPS, middle portion of the dIPS (dIPSm) and IFG. Greater right-hemisphere activation was observed in the fusiform gyrus (FFG) and the cerebellum, while other activation clusters showed greater activation on the left. The lateralisation effects in the motor system probably reflect activation elicited by right-handed responses, while the differences in lateralisation within the dIPSm, vIPS, IFG and FFG cannot be directly attributed to response-related activations, but probably reflect consistent left-hemisphere involvement in both tasks, as indicated by the descriptive analysis.

It should be noted that none of the significant voxels reported above were a part of the task-by-hemisphere interaction, although the vIPS and dIPSm clusters showed significant task effects.

Task-related modulation

Summary statistics for task-related differences at peak-activation voxels – with MNI coordinates and corresponding anatomical labels – are represented in Table 2.2 and significant activation clusters and associated parameter estimates for peak-activation voxels are represented on cortical surface rendering and glass brain statistical parametric map (SPM) in Figure 2.4.

Table 2.2: Brain areas showing significant differences between tasks and cluster extent in mm^3, with MNI-coordinates for the peak activation voxel, and corresponding summary statistics (F- and FWE corrected p-values). Three local maxima more than 8mm apart are shown for the largest cluster. Direction of differences is also indicated. Note that a single voxel extent is $45mm^3$.

Label	**Location**	**Brodmann areas**	**Cluster extent mm3**	**x y z (mm)**	**F-value**
Parity > category					
3.	dIPSa	BA 7	26370	15 -69 55	119.87***
4.	dIPSm	BA 7		33 -51 55	87***
5.	dIPSa/m	BA 7		27 -57 55	85.89***
1.	ITG	BA 37	10710	48 -63 -5	61.43***
2.	MOG/MT	BA 19		39 -81 10	46.12***
8.	Anterior insula	BA 13	1755	30 24 5	47.54***
6.	IFG	BA 44	2790	54 9 25	39.72***
9.	lateral pre-SMA	BA 6	1530	27 0 55	33.26***
7.	IFG	BA 46	90	51 30 25	23.58*
10.	medial pre-SMA	BA 6	90	3 15 50	21.51*
Category > Parity					
11.	Midorbital gyrus	BA 11	45	6 27 -10	22.71*

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

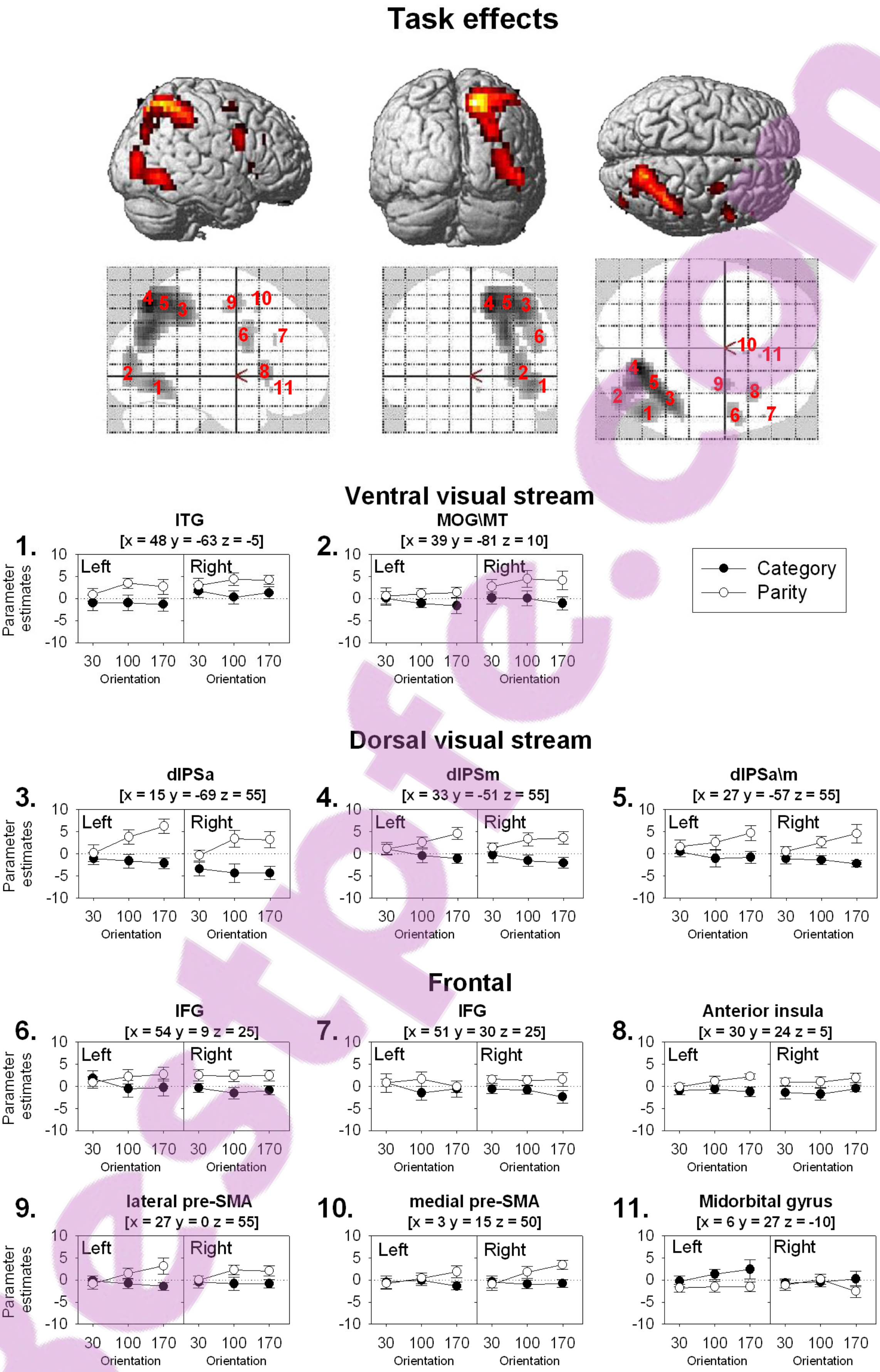


Figure 2.4: Significant differences between the tasks displayed on cortical surface rendering and glass brain SPMs. Peak voxels within the clusters are labelled on the SPMs and corresponding parameter estimates as a function of task, orientation and hemisphere are plotted below. Error bars indicate 95% confidence interval of the mean.

The parity task elicited greater activation than the category task in the posterior portion of the inferior temporal gyrus (ITG), middle occipital gyrus (MOG), and throughout the IPS extending from the traverse-occipital sulcus to the postcentral sulcus, including the vIPS, and middle and anterior portions of dIPS (dIPSm and dIPSa). Additionally, greater activation in response to the parity task was observed in the anterior insula, IFG, medial and lateral pre-SMA. A single voxel showing the reverse pattern was observed in the midorbital gyrus, where amplitude of parameter estimates was more positive for categorisation than rotation tasks. Only a portion of the vIPS was involved in task-by-hemisphere interaction which is examined in the following section.

Task-by-hemisphere interaction

A significant task-by-hemisphere interaction was observed in the vIPS, as well as in lateral and medial pre-SMA, and a portion of the middle frontal gyrus corresponding to the DLPFC. Significant activation clusters for the task-by-hemisphere interaction and associated parameter estimates peak-activation voxels are represented on a glass brain SPMs and cortical surface rendering in Figure 2.5 and summary statistics for peak activation voxels are represented in Table 2.3.

Table 2.3: Brain areas showing significant task-by-hemisphere interaction and cluster extent in mm^3, with MNI-coordinates for the peak activation voxel, and corresponding summary statistics (F- and FWE corrected p-values). Three local maxima more than 8mm apart are shown for the largest cluster. Direction of differences is also indicated. Note that a single voxel extent is 45mm^3.

Label	Location	Brodmann areas	Cluster extent mm3	x y z (mm)	F-value
1.	poIPS/vIPS	BA 39	2520	39 -63 25	34.12***
2.	poIPS/vIPS	BA 39		36 -69 35	32.99***
3.	MFG	BA 6	225	48 9 50	26.03**
4.	medial pre-SMA	BA 32	90	9 24 45	23.43*
5.	lateral pre-SMA	BA 8	45	30 12 40	21.59*

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

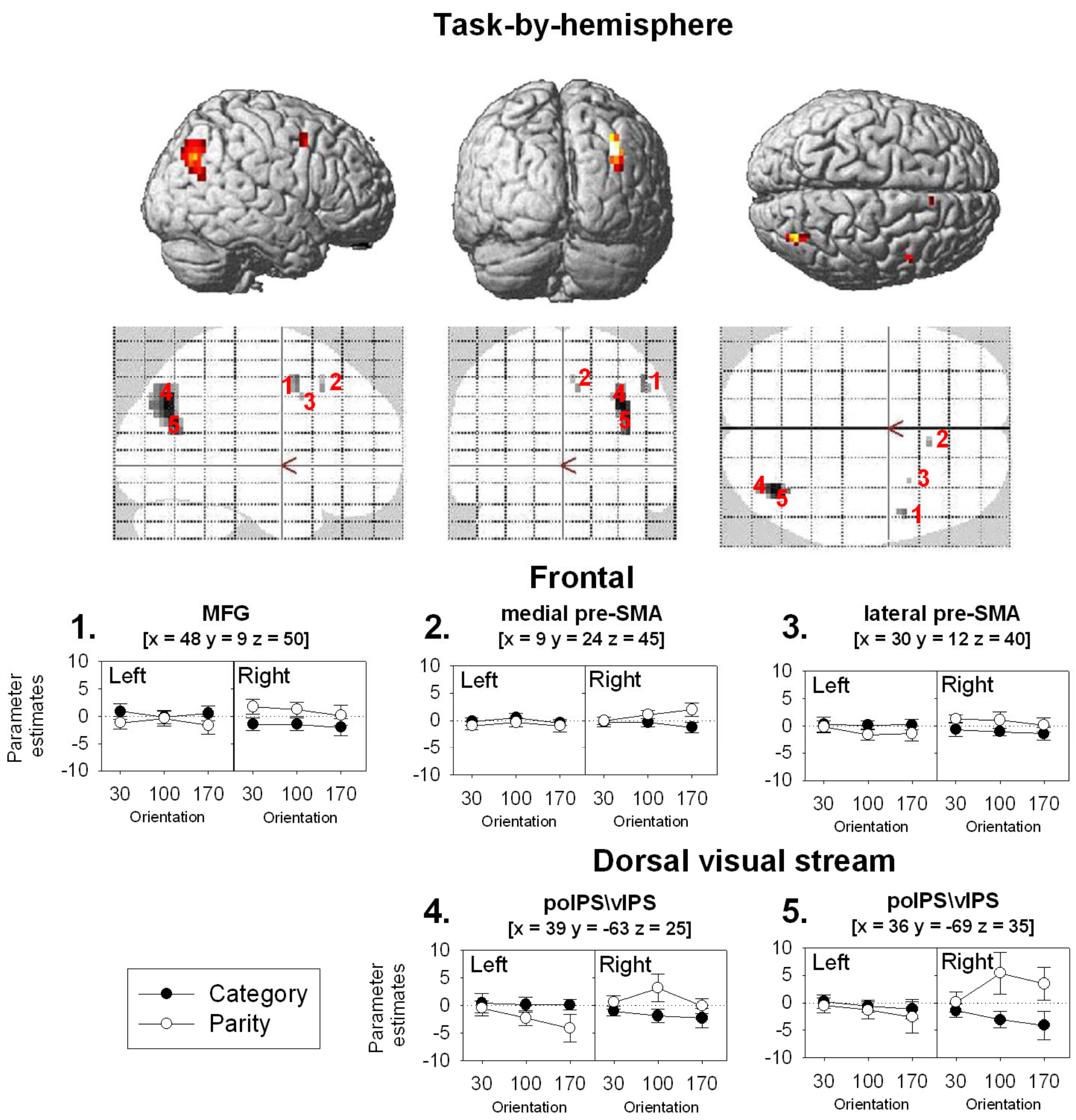


Figure 2.5: Significant voxels showing task-by-hemisphere interaction displayed on cortical surface rendering and glass brain SPMs. Peak voxels within the clusters are labelled on the SPMs and corresponding parameter estimates as a function of task, orientation and hemisphere are plotted below. Error bars indicate 95% confidence interval of the mean.

The parameter estimates, plotted in Figure 2.5, can be used to characterise the task-by-hemisphere interaction in distinct cortical regions. Larger differences in activation levels were observed on the right than the left in the three clusters within the prefrontal areas – the middle frontal gyrus, medial pre-SMA, and lateral pre-SMA. The pattern of BOLD responses in the vIPS is somewhat different. For both voxels of interest, the right-hemisphere activation is lower for the category task, and higher for the parity task, when compared to the left-hemispheric activation.

Simple effects of task for each hemisphere, and of hemisphere for each task, are represented on cortical surface rendering in Figure 2.6. Significant differences between the tasks are observed within similar regions in both hemispheres: the dIPS, vIPS, MOG and IFG, lateral pre-SMA, DLPFC, and anterior insula. Only a cluster in the midline pre-SMA showed significant task differences on the right but not on the left. It is also evident from these figures that the task effects appear to be more pronounced on the right than the left, particularly in the frontal regions.

A similar pattern of results was also observed for the difference between hemispheres for each task, with significant differences in activation between sensory-motor hand area, ventral and dorsal cerebellum, vIPS and posterior insula. Task-specific hemispheric lateralisation effects were also observed, with category task eliciting greater left-hemispheric activation in the dIPSm, and the dorsolateral prefrontal cortex. The parity task elicited greater activation on the left within the midline SMA, and fusiform and ITG on the right.

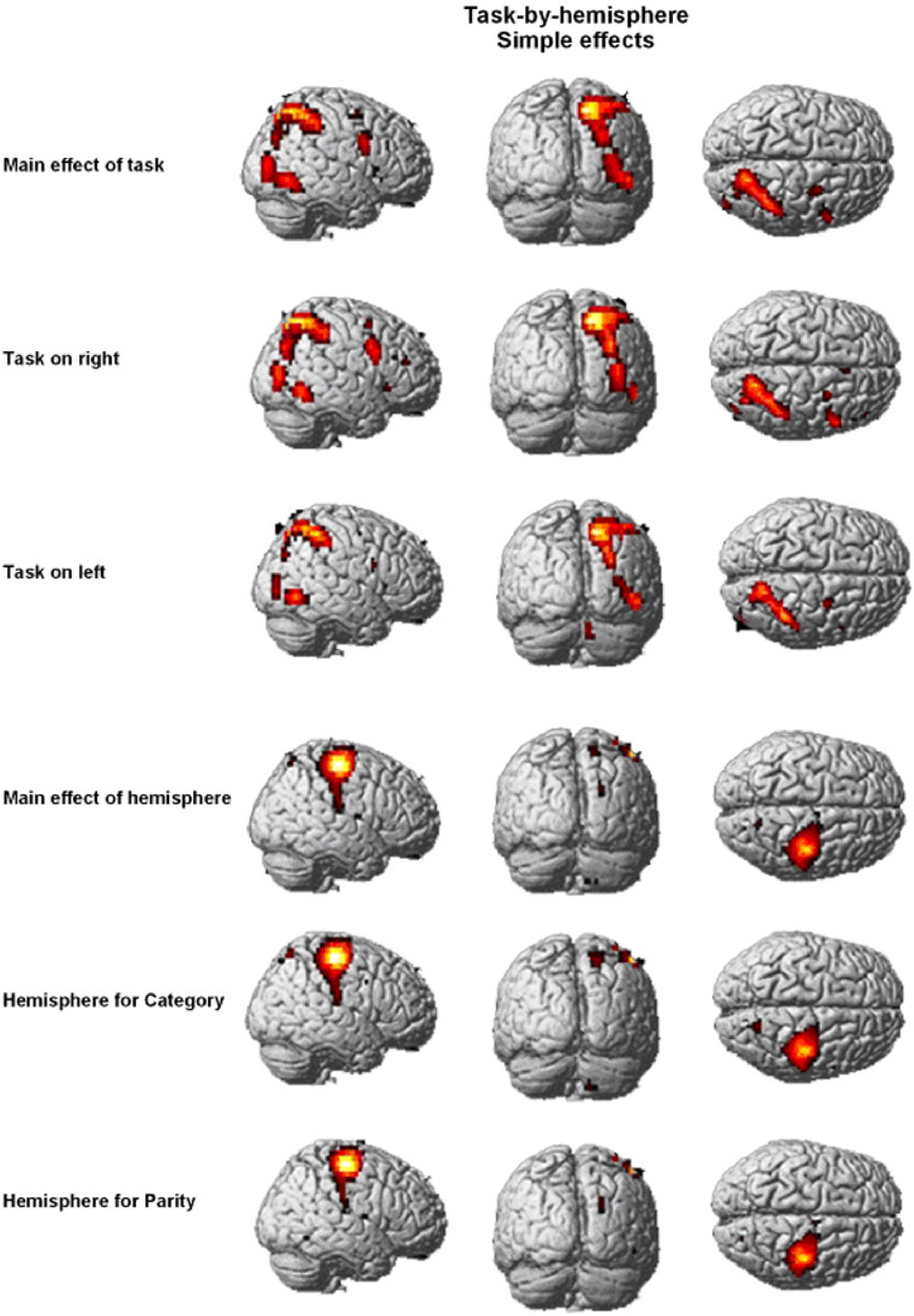


Figure 2.6: Significant voxels showing main effects of task and hemisphere and simple effects for the task-by-hemisphere interaction displayed on cortical surface rendering. Again, activation is shown only on the nominal "right" hemisphere.

Effects of stimulus orientation

Significant activation clusters for the effects of orientation and associated parameter estimates, are represented on a glass brain SPMs and cortical surface rendering in Figure 2.7. Summary statistics for orientation effects at peak-activation voxels, with MNI coordinates and corresponding anatomical labels are represented in Table 2.4. Same information is also presented for the linear and quadratic trend components.

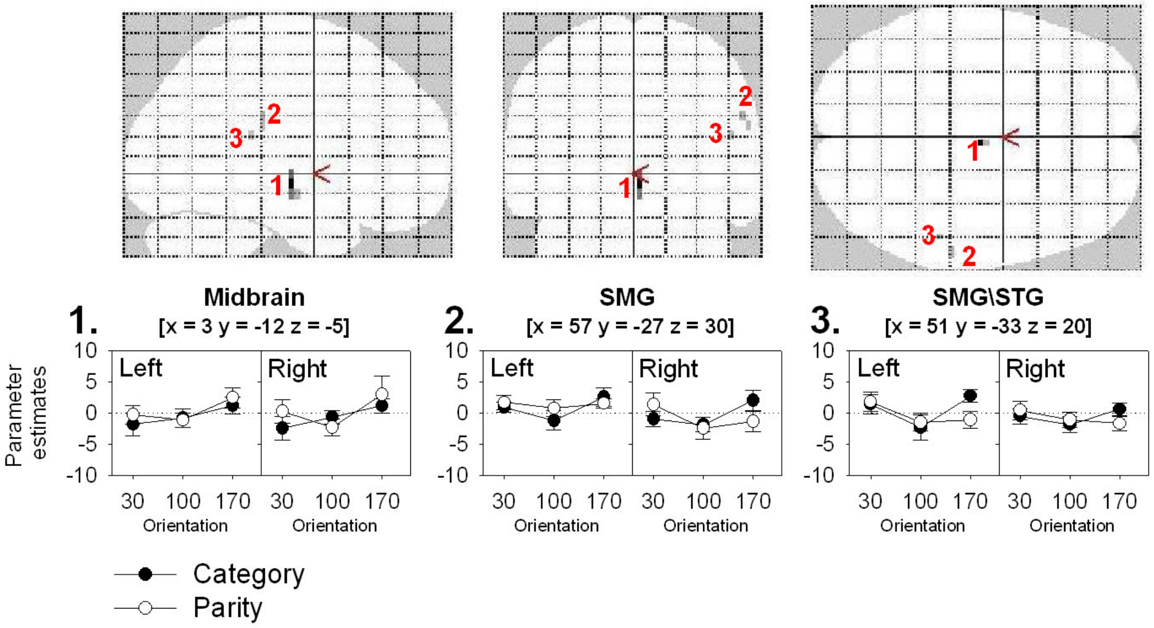
Table 2.4: Brain areas showing significant orientation effects and cluster extent in mm^3, with MNI-coordinates for the peak activation voxel, and corresponding summary statistics (F- and FWE corrected p-values). Linear and quadratic trend components are shown separately. Note that a single voxel extent is 45mm^3.

Label	**Location**	**Brodmann areas**	**Cluster extent mm3**	**x y z (mm)**	**F-value**
Overall					
1.	Midbrain	---	180	3 -12 -5	15.8**
2.	SMG	BA 40	90	57 -27 30	12.72*
3.	STG/SMG	BA 13	45	51 -33 20	12.48*
Linear					
4.	Midbrain	---	135	'3 -9 -10	24.53*
Quadratic					
5.	SMG	BA 40	675	60 -27 25	25.05**
6.	STG/SMG	BA 13		51 -33 20	23.71*

$p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Significant orientation effects, consisting of combined linear and quadratic trend, orientation trends, were observed within the supramarginal gyrus (SMG) and the midbrain. The supramarginal activation was characterised in terms of a quadratic trend, and showed lower parameter estimates for the 100° rotations compared to 30° and 170° rotations as indicated by parameter estimates displayed in Figure 2.7. The midbrain activation was characterised in terms of a linear increases in BOLD activity associated with increase in stimulus orientation.

Orientation



Trend components

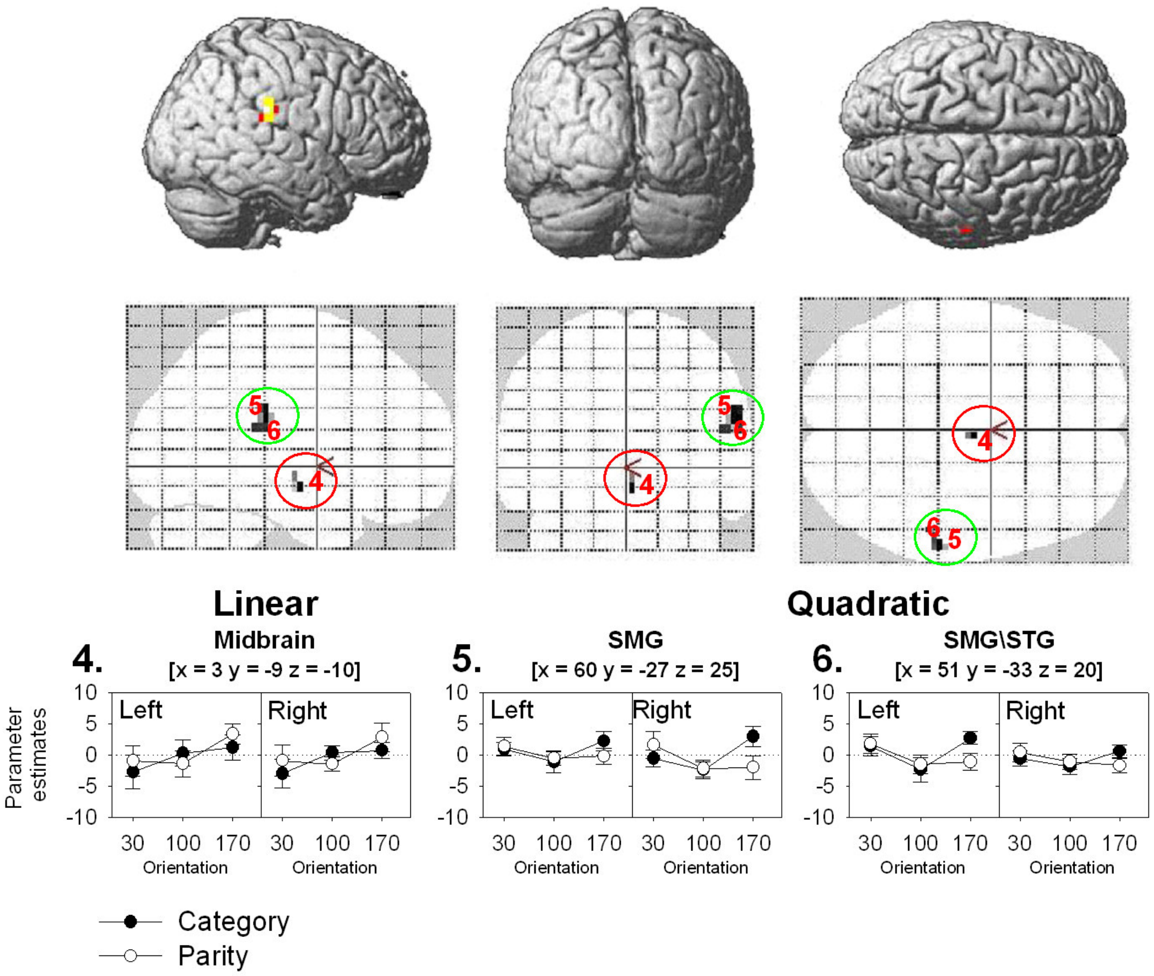


Figure 2.7: Significant voxels showing main effect of orientation displayed on a glass brain SPM and linear and quadratic trend components displayed on cortical surface rendering and a glass brain SPM. Peak voxels within the clusters are labelled on the SPMs and corresponding parameter estimates as a function of task, orientation and hemisphere are plotted below. Error bars indicate 95% confidence interval of the mean.

Task-by-orientation interaction

Summary statistics for peak activation voxels are presented in Table 2.5. Significant interaction was observed in lateral and medial pre-SMA, vIPS and dIPSm and SMG. Figure 2.8 shows significant task-by-orientation interaction clusters on a glass-brain SPM. Significant clusters exhibiting the linear component of the task-by-orientation interaction on a rendered brain surface and glass brain SPM are also presented in Figure 2.8. It is evident from these plots that the task-by-orientation interaction overlaps with the linear terms of this interaction. The parameter estimates plotted in Figure 2.8 indicate that the interaction could be attributed to linear modulation of the BOLD signal as a function of orientation, for the parity task with no comparable effects for the category task. Significant linear increases in the BOLD signal with increase in stimulus orientation were observed in the pre-SMA, vIPS, and dIPSm, while significant *decreases* in BOLD signal were observed within the SMG. The cluster in the SMG overlapped partially with the quadratic orientation trend and showed a decrease with larger orientations for the parity task.

Table 2.5: Brain areas showing significant linear trend of the task-by-orientation interaction and cluster extent in mm^3, with MNI-coordinates for the peak activation voxel, and corresponding summary statistics (F- and FWE corrected p-values). Three local maxima more than 8mm apart are shown for the largest cluster. Linear and quadratic trends are shown separately. Note that a single voxel extent is 45mm^3.

Label	**Location**	**Brodmann areas**	**Cluster extent mm3**	**x y z (mm)**	**F-value**
Overall					
	SMG	BA 40	180	60 -24 20	14.02***
	dIPSm	BA 7	90	15 -69 55	12.96***
	Lateral pre-SMA	BA 6	45	30 0 60	12.70***
Linear trend					
6.	SMG	BA 40	360	60 -24 20	25.35**
5.	lateral pre-SMA	BA 6	45	30 0 60	22.03*
2.	dIPSm	BA 7	90	30 -54 55	21.78*
3.	vIPS	BA 7	45	27 -63 35	21.53*
4.	medial pre-SMA	BA 6	45	3 15 50	21.26*
1.	poIPS/dIPSm	BA 7	90	15 -66 55	20.92*

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

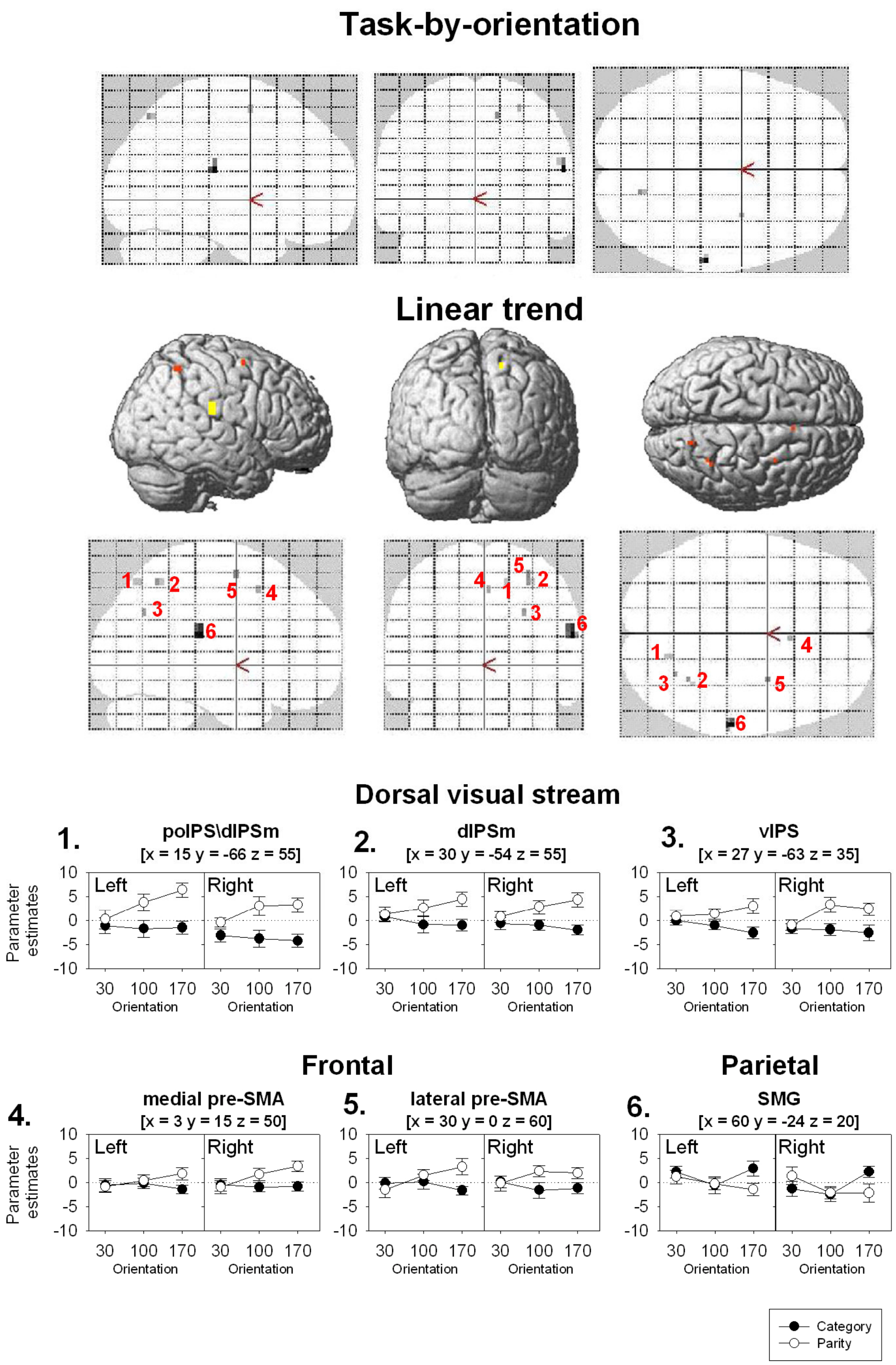


Figure 2.8: Significant voxels showing linear trend component of the task-by-orientation interaction displayed on cortical surface rendering and glass brain SPMs. Peak voxels within the clusters are labelled on the SPMs and corresponding parameter estimates as a function of task, orientation and hemisphere are plotted below. Error bars indicate 95% confidence interval of the mean.

Simple effects of linear increase with increase in stimulus orientation were observed only for the parity task, with no reliable effects for the category task. Significant activation clusters for linear trends in the parity task and associated parameter estimates peak-activation voxels are represented on a glass brain SPM in Figure 2.9.

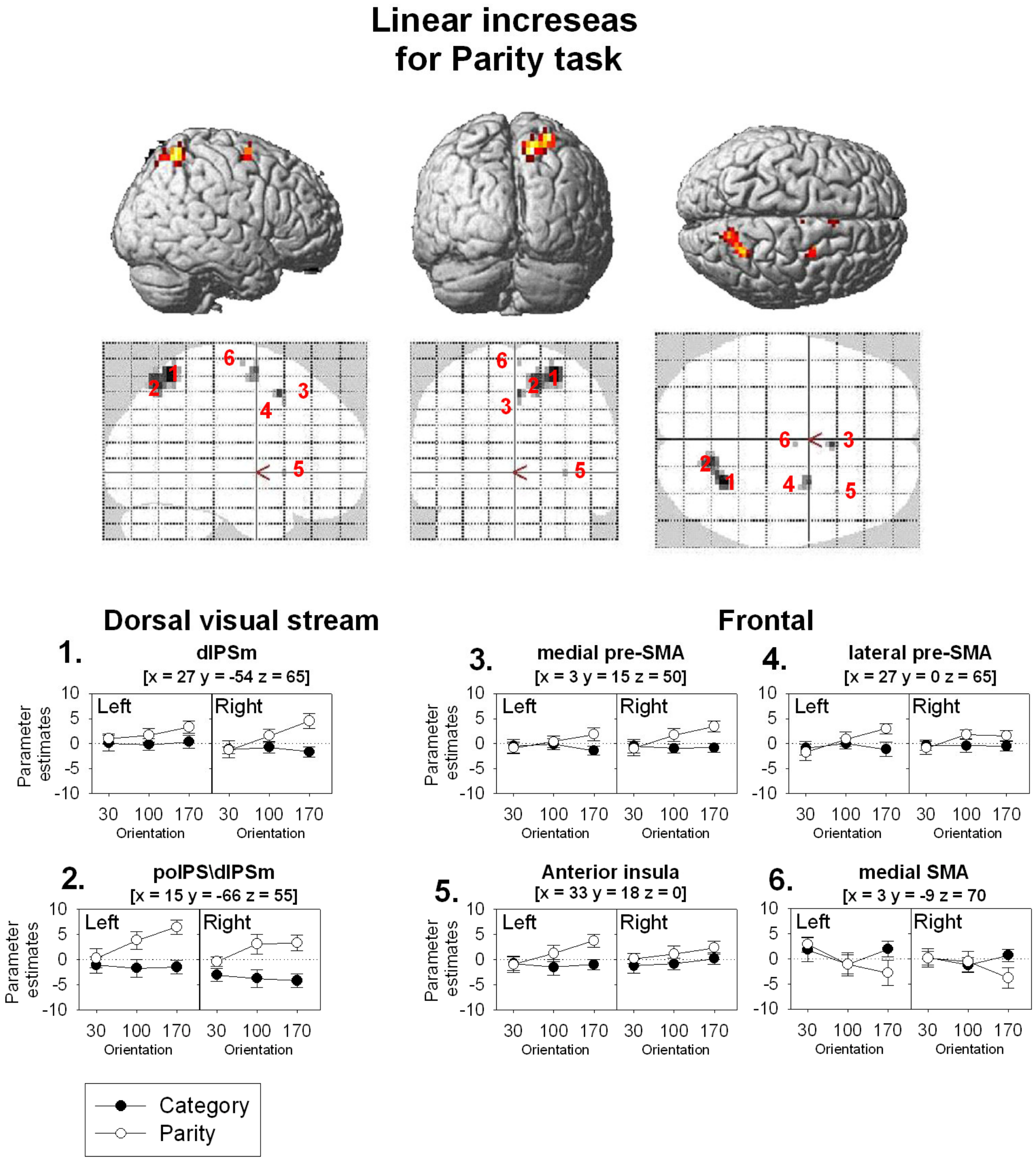


Figure 2.9: Significant voxels associated with linear modulation during the parity task displayed on cortical surface rendering and glass brain SPMs. Peak voxels within the clusters are labelled on the SPMs and corresponding parameter estimates as a function of task, orientation and hemisphere are plotted below. Error bars indicate 95% confidence interval of the mean.

The linear trend in the parity task was observed in six discrete clusters: in the dIPSm, midline and lateral pre-SMA, in addition to midline SMA and anterior insular region (see Table 2.6 for summary statistics, anatomical labels and MNI coordinates).

Table 2.6: Brain areas showing significant linear trend for the parity task and cluster extent in mm^3, with MNI-coordinates for the peak activation voxel, and corresponding summary statistics (F- and FWE corrected p-values). Three local maxima more than 8mm apart are shown for the largest cluster. Linear and quadratic trends are shown separately. Note that a single voxel extent is $45mm^3$.

Label	**Location**	**Brodmann areas**	**Cluster extent mm3**	**x y z (mm)**	**F-value**
1.	dIPSm	BA 7	2835	27 -54 65	37.28***
2.	poIPS/dIPSm	BA 7		15 -66 55	32.91***
3.	medial pre-SMA	BA 6	225	3 15 50	31.1**
4.	lateral pre-SMA	BA 6	585	27 0 65	29.05**
5.	Anterior insula	BA 47	45	33 18 0	22.96*
6.	medial SMA	BA 6	45	3 -9 70	22.15*

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

There were no significant voxels for the orientation-by-hemisphere and task-by-orientation-by-hemisphere interactions, indicating that the task-independent and mental-rotation related effects of orientation are comparable between the hemispheres.

Discussion

The aims of the current study were to identify cortical regions that show increases in activation in response to alphanumeric categorisation and parity discriminations of rotated letters and numbers, and to investigate which cortical regions show BOLD signal correlates of changes in stimulus orientation. I reasoned that both tasks should involve object recognition, and that only the parity task would elicit the process of mental rotation. Mental rotation is associated with linear increases in RTs as a function of stimulus orientation, and I hypothesised that a similar relationship between angular departure from upright and the BOLD signal should be observed in areas that are involved in mental rotation. The act of object recognition might also show some dependence on orientation, and I expected that this would be reflected in quadratic rather than linear modulation of activity.

Alphanumeric categorisation

Increases in activation in response to the category task were observed in the ventral visual stream bilaterally, left dIPS, left IFG, lateral and medial pre-SMA, left sensory motor cortex, and right cerebellum. The ventral stream activation can be attributed to visual processing, the activation in the left IFG has been reported in a number of studies investigating alphanumeric categorisation and character identification (Garrett *et al*., 2000; K. H. James & Gauthier, 2006; Joseph *et al*., 2006; Pernet *et al*., 2004) and has been related to linguistic processing (Joseph *et al*., 2006) or attentional demands (Garrett *et al*., 2000). Activation within the dIPS is not commonly associated with character recognition, although Joseph *et al*. (2006) have reported activation within this area, and attributed it to character naming. However, other studies have identified left dIPS as important in verbal working memory and attention which remains a possibility for the current study. Given the importance of the medial pre-SMA for cognitive control (Dreher & Berman, 2002) the activation within the medial pre-SMA could be attributed to task monitoring or response selection, although there is some evidence that perception of (kanji) characters may also elicit activation within this area (Kato *et al*., 1999) – a finding comparable to that of James and Gauthier (2006) who also found that visual processing of letters recruits regions involved in motor execution. The activation within the sensory-motor cortex and the cerebellum are probably related to right-handed responses, rather than any other cognitive or perceptual processes specific to category judgements.

Parity discrimination

The parity task elicited increases in BOLD signal activation bilaterally within the ventral stream, IFG, dorsal (dIPS) and ventral (vIPS) intraparietal sulci, anterior insula, lateral and medial pre-SMA. Unilateral activation was also observed within the somatosensory cortex on the left and in the right cerebellum. The distribution of the activation in response to the parity task was similar to the pattern of activation in response to the category task on the left, with the exception of the vIPS which was only active in response to the parity task. The parity task also elicited increases in activation on the right in comparable regions. However, the magnitude of the activation on both the left and the right was significantly greater in all of these regions for the parity task, with the exception of the sensory motor and cerebellar activation.

Therefore, parity-task related increases in activation were observed in the ventral stream, vIPS and dIPS, inferior frontal gyrus, anterior insula, lateral and medial pre-SMA.[4] In some respect, at least, this pattern of results is not unexpected. The parity task likely involves all the perceptual, cognitive and response-related processing stages involved in category judgements, in addition to the shared processing steps, parity judgements are also likely to require additional spatial processing of the stimuli, such as determining the orientation of the object, deciding which way to rotate it to upright, generating a mental image, mental rotation to upright and finally parity discrimination. Thus, it is not surprising that the parity judgement task elicited a greater degree of activation than the category task.

Ventral stream

In addition to the regions that showed linear increases in activation, that I attributed to mental rotation *per se*, increases in activation for the parity task, relative to the category task, were observed in the ventral stream, throughout the IPS, and dorsolateral prefrontal regions. These areas, however, did not show linear increases with angular orientation. Alivisatos and Petrides (1997) also reported increases in these areas in a PET study for parity judgements relative to category judgements, although the category task was performed only with upright non-mirrored characters. They suggested that the increases in the ventral stream were

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[4] A small area within the midorbital gyrus showed larger activation in response to the category task than the parity task – however increases in activation within this region is usually correlated with rest periods, and may reflect smaller cognitive demands of the category task, rather than cognitive processes unique to this task.

associated with increased difficulty in processing of mirror-reversed and misoriented stimuli, rather than task-related demands. This conclusion is not supported by the current data, since the stimuli were identical for the two tasks. The results from the present study therefore suggest that the parity task required more perceptual processing than the category task. This extra processing may have involved the identification of orientation itself, which is necessary for mental rotation but not for categorisation.

It is also possible that categorization does not require that individual letters and digits be identified; experiments on visual search show, for example, that search for individual digits among letters is accomplished in parallel, whereas searching for letters among letters requires serial search (Schneider & Shiffrin, 1977). Parity judgements may therefore require that the characters be individually identified, whereas category can be accomplished without this further step. Given that mental image formation recruits similar cortical regions as perception (e.g. Kosslyn, Ganis, & Thompson, 2001), another possible reason for greater involvement of ventral-stream areas in parity judgements is the requirement that participants form a mental image of the character prior to mental rotation.

Posterior parietal cortex

Our results are consistent with those of previous studies in showing activation in the intraparietal sulcus (IPS) elicited by the parity task. This activation was bilateral, in conformity with some previous studies (e.g. Podzebenko *et al.*, 2002), but contrary to those showing unilateral activation in the right (e.g. Harris *et al.*, 2000) or the left (e.g. Alivisatos & Petrides, 1997) IPS. Further, the linear increase in activation with angular orientation was evident only in the posterior portion of the dorsal IPS, suggesting that only this portion of the IPS is involved in the process of mental rotation itself. This explanation is consistent with previous studies showing that the IPS consists of a number of functionally distinct regions, both in humans and monkeys (Orban *et al.*, 2006).

Activation unique to the parity task was observed within the vIPS, an area posterior to the portion of the IPS involved in mental rotation (see below). This area corresponds to one of the four motion sensitive sections of the IPS (Orban *et al.*, 2006), in particular Orban *et al.* (2006) suggested that this area is a human homologue of the LIP area in the macaque cortex. The LIP has been shown to be involved in visuo-spatial attention, motor planning and decision-making (Freedman & Assad, 2006). Hemispheric asymmetries were also observed within this region for the parity task, with larger activation on the right than the left.

Inferior frontal gyrus

The only prefrontal region that showed increases in response to the parity task, but not as a function of stimulus orientation, was the inferior frontal gyrus. Activation in areas that do not show orientation dependence might reflect areas that respond to the increases in attentional and working-memory demands for the parity task, rather than areas involved in the process of mental rotation *per se*. Task-related hemispheric differences were also observed in this area, with increases in activation in on the left for both category and parity tasks, and only parity task related increases on the right.

Mental rotation

Linear increases in RTs and the BOLD signal as a function of angular orientation were found only observed in response to the parity task. Linear increases in the RTs for parity tasks are commonly associated with mental rotation. I hypothesised that comparable effects should be seen in the BOLD signal originating in the areas that are involved in mental rotation *per se*. The observation that linear effects were only observed in the parity task provides additional support for the idea that linear increases in the BOLD signal are indeed neural correlates of mental rotation. Only a subset of areas involved in the parity judgement task showed linear increases in BOLD activation with larger angular orientations. The mental-rotation related effects were restricted to a subregion of the IPS – the middle portion of the dorsal IPS (dIPSm), and specific prefrontal areas – the lateral and the medial pre-SMA. These findings support the notion that mental rotation is subserved by both parietal and higher-order premotor regions.

The frontal modulation with increased mental rotation demands with the alphanumeric parity task is of particular significance because some models of mental rotation, namely those of Carpenter et al. (1999), have attributed activation within those regions to eye movements or shifts of attention between simultaneously presented stimuli, as is typically the case in paradigms using torus shapes.

Given that the current paradigm involved single stimulus displays, it is highly unlikely that the higher-order pre-motor activation was due to shifts of attention or eye movements between stimuli. However, a possibility remains that eye movements or shifts of attention were occurring during mental rotation. There is some evidence that some mental rotation tasks involve eye movements. De'Sperati (2003) tracked eye movements while participants performed a variant of the visuomotor mental rotation task (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989). The participants were shown an angle, with a starting point at the 3 o'clock position. The starting point was then presented at another location on the circle. After changing the location of the starting-point on the circle, the participants were asked to imagine where the end point of the angle would lie, and then indicate they have done so by pressing a button. RTs increased as a function of the size of the angle. This increase in RTs was accompanied by eye movements from the new starting point of the angle, to the imagined location of the ending point of the angle.

It is plausible that the task itself induced eye movements, while the current paradigm might not. Possibility remains, however, that participants may track the imagined motion of the top of the presented stimulus to its canonical upright. If such eye movements accompanied mental rotation of alphanumeric characters, than this would also vary as a function of angular departure from upright, and may be reflected as linear increases in pre-SMA activation.

The involvement of the prefrontal areas has frequently been attributed to attention or working-memory functions, while the parietal involvement has been assigned to mental rotation *per se*. Mental rotation has been reported to be impaired following either left (Mehta & Newcombe, 1991) or right (Ditunno & Mann, 1990) damage to the PPC, or by stimulation of the parietal lobe with TMS (Harris & Miniussi, 2003), or deep cortical stimulation (Zacks *et al*., 2003), but is apparently unaffected by lobotomy of either the left or the right prefrontal cortex (Alivisatos, 1992).

Therefore, the possibility remains that the prefrontal activation may be a result of prominent anatomical connections between the PPC and the pre-motor areas, given that in some cases anatomically-connected cortical regions will show co-activation even if only one of those areas is actively involved in the task (Rorden & Karnath, 2004). What seems certain is that, based on the current results, it is not possible to attribute activation within the parietal lobe to mental rotation *per se* and within the higher-order pre-motor areas to processes other than mental rotation.

Orientation effects common to both tasks

Quadratic modulation for both tasks was observed within the SMG, an area anatomically distinct from regions that showed task differences. The quadratic effect was such that activation was greater for 30° and 170° orientations than for the 100° orientation. Since there was no evidence for an overall difference between tasks in this area, the orientation-dependent activation in the SMG is presumably due to the common process of shape recognition required for both tasks. Previous research has shown that letter naming, but not letter matching elicits activation in this area (Joseph *et al*., 2006) which indicates that these effects may be related to character recognition.

Hemispheric asymmetries

In terms of hemispheric lateralisation, both tasks activated comparable regions in the left hemisphere, but the parity task differed from the category task in that activity tended to be bilateral and symmetrical. Both tasks elicited activation within response-related sensory-motor regions which can be related to right-handed responses. Additionally, the preferential involvement of the left hemisphere in the category task may also reflect the effects stimulus type, i.e. alphanumeric characters (Garrett *et al*., 2000; K. H. James *et al*., 2005; Joseph *et al*., 2006; Pernet *et al*., 2005; Pernet *et al*., 2004; Polk & Farah, 1998).

The main effect of hemisphere indicated greater activation within the posterior portion of the dorsal stream and inferior frontal gyrus in the left hemisphere compared to the right. Since the left-hemispheric involvement within these regions was present for both tasks, and right-hemisphere activation was only elicited by the parity task, these overall effects reflect bilateral involvement in the parity task and left-hemisphere involvement in the category task. These areas also show increases in overall activation in response to the parity task relative to the category task. Task-specific hemispheric asymmetries, as indicated by the interaction between task and hemisphere, suggest that the right hemisphere might show dominance for cognitive processes involved in the parity task, but not mental rotation *per se*. The task-by-hemisphere interaction also indicates that the extent of activation elicited by the parity task is larger, compared to the category judgement, on the right, although the specific differences between the hemispheres in terms of the degree of activation within a task are restricted to the parity task. Hemispheric asymmetries might therefore be interpreted as left-hemispheric dominance for perception, recognition and categorisation of alphanumeric characters, as well as for response generation, and additional recruitment of the right hemisphere for mental-image generation and transformation, and mirror-normal judgement.

Conclusion

Quadratic modulation with stimulus orientation was observed within the SMG and did not differ between the tasks. It was characterised by larger activation in response to stimuli presented at 30° and 170° orientations than in response to stimuli presented at 100°. Linear modulation of the BOLD response was only observed for the parity task and was characterised by increases in activation with increase in angular rotation from upright. These effects were restricted a subset of areas that showed increases in activation in response to the parity task and included posterior portion of the dIPS, lateral and medial pre-SMA and anterior insular region. No hemispheric asymmetries were observed for the effects of orientation, indicating that neither hemisphere can be seen as dominant for mental rotation.

Hemispheric asymmetries *were* observed for the parity task, but not in the areas that showed linear increases in BOLD signal amplitude associated with mental rotation. Firstly, larger right, than left, hemispheric activation was observed in the vIPS. Secondly, the parity task elicited more activation than the category task within the IFG, lateral and medial pre-SMA (anterior to the areas that showed linear increases in response to the parity task) on the right, but not on the left. This pattern of results suggests that the hemispheric asymmetries may be related to visuospatial processing and attention rather than mental rotation *per se*.

Chapter 3: ERP correlates of misoriented object processing during category and parity judgements

Introduction

Chapter 2 showed that the time to categorise alphanumeric stimuli does not depend on stimulus orientation. In contrast, parity judgement time of the same alphanumeric stimuli does increase with stimulus orientation. It was argued that common cognitive processes underlie both tasks up to the point of object-recognition, thus implying comparable visual-processing demands. Subsequent to recognition only the parity discrimination task would require additional processes that 1) establish the orientation of the stimulus, 2) mentally rotate the stimulus, and 3) decide whether the character is normal or backward.

A difficulty with studies using fMRI is that this technique has relatively poor temporal resolution. In Chapter 2 I used parametric-block design which involved averaging activity over two 18 second blocks per experimental run. As a consequence, the fMRI results are likely to provide a temporally smeared image of sensory, perceptual, cognitive and motor elements of the category and parity tasks.

The aim of the present study is to examine temporal sequence of processing stages preceding mental rotation, mental rotation itself and parity discrimination by using high-density EEG recordings while participants perform category and parity judgements about upright and misoriented alphanumeric characters. The utility of EEG in this context is two-fold. Firstly, EEG has excellent temporal resolution and can provide information regarding the time course of neural events underlying the different stages of processing. Secondly, mental rotation has well-established electrophysiological markers, which can be used as a temporal marker to differentiate between processing preceding mental rotation and mental rotation itself.

Electrophysiological correlates of mental rotation

Amplitude modulation of the circa 400–700 ms parietal ERP component during mental rotation of letters was initially described in 1989 by Peronnet and Farah (1989) and Wijers *et al*. (1989) and the basic phenomenon has been extensively replicated since then. Wijers *et al*. (1989) interpreted this amplitude effect as a slow parietal negative wave superimposed upon a temporally- and spatially-coincident, but functionally independent, P300 complex. The amplitude of the slow parietal negativity increases monotonically as a function of the angular disparity of stimuli from the upright position, mirroring the RT results and suggesting that this ERP component is closely tied to the neurophysiological operations underlying mental rotation. This inference has been strongly validated in a series of experiments by Heil and colleagues, who have systematically elucidated the functional and temporal characteristics of this component (see Heil, 2002 for a review). Taken together, the studies of Heil and colleagues (Bajric *et al*., 1999; Heil, 2002; Heil *et al*., 1998) provide compelling evidence for the hypothesis that the parietal amplitude modulation is an electrophysiological marker for the process of mental rotation.

Hemispheric lateralisation

As discussed in Chapter 1 and 2, the issue of hemispheric lateralisation of the process of mental rotation function is still unresolved although it is often suggested that mental rotation is more dependent on processes in the right than in the left hemisphere (Corballis, 1997). The empirical evidence for this greater right hemisphere involvement supposition is currently equivocal: while a number of neuroimaging and neuropsychological studies have reported evidence for a right hemispheric superiority for mental rotation (Farah & Hammond, 1988; Harris *et al*., 2000; Harris *et al*., 2002), others have reported evidence for bilateral involvement (Cohen et al., 1996; Kosslyn et al., 1998; Tagaris et al., 1996; e.g. Tagaris et al., 1997) or even a *left*-hemisphere superiority (Alivisatos & Petrides, 1997; Mehta &

Newcombe, 1991). The results from Chapter 2 indicate that bilateral cortical regions in the IPS, medial and lateral pre-SMA, and insular regions are related to mental rotation.

Although the spatial resolution of EEG is considerably poorer than that of fMRI, the question of hemispheric lateralisation can be addressed with high density EEG if the cortical generators of the activity are sufficiently distant from the midline, as seems to be the case for cortical regions involved in mental rotation (see Chapter 2). The combination of both of these methods may provide a clearer picture in regards to the question of hemispheric dominance for mental rotation. The existing electrophysiological evidence is similarly inconclusive: while several studies have reported a right parietal bias for the orientation-dependent ERP amplitude effect (e.g. Johnson, McKenzie, & Hamm, 2002; Milivojevic, Johnson *et al*., 2003; Pegna *et al*., 1997), a number of others have reported no significant lateralisation effects (Heil, 2002; Peronnet & Farah, 1989; Wijers *et al*., 1989).

Corballis (1997) suggested that some of the conflicting results reported in the literature could be explained as relative superiority of the right hemisphere in terms of the rate of mental rotation. If this is indeed the case, then superior temporal resolution of the ERPs would allow for the relative timing of the mental rotation effects over the left and the right hemispheres to be examined.

Parity discrimination

In the context of parity discrimination tasks, the role of mental rotation is to mentally transform the image into alignment with a target image, or the canonical upright of an object. Therefore, parity discrimination should follow mental rotation. A common observation with mirror-normal judgements about alphanumeric characters is that the mirror-reversed stimuli typically elicit longer RTs than normal stimuli at all orientations (Cooper & Shepard, 1973).

Since character version bears directly on response selection in the parity task, Cooper and Shepard (1973) suggested that the RT cost associated with mirror-reversed characters is related to response selection processes. Cooper and Shepard (1973) reasoned that participants anticipated normal characters and therefore prepared for "normal" responses prior to mental rotation. Mental rotation would then be used as a check for the prepared response. When mirror-reversed characters were encountered, the participants would need to inhibit the prepared "normal" response and subsequently prepare and execute the "mirrored" response. According to this explanation, RT cost associated with mirror-reversed characters reflects processes directly related to response selection.

An alternative explanation was proposed by Hamm, Johnson and Corballis (2004) who found that the RT cost associated with mirror-reversed characters is highly correlated with the rate of mental rotation. They also found that the difference between ERPs to mirror-reversed and normal characters is similar to the difference between rotated and unrotated characters, and that these mirror-reversal effects occur after mental rotation effects. Hamm *et al*. (2004) suggested that this pattern of results indicates that mirror-reversed characters undergo an additional mental transformation – a flip out of the picture plane into alignment with the canonical template representation of the character – and that this additional processing step occurs after mental rotation within the picture plane is finished. According to Hamm et al. (2004), this additional transformational step is used to increase confidence by providing a match with the canonical representation of the characters and may thus be restricted to experimental paradigms in which highly familiar stimuli with clearly defined parity are used, such as alphanumeric characters.

Although their results are fairly convincing, these findings have not been extensively replicated. Thus, one of the aims of the current experiment is to investigate the effects of mirror-reversal and provide a more detailed time-course of parity effects before and after mental rotation itself.

In their investigation of functional properties of the mental rotation component, Heil *et al.* (1998) compared parity and category judgements of alphanumeric characters. They found that increases in parietal negativity were only correlated with the parity judgement task which also elicited increases in RTs as a function of stimulus orientation. In contrast, the P300 and the RTs in the category judgement task were not modulated by changes in stimulus orientation. Therefore, category judgements do not elicit ERP correlates of mental rotation.

However, given the behavioural evidence that misoriented stimuli impose extra processing demands, independently of any "correction" for orientation through mental rotation (Jolicoeur & Landau, 1984; Lawson & Jolicoeur, 2003) it seems reasonable to expect that misorientation would have an effect on neural processing. If this is the case then it might be useful to examine orientation-specificity of neural activity preceding mental rotation. Since the ERP correlates of mental rotation start at approximately 400 ms, examination of the P1-N1-P2[5] complex of the VEP may provide information regarding perceptual processing and visual processing associated with recognition. Note that nearly all of the mental-rotation studies described above analysed data only from relatively few parietal electrodes and have omitted a detailed analysis of occipito-temporal leads which typically exhibit the strongest VEP responses.

The early visual processing can be correlated with the P1 and the N1 ERP components. The P1 and N1 typically have occipito-temporal distribution and occur between 80-120 ms and 140-200 ms, respectively. Both of these components are affected by attentional demands. The P1 component is particularly sensitive to exogenous attentional

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[5] The convention used for naming of the visual-evoked components is P for positive and N for negative. The numbers 1 and 2 simply denote first positive or negative component (P1 and N1) and second positive (P2) component. An alternative naming convention is also used whereby the approximate latency of the component is denoted instead of the sequential numbering used here. In reference to the N1 component, face responsive N1 is usually referred to at the N170 (e.g. Rossion et al., 2000) and cortical-surface recorded N1 was referred to at the N200 (Allison, Puce, Spencer, & McCarthy, 1999).

cues, while the N1 component is particularly sensitive to endogenous attentional cues and top-down task demands (Luck, 2005; Martinez *et al*., 2001).

The cortical generators of the P1 and the N1 differ although both components are generated by multiple extrastriate regions (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). The P1 component originates from both the dorsal and ventral extrastriate areas. More specifically, the initial stages of the P1 have been localised to the middle occipital gyrus and the later stage of the P1 has been localised to the fusiform gyrus. The P1 component is sensitive to simple properties of visual stimuli such as luminance, contrast and spatial frequency (Luck, 2005) and has been related to visual feature processing (Muthukumaraswamy, Johnson, & Hamm, 2003). Additionally, the P1 has been shown to be affected by global stimulus transformations and some authors have suggested that it may reflect a global encoding stage of stimulus processing (Boutsen, Humphreys, Praamstra, & Warbrick, 2006; Itier & Taylor, 2004; Taylor, 2002).

Cortical generators of the N1 have been localised to both the parietal, lateral occipital and inferior temporal regions (Di Russo *et al*., 2002; Rossion, Joyce, Cottrell, & Tarr, 2003). The later stages of the N1 are selective to object information, with somewhat different latencies and distributions for distinct classes of objects (Rossion *et al*., 2000). Cortical surface recorded ERPs also show that proximal cortical regions within the inferior temporal cortex elicit maximal N1 amplitudes to specific objects such as sinusoidal gratings, faces, letter strings and houses.

In an earlier mental-rotation study, Milivojevic, Johnson *et al.* (2003) reported orientation-related modulation of ERPs as early as 140 ms, corresponding to the N1 component. The distribution of this modulation was over occipito-temporal leads. This early orientation-related modulation was not associated with mental-rotation demands because the effects were better characterised with a quadratic, rather than a linear, trend. The largest N1 amplitudes evoked by stimuli presented at 60 and 120 degree orientations, followed by inverted stimuli, and the lowest amplitudes were observed for the upright stimuli. The authors attributed the increase in N1 to fairly low-level processing of orientation by cells in visual cortex. This is certainly a possibility, particularly since Ito, Sugata, and Kuwabara (1997) found that the amplitudes of the N1 component were larger for triangles and diamonds than to circles and squares. However, the fact that the inverted characters elicited larger N1 amplitude compared with the upright characters would suggest that the orientation processing is related to the orientation of the object itself.

The amplitude and the latency of the N1 have been shown to be specific to various object classes (Rossion *et al.*, 2000). Additionally, evidence from cortical-surface VEP recordings indicate that the N1 responses to different stimulus classes (faces, objects, letter-strings etc.) originate from adjacent, but non-overlapping cortical regions (Allison et al., 1999). This indicates that the N1 may mark the first stage by which object recognition, at least to some level of classification, is accomplished. Further, N1 amplitude and latency have been shown to increase with stimulus inversion, and is thought to reflect a disruption of configural object processing (e.g. Rebai, Poiroux, Bernard, & Lalonde, 2001; Rossion *et al.*, 2000). Although the effects of stimulus inversion on the amplitude and the latency of the N1 are best documented with face stimuli (e.g. Rossion *et al.*, 2000) there is some evidence that the amplitude of the N1 also increases with inversion of complex objects such as cars (Rebai *et al.*, 2001). However, in the Rebai *et al.* (2001) study other objects, such as cups, did not elicit comparable inversion effect.

The functional properties of the posterior P2 component are relatively poorly understood. Luck (2005) noted that this may be related to the fact that the posterior P2 is often difficult to distinguish from the subsequent P300 wave, although they differ in distribution. The P2 is distributed over the posterior-parietal and dorsal occipital electrode sites while the P300 is distributed over dorso-parietal electrodes. In a mental-rotation study, Muthukumaraswamy *et al*. (2003) found larger P2 amplitude is associated with trials in which random 2D shapes were misoriented with respect to a preceding sample stimulus, but this increase was not systematically related to the degree of misorientation. Milivojevic, Clapp, Johnson & Corballis (2003) found that the P2 amplitude difference between ERPs evoked by normal and thatcherised faces showed linear reduction as a function of angular rotation from upright. The authors interpreted these results as indicative of a gradual reduction of configural processing mechanisms with misorientation. Similar findings were reported by Boutsen *et al*. (2006) who showed that P2 is modulated by inversion of faces and houses. However, Boutsen *et al*. (2006) suggested the P2 component reflects local processing of configural information, in contrast to the P1 which reflects global processing of configural information.

The present experiment

The evidence reviewed above suggests that mental rotation is involved in parity judgements about rotated objects, but is not involved in the categorisation of rotated alphanumeric characters. Additionally, I have argued that mental rotation of familiar shapes should not be part of object recognition itself, but should follow it. Therefore, the onset of mental rotation can be used as an indication that object recognition has been accomplished and orientation-specificity of neural processing preceding mental rotation can be investigated. The aims of the present experiment are to 1) characterise the orientation sensitivity of the VEPs preceding mental rotation, 2) examine hemispheric asymmetries of the mental-rotation component itself and 3) assess the time course of parity discrimination which follows mental rotation.

Methods

Participants

Eighteen neurologically normal volunteers were recruited from students and faculty at the University of Auckland for approximately two hours of participation. All had normal or corrected-to-normal vision and were right-handed (LQ range: 60-100, mean 94.28), as determined by Edinburgh handedness inventory (Oldfield, 1971). The procedures were approved by the University of Auckland Human Subjects Ethics Committee, and all participants gave their informed consent to participate in the experiment. Four were excluded from analysis due to ocular and/or movement artefact during recording. Thus, 14 participants (7 women) were included in the final analysis. They ranged in age from 18 years to 47 years, with a mean of 27.57 years.

Visual Displays

The stimuli consisted of four uppercase letters (R, F, L, and P) and four digits (2, 4, 5, and 7) printed in black 72-point Arial font on white background. At upright, the characters subtended a vertical visual angle of 2º and a horizontal visual angle of 1.45º, on average, although small differences in the horizontal visual angle were present due to the shape of the characters (range: 1.3-1.8°). Each character was presented in both a normal and backward (mirror-reversed) form at angular departures of 0º, 60º, 120º, 180º, 240º, and 300º clockwise from the upright. Manipulation of visual displays was performed using Microsoft Office Picture Editor (MS). Stimuli were displayed on an SVGA computer monitor (1024×768 pixel resolution; 60 Hz refresh rate) from a distance of 57 cm. Stimulus presentation was controlled using E-Prime v1.1.4.1 (Psychology Software Tools, Pittsburgh, Pennsylvania, USA). TTL pulses generated via the parallel port of the display computer provided synchronization of stimulus events with EEG acquisition. Millisecond timing routines for the visual displays and pulse generation were conducted as outlined in the E-Prime User Guide (Schneider, Eschmann, & Zuccolotto, 2002).

Tasks

The participants performed two tasks, a mirror-normal judgement task (parity task) and a letter-digit judgement task (category task). In the parity task, the participants were required to press the left mouse button if they judged the character to be normal and the right mouse button if they judged it to be mirrored. In the category task, the participants were required to press the left mouse button if they judged the character to be a letter, and the right mouse button if they judged the character to be a digit. In both the cases they were instructed to respond as quickly as possible without sacrificing accuracy.

Procedure

Participants performed a practice block for each task immediately prior to the experiment. The parity task practice consisted of 48 randomly selected trials. The probability of stimulus presentations was weighted in favour of larger angular orientations with 32% of possible trials involving inverted stimuli, 21% involving stimuli presented at 120 and 240 orientations, 12% involving stimuli rotated by 60 or 300 degrees, and 5% involving upright stimuli. Mirrored and normal stimuli were equiprobable. Since the category task was easier, only 16 randomly selected trials were used, with the same probability of stimulus orientations as in the experimental blocks.

Over the course of the experiment, 512 trials were presented for each task. As per method used by Milivojevic, Johnson *et al*. (2003), twice as many stimuli were presented for the 0º and 180º orientations, compared to those at 60º, 120º, 240º and 300º, and clockwise and anticlockwise rotations were treated as equivalent, due to the symmetry of RTs and ERP effects around the 180º orientation. Thus, 128 stimuli were presented at each orientation for each task.

The experiment was conducted over four blocks of trials, and task order was randomised across the blocks. Within each block, each stimulus was presented four times at each orientation, and the order of stimulus presentations was randomised. Stimuli were presented centrally for up to 10 s or until a response was detected, whichever was sooner. Participants were instructed to keep looking at the stimulus, avoid eye movements, and withhold blinking until after the response was made. Following stimulus offset, the participants were instructed to keep fixation on a small '+' which was presented for 1000 ms.

EEG Apparatus

Electrical Geodesics Inc. 128-channel Ag/AgCl electrode nets (Tucker, 1993) were used. EEG was recorded continuously (250Hz sampling rate; 0.1–100Hz analogue bandpass) with Electrical Geodesics Inc. amplifiers (200 MΩ input impedance) and acquisition software running on a Macintosh G4 computer with a 16-bit analogue-to-digital conversion card bit. Electrode impedances were below 50 kΩ (range 30–50 kΩ), an acceptable level for this system (Ferree, Luu, Russell, & Tucker, 2001). EEG was acquired using a common vertex (Cz) reference.

Pre-processing

Pre-processing was performed with custom (in-house) software. Following data collection, the EEG files were segmented with respect to event triggers in 1000 ms epochs including a 200 ms pre-stimulus baseline and 800 ms post-stimulus epoch. Voltages were sampled every 4 ms over this epoch. Only the trials on which the participants responded correctly were included in the analyses. Eye-movement correction was made on all segments using the method of Jervis, Nichols, Allen, Hudson, and Johnson (1985). The corrected data from each subject were then averaged to produce a total of 16 ERPs (two tasks, two character versions, and four orientation conditions). DC offsets were calculated from the pre-stimulus baseline and removed from all waveforms. The individual waveforms were digitally filtered with a band-pass filter for 0.01–30 Hz range using a bi-directional 3 Pole Butterworth filter (Alarcon, Guy, & Binnie, 2000). Averaged and filtered ERPs were re-referenced to the average reference off-line.

Results

Behavioural data

RTs for accurate responses and accuracy, as percent correct, were analysed with a 2 x 2 x 4 repeated measures ANOVA with task, stimulus version (normal or mirror-reversed) and orientation as factors. The mean RTs and accuracy as a function of task, version and orientation are plotted in Figure 3.1. Huynh-Feldt ε value correction was used to correct for sphericity violations associated with repeated-measures effects (Huynh & Feldt, 1976).

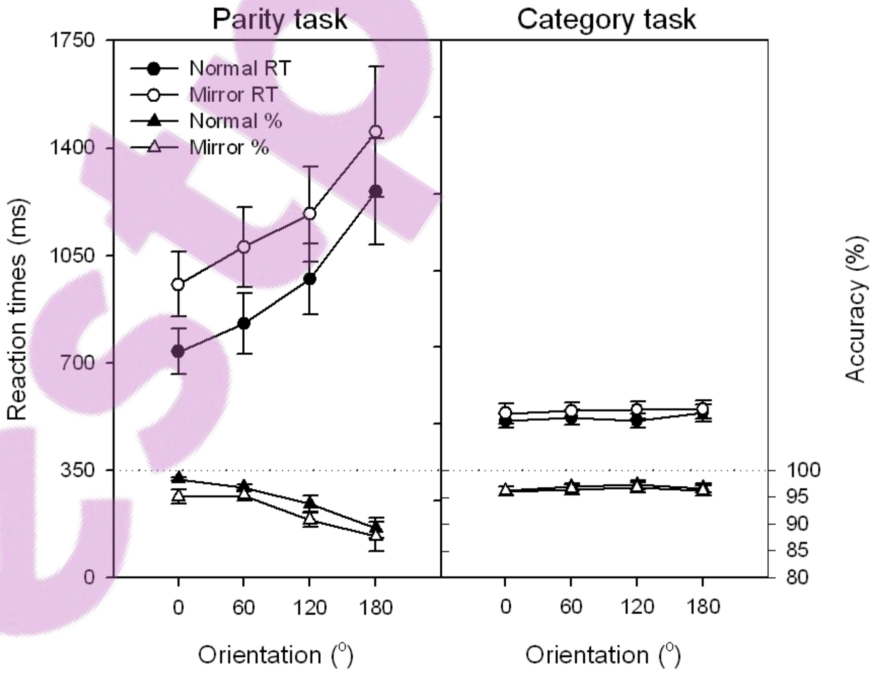

Figure 3.1: Reaction times (RT) in milliseconds (ms) and accuracy (%) as percent correct for category and parity tasks as a function of stimulus version and orientation. RTs are plotted as circles, accuracies as triangles.

RTs were significantly longer for the parity, compared with the category, task (F(1, 13) = 23.79, $p < 0.001$), with the parity task eliciting RTs of 1058.5 ms on average (SE = 128.61), and the category task eliciting 531.6 ms on average (SE = 26.55). Mirror-reversed characters elicited significantly longer RTs than normal characters (F(1, 13) = 25.82, $p < 0.001$; normal: 734.7 ms, SE = 66.08, mirrored 855.46 ms, SE = 85.58). A significant interaction between character version and task was also observed (F(1, 13) = 16.55, p = 0.001) which could be attributed to a smaller effect of stimulus version for the category task (mean: 22.8, SE: 6.76, p = 0.005) than for the parity task (mean: 218.8 ms, SE: 47.40, $p < 0.001$).

The orientation-by-version interaction was not significant (F(3, 39) <1) and neither was task-by-orientation-by-version interaction (F(3, 39) <1). Given that some evidence suggests that orientation effects on letter/digit *identification* are only apparent when mirror-reversed stimuli are used (Corballis et al., 1978), orientation-by-version interaction was examined for each task separately. Orientation-by-version interaction was not significant for neither the parity (F(3, 39) < 1) or the category (F(3, 39) = 1.78, p = 0.177, e = 0.839), indicating that effects of orientation did not differ between mirror-reversed and normal characters.

Main effect of stimulus orientation was also observed (F(3, 39) = 17.51, p = 0.001, ε = 0.372), as was the orientation-by-task interaction (F(3, 39) = 18.26, $p < 0.001$, ε = 0.394). The parity task elicited significantly longer RTs than the category task at all orientations, ranging from 323.6 ms (SE = 67.49) for upright characters to 813.3 ms (SE = 169.70) for inverted characters ($p < 0.001$). Simple effects of orientation were then examined for each task separately. The effects of orientation did not reach significance for the category task (F(3, 39) = 2.53, p = 0.083, ε = 0.848), although a significant linear trend was observed (F(1, 13) = 7.61, p = 0.016; 80.51% of variance explained) reflecting a small increase in RTs with stimulus misorientation. The slope of the linear component of the RT function was 0.09, indicating that if this increase in RTs was due to mental rotation; the rate of mental rotation would have been approximately 10,832° per second.

The effect of orientation was highly significant for the parity task (F(3, 39) = 18.00, p = 0.001, ε = 0.379). A significant linear (F(1, 13) = 20.02, p = 0.001) trend accounted 94.46% of variance, although quadratic (F(1, 13) = 6.75, p = 0.022) and cubic (F(1, 13) = 5.58, p = 0.034) trends, which accounted for 4.95% and 0.58% of variance, respectively, were also significant. The slope of the linear component of the RT function was 2.76, indicating that the rate of mental rotation was approximately 363° per second.

Participants performed the category task (96.6% correct) more accurately than the parity task (93.4% correct, F(1, 13) = 15.11, p = 0.002). The main effect of stimulus version was also significant (F(1, 13) = 4.98, p = 0.044) and reflected higher accuracy for normal (95.7%), compared to mirror-reversed (94.3%), characters. Furthermore, the main effect of orientation was significant (F(3, 39) = 16.95, p < 0.001, ε = 0.667), as was the task-by-orientation interaction (F(3, 39) = 17.34, p < 0.001, ε = 0.895).

Simple effects were analysed by examining the effects of orientation for each task separately. The effects of orientation did not reach significance for the category task (F(3, 39) < 1, ε = 0.799), but did for the parity task (F(3, 39) = 21.32, p < 0.001, ε = 0.720). A significant linear trend (F(1, 13) = 38.49, p < 0.001) accounted for 93.37% of variance. A quadratic trend was also significant (F(1, 13) = 5.57, p = 0.035) and accounted for 5.48% of variance.

Summary of behavioural results

In summary, the parity task elicited longer RTs and lower accuracy than the category task, consistent with the notion that decisions based on the parity of alphanumeric characters required processing steps additional to those based on the letter-number category. The data also support the notion that the parity-judgement task elicited mental rotation, at a rate of approximately 363°/second, as indicated by significant effects of orientation on RTs characterised by linear and quadratic trends. Effects of orientation on RTs for the letter-digit categorisation task were not significant, although a significant linear trend was apparent. This effect is unlikely to be related to mental rotation because the rate of mental rotation would have been 10,832°/second.

Additionally, mirror-reversal of characters made both tasks more difficult, as indexed by reduced accuracy and increased RTs. The increase in RTs was considerably greater for the parity task than for the category task indicating that the RT cost associated with mirror-reversed characters does not reflect the same underlying cognitive or perceptual processes for both tasks. Character version bears directly on response selection in the parity task but not the category task, and as Hamm *et al.* (2004) suggested, in the parity task the mirror-reversed characters are probably rotated out of the picture plane into alignment with a canonically-oriented character representation.

Therefore, the RT cost associated with mirror-reversed stimuli is probably accrued after mental rotation within the picture plane is completed. As mentioned above, the RTs for the category task show no indication of mental rotation and the RT cost associated with mirror-reversed stimuli is considerably smaller for this task. Therefore, it is likely that mirror-reversed stimuli affect visual processing at a stage prior to mental rotation as well and may be associated with character recognition. In a letter-identification task, Corballis *et al.* (1978) reported an ‘M’-shaped RT function only for mirror-reversed characters while comparable effects for normal characters were not observed. One possible explanation relates to relative visual familiarity of normal and mirror-reversed characters. Perrett *et al.* (1998) found that extensive visual familiarity with objects at specific orientations is related to a larger number of orientation-specific neurons for that particular view-point of an object. These findings may extend to familiarity with alphanumeric characters - since mirror-reversed characters are less commonly encountered smaller number of neurons may be tuned for their configurations than for normal characters. It would then follow that the smaller neural population takes longer to accumulate sufficient amount of neural activity for recognition. Koriat and Norman (1985) showed that RT function for mirror-reversed characters was predominantly linear, while the RT function for normal characters was explained by both linear and quadratic trends. They argued that this pattern of results indicates that alphanumeric characters (in this case Hebrew characters) have relatively broad tuning curves that reflect the degree of visual familiarity with the stimulus. Since mirror-reversed characters are less familiar, their recognition tuning curves are narrower. Although a comparable pattern was not observed in the current data, as indicated by the lack of version-by-orientation interaction, it is possible that visual familiarity with the stimulus affects visual processing to a certain degree. If this is the case, then both tasks should show effects of mirror-reversal prior to mental rotation. Subsequently to these effects, the parity task should show mental-rotation effects in the ERPs which would last longer for the mirror-reversed than for the normal characters.

EEG data

The aim of the ERP analysis is to determine the time-course and spatial distribution of orientation-related modulation of neural activity. Therefore, time windows and electrodes of interest need to be selected for detailed analysis. The first step, though, is to identify the components of interest. If one adopts the physiological approach for definition of ERP components (Näätänen & Picton, 1987), then an ERP component is defined in terms of the anatomical source within the brain. The topographic distribution of scalp potentials provides information regarding the configuration of underlying sources of activity and the amplitude of scalp ERPs provides information regarding the strength of that activity. However, in the context of high-density ERP recording, the time-periods and electrodes of interest for detailed analyses can be problematic because ERP components of interest are typically distributed over many electrodes, and amplitudes often vary widely over space and time (see Figure 3.2).

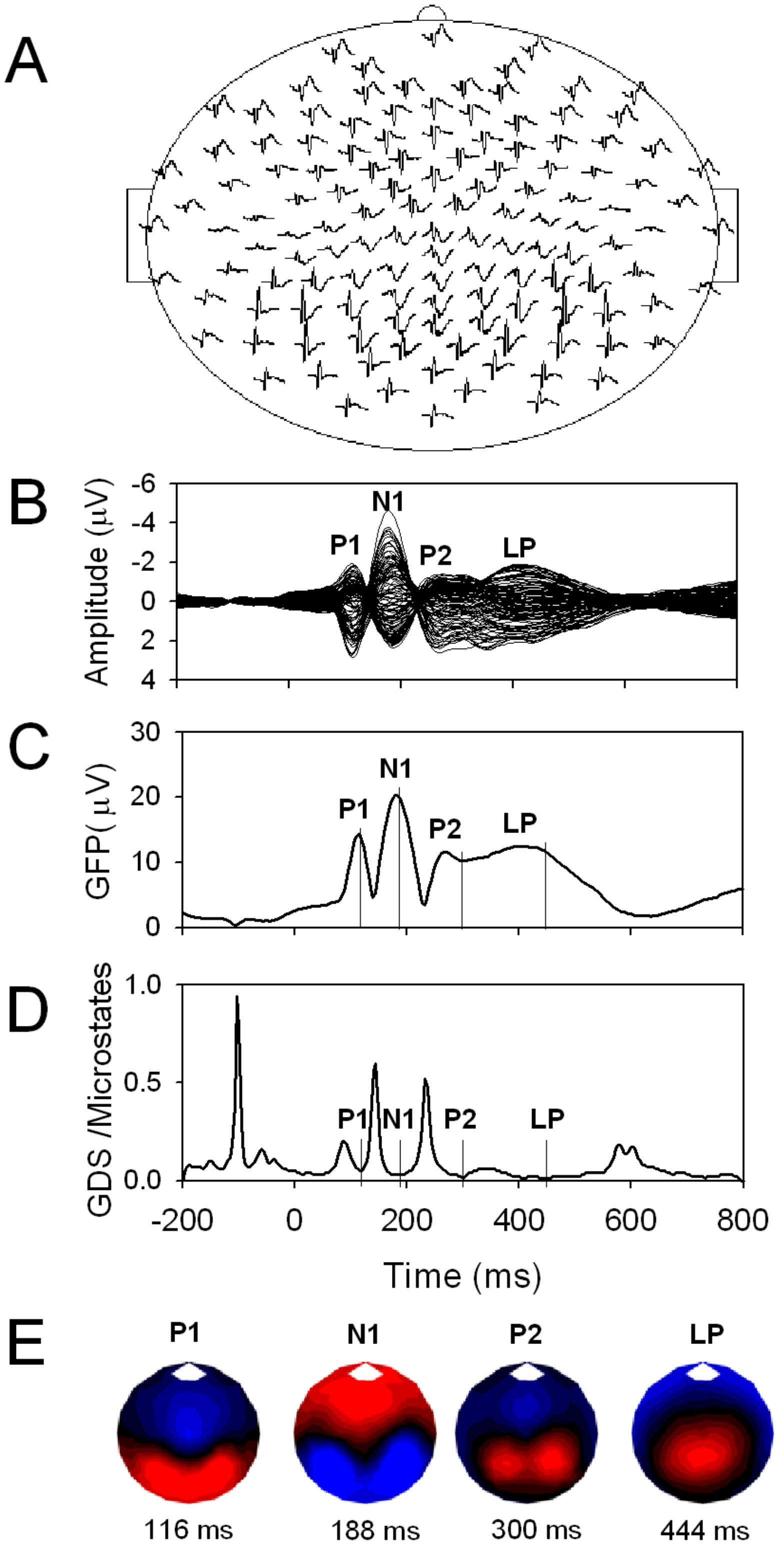

Figure 3.2: Relationship between event-related potentials, global field power, microstates and topographic distributions of ERPs. A. Event related potentials displayed on a head-map with electrode positions. B. An ERP overlay. C. Global field power. D. Time-series of global dissimilarity scores/microstates. E. Topographic distributions of ERPs at time points corresponding to low microstate scores, within time periods corresponding to high GFP. The main ERP components have been labelled.

Even when a given component is well localised to a spatial cluster of electrodes, there is typically a polarity-reversed version at a distant location or locations on the head, because of the dipolar nature of the generators of surface ERPs. Figure 3.2 illustrates a grand-average ERP waveforms averaged over the eight conditions plotted at each electrode position (part A) and all waveforms superimposed as an overlay plot (part B). Identification of time periods showing ERP amplitude variation is easier when all the electrodes are plotted in overlay, although it is still difficult to determine at what point in time the topography, and thus the configuration of the underlying generators, changes. Thus, it may be useful to adopt methods for data reduction which would utilise both the amplitude and topography information.

Data reduction

A useful method for spatial-data reduction is the Global Field Power (GFP, Lehmann & Skrandies, 1984) descriptor, which has the advantage of reducing the data from multiple electrodes into a single time series. GFP is calculated as:

$$GFP=\sqrt{\frac{1}{2n}\sum_{i=1}^{n}\sum_{j=1}^{n}\left(u_i-u_j\right)^2}$$

where n is the number of electrodes which measure the potentials e_i and e_j; $i,j = 1 \ldots n$; the observed voltages are $u_i = e_i - e_{common\ reference}$ and describes the degree of global relief (or “hilliness”) of the voltage topography at each point in time by quantifying the variability between electrodes at each time point (Figure 3.2 illustrates the relationship between ERPs (part B) and GFP (part C).

Although useful as a compact descriptor of time-series information, GFP loses all spatial information. Given that changes in scalp topographies imply a change in the underlying neural generators, it is important to select time periods that show similar topographic distributions. One method for comparison between scalp topographies is to calculate a global dissimilarity score (GDS, Lehmann & Skrandies, 1980) between sequential time points. GDS is calculated as:

$$GSD = \frac{\sqrt{\frac{\sum_{i=1}^{n}\left(e_{it} - e_{it+1}\right)^2}{n}}}{GFP_t}$$

where *n* is the number of electrodes which measure the potentials e_i, $i = 1\ldots n$, at time point *t* and sequential point $t+1$, and GFP refers to average-reference GFP, which has lower amplitudes than reference-free GFP described above. GDS values can range between 0 (identical) and 2 (complete inversion). Each time period of stable topographies is called a microstate, and corresponds to a period of low global dissimilarity scores. Part D of Figure 3.2 illustrates a plot of microstates over the entire epoch, while part E of the same figure illustrates the topographies at the time period corresponding to the lowest microstate value.

Although the most stable topographic distributions for the P1 and the N1 components correspond well to the peak of the GFP for the same components, the same is not true of the P2 and the LP components. Thus, the GFP and the microstate plots can be used in combination for data reduction of multi-channel data into two complementary time series, representing variability between electrodes and stability of spatial distributions over time. A combination of these methods can be useful for selection of time windows for further analysis.

Effects of interest

ERP components are also commonly defined in terms of their functional significance (e.g. Heil, 2002). However, the relationship between the peaks and troughs of scalp recorded ERPs and the underlying functionally-defined latent components of interest may not be obvious (Luck, 2005). For example, ERP correlates of mental rotation are manifest as increases in parietal negativity with larger angular rotations from upright during 400 to 700 ms time period (e.g. Peronnet & Farah, 1989; Wijers *et al*., 1989). These increases in negativity, however, coincide with a late parietal (LP) positivity elicited by stimulus recognition (Heil, 2002). Thus the distribution of the ERP waveforms over that time period does not show absolute parietal negativity for any of stimulus orientations. Subtracting ERPs for smallest angle from those for larger ones, however, reveals the parietal negativity associated with increasing angular misorientation.

Therefore, one method of selecting the time periods reflecting the latent components of interest is to plot the time course of a difference between the experimental conditions. With only two experimental conditions, this can be accomplished by a simple subtraction. However, when more than two experimental conditions are used, the solution may not be so obvious. A simple way to circumvent this problem is to use orthogonal contrasts. Given that the stimuli were presented at four angular rotations from upright, the effects of stimulus orientation can be fully described with linear, quadratic and cubic contrasts. The contribution of each trend was calculated for each subject, by multiplying the ERPs evoked by four stimulus orientations with contrast weights corresponding to a linear (-3 -1 1 3), quadratic (-1, 1, 1, -1) and cubic (-1 3 -3 1) trends and calibrated to have equal variance, at each electrode and each time point. This calculation was performed within each task, and the resulting six trend coefficients were grand-averaged across subjects.

Time periods of interest

Two types of orientation-related effects were discussed in the introduction of this chapter, effects related to mental rotation and effects related to stimulus obliqueness. In this sense, linear and quadratic functions can be seen as particularly important given that mental rotation might be expected to induce linear increases in parietal negativity with larger angular rotation from upright, and effects of orientation associated with obliqueness of stimuli can be described in terms of a quadratic trend. Thus, the time-windows for further analysis were chosen based on linear and quadratic trends evident in ERPs. Since the orientation-related modulation is likely to differ between tasks and the two stimulus versions, at least over the LP component, the selection of time windows interest was based on linear and quadratic trends for the two stimulus version in each task separately.

The GFP and microstate time series of linear and quadratic trends for ERPs in each task are plotted in Figure 3.3. Time periods associated with increases in GFP and decreases in global dissimilarity scores were considered of interest. Linear changes in the ERP amplitudes between 300 and 800 ms are taken to be related to mental rotation (e.g. Peronnet & Farah, 1989; Wijers *et al.*, 1989). Linear modulation over this time period is observed for both normal (356-636 ms) and mirror-reversed (492-712 ms) stimuli during the parity task. No comparable effects are observed for the normal stimuli in the category task although there were smaller linear and quadratic changes between 340 and 480 ms for the mirror-reversed stimuli. These time periods are indicated by arrows in Figure 3.3.

Furthermore, linear changes in the ERPs are predominant in the parity task between 248-320 ms which correspond to the P2 component. The P2 component was also associated with quadratic modulation for the category task, and to a lesser extent, the parity task. Quadratic modulation for both tasks was evident over 96-136 ms, and 160-216 ms, corresponding to the P1 and the N1 ERP components. Additionally, linear modulation was observed over the N1 component for the normal stimuli in the category task. Increases in GFP over the N1 component are also observed for the normal stimuli in the parity task, although this increase seems continuous with the P2 linear increases. The microstates plots indicate that the topographies between these time periods do change for the parity task, although the differences are not as clear cut as for the category task. Topographic distribution of the P1 and the N1 quadratic trends resembles the topographic distribution of the ERPs, suggesting that the effects reflect increases in amplitudes for oblique stimuli.

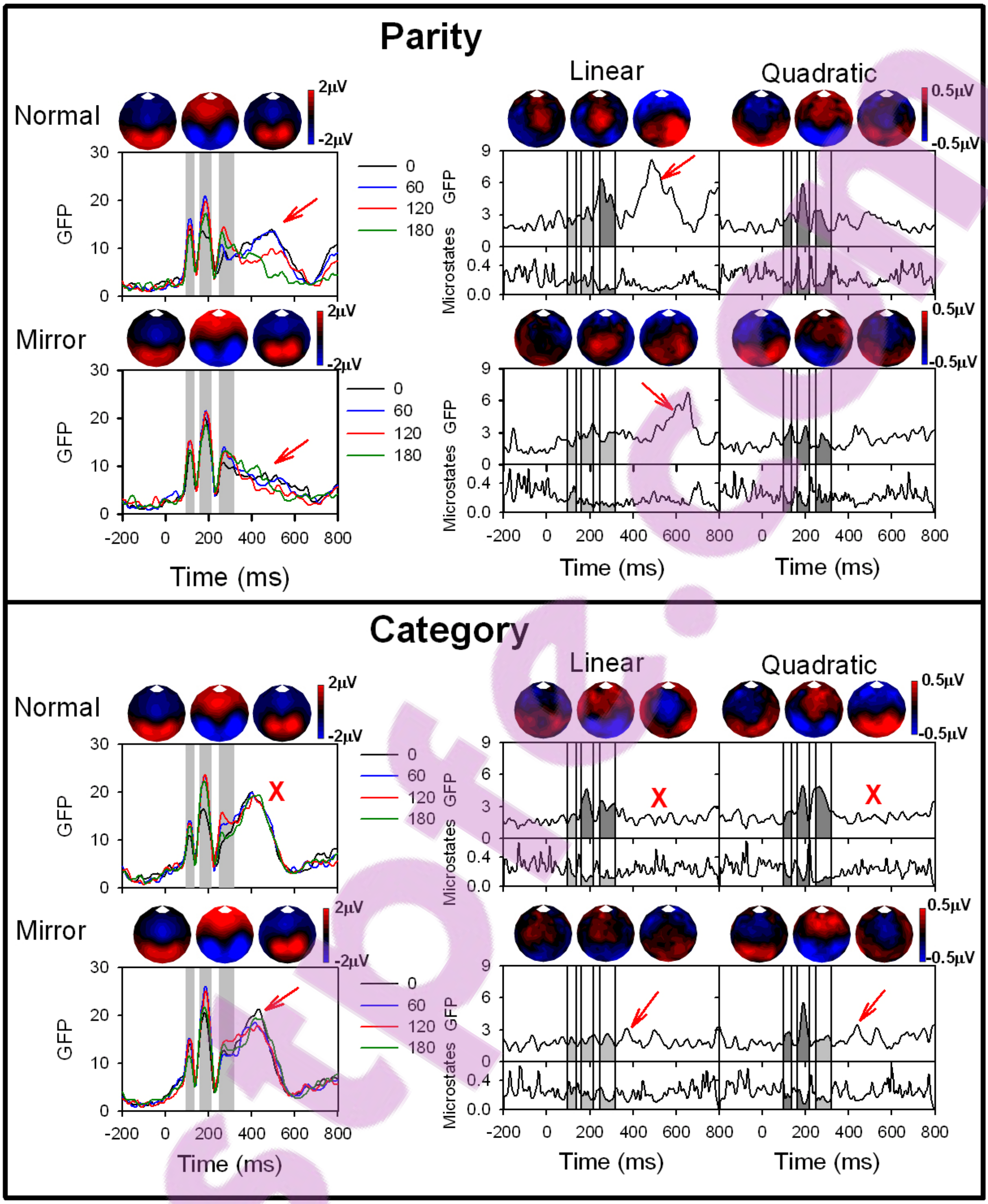

Figure 3.3: Global field power and microstates plots of original ERPs at all four orientations and linear and quadratic trends associated with stimulus orientations ERP effects for category and parity tasks. Time windows of interest are shaded in dark-grey in plots that guided their choice, and light-grey for other plots. Spatial distributions for the time windows are plotted above the GFP plots. For the parity task red arrows indicate the mental-rotation component evident in the GFP plots. For the category task the red arrows indicate a mental-rotation component for the mirror-reversed stimuli, and red Xs indicate that no comparable effect was observed for normal stimuli.

A linear relationship between angle of stimulus orientation and ERP amplitude may be suggestive of mental rotation. Linear modulation of the ERPs was observed over two ERP components – the P2 and the late-parietal components – during the parity task. For the P2 component, linear increases in positivity were observed over posterior-parietal leads. Modulation of the P2 component is not commonly associated with mental rotation *per se* although Muthukumaraswamy *et al.* (2003) found similar increases in response to stimuli that needed to be rotated, but these increases did not vary as a function of orientation. For the late-parietal component linear increases in *negativity* were observed over the centro-parietal electrodes. The distribution and the direction of these effects conforms to the typical distribution of the ERP mental-rotation effect (e.g. Milivojevic, Johnson *et al.*, 2003).

Effects of orientation on the early VEPs

Since the late-parietal effects clearly differ between the tasks in terms of magnitude and temporal characteristics but appear relatively similar for the P1, N1 and P2 components, the effects of orientation on these early VEPs were initially examined with task as a factor. Three time windows of interest were chosen: 96-136 ms, 160-216 ms, corresponding to the P1 and N1 components, respectively, and 248-320 ms corresponding to the P2 component. Two electrode clusters – one over each hemisphere – were used for each of the time windows. Occipito-temporal electrode clusters were used for the P1 and the N1 components (see Figure 3.4, Part A for illustration of electrode positions in reference to the whole electrode montage) which corresponds to the areas of interest based on topographic distributions of the effects (also see Figure 3.4, Part A) and previous findings (Milivojevic, Johnson *et al.*, 2003). The P2 analysis was restricted to a cluster of parieto-temporal electrodes which showed a maximal P2 amplitude (see Figure 3.5 for illustration of electrode position and spatial topography of the P2 effects), and have previously been associated with increases in response to misoriented stimuli (Muthukumaraswamy *et al.*, 2003). Mean amplitudes over these time windows were then analysed in a 2x2x4x2 repeated measures ANOVA with task, character version, orientation and hemisphere as within-subject factors. Violations of the sphericity assumption were corrected using Huynh-Feldt ε value correction (Huynh & Feldt, 1976)[6].

P1 and N1 effects

As indicated above, the effects of orientation on the P1 and the N1 had similar occipito-temporal topographic distribution, and same occipito-temporal electrode clusters were used for the analysis (see Part A of Figure 3.4). The ERPs collapsed over the electrode clusters of interest are presented in Par B of Figure 3.4, and time windows of interest are shaded in gray. Part C of Figure 3.4 depicts average amplitude over the P1 (96-136 ms) and the N1 (160-216 ms) time windows over the electrode clusters of interest as a function of task, orientation, character version, and hemisphere.

For the P1 component, the main effect of stimulus orientation was significant ($F(3,39) = 10.1$, $p < 0.001$, $\varepsilon = 1$) and could be attributed to a significant quadratic trend ($F(1,13) = 21.12$, $p = 0.001$), which explained 99.97 % of variance. Main effect of task was also significant ($F(1,13) = 9.15$, $p = 0.01$) as was the task-by-version-by-hemisphere interaction ($F(1,13) = 9.82$, $p = 0.008$). Larger P1 amplitudes were evoked by the parity task than the category task, although the differences between the tasks only reached significance over the right hemisphere for normal stimuli ($p = 0.001$), and over the left hemisphere for the mirrored stimuli ($p = 0.045$). Furthermore, significant effects of stimulus version, with larger amplitudes in response to mirror-reversed, in comparison to normal, stimuli, were observed for the category task only, and this effect was only evident over the right hemisphere ($p = 0.016$).

For the N1 component, the main effect of task was significant ($F(1, 13) = 5.32$, $p = 0.038$), with larger N1 amplitudes in response to the category task than to the parity task. The

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[6] Although the Greenhouse-Geisser correction for sphericity violations (Greenhouse & Geisser, 1959) is more commonly used in psychology-research than Huynh-Feldt method (Huynh & Feldt, 1976), some authors suggest that the Greenhouse-Geisser method is overly conservative (e.g. Howell, 1997). In the article on guidelines for ERP data analysis and interpretation for cognitive science, Picton et al. (2000) suggest that either Greenhouse-Geisser *or* Huynh-Feldt method can be used, as long as a correction for the *df* is applied. Huynh-Feldt method was used throughout this thesis because it provides more power in the test.

task-by-hemisphere interaction was also significant (F(1, 13) = 5.86, p = 0.031) and could be attributed to significant differences between the tasks over the right hemisphere only (p = 0.021).

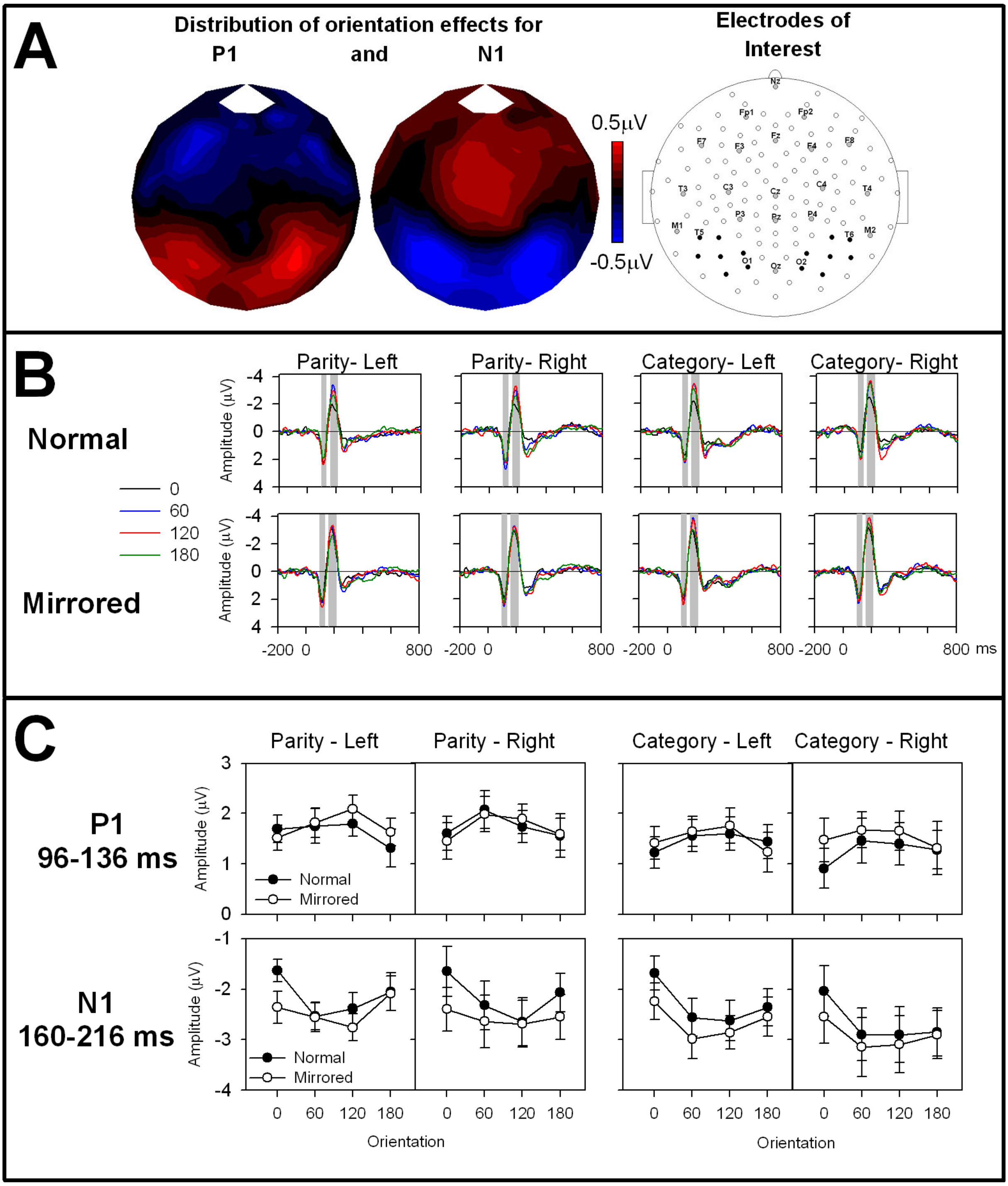

Figure 3.4: A distribution of orientation effects collapsed over trend component (linear and quadratic), stimulus version and task for the P1 and the N1 time windows of interest and the electrode cluster in reference to 10-20 system labels and the rest of the electrode montage. B: ERPs at the electrode clusters of interest as a function of task, stimulus version, orientation and hemisphere. Time windows of interest are shaded in grey. C. Mean amplitudes over the time windows of interest as a function of task, stimulus version, orientation and hemisphere. Error bars represent standard errors of the mean.

The main effect of orientation was significant ($F(3, 39) = 29.62$, $p < 0.001$, $\varepsilon = 0.994$), and could be attributed to significant linear ($F(1, 13) = 31.77$, $p < 0.001$, 21.19% variance explained) and quadratic ($F(1, 13) =50.71$, $p < 0.001$, 77.80% variance explained) trends. The modulation of the N1 is unlikely to reflect mental rotation because the amplitudes increase more for 60° and 120° orientations than for the 180°, and there is no difference between 60° and 120° orientations, conforming to a predominantly quadratic trend, and a smaller linear trend. Linear and quadratic trends are also evident in the RT function for parity judgements, but in that case, the linear trend is dominant, with a smaller quadratic contribution. The direction of the quadratic trend is also inconsistent with the mental rotation – the quadratic trend in mental rotation is characterised by smaller differences between 0° and 60°, than between 60° and 120°, and sharpest increases between 120° and 180° rotations. In contrast, the quadratic effect corresponds to large increase between 0° and 60°, no change between 60° and 120°, and then a dip between 120° and 180° orientations. Thus, these effects are unlikely to reflect mental-rotation related processing.

The main effect of stimulus version was also significant ($F(1, 13) = 40.66$, $p < 0.001$) and was characterised by larger N1 amplitudes in response to mirror-reversed stimuli than to normal stimuli. The version-by-orientation interaction was also significant ($F(3, 39) = 4$, $p = 0.018$, $\varepsilon = 0.887$) and could be attributed to significant increases in amplitudes with mirror-reversal for upright stimuli only ($p < 0.001$). The version-by-orientation interaction could be attributed to a significant interaction of the linear trend ($F(1, 13) = 17.98$, $p = 0.001$) which explained 71.32% of the interaction variance. This increase in amplitude with mirror-reversal for upright stimuli resulted in attenuation of the linear orientation effects for mirror-reversed characters, which accounted for 5.55% of variance, compared with the linear orientation effects for normal characters, which accounted for 33.03% of variance, although the linear trend was significant for both stimulus versions (mirrored: $F(1, 13) = 5.75$, $p = 0.032$, normal: $F(1, 13) = 32.24$, $p < 0.001$). Changes in orientation for both stimulus versions also conformed to significant quadratic trends (mirrored: F(1, 13) = 17.32, p = 0.001, 65.32 % variance explained; normal: F(1, 13) = 60.95, p < 0.001, 94.24 % variance explained).

Furthermore, there was a significant task-by-orientation interaction (F(3, 39) = 3.2, p = 0.046, ε = 0.796). Although the category task elicited larger N1 amplitudes than the parity task at all orientations, the significant differences were observed at 60° and 180° orientations, only. This pattern of results could be attributed to differential effect of stimulus orientation for the two tasks. Stimulus orientation effects could be attributed to significant linear (F(1,13) = 38.36, p < 0.001, 32.77% variance explained), quadratic (F(1,13) = 35.55, p < 0.001, 62.14% variance explained) and cubic (F(1,13) = 6.25, p = 0.027, 5.08% variance explained) trends for the category task, while the effects of orientation for the parity task were predominantly in terms of significant quadratic trend (F(1,13) = 34.78, p < 0.001, 90.98% variance explained), although the linear trend also approached significance (F(1,13) = 3.36, p = 0.09, 8.7% variance explained).

Although the task-by-version-by-orientation interaction did not reach significance, the plots in Figure 3.4 indicate that the effects of orientation were minimal for mirror-reversed characters in the parity task, while the effects of orientation were similar for normal and mirror-reversed characters for the category task. Normal characters for both tasks elicited larger amplitudes for the inverted, compared to upright characters, implying a presence of a linear trend for both tasks.

P2 effects

ERPs at electrodes of interest with P2 time-window shaded in grey are plotted in Figure 3.5 as are the average amplitudes over the time window as a function of task, character version and orientation. The main effect of orientation was significant (F(3, 39) = 27.47, p < 0.001, ε = 1). Significant two-way interactions between orientation and all other factors were also observed (orientation-by-hemisphere: F(3, 39) = 6.84, p = 0.001, ε = 1; task-by-orientation: F(3, 39) = 3.6, p = 0.022, ε = 1; version-by-orientation: F(3, 39) = 5.4, p = 0.004, e = 0.984), as was a significant three-way task-by-version-by-orientation interaction (F(3, 39) = 4.24, p = 0.013, ε = 0.946).

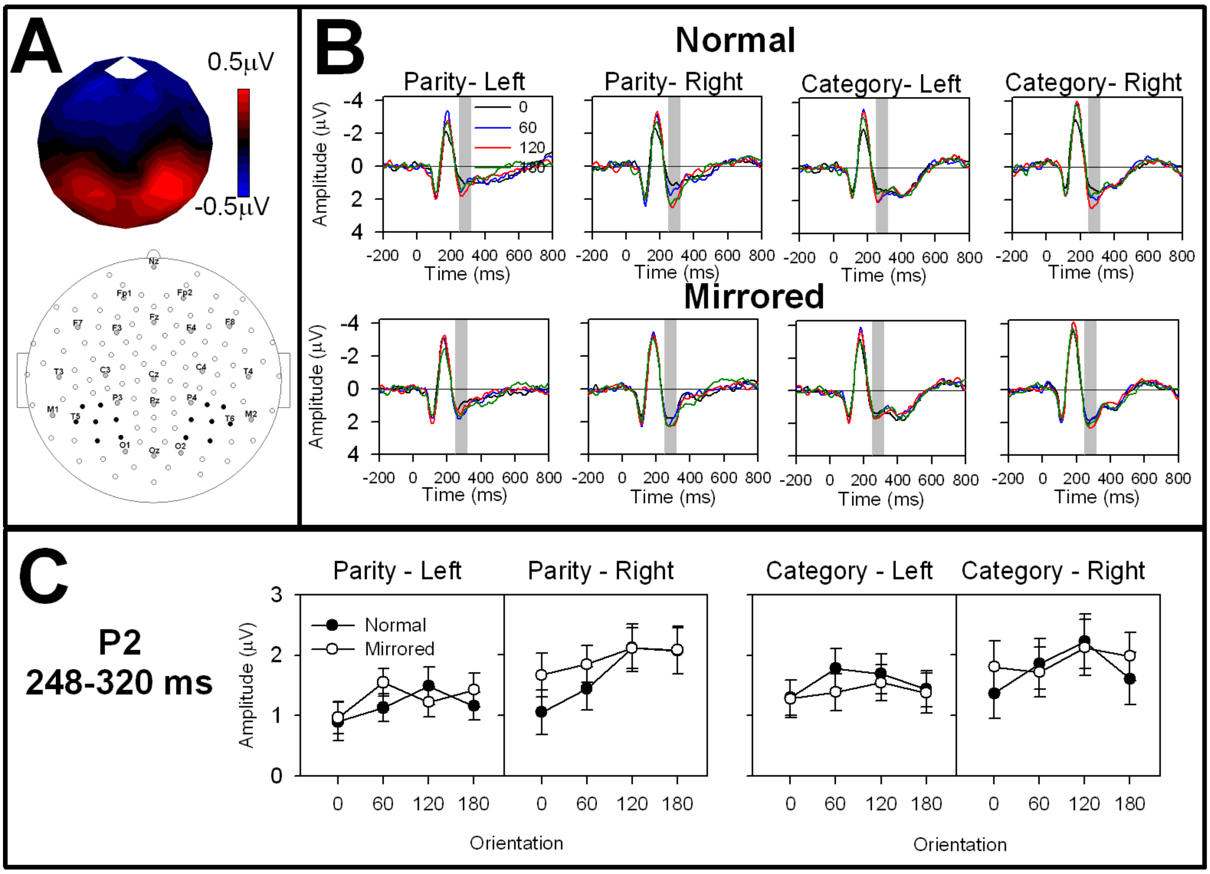

Figure 3.5: A distribution of orientation effects collapsed over trend component (linear and quadratic), stimulus version and task for the P2 time window of interest and the electrode cluster in reference to 10-20 system labels and the rest of the electrode montage. B: ERPs at the electrode clusters of interest as a function of task, stimulus version, orientation and hemisphere. Time window of interest are shaded in grey. C. Mean amplitudes over the time window of interest as a function of task, stimulus version, orientation and hemisphere. Error bars represent standard errors of the mean.

In order to characterise the three-way interaction, effects of character version and orientation on the other factors were examined. In terms of character version, significantly greater amplitudes were elicited by mirror-reversed than normal stimuli. This effect was observed for upright stimuli for both tasks, and for stimuli at 60° ($p \leq 0.033$) for the parity task only. No significant differences were observed between normal and mirror-reversed stimuli for stimuli presented at 120° and inverted stimuli ($p \geq 0.133$).

Simple effects of orientation were then examined. Significant orientation effects were observed for both tasks for both character versions (see Table 3.1). It would be useful to consider the magnitude of the effect size of the orientation effects. For both tasks, the orientation effect was stronger for normal characters ($\eta^2 \geq 0.530$) than for mirror-reversed characters ($\eta^2 \leq 0.346$). As indicated in Table 3.1, significant linear, quadratic, and cubic trends are evident for both tasks when normal stimuli are used. For mirror-reversed stimuli, orientation effects differed between the tasks in terms of constituent trend components. For the parity task, only the linear trend reached significance ($F(1, 13) = 21.04$, $p = 0.001$) and explained 70.08% of variance. For the category task, only the cubic trend reached significance ($F(1, 13) = 9.39$, $p = 0.009$) and explained 45.11% of the variance.

Table 3.1: Results for the simple effects of orientation as a function of task and stimulus version with the observed effect size (η^2).

Stimulus version	**Task** Parity	 Category
Normal	$F(3,39) = 14.961, p < 0.001, \varepsilon = 0.965, \eta^2 = 0.535$	$F(3,39) = 14.681, p = < 0.001, \varepsilon = 1, \eta^2 = 0.530$
- Linear	$F(1,13) = 34.71, p < 0.001, \eta^2= 0.728, 73.99\%$	$F(1,13) = 5.12, p = 0.041, \eta^2= 0.283, 10.6\%$
- Quadratic	$F(1,13) = 6.66, p = 0.023, \eta^2= 0.339, 15.48\%$	$F(1,13) = 29.24, p < 0.001, \eta^2= 0.692, 88.34\%$
- Cubic	$F(1,13) = 4.73, p = 0.049, \eta^2= 0.267, 10.53\%$	$F(1,13) = 0.62, p = 0.446, \eta^2= 0.045, 1.07\%$
Mirrored	$F(3,39) = 6.876, p = 0.001, \varepsilon = 0.993, \eta^2= 0.346$	$F(3,39) = 3.276, p = 0.031, \varepsilon = 0.992, \eta^2= 0.201$
- Linear	$F(1,13) = 21.04, p = 0.001, \eta^2= 0.618, 70.08\%$	$F(1,13) = 2.69, p = 0.125, \eta^2= 0.172, 42.4\%$
- Quadratic	$F(1,13) = 2.65, p = 0.127, \eta^2= 0.169, 18.17\%$	$(1,13) = 1.25, p = 0.284, \eta^2= 0.088, 12.49\%$
- Cubic	$F(1,13) = 2.7, p = 0.125, \eta^2= 0.172, 11.75\%$	$F(1,13) = 9.39, p = 0.009, \eta^2= 0.419, 45.11\%$

Nevertheless, in terms of percentage of variance explained and effect size, orientation effects differed between the tasks, even for normal stimuli. For the parity task, effects of orientation were predominantly linear for both the normal ($F(1, 13) = 34.71$, $p < 0.001$, $\eta^2= 0.728$, 73.99% variance explained) and mirror-reversed characters ($F(1, 13) = 21.04$, $p = 0.001$, $\eta^2= 0.618$, 70.08% variance explained). Both the quadratic ($F(1,13) = 6.66$, $p = 0.023$, $\eta^2= 0.339$, 15.48% variance explained) and the cubic ($F(1,13) = 4.73$, $p = 0.049$, $\eta^2= 0.267$, 10.53% variance explained) trends also reached significance for normal characters, but not for mirror-reversed characters (quadratic: $F(1,13) = 2.65$, $p = 0.127$, $\eta^2= 0.169$, 18.17% variance explained, cubic: $F(1,13) = 2.7$, $p = 0.125$, $\eta^2 = 0.172$, 11.75% variance explained). Therefore, for the parity task, largest effect and the largest proportion of variance explained could be attributed to the linear trend. The proportion of variance explained by the quadratic and the cubic trends was also comparable between the two character versions, even though these trend components reached significance for the normal characters, but not for the mirror-reversed characters.

For the category task, the effects of orientation for normal characters were best characterised in terms of a significant quadratic trend ($F(1, 13) = 29.24$, $p < 0.001$, $\eta^2 = 0.692$, 88.34% variance explained), with smaller contribution of a significant linear trend ($F(1, 13) = 5.12$, $p = 0.041$, $\eta^2 = 0.283$, 10.6% variance explained). The cubic trend did not reach significance ($F(1, 13) = 0.62$, $p = 0.446$, $\eta^2 = 0.045$, 1.07% variance explained). The effects were considerably different for mirror-reversed characters, whereby only the cubic trend reached significance ($F(1, 13) = 9.39$, $p = 0.009$, $\eta^2 = 0.419$, 45.11% variance explained) while the linear ($F(1, 13) = 2.69$, $p = 0.125$, $\eta^2 = 0.172$, 42.4% variance explained) and quadratic ($F(1, 13) = 1.25$, $p = 0.284$, $\eta^2 = 0.088$, 12.49% variance explained) trends did not.

As noted earlier, the orientation-by-hemisphere interaction was also significant. Simple effects of orientation were significant for both hemispheres although they were more pronounced over the right hemisphere ($F(3, 39) = 24.62$, $p < 0.001$, $\varepsilon = 1$, $\eta^2 = 0.654$) than over the left ($F(3, 39) = 10.97$, $p < 0.001$, $\varepsilon = 0.851$, $\eta^2 = 0.458$). Furthermore, the effects of orientation over the right hemisphere were best characterised in terms of a significant linear trend ($F(1, 13) = 39.67$, $p < 0.001$) which accounted for 66.17% variance, as well as significant quadratic ($F(1, 13) = 13.82$, $p = 0.003$, 20.26% variance explained) and the cubic trends ($F(1, 13) = 14.63$, $p = 0.002$, 13.57% variance explained). The effects of orientation over the left hemisphere were best characterised in terms of a significant quadratic trend ($F(1, 13) = 13.11$, $p = 0.003$) which accounted for 67.44% variance explained, and a significant linear trend (F(1, 13) = 13.67, p = 0.003) which accounted for 31.10% of variance. The cubic trend did not reach significance (F(1, 13) = 0.86, p = 0.37, 1.46% variance explained). This pattern of results indicates that effects of orientation were predominantly linear on the right, and quadratic on the left.

Although the P2 amplitudes were generally larger over the right than the left hemisphere, differences between the hemispheres were only significant for stimuli presented at 120° orientation (p = .047), although they also approached significance when the stimuli were inverted position (p = 0.075). A significant version-by-hemisphere interaction was also observed (F(1, 13) = 4.72, p = 0.049) and was characterised by larger P2 amplitudes in response to mirror-reversed characters, in comparison to normal characters, over the right hemisphere (p = 0.003), and no differences between normal and mirror-reversed characters over the left hemisphere (p = 0.835).

Bearing in mind that spatial topography of ERPs does not necessarily correspond to the localisation of the sources, this pattern of results indicates that the right hemisphere is more sensitive to stimulus misorientation with reference to the canonical position, as indicated by the more prevalent contribution of the linear trend. Not surprisingly then, the right hemisphere also showed stronger effects of stimulus version.

Summary of orientation effects on the early VEPs

In summary, changes in stimulus orientation initially elicit comparable effects for both tasks over the P1 time period. These early effects, characterised by an increase in amplitude in response to stimuli presented at oblique orientations, were distributed bilaterally over occipito-temporal electrodes with a distribution similar to that of the P1 component. Task-related orientation effects are observed as early as the N1 although both tasks elicited combined linear and quadratic modulation of the ERPs. This linear-quadratic combination reflects as larger increases in N1 amplitudes for stimuli presented at oblique orientations than those elicited by character inversion.

Further, the version-by-orientation interaction indicated that while the effects of orientation for normal characters was characterised as a combined linear and quadratic function, the effects of orientation for mirror-reversed characters were characterised by a quadratic function only. This observation reflects an increase in amplitude for mirror-reversed characters when the stimuli are presented at upright, and this increase in amplitude is comparable to the increase observed with inversion. This pattern of results is particularly interesting for two reasons. Firstly, it suggests that the effects of inversion on the N1 are comparable to those of mirror-reversal, and secondly it suggests that the effects of mirror-reversal attenuate with misorientation.

Effects of orientation over the P2 time window also differed between tasks and stimulus versions. For normal characters, the effects of orientation were predominantly linear for the parity task and quadratic for the category task, although both tasks elicited both types of effects. Character version had an effect on the amplitude of the P2, with larger P2 amplitudes in response to mirror-reversed stimuli. This effect of mirror-reversal was attenuated with increase in angular displacement from upright, resulting in an apparent attenuation of orientation effects for mirror-reversed characters.

For the parity task, this is reflected as larger differences between normal and mirror-reversed stimuli when the stimuli were presented at upright and 60° orientations than when the stimuli were presented at 120° and inverted orientations. In reference to the canonical, parity-defined, orientation, mirror-reversed characters are also misoriented. The apparent attenuation of orientation effects on the P2 component corresponds to an increase in P2 amplitude with mirror-reversal at smaller angular departures from upright. On the other hand, mirror-reversed and normal stimuli elicit comparable P2 amplitudes, for larger angular orientations. This pattern of results is suggestive of P2 sensitivity to misorientation from a canonical orientation – irrespective of whether the misorientation is due to rotation in the picture plane or a flip out of the picture plane. Furthermore, this patters of results indicates that for large rotations in the picture plane, normal and mirror-reversed stimuli may become less differentiable – a possible reason for why mental rotation to a canonical upright is needed prior to parity-discrimination. For the category task, where character version was of no importance, the differences were larger at vertical orientations (upright and inverted) than at the oblique orientations (60° and 120° orientations), possibly due to a "dip" in the P2 amplitude when *normal* characters were presented at 180° orientation. Therefore, the task specificity over the P2 component was manifested as different patterns of orientation effects for these two tasks, while the task specificity of the orientation effects over the N1 component was manifest as an attenuation of orientation effects for the parity task.

Effects of orientation on the P2 component differed between the hemispheres. Firstly, effects of orientation were larger over the right than over the left hemisphere. Secondly, the effects of orientation on the left were best characterised by a quadratic function, while the effects of orientation on the right reflected predominantly linear increases in P2 amplitudes, although quadratic modulation was also observed.

Late parietal complex effects

The effects of orientation over the LP component were analysed separately for the two tasks since the linear changes associated with the parity task extend beyond the actual response period during the category task.

Category task

Figure 3.6 illustrates the GFP and microstate plots for the linear and quadratic trends associated with normal and mirror-reversed stimuli during the category task. These plots show that linear and quadratic trends may be apparent for mirror-reversed stimuli during two consecutive time periods, with linear effects starting at 340 ms and lasting till approximately 400 ms and quadratic effects starting at 400 ms and lasting for 80 ms, till 480 ms. The ERPs over the parietal leads also seem to show modulation with orientation for mirror-reversed characters, but not the normal ones.

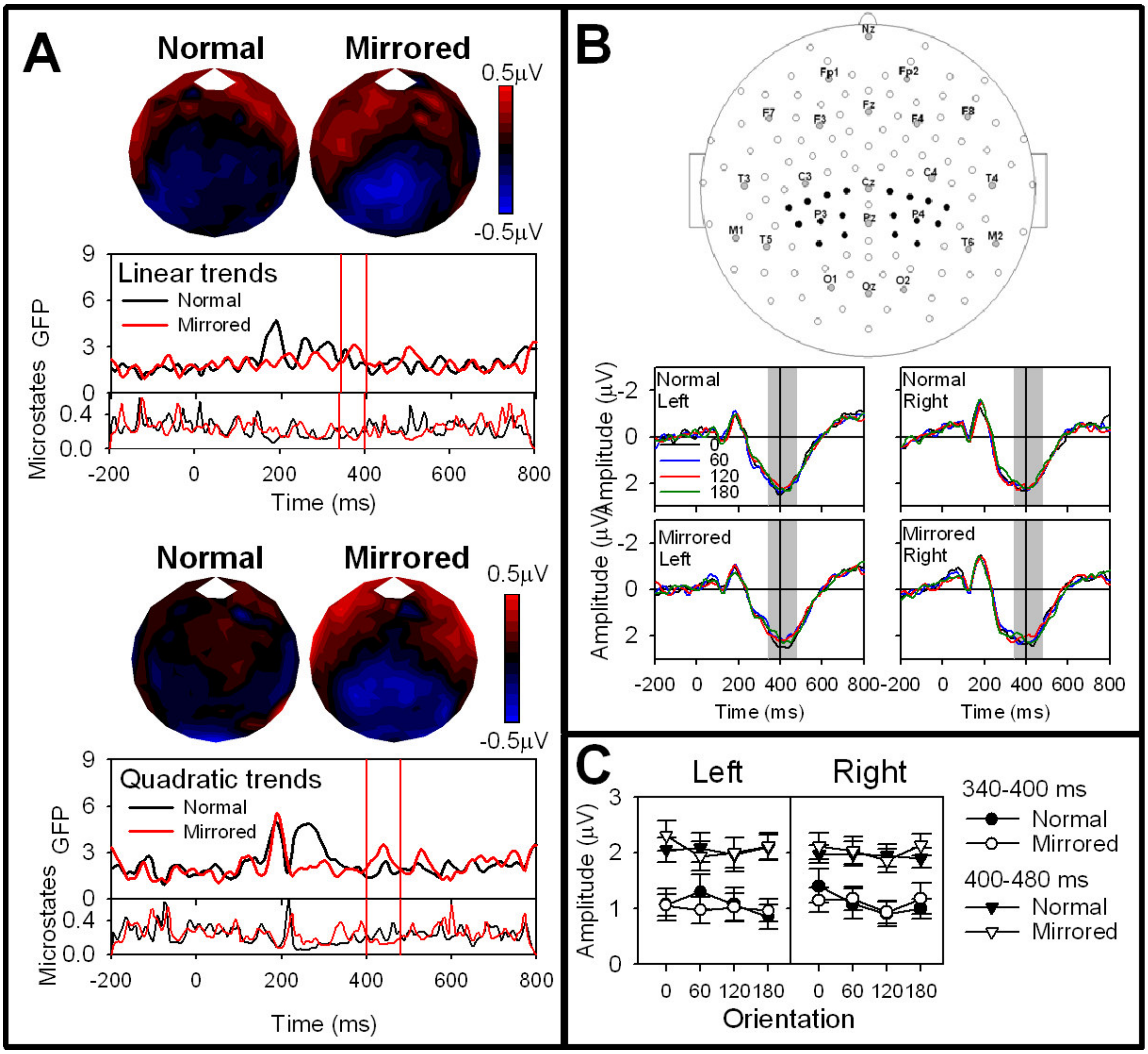

Figure 3.6: Late-parietal effects in the category task. A: GFP and microstate plots for linear and quadratic orientation effects for normal and mirror-reversed characters and the topographic distribution of linear effects over the time window of interest. B: Distribution of electrode clusters of interest in reference to the whole net montage and ERPs at clusters of interest as a function of version and orientation for the parity task. Time windows of interest are shaded in grey. C: mean amplitudes over the time window of interest as a function of time window, stimulus version, orientation and hemisphere. Error bars represent standard errors of estimates.

Since linear and quadratic trends were evident in consecutive time periods, the effects of stimulus orientation and version were examined while taking time window as a factor. The effects of version, orientation and hemisphere were examined with a four-way 2x2x4x2 repeated measure ANOVA, with time, version, orientation and hemisphere as factors and

Huynh-Feldt ε value was used for correction of sphericity violation (Huynh & Feldt, 1976). Average amplitudes over the time windows of interest are plotted as a function of time, character version, hemisphere and orientation in Figure 3.6 part C. The main effect of time window was significant (F(1, 13) = 15.79, p = 0.002), with larger amplitudes over the 400-480 ms time window, than over the 340-400 ms time window. The only other significant effect was a three-way version-by-orientation-by-hemisphere interaction (F(3, 39) = 3.13, p = 0.045, ε = 0.862). Significant effects of stimulus version were observed over the left hemisphere only, and only when characters were presented at 60° orientation (p = 0.018), with larger amplitudes in response to normal than mirror-reversed characters. No other significant differences were observed. And no significant simple effects of orientation for either stimulus version over either hemisphere were significant (see Table 3.2).

Table 3.2: Results for the simple effects of orientation as a function of stimulus version and hemisphere for the category task.

Hemisphere	**Stimulus version**	
	Normal	Mirrored
Left	F(3,39) = 1.34, p = 0.279, ε = 0.840	F(3,39) = 1.74, p = 0.181, ε = 0.908
Right	F(3,39) = 1.89, p = 0.155, ε = 0.888	F(3,39) = 2.68, p = 0.060, ε = 1

Parity task

For the parity task, linear increase in parietal negativity over a later time period between approximately 400 and 800 ms is thought to index mental rotation (Heil, 2002; Peronnet & Farah, 1989; Wijers *et al.*, 1989). Two clusters of parietal electrodes – one over each hemisphere – were selected and ERPs over these electrode clusters are plotted in Figure 3.7. The typical linear increase in parietal negativity –associated with mental rotation – is evident in the ERP plots. The GFP and microstate plots of the linear trends associated with normal and mirror-reversed stimuli during the parity task are also plotted in Figure 3.7 and the topographic distribution of the linear increases indicates that the effects are indeed distributed over the parietal region.

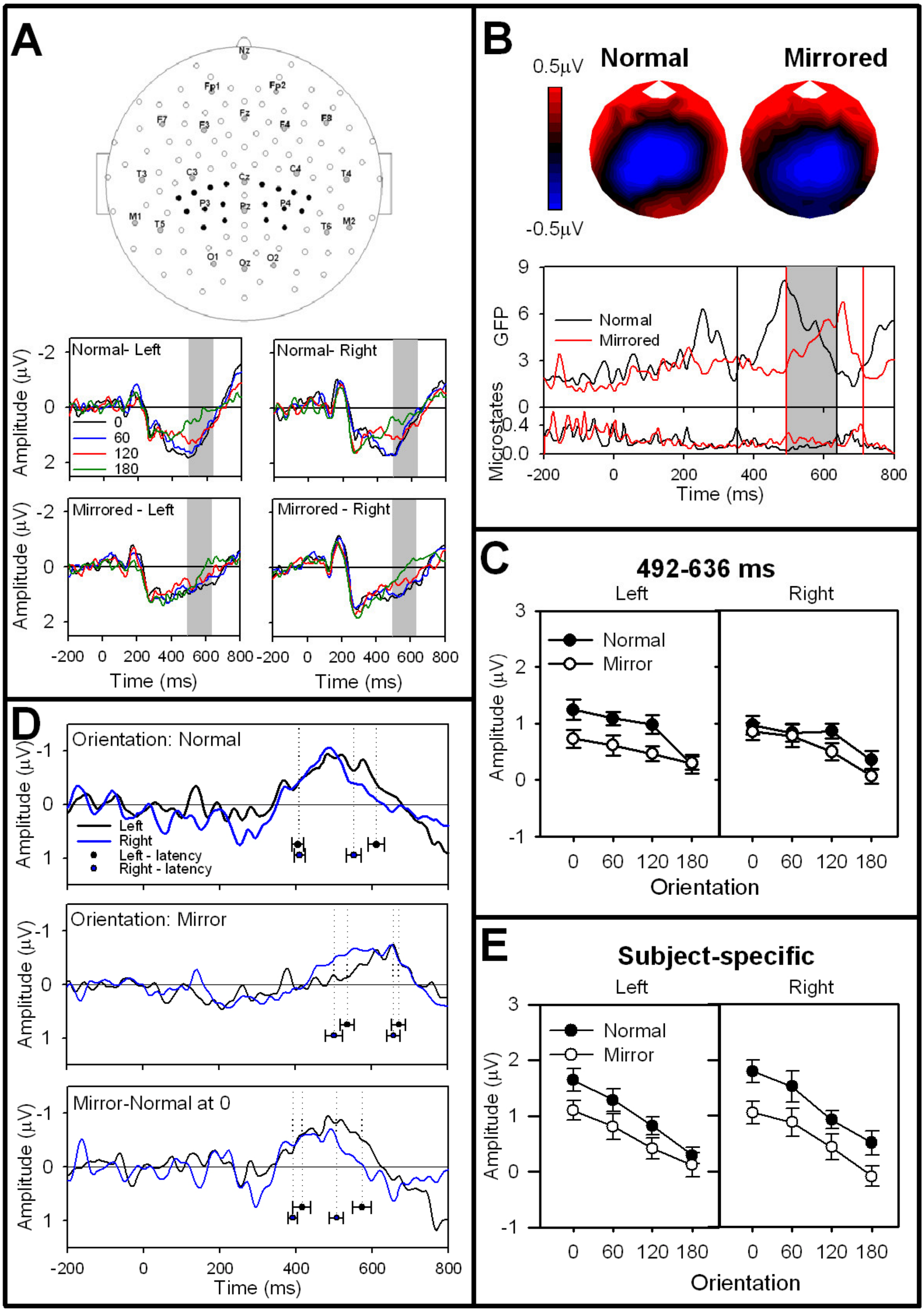

Figure 3.7: Late-parietal effects in the parity task. A: Distribution of electrode clusters of interest in reference to the whole net montage and ERPs at clusters of interest as a function of version and orientation for the parity task. B: GFP and microstate plots for linear orientation effects for normal and mirror-reversed characters and the topographic distribution of linear effects over the time window of interest (shaded in grey). C: mean amplitudes over the time window of interest as a function of stimulus version, orientation and hemisphere. Error bars represent standard errors of estimates. D: Waveforms represent linear effects of orientation for normal and mirror-reversed characters and difference between mirror-reversed and normal characters at 0° orientation as a function of hemisphere. Scatter plots represent mean latency, with standard errors, of onsets and offsets of these effects. E: Mean amplitudes over parietal electrodes of interest as function of stimulus version, orientation and hemisphere. Time windows were based on subject-specific duration of linear orientation effects.

The linear increases in parietal negativity are evident over two partially overlapping time periods for normal and mirror-reversed stimuli. For normal stimuli, the time period which shows linear increases in parietal negativity spans between 356 and 636 ms, while for mirror-reversed stimuli, this time period begins considerably later, at about 492 ms and lasts until 712 ms after stimulus onset. As proposed by Hamm *et al.* (2004), an interpretation for this time delay, and similarly for the overall, orientation-independent, increase in RTs in response to mirror-reversed stimuli, may be that mirror-reversed stimuli also elicit mental rotation out of the picture plane to restore the stimulus to its normal version. In order to examine effects of orientation, it seemed reasonable to select a time period that encompassed linear increases in parietal negativity for both stimulus versions. A single time period, spanning between 492 ms and 636 ms was, therefore, chosen for this analysis. Mean amplitudes over this time period were then analysed in a 2x4x2 repeated measures ANOVA with stimulus version, orientation and hemisphere as factors.

The main effects of version ($F(1, 13) = 9.40$, $p = 0.009$) and orientation ($F(3, 39) = 18.31$, $p < 0.001$, $\varepsilon = 0.955$) were significant. The orientation effects were characterised by a significant linear trend ($F(1, 13) = 43.25$, $p < 0.001$) which accounted for 88.46% of the variance. The version-by-orientation-by-hemisphere interaction ($F(3, 39) = 7.32$, $p = 0.001$, $\varepsilon = 1$) was also significant. Pair-wise comparisons indicated that significant differences between the hemispheres were evident only for normal, upright, stimuli ($p = 0.030$), with larger amplitudes over the left hemisphere. Additionally, differences between mirror-reversed and normal stimuli were evident over both hemispheres for stimuli presented at 120° ($p \leq 0.013$), and over the left hemisphere only when the stimuli were presented at 60° orientation ($p = 0.014$). Simple effects of orientation were evident for both stimulus types over both hemispheres and in each case, the effects of orientation, could be attributed to a significant linear trend, although the effects of orientation for normal characters also consisted of a significant cubic trend on the left and a significant quadratic trend on the right (see Table 3.3).

It is also noteworthy that the effect of orientation was larger on the left ($\eta^2 = 0.454$) than the right ($\eta^2 = 0.267$) for normal characters, while for mirror-reversed characters the opposite was true, with larger orientation effects over the right ($\eta^2 = 0.434$) than the left ($\eta^2 = 0.264$).

Table 3.3: Results for the simple effects of orientation as a function of stimulus version and hemisphere for the parity task.

Hemisphere	**Stimulus version**	
	Normal	Mirrored
Left	$F(3,39) = 10.79$, $p < 0.001$, $\varepsilon = 0.746$, $\eta^2 = 0.454$	$F(3,39) = 4.674$, $p = 0.007$, $\varepsilon = 0.980$, $\eta^2 = 0.264$
- Linear	$F(1,13) = 15.57$, $p = 0.002$, $\eta2 = 0.545$, (82.47%)	$F(1,13) = 9.03$, $p = 0.01$, $\eta^2 = 0.41$, (99.4%)
- Quadratic	$F(1,13) = 4.2$, $p = 0.061$, $\eta^2 = 0.244$, (13.79%)	$F(1,13) = 0.1$, $p = 0.756$, $\eta^2 = 0.008$, (0.55%)
- Cubic	$F(1,13) = 5.43$, $p = 0.037$, $\eta^2 = 0.295$, (3.74%)	$F(1,13) = 0.01$, $p = 0.921$, $\eta^2 = 0.001$, (0.05%)
Right	$F(3,39) = 4.74$, $p = 0.010$, $\varepsilon = 0.846$, $\eta^2 = 0.267$	$F(3,39) = 9.96$, $p < 0.001$, $\varepsilon = 0.823$, $\eta^2 = 0.434$
- Linear	$F(1,13) = 6.36$, $p = 0.025$, $\eta^2 = 0.329$, (73.98%)	$F(1,13) = 23.43$, $p < 0.001$, $\eta^2 = 0.643$, (91.67%)
- Quadratic	$F(1,13) = 6.02$, $p = 0.029$, $\eta^2 = 0.317$, (15.66%)	$F(1,13) = 1.65$, $p = 0.221$, $\eta^2 = 0.113$, (8.29%)
- Cubic	$F(1,13) = 1.51$, $p = 0.241$, $\eta^2 = 0.104$, (10.37%)	$F(1,13) = 0.03$, $p = 0.857$, $\eta^2 = 0.003$, (0.04%)

An orientation-by-hemisphere interaction was then also examined for each stimulus type separately, and significant interactions were observed for both normal ($F(3, 39) = 3.17$, $p = 0.003$, $\varepsilon = 1$) and mirror-reversed characters ($F(3, 39) = 4.01$, $p = 0.015$, $\varepsilon = 0.975$). This pattern of results suggests that mental rotation of normal characters is predominantly subserved by the left hemisphere, while the mental rotation of mirror-reversed characters is predominantly subserved by the right hemisphere. This interpretation would indicate that hemispheric asymmetries are dependent on stimulus type, and thus, by inference, would indicate that stimulus parity is known prior to the onset of mental rotation itself. If this is indeed the case, one may wonder why mental rotation would be necessary if parity is already known. An alternative explanation is that the observed hemispheric asymmetries reflect a change in hemispheric dominance over time. That is, left hemispheric dominance is associated with the later phase of orientation-dependent increases in negativity for normal characters, and the right hemispheric dominance is observed over an earlier phase of orientation-dependent increases in negativity for mirror-reversed characters.

To investigate this possibility, linear-trend ERP waveforms for both stimulus versions were plotted and superimposed for the left and the right hemispheres (see Figure 3.7 part D). It is obvious from this figure that, for normal characters, the onset of the linear increases is comparable between the hemispheres, but that the return to baseline occurs later over the left than the right hemisphere. For mirror-reversed characters, the linear increases appear earlier over the right than the left hemisphere, and return to baseline around the same time. As noted earlier, mirror-reversed characters may elicit an additional rotation component, a “flip” out of the picture plane. If this is the case, parity judgements of mirror-reversed stimuli at upright would also elicit increases in parietal negativity when compared with normal characters. The difference between normal and mirror reversed characters is also plotted in Figure 3.7, and it appears that the onset of the increase in negativity is similar between the left and the right hemisphere, but that the return to baseline occurs earlier over the right hemisphere than the left hemisphere.

To test this observation statistically, the beginning and end of linear effects for normal and mirror-reversed characters, and the difference between normal and mirror-reversed characters at upright, were estimated over the left and the right hemispheres for each subject individually. This was done by selecting peak amplitude within a time period between 340 and 600 ms for normal characters, 400 to 700 ms for mirror-reversed characters and between 280 and 600 ms for the difference between normal and mirror-reversed characters. The onset of the effects was defined as the earliest time point at which the amplitude of the effects exceeded 20% of the peak amplitude and the offset was defined as the last time point for which the effects were greater than the 20% of the peak amplitude within a continuous time period. The time period was deemed non-continuous if it was disrupted for more than three consecutive sample points (corresponding to duration over 12 ms). Demarcation points were successfully obtained for all fourteen participants and all three effects of interest.

The data were then analysed in a 3x2x2 repeated measures ANOVA, with comparison of interest (orientation effects for normal characters, orientation effects for mirror-reversed characters and difference between normal and mirror-reversed characters), onset/offset and hemisphere as within subject factors.

The main effects of comparison ($F(2, 26) = 51.86$, $p < 0.001$, $\varepsilon = 1$), hemisphere ($F(1, 13) = 10.34$, $p = 0.007$) and onset/offset ($F(1, 13) = 275.50$, $p < 0.001$) were significant. The onset/offset-by-hemisphere interaction was also significant ($F(1, 13) = 4.90$, $p = 0.045$), as was the three-way interaction involving all of the factors ($F(2, 26) = 7.10$, $p = 0.007$, $\varepsilon = 0.811$). Pair-wise comparisons were then examined to assess whether there were hemispheric differences for the onsets and offsets for orientation effects associated with normal and mirror-reversed characters and the difference between normal and mirror-reversed characters at upright. The onset of the linear increases evoked by the mirror-reversed stimuli occurred significantly earlier over the left hemisphere ($p = 0.028$), while no significant differences between the hemispheres were observed for the onsets of linear increases in negativity evoked by the normal stimuli ($p = 0.693$) or for the onsets of the mirror-normal differences ($p = 0.219$). On the other hand, significantly later offsets were observed over the left hemisphere, compared with the right hemisphere, for both the linear increases evoked by normal stimuli ($p = 0.001$) and the mirror-normal difference ($p = 0.008$), but not for the linear increases evoked by the mirror-reversed stimuli ($p = 0.418$). This pattern of results confirms the observations made above.

Furthermore, the onsets of linear increases evoked by the normal stimuli and of mirror-normal difference did not differ over either the left or the right hemisphere ($p \geq 0.355$) and both occurred earlier than the linear increases evoked by the mirror-reversed stimuli for both hemispheres ($p > 0.001$). The offsets of linear increases evoked by the normal stimuli and of mirror-normal difference also occurred earlier than the linear increases evoked by the mirror-reversed stimuli ($p \leq 0.027$). The offsets of rotation effects evoked by normal stimuli and the mirror-normal difference differed significantly over the right hemisphere ($p = 0.004$), but not the left ($p = 0.109$), with earlier offset for the mirror-normal difference on the right, indicating that the "flip" out of the picture plane can be performed faster than the 180° rotation within the picture plane, which is also evident from the RT data.

It is also noteworthy that during the "on" state, the amplitudes of the effects of interest do not appear to differ between the two hemispheres. In order to assess this statistically, mean amplitudes were calculated within the time periods that showed linear increases in negativity evoked by normal and mirror-reversed stimuli. These time periods were based on the onsets and offsets for each subject, stimulus version and hemisphere separately, as outlined above. The mean amplitudes were then analysed in a 2x4x2 repeated measures ANOVA with version, orientation and hemisphere as factors. The main effect of orientation was highly significant ($F(3, 39) = 60.69$, $p < 0.001$, $\varepsilon = 0.811$) and consisted of a significant linear trend ($F(1, 13) = 235.35$, $p < 0.001$) which accounted for 98.83% of the variance. Significant main effect of character version ($F(1, 13) = 27.64$, $p < 0.001$) was observed, with larger positive amplitudes evoked by normal stimuli at all orientations, as illustrated in Figure 3.7. Most notably, there were no significant differences between the hemispheres ($F(1, 13) < 1$), or interactions between version and hemisphere ($F(1, 13) = 2.81$, $p = 0.118$), orientation and hemisphere ($F(3, 39) < 1$, $\varepsilon = 0.879$) version, orientation and hemisphere ($F(3, 39) = 1.21$, $p = 0.318$, $\varepsilon = 1$). These results confirm the observation that there are no differences between the hemispheres in terms of the amplitudes of linear increases in parietal negativity.

The results presented in this section indicate that mental rotation, both in the picture plane and out of the picture plane, recruits both hemispheres at a similar time period.

However, mental rotation appears to be performed more quickly, and therefore more efficiently, by the right hemisphere. This conclusion is based on the difference in the duration of the effects between the left and the right hemisphere for normal characters and for mirror-normal effects at upright, and the difference in the onset of the effects for mirror-reversed characters[7]. These results are particularly noteworthy because they may offer an account for the apparent discrepancies in literature regarding hemispheric dominance for mental rotation.

Discussion

The contribution of this study is two-fold. Firstly, it presents evidence that the ERP correlates of early visual processing, investigated in terms of the P1, N1 and P2 ERP components, show orientation-specificity. Secondly, the findings suggest that the hemispheric differences in mental rotation may be related to the relative speed at which each hemisphere carries out the operation.

Early visual processing

In this study, the ERP correlates of early visual processing were represented by the P1, N1 and the P2 components. The effects of orientation on both category and parity judgements were manifest in terms of increases in amplitude with stimulus misorientation over the P1, N1 and P2 components. These effects were present for both category- and parity-judgement tasks, suggesting that they had to do with perception or recognition of the stimuli, and not with processes to do with mental rotation.

The earliest component to be investigated was the P1. The orientation for this component was best characterised by a quadratic function with larger P1 amplitudes in response to stimuli presented at oblique orientations (±60° and ±120°) than to stimuli

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[7] If upright mirror-reversed characters are rotated out of the picture plane into alignment with a canonically oriented template, then, at early stages of the process, both upright and rotated mirror-reversed characters would show evidence of mental rotation. The characteristic mental-rotation ERP effects would be evident between rotated and upright mirrored characters only once the mental rotation of upright mirrored characters is finished.

presented at the vertical orientations (upright and inverted). Since no difference was observed between upright and inverted stimuli, the effect of orientation on the P1 could be related to the oblique effect described in Chapter 1. Li and Westheimer (1997) suggested that perception of shape orientation is based on the principal axis of elongation rather than orientation of the parts of the shape. If this is the case then it follows that both the upright and inverted stimuli would have the same perceived – vertical – orientation.

This can only be the case if the perception of shape orientation occurs prior to object recognition since the discrimination between the upright and the inverted orientation would be dependent on identification of the direction of the top and bottom of the stimulus. In order to recognise which part of the stimulus is the top of the object, one must firstly know what the object is. Therefore, one must first recognise an object and then determine its orientation. The same reasoning applies to discrimination between stimuli rotated by 60° and 240° or by 300° and 120° in the clockwise direction from upright. As mentioned in Chapter 1, Corballis *et al.* (1978) showed that RTs to name letters are shorter than RTs to identify their orientations, indicating that object recognition precedes object-orientation recognition. It is conceivable that stimulus orientation is initially extracted based on the orientation of the principal axis of elongation, and then, following object recognition, top-bottom direction can be "superimposed" on the orientation of the shape. If this is the case, then the effect of stimulus orientation on the P1 component may reflect the first instance of orientation perception based on a principal axis of shape elongation.

It seems reasonably certain that the orientation effects on the P1 component are not related to object recognition. Firstly, no difference was observed between upright and inverted stimuli, indicating that the top and the bottom of the stimuli have not been differentiated. Secondly, the P1 component is not sensitive to object type. Rossion *et al.* (2000) showed that while distinct classes of objects, such as cars, houses and faces evoked different N1 amplitudes, no effect of object class was apparent over the P1. Therefore, the orientation-specificity of the P1 component must reflect perceptual processing preceding object recognition. This may either be related to perception of orientation or a flow-on effect from a disruption of lower-level visual processing related to the oblique effect.

The second component investigated was the N1. The effect of orientation on the amplitude of this component was characterised as an increase with misorientation, but the increase was smaller for inverted stimuli than for most other orientations. These results replicate findings from a previous mental-rotation study by Milivojevic, Johnson et al. (2003). Despite the fact that these authors attributed the N1 effects to stimulus "obliqueness", the increase in response to the inverted stimuli, albeit smaller than that observed with the stimuli at intermediate orientations, brings this interpretation in question. It is important to note here that the amplitude of the N1 can be used to differentiate between upright and inverted stimuli.

The results also showed that mirror-reversal and inversion increased the N1 response by about the same amount. Given that alphanumeric characters have a clear canonical orientation both for the left-right and top-bottom axes, these results suggest that mirror-reversal and inversion have a similar effect on neural processing. It is also of note that mirror-reversed characters do not elicit responses that differ from those to normal characters when the characters are presented upside-down. This is particularly important because it suggests that parity information is lost with inversion, which in turn supports the notion that decisions based on parity information, such as left-right or mirror-normal judgements, would require mental transformation to the upright.

There is some evidence to suggest that N1 amplitude reduces with repeated presentation of a specific view of a particular object (Schendan & Kutas, 2003). It may be of note that clockwise and counter-clockwise rotations were treated as equivalent. Therefore, there were twice as many trials in which stimuli were at upright or upside-down than at any of the other orientations (e.g. rotated by 60° in clockwise direction). It is possible that this method resulted in overexposure to the inverted stimuli. However a similar pattern, with larger increases in N1 amplitude for stimuli rotated by ±60° and ±120° than for upside-down stimuli was observed by Milivojevic, Johnson *et al.* (2003). In this study, it was intended that the letters presented at upright and upside-down would be presented twice as often as letters at 60°, 120°, 240° and 300°, since the 60° and 120° orientations were to be treated as equivalent to 300° and 240°, respectively. However, due to a programming error which was not discovered until after completion of the data collection, the letters at 120° orientations were presented twice as often as the letters at 60°, 180°, 240° and 300° orientations. This resulted in 60:60:90:30 presentations for 0°, 60°, 120° and 180° orientations, respectively. Therefore, if the misoriented character N1 amplitude is specifically related to within-experiment presentation frequency**,** the pattern observed by Milivojevic, Johnson *et al.* (2003) should have been different from the results from the current study, and we should have seen a “dip” around 120° orientation, rather than the observed “dip” when the stimuli were upside-down. This suggests that the dip at 180° was indeed a function of inversion, and not of frequency of presentation.

There is convincing evidence that the N1 component reflects object recognition. Firstly, as mentioned earlier, distinct classes of objects, such as cars, houses and faces evoked different N1 amplitudes (Rossion *et al.*, 2000). Secondly, cortical-surface VEP recordings indicate that the maximal N1 responses to different stimulus classes (faces, objects, letter-strings etc.) originate from adjacent, but non-overlapping cortical regions (Allison *et al.*, 1999). This characteristic is probably related to the observation that some classes of objects, most notably faces and houses but also alphanumeric characters (Polk & Farah, 1998), elicit larger neural activation than other object classes within specific subregions of the ventral visual stream.

Additionally, N1 amplitude and latency have been shown to increase with stimulus inversion, and is thought to reflect a disruption of configural object processing (Rebai *et al.*, 2001; Rossion *et al*., 2000). Although the effects of stimulus inversion on the amplitude and the latency of the N1 are best documented with face stimuli (e.g. Rossion *et al*., 2000), there is some evidence that indicates that the amplitude of the N1 also increases with inversion of complex objects such as cars (Rebai *et al*., 2001), although in that particular study cups did not elicit comparable effects.

However, it is still unclear whether the N1 is the EEG correlate of object recognition or of perceptual encoding of the stimulus (see Pernet *et al*., 2003). Pernet *et al*. (2003) argued that the N1 does not mark object recognition in the sense of matching to a long-term memory representation; rather the N1 should be thought of representing a generation of a stimulus-driven mental representation which could then be compared to a mental representation stored in long-term memory. This interpretation would suggest that the N1 increase with stimulus misorientation is not an effect of increased difficulty with character recognition, but that it reflects increased lower-level visual processing demands.

If this is the case, then the larger N1 amplitude evoked by the stimuli whose principal axis is not aligned to the upright characters is related to a flow-on effect of earlier cortical processing. The results indicated that the obliquely presented stimuli elicited greater P1 amplitudes than the upright or inverted stimuli. This increase in processing may have resulted in increased processing demands at the subsequent processing stage reflected by the N1.

This explanation would certainly account for the increase in the amplitude associated with stimuli at ±60° and ±120°. This explanation, however, does not account for the difference observed between upright and inverted stimuli, or the difference observed between normal and mirror-reversed stimuli at upright. It is possible that multiple, and distinct, neural processes are responsible for the orientation effects observed over this component. One mechanism may reflect a flow-on effect of earlier cortical processing, while another may reflect an increase in amplitude related to visual processing of objects at non-canonical orientations. If these effects are additive, then an increase in amplitudes may be observed for all misoriented characters, with an additional increase for characters presented at oblique orientations.

It is of note that in the study by Pernet *et al.* (2003) participants passively viewed the stimuli, and no explicit recognition or categorisation task was administered during the EEG recording. Given that the tasks in this study required character recognition, it is plausible that the task-demands elicited earlier object recognition effects than the non-speeded passive-viewing conditions (see Pernet et al., 2003 for a similar interpretation).

The P2 was the third part of the VEP complex investigated. The results from the current study indicate that the P2 amplitude may be important in differentiating the parity and the category tasks. For both tasks, a linear increase in P2 amplitude was associated with angular orientation from 0° to 120°. For the parity task, the amplitude for 120° and 180° stimuli were comparable, while for the category task the amplitude decreased for the stimuli presented at 180°. It is also of note that in the parity task, the amplitude of the P2 was larger for mirror-reversed than for normal characters at both upright and 60° orientation for the parity task. This is an important observation because it indicates that the cognitive processes marked by the P2, at least in the parity task, provide information regarding stimulus orientation primarily in reference to the canonical position, i.e. normal, upright characters. It is possible, therefore, that the modulation of the P2 amplitude in the parity task reflects recognition of the degree of stimulus misorientation with respect to the canonical stimulus orientation, which may be a necessary step prior to mental transformation.

If this is the case, then the modulation of P2 amplitude for the category task may also index the recognition of stimulus orientation. Orientation perception in this case may depend on both the top-bottom axis inversion and any additional changes in orientation, such as a tilt away from the top-bottom axis. Amplitude increase would be characterised by an increase with inversion in addition to an increase with misalignment of the top-bottom axis from the vertical. Although no behavioural correlates of these effects were observed with the current stimulus set consisting of overlearned alphanumeric characters, this interpretation would fit well with the observation that recognition of stimuli may be easier when the stimuli are inverted than when the stimuli are presented at orientations around the 120° point.

The results, therefore, indicate that the task-specific orientation effects begin prior to the beginning of mental rotation, and are concurrent with the P2 ERP component. The shape of the orientation-related functions differed between tasks, with linear modulation associated with the parity task, and a combination of linear and quadratic effects for the category task. The shape of the orientation-effects for the category task may be related to the 'M'- shaped function commonly associated with orientation-dependent object-identification performance (e.g. Jolicoeur, 1985).

Linear modulation of neural activity was hypothesised to relate to mental rotation. Although linear increases of P2 amplitudes were observed, the direction of this effect was opposite to the effects commonly associated with mental rotation. The effects on the P2 had similar distribution and temporal characteristics as those reported previously (Muthukumaraswamy et al., 2003). However, orientation-dependence of this component has not been reported previously for parity-judgement tasks.

The functional properties of the P2, unlike those of the N1, are not well understood. It seems reasonable to assume that it has to do with perception of orientation. As noted earlier, both empirical evidence (Corballis et al., 1978; DeCaro, 1998; DeCaro & Reeves, 2002) and logic suggest that perception of object orientation should follow object recognition. Nevertheless I also suggested that an early, pre-recognition sense of orientation might be extracted from the orientation of the principal axis of elongation, and reflected in the P1 component. A full understanding of orientation, following object recognition, might then require top and bottom to be "superimposed" on this initial impression. If this is the case, then the effect of stimulus orientation on the P2 component may reflect the second step in orientation perception based on mapping of object identity on the principal axis of shape elongation.

Furthermore, the orientation effects on the P2 component were right lateralised. Therefore, these results suggest that the right hemisphere is more responsive to stimulus orientation, which may depend on holistic or configural processing of the stimulus. In contrast, the left hemisphere may not be as responsive to stimulus orientation because it uses feature-based recognition mechanisms. Milivojevic, Clapp *et al.* (2003) suggested that the P2 may reflect configural processing. In a study that investigated effects of thatcherisation on upright and rotated faces it was found that the effects of thatcherisation on the P2 component linearly decreased as a function of face orientation. It has also been suggested that face recognition based on configural information deteriorates as a linear function of face orientation (Collishaw & Hole, 2002). The linear decrease shown for face recognition and thatcherisation led Milivojevic, Clapp *et al.* (2003) to speculate that the P2 reflects configural processing. If this is an accurate interpretation, then lateralisation of P2 effects could reflect right-hemispheric specialisation for holistic encoding.

Mental rotation

Behavioural results and the ERP analysis indicated that mental rotation was elicited by the parity task. There was no evidence that mental rotation was elicited by the category task. The ERP effects of mental rotation were manifest in terms of a reduction in parietal positivity between 350 and 700 ms which in this context is interpreted as an increase in a latent negative component, temporally coincident, but functionally independent from the P3 associated with stimulus recognition. These results fit well with the previous findings in this area (Heil, 2002).

Furthermore, this study replicates the findings by Hamm *et al*. (2004) that, subsequent to mental rotation within the picture plane to the upright, mirror-reversed characters are then flipped out of the picture plane, into alignment with the canonical parity-defined position. This conclusion is supported by two observations. Firstly, compared with upright normal characters, upright mirror-reversed characters elicit a negative-going deflection over the parietal leads. This negative going deflection follows the same temporal and spatial characteristics of the ERP correlates of the mental rotation. Secondly, mental-rotation ERP component for mirror-reversed characters is temporally delayed compared to the one observed for normal characters, because when the upright mirror-reversed characters are used as a baseline, the initial mental rotation stages are shared between upright and rotated mirror-reversed characters. The mental rotation component for mirror reversed characters also lasts longer than that for normal characters, thus mimicking the behavioural RT cost associated with mirror-reversal.

The current results also indicate that mental rotation may be performed more quickly by the right hemisphere. This conclusion is based on the relatively shorter duration of the mental-rotation effects over the right hemisphere for normal characters and the earlier onset of the effects for mirror-reversed characters. The idea that the right hemisphere may perform the mental rotation faster than the left is not new. Corballis (1997) noted that there is a possibility that the right hemisphere performs mental rotation more efficiently and more quickly than the left hemisphere. He based this conclusion on findings from studies investigating the effects of attentional load on the rate of mental rotation. In one study, Corballis and Sidey (1993) showed that mental-rotation rate increased when the left hemisphere was primed through concurrent verbal load. In this case, Corballis (1997) suggested, the effect of the concurrent verbal load in that study was to "occupy left-hemispheric resources, and right-hemifield presentation of the letter to be rotated may have further occupied the left hemisphere in identification, leaving the right hemisphere free to accomplish the rotation itself" (p. 114). In another study, Corballis and Manalo (1993) directed the participants' attention to the left or the right with an arrow preceding the stimulus presentation. Although the overall RTs were faster when the arrow correctly identified the subsequent stimulus location, the rate of mental rotation increased when attention was directed toward the left visual field. The greatest effect on mental-rotation rate was observed when attention was directed towards the left, but the stimulus was presented on the right. In this case, the division of labour between the hemispheres should be most notable because the right visual field presentation may result in the left hemisphere performing the character identification, while the primed right hemisphere would perform the mental rotation. To my knowledge, the current study is the first to show ERP evidence of faster right-hemispheric mental rotation effects.

Corballis (1997) also noted that the apparent right hemispheric superiority for the speed of mental rotation may, in fact "reflect variations in the effect of orientation on the *identification* of the stimulus to be rotated" (p.114). The findings reported in this study provide some evidence for this suggestion. Namely, the P2 effects observed for both the category and the parity tasks indicate that the right hemisphere is more responsive to stimulus orientation than the left hemisphere. As discussed earlier the P2 effects could reflect the second step in orientation perception based on mapping of object identity on the principal axis of shape elongation. This may be a processing step preliminary to mental rotation, and may effectively be informative in terms of the degree and the direction of required transformation. If this is the case, the right-hemispheric orientation sensitivity may effectively reduce the time required to mentally rotate the stimulus.

Conclusion

This study was designed to examine the temporal sequence of processing stages preceding mental rotation and mental rotation itself. The results suggest that there are at least three distinct processing stages preceding mental rotation that show orientation dependence.

Furthermore, three distinct orientation-related effects were observed: (1) an oblique effect evident over the P1 component between 96 and 136 ms after stimulus onset; (2) an effect that increases with misorientation, but with a dip at 180 degrees evident over the N1 component between 160 and 216 ms after stimulus onset for both tasks, and over the P2 component for the category task, and (3) a linear effect, evident over the P2 and the late-parietal component for the parity task and reflecting preparation for mental rotation and mental rotation *per se*, respectively.

Chapter 4: ERP correlates of stimulus-orientation effects in a letter-number categorisation task, and a colour-judgement task

Introduction

Chapter 3 showed that effects of orientation on both category and parity judgements were manifest in terms of increases in amplitude with stimulus misorientation over the P1 and the N1 components. These effects were present for both category-and parity-judgement tasks, suggesting that they had to do with perception or recognition of the stimuli, and not with processes to do with mental rotation. I argued that these effects may somehow reflect an increase in visual processing demands with stimulus misorientation, although their precise nature remains unclear. Orientation effects on the P2 component were of particular interest because they differed between the tasks. Both tasks elicited increases in amplitude for orientations up to the 120°. Task differences were apparent when stimuli were presented at 180° orientation – P2 amplitudes decreased in comparison to 120° for the category task, while no reduction in amplitude was apparent for the parity task.

Increases in amplitude of the P2 component are not commonly observed in response to parity-judgement tasks. Nevertheless, I reasoned that these effects may reflect a processing stage that depends on the assigning of orientation, which may be a necessary preliminary to mental rotation, and the subsequent judgement of parity. The modulation of P2 amplitude for the category task may also index the recognition of stimulus orientation.

Furthermore, the effects of orientation differed across the three VEP components, indicating that changes in stimulus orientation affect neural processing at several different processing stages. I argued that the effects on the P1, with no difference between upright and inverted characters, and an increase in amplitude for characters presented at oblique orientations, are related to initial stages of orientation perception based on the principal axis of elongation (W. Li & Westheimer, 1997). The increase in amplitude for stimuli presented at the oblique orientations may reflect an oblique-effect related flow-on from a disruption of lower-level visual processing in the primary visual cortex (B. Li *et al.*, 2003). Alternatively, the increase in amplitude for oblique presentations may be directly related to an oblique effect in higher order visual areas such as the middle temporal (Xu *et al.*, 2006) or inferior temporal regions (Orban & Vogels, 1998). In either case, if the orientation-related modulation of the P1 is related to the obliqueness of the stimulus orientation, than one would expect that vertically and horizontally oriented stimuli would elicit comparable ERP amplitudes. Based on the results from Chapter 3, P1 amplitude should be larger for obliquely oriented stimuli than for the vertically oriented stimuli.

It may seem somewhat counterintuitive that effects of obliqueness may be reflected as increases in amplitudes, given that there are larger numbers of cells tuned to cardinal orientations, compared to any of the oblique orientations. There are two possible explanations for this. The first is that the tuning curves are wider for oblique than for cardinal orientations, and thus the overall number of cells that respond to any particular orientation may result in a larger combined response. If the P1 orientation effects are related to obliqueness and reflect the contribution of the oblique effect originating from, say, the inferior temporal cortex, than this explanation would make more sense. The alternative explanation would be that the orientation-sensitivity of the P1 reflects a carry-over effect from the relatively poorer processing by the primary visual cortex, and may act as a compensatory mechanism at this later visual processing stage, resulting in increased processing demands required to reach the same signal level that would then feed forward.

Orientation effects on the N1 component were characterised as an increase with misorientation, but the increase was smaller for inverted stimuli than for most other orientations. Based on the observation that the amplitude of the N1 can be used to differentiate between upright and inverted stimuli, I argued that the N1 reflects the earliest stages of shape recognition or structural encoding of the stimulus prior to matching to a memory representation. This interpretation is supported in part by the observation that the amplitude and the latency of the N1 have been shown to be specific to various object classes (Rossion *et al*., 2000). Furthermore, N1 amplitude and latency have been shown to increase with stimulus inversion, and is thought to reflect a disruption of configural object processing (Rebai *et al*., 2001; Rossion *et al*., 2000; Rossion *et al*., 2003).

The functional significance of the P2 component is not as well documented, although results from Chapter 3 indicate that its amplitude may be important in differentiating the parity and the category tasks and there is some evidence that the P2 component may show sensitivity to configural information. I argued that the P2 component reflects a second step in orientation perception based on mapping of object identity onto the principal axis of shape elongation. Namely, if the P1 reflects an early, pre-recognition sense of orientation which might be based on the orientation of the principal axis of elongation, the P2 component may reflect a full understanding of orientation, subsequent to object recognition, and based on "superimposing" the *direction* of the top-bottom axis on this initial impression.

Furthermore, the orientation effects in Chapter 3 on the P2 component were right lateralised. Therefore, the right hemisphere may be more responsive to stimulus orientation. It is conceivable that orientation-perception may depend on holistic or configural processing of the stimulus. If that is the case, then the left hemisphere may not be as responsive to stimulus orientation because it uses feature-based recognition mechanisms. The link between the P2 and configural processing is based on a study that investigated effects of thatcherisation on upright and rotated faces (Milivojevic, Clapp *et al*., 2003). Milivojevic, Clapp *et al*. (2003) showed that the effects of thatcherisation on the P2 component showed linear decreases with angular displacement from upright. Based on these findings and previous research which suggested that face recognition based on configural information deteriorates as a linear function of angular displacement from upright (Collishaw & Hole, 2002), Milivojevic, Clapp *et al*. (2003) speculated that P2 reflects gradual reduction in the contribution of configural information to perception of thatcherisation. Similar effects on the amplitude of the P2 of thatcherisation and inversion were observed by Boutsen *et al.* (2006). They also suggested that the P2 component reflects configural processing. More specifically, however, they argued that the P2 component reflects local processing of configural information, in contrast to the P1 which reflects global processing of configural information. Nevertheless, there is some evidence that the P2 reflects configural processing and that it may reflect a perceptual stage related to the P1.

The present experiment

The present experiment examines the effects of orientation at a more fine-grained orientation resolution by increasing the number of orientations used. Thus, I chose to use a set of seven orientations at 30° clockwise or counter-clockwise rotations from 0°. Furthermore, visual inspection of the data in Chapter 3 also indicated that the effects on the N1 occurred over the later phase of the N1, and small differences in peak N1 latency between upright and misoriented stimuli were evident in the grand-average waveforms. However, the effects on the latencies of the components were not investigated due to a relatively low sampling rate of 250Hz. To allow for a more accurate investigation of the effects of latency on the early VEPs, the sampling rate for the current study was increased to a 1000 Hz.

In an attempt to elucidate the effects of orientation on early visual processing, I introduced an additional task involving judgements of colour for comparison with the category task. There is a distinct possibility that the effects of orientation on the N1 and the P2 reflect access to object information. In the case of the N1 these effects may reflect early stages of object recognition while in the case of the P2 these effects may reflect a secondary stage of orientation perception, subsequent to recognition. Therefore, it seems reasonable to suppose that orientation effects on these components should only be observed for the task that requires object recognition, such as the category-judgement task, but not for the task that does not require object recognition. One such task may be a colour-judgement task given that there is some evidence that colour identification can be accomplished independently of object recognition (Boucart *et al*., 2000; Pins *et al*., 2004).

Methods

Participants

Fifteen neurologically normal volunteers (7 women) were recruited from students and faculty at the University of Auckland for approximately two hours of participation. All had normal or corrected-to-normal vision and were right-handed (LQ range: 60- 100, mean 85.03), as determined by Edinburgh handedness inventory (Oldfield, 1971). They ranged in age from 21 years to 35 years, with a mean of 26.2 years. The procedures were approved by the University of Auckland Human Subjects Ethics Committee, and all participants gave their informed consent to participate in the experiment.

Visual Displays

The stimuli consisted of eight uppercase alphanumeric characters - four letters (R, F, L, and P) and four digits (2, 4, 5, and 7) – presented in red and in blue 72-point Arial font on white background. At upright, the characters subtended a vertical visual angle of 2º and a horizontal visual angle of 1.45º, on average, although small differences in the horizontal visual angle were present due to the shape of the characters (range: 1.3-1.8°). Each character was presented at twelve clockwise angular departures ranging from 0º to 330º, in 30º increments. Manipulation of visual displays was performed using Microsoft Office Picture Editor (MS). Stimuli were displayed on an SVGA computer monitor (1024×768 pixel resolution; 60 Hz refresh rate) from a distance of 57 cm. Stimulus presentation was controlled using E-Prime v1.1.4.1 (Psychology Software Tools, Pittsburgh, Pennsylvania, USA). TTL pulses generated via the parallel port of the display computer provided synchronization of stimulus events with EEG acquisition. Millisecond timing routines for the visual displays and pulse generation were conducted as outlined in the E-Prime User Guide (Schneider *et al.*, 2002).

Twice as many stimuli were presented for the upright and inverted (180º) orientations, compared to those at the other ten orientations, since clockwise and counterclockwise rotations were treated as equivalent, thus resulting in seven orientation conditions.

Tasks

The participants performed two tasks, a red-blue discrimination task (colour judgement) and a letter-digit discrimination task (category judgement). In the colour-judgement task, the participants were required to press the left mouse button if they judged the character to be blue and the right mouse button if they judged it to be red. In the category-judgement task, the participants were required to press the left mouse button if they judged the character to be a letter, and the right mouse button if they judged the character to be a number. In both the cases they were instructed to respond as quickly as possible without sacrificing accuracy.

Procedure

Participants performed two practice blocks, one for each task, immediately prior to the experiment. Each practice block consisted of 20 randomly selected trials. Over the course of the experiment, 448 trials were presented for each task. The experiment was conducted over four blocks of trials, and task order was randomised across the blocks. Within each block, each stimulus was presented twice at each orientation, and the order of stimulus presentations was randomised. Stimuli were presented centrally for up to 4 s or until a response was detected, whichever was sooner. The inter-trial interval varied between 733 and 1566 ms and participants were instructed to keep fixation on a small '+' presented on the screen during that interval. Participants were also instructed to keep looking at the stimulus, avoid eye movements, and withhold blinking until after the response was made.

EEG apparatus

Electrical Geodesics Inc. 128-channel Ag/AgCl electrode nets (Tucker, 1993) were used. EEG was recorded continuously (1000 Hz sampling rate; 0.1–100Hz analogue bandpass) with Electrical Geodesics Inc. amplifiers (200 MΩ input impedance) and acquisition software running on a Macintosh G4 computer with a 16-bit analogue-to-digital conversion card bit. Electrode impedances were below 50 kΩ (range 30–50 kΩ), an acceptable level for this system (Ferree *et al*., 2001). EEG was acquired using a common vertex (Cz) reference.

Pre-processing

Pre-processing was performed with custom (in-house) software. Following data collection, the EEG files were segmented with respect to event triggers in 800 ms epochs including a 200 ms pre-stimulus baseline and 600 ms post-stimulus epoch. Voltages were sampled every millisecond over this epoch. Only the trials on which the participants responded correctly were included in the analyses. Eye-movement correction was made on all segments using the method of Jervis et al. (1985). The corrected data from each subject were then averaged to produce a total of 14 ERPs (two tasks and seven orientation conditions). DC offsets were calculated from the pre-stimulus baseline and removed from all waveforms. The individual waveforms were digitally filtered with a band-pass filter for 0.01–30 Hz range using a bi-directional 3 Pole Butterworth filter (Alarcon *et al*., 2000). Averaged and filtered ERPs were re-referenced to the average reference off-line.

Results

Behavioural Results

Mean RTs for correct responses, and accuracy, as percent correct, were analysed in a 2x7 repeated measures ANOVA with task and orientation as factors and plotted in Figure 4.1. Sphericity violations arising from repeated measures were corrected for using the reduced df approach, corrected by the Huynh-Feldt ε value (Huynh & Feldt, 1976).

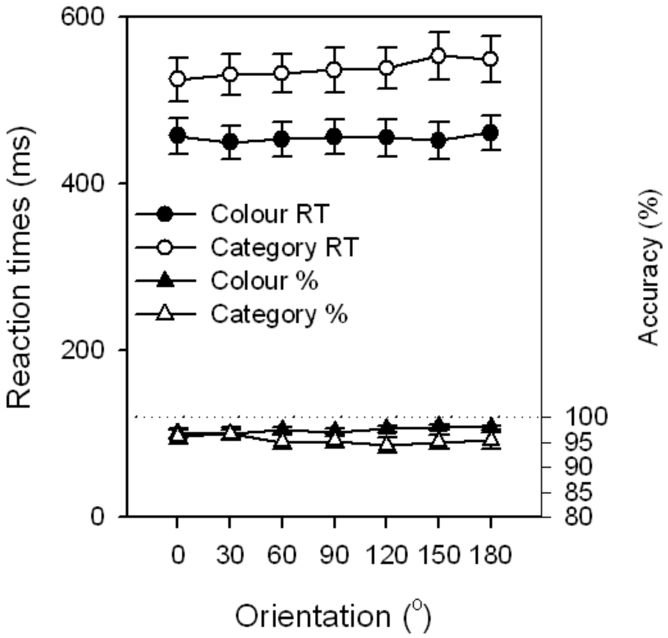

Figure 4.1: Reaction times (RT) and accuracy (%) as percent correct, as a function of task and orientation. RTs are plotted as circles, accuracies as triangles.

In terms of accuracy, the main effects of task (F(1, 14) = 3.330, p = 0.089) and orientation (F(6, 84) < 1, ε = 0.928) were not significant, and the task-by-orientation interaction was only marginally significant (F(6, 84) = 2.207, p = 0.05, ε = 1). This interaction was characterised by significantly lower accuracy for the categorisation task than for the colour judgement task at 120° and 150° orientations (p ≤ 0.038). Using pair-wise comparisons, no significant differences were observed between the orientation conditions within either task. Simple effects of orientation for each task were also examined. No significant orientation effects were observed for neither the colour (F(6, 84) = 1.06, p = 0.392,

$\varepsilon = 0.810$) nor the category ($F(6, 84) = 1.87$, $p = 0.102$, $\varepsilon = 0.923$) tasks, although a significant linear trend was observed for the category task ($F(1, 14) = 7.20$, $p = 0.018$) and explained 39.14% of the variance.

With respect to RTs, the category task elicited significantly longer RTs than the colour task ($F(1, 14) = 57.475$, $p < 0.001$). The main effect of orientation was not significant ($F(6, 84) = 2.625$, $p = 0.061$, $\varepsilon = 0.515$), although there was a significant task-by-orientation interaction ($F(6, 84) = 3.145$, $p = 0.010$, $\varepsilon = 0.910$). The interaction was further investigated by examining the effects of orientation for each task separately. The effect of orientation was not significant for the colour task ($F(6, 84) = 1.003$, $p = 0.423$, $\varepsilon = 0.846$), but was for the category task ($F(6, 84) = 3.760$, $p = 0.017$, $\varepsilon = 0.508$). The effect of orientation was best characterised in terms of linear increases with increased angle of orientation ($F(1,14) = 14.782$, $p = 0.002$; 88.26%), and pair-wise comparisons indicated that significantly longer RTs were elicited by stimuli presented at 150° and 180° orientations than at 0° orientation ($p < 0.05$, with Bonferroni correction). The orientation-dependent increase in RTs is unlikely to reflect mental rotation as the slope of the function is too low, indicating that *if* this effect was due to mental rotation, the rate would have been approximately 49,148°/second. In contrast, the mental rotation rates in Experiment 1 and 2 were closer to 577°/second and 363°/second, respectively.

EEG results

Figure 4.2 illustrates GFP plots for category and colour tasks at each of the stimulus orientations. Spatial topographies, averaged across the seven orientation conditions, are illustrated for each task at each of the VEP components of interest. Two clusters of occipito-temporal electrodes – one over each hemisphere – were selected for further analysis. Electrodes of interest in reference to the entire electrode montage are illustrated in part B of Figure 4.2, and the ERPs at these electrodes are plotted in part C of the same figure.

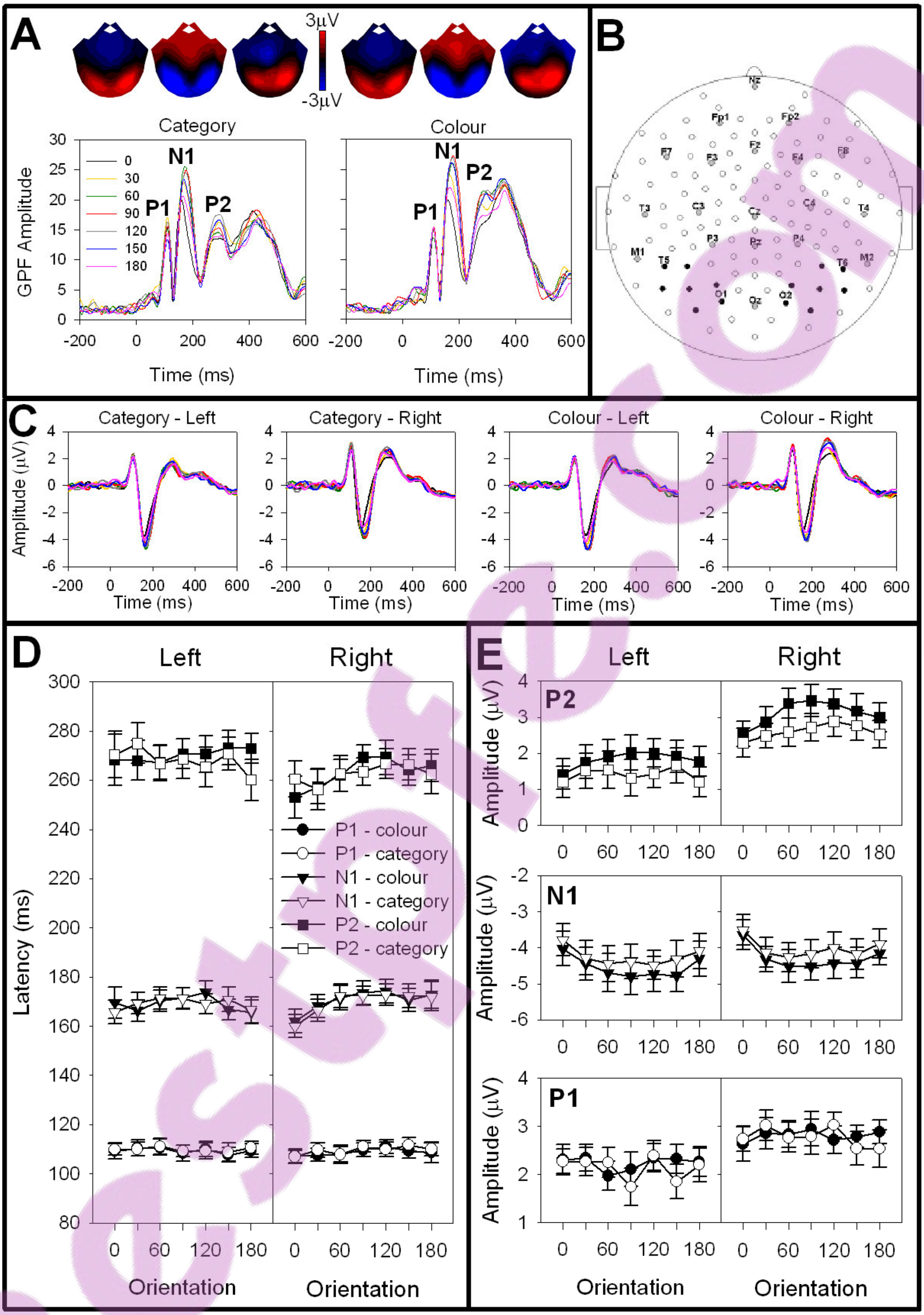

Figure 4.2: A: Global field power as a function of stimulus orientation and task and distributions of the P1, N1 and P2 components for each task. B: Electrode clusters of interest in reference to the entire electrode montage. Electrodes closest to the standard 10-20 system positions are labelled. C: ERPs as a function of task, hemisphere and orientation at the electrode clusters of interest. D: P1, N1 and P2 latency as a function of orientation, hemisphere and task. E: P1, N1 and P2 amplitudes as a function of orientation, hemisphere and task.

For each VEP component, peak latency and amplitude were estimated at the two electrode clusters of interest for each participant individually. The peak latency for the P1, the N1 and the P2 components was estimated as the latency at which the components reached their maximal amplitude. Mean latencies, with standard errors of the mean, for each component as a function of orientation and hemisphere are depicted in Figure 4.2 D and also presented in Table 4.1. For the P1 and the N1 components, the component amplitude was estimated as average amplitude over the time period corresponding to the full-width-at-half maximum for these components. Since the late-parietal positivity was relatively continuous with the P2 component for the colour task (see the GFP plots in Figure 4.2 part A) the P2 amplitude was estimated as the time period of 60 ms surrounding the P2 peak latency (30 ms before and 30 ms after the peak). This time period was chosen based on the grand-average GFP plots which suggested that the orientation effects for the average waveforms were evident over a 60-ms time period surrounding the peak. The latency and amplitude data were then analysed with a 2x7x2 repeated measures ANOVA with task, orientation and hemisphere as within subject factors and Huynh-Feldt ε correction was used for sphericity violations (Huynh & Feldt, 1976).

Table 4.1: Mean latency as a function of orientation and hemisphere (standard errors of estimate in brackets) for the P1, N1 and P2 components. Significant orientation-by-hemisphere interactions were only observed for the N1 and the P2 components. Values are rounded to the nearest whole number to reflect the sampling of EEG.

Component	**Hemisphere**	**Orientation**						
		0	**30**	**60**	**90**	**120**	**150**	**180**
P1	Left	110 (3)	110 (3)	111 (3)	109 (3)	110 (3)	108 (3)	110 (3)
	Right	107 (3)	109 (3)	108 (3)	110 (2)	110 (3)	111 (3)	109 (3)
N1	Left	168 (5)	168 (4)	171 (4)	171 (4)	171 (4)	169 (4)	166 (5)
	Right	161 (5)	167 (5)	172 (5)	173 (4)	174 (5)	172 (5)	172 (6)
P2	Left	269 (10)	271 (7)	267 (7)	270 (7)	268 (7)	272 (6)	267 (6)
	Right	257 (8)	257 (7)	262 (7)	266 (5)	268 (6)	265 (6)	264 (7)

Latency effects

Effects of orientation, task, and hemisphere were examined for the latencies of the P1, N1, and P2 components. For the P1 component, no significant effects of task (F(1, 14) = 1.77,

$p = 0.205$), orientation ($F(6, 84) < 1$, $\varepsilon = 0.671$), or hemisphere ($F(1, 14) < 1$) on the latency of the P1 were observed.

For the N1 component, a significant main effect of orientation ($F(6, 84) = 8.53$, $p < 0.001$, $\varepsilon = 0.419$) and a significant orientation-by-hemisphere interaction ($F(6, 84) = 5.18$, $p = 0.005$, $\varepsilon = 0.470$) were observed. Significant effects of orientation were observed over both the left ($F(6, 84) = 3.33$, $p = 0.025$, $\varepsilon = 0.532$) and the right hemispheres ($F(6, 84) = 9.37$, $p = 0.002$, $\varepsilon = 0.271$). The orientation effects over the left were characterised by a significant quadratic trend ($F(1, 14) = 5.69$, $p = 0.032$) which explained 84.69% of variance. On the right, effects of orientation were best characterised with significant linear ($F(1, 14) = 10.03$, $p = 0.007$) and quadratic ($F(1, 14) = 22.27$, $p < 0.001$) trends, which explained 58.26% and 36.16% of variance, respectively.

For the P2 component, the orientation-by-hemisphere interaction was significant ($F(6, 84) = 5.18$, $p = 0.005$, $\varepsilon = 0.470$). Significant effects of orientation were observed over the right ($F(6, 84) = 4.12$, $p = 0.002$, $\varepsilon = 0.923$), but not the left hemisphere ($F(6, 84) < 1$, $\varepsilon = 0.835$). The orientation effects over the right were characterised by significant linear ($F(1, 14) = 9.83$, $p = 0.007$) and quadratic ($F(1, 14) = 5.22$, $p = 0.038$) trends which explained 59.32% and 26.46% of variance, respectively.

To investigate whether the effects of orientation on the latency of the P2 depended on the latency shifts of the N1 components, ANOVA was conducted on the difference between the P2 and the N1 latencies. No significant effects were observed, indicating that the observed effects of latency on the P2 were due to delays at the N1 processing stage.

Amplitude effects

Effects of orientation, task, and hemisphere were examined for the amplitudes of the P1, N1, and P2 components. For the P1 component, only the main effect of hemisphere was significant ($F(1, 14) = 4.74$, $p = 0.047$), characterised by larger P1 amplitudes on the right.

For the N1 component, the main effect of task was significant ($F(1, 14) = 6.55$, $p = 0.023$) and was characterised by larger N1 amplitudes in response to the colour-judgement task. The main effect of orientation was also significant ($F(6,84) = 7.14$, $p = 0.001$, $\varepsilon = 0.449$) and was predominantly characterised by significant quadratic ($F(1,14) = 11.39$, $p = 0.005$, 76.79 % variance explained) and linear ($F(1,14) = 5.75$, $p = 0.031$, 13.97% variance explained) trends, although the cubic trend was also significant ($F(1,14) = 7.36$, $p = 0.017$, 3.80% variance explained).

For the P2 component, the main effect of task was significant ($F(1, 14) = 10.71$, $p = 0.006$) and was characterised by larger P2 amplitudes in the colour-judgement task. Significant main effects of orientation ($F(6, 84) = 5.28$, $p < 0.001$, $\varepsilon = 0.905$) and hemisphere ($F(1, 14) = 19.55$, $p = 0.001$), characterised by larger P2 amplitudes over the right hemisphere, were also observed.

The task-by-orientation interaction did not reach significance ($F(6, 84) = 1.99$, $p = 0.095$, $\varepsilon = 0.795$), but the orientation-by-hemisphere interaction did ($F(6, 84) = 2.40$, $p = 0.048$, $\varepsilon = 0.805$). This interaction was characterised by significant effects of orientation on the right ($F(6, 84) = 7.83$, $p < 0.001$, $\varepsilon = 0.985$), but not the left ($F(6, 84) = 2.32$, $p = 0.056$, $\varepsilon = 0.785$). The effects of orientation on the right were best characterised by significant linear ($F(1, 14) = 8.89$, $p = 0.010$, 28.68 % variance explained) and quadratic trends ($F(1, 14) = 26.50$, $p < 0.001$, 69.88 % variance explained).

Discussion

This study was designed to further elucidate the effects of orientation on ERP correlates of early visual processing. The amplitudes and latencies of the P1, N1 and P2 visual components were examined during a letter-digit category judgement – a task that required object recognition – and a red-blue colour judgement task which did not require object recognition. The stimuli were presented at seven orientations ranging from upright to inverted at 30° increments.

It was hypothesised that the effects of orientation on the P1 component were related to stimulus obliqueness. Based on results reported in Chapter 3, it was expected that the amplitudes of the P1 would be larger for obliquely oriented stimuli than for the vertically oriented stimuli. The current study did not replicate the effects of orientation on the P1 component.

It is not entirely clear what factors may have contributed to the absence of orientation effects on the P1 in this study. It is possible that the effects of orientation on this component were context specific. In Chapter 3, participants performed parity judgements where orientation information is critical. Therefore, stimulus orientation may have been perceived to be of particular importance in that experiment. In contrast, orientation information was not of particular relevance to either the colour or the category task in this study.

However, if orientation specificity of the P1 depended on whether orientation was of particular relevance to the task, then one would expect the orientation specificity of the P1 in Chapter 3 to differ between the parity-judgement task, where orientation was critical, and the category-judgement task, where orientation was irrelevant. This was not the case. It is also worth a mention that changes in stimulus orientation in a previous mental-rotation study did not affect the amplitude of the P1, although effects of orientation on the N1 were observed (Milivojevic, Johnson *et al.*, 2003). It is therefore possible that the effects of orientation on the P1 are not reliably elicited even when identical experimental manipulations are used. This certainly seems to be the case in face-inversion studies where some have found P1 increases with stimulus inversion (e.g. Itier & Taylor, 2002, 2004; Rebai *et al.*, 2001), while others have not (e.g. Rossion *et al.*, 1999).

The effects of orientation on the N1 and the P2 components were hypothesised to depend on object recognition. Thus, it was expected that the category task would elicit orientation effects on these ERP components, while the colour task would not. Visual inspection of the current results and the results reported in Chapter 3 indicated that the patterns of the orientation effects for these two ERP components were comparable. However, no task-by-orientation interactions were observed in the current study for either of these components. The current data, therefore, do not support the idea that these are specifically related to character recognition – which would only be required for successful completion of the category task, but not the colour task – and a possibility remains that some level of recognition took place even in the colour-judgement task, since the stimuli are highly overlearned.

This is suggested by performance on colour-Stroop tasks, whereby colour-word reading may interfere with ink-colour identification (MacLeod, 1991). Since in this experiment participants responded by clicking either the left or the right mouse button with their right hand for both tasks, it is possible that stimulus-response matching was learned during the experiment. In the colour task, the participants pressed the right button when the characters were red, and in the category task the participants pressed the right button when the characters were digits. Left responses were associated with blue characters, in the colour task, and letters, in the category task. It is possible that participants learned the association between letters and blue stimuli, and between digits and red stimuli. If this was the case, then response congruency between the categorisation and colour tasks, for example, when the stimulus is a blue ‘R’, may result in faster RTs, while response incongruent stimuli, such as a red ‘R’ may result in slower RTs. I would expect that the decisions about the colour of the stimuli would be more sensitive to the congruency effects, simply because character recognition may be an automatic response. Clearly, the response-congruency effects on the colour task would only apply in cases where participants had already performed the category task. Since the participants completed practice blocks for both tasks immediately prior to the onset of the experiment, this would certainly be the case for all of the data collected.

The response-congruency effects were assessed by comparing the RTs in response to stimuli that required identical responses in both tasks (response-congruent) to those that required opposite responses in the two tasks (response-incongruent). The results for the colour task indicate that the RTs were significantly faster for response-congruent trials (451.93 ms, SE = 20.45) than for response-incongruent trials (459.16 ms, SE = 21.51; t(14) = -2.53, p = 0.023). No significant effect of response congruency was observed for the category task (t(14) < 1). Therefore, the behavioural data indicate that colour judgements may have been accompanied by character recognition, in some trials at least, and the question of whether the orientation effects on the N1 reflect disruption of access to object information remains inconclusive.

It is of note that only small orientation effects were observed for the category task RTs, while no effects of orientation were observed for the accuracy on this task, or either behavioural measures for the colour task. Therefore, the ERP correlates of stimulus orientation do not correspond to changes in behavioural data and ERP orientation effects are observed in a task that does not require recognition, even if participants may be unable to suppress recognition.

The results indicate that the N1 shifts in time with stimulus misorientation and that the amplitudes increase in response to misoriented stimuli. The shifts in latency can be observed at the onset of the N1, and cannot, thus, be attributed to increases in the duration to reach the peak amplitude. This shift in latency cannot be attributed to delays of the P1 component either, indicating that the latency shifts are most likely to be related to a delay in the recruitment of the neural generators underlying the N1.

Hemispheric differences were also observed for the latency shifts of the N1 component. Over the left hemisphere the latencies increased gradually with stimulus rotation away from the vertical (upright and inverted) up to the 90° orientation, while over the right hemisphere the latencies increased with increased misorientation from upright. Interestingly, the left hemisphere responded later than the right hemisphere when the stimuli were presented at upright. If the left hemisphere subserves featural recognition mechanisms, while the right subserves configural or holistic processing (Bradshaw & Nettleton, 1981) then these results could be interpreted as an indication that the feature- based processing is slower than holistic processing when the stimuli are presented at upright and that the holistic processing is delayed as a function of rotation from upright, while feature-based processing is delayed as a function of rotation from vertical. Feature-based processing may be more similar between the upright and inverted stimuli because the vertical axis is in alignment for stimuli presented at these two orientations (Hummel & Biederman, 1992).

Amplitudes of the N1 also increased as a function of stimulus orientation, with a smaller increase between upright and inverted, and larger increases from upright to all other orientations. Thus, irrespective of the relative timing of the effects, stimulus misorientation elicited increases in amplitudes of the N1 component that were not related to stimulus obliqueness, and thus can not be easily attributed to simple visual features of misoriented stimuli. Rather, the results indicate that the effects of orientation on the N1 component reflect a complex interplay between relative timing of the N1 component and increases in amplitudes, suggestive of increased processing demands.

Similar effects were observed over the P2 component, with linear and quadratic increases in P2 amplitudes with stimulus rotation from upright. However, these effects were only evident over the right hemisphere. These findings are in line with the results reported in Chapter 3 which indicated that the effects of orientation were more prominent over the right hemisphere. Further, although no significant interaction between the effects of orientation and task were observed, the pattern of amplitudes for the category task closely matched results presented in Chapter 3, with largest amplitudes at 120° orientation. The peak amplitudes for the colour task were observed at 90°. The results from Chapter 3 indicated that the P2 component is also the first stage at which task-specific orientation effects are observed, and I speculated that these results were related to assignment of top-bottom coordinates, or binding of orientation and identity, which may be necessary for the parity task, but not the category task. Thus, the present results indicate that the "default" orientation-specificity of this component may be a quadratic function, similar to that of the earlier visual components. Meanwhile, the category task, which requires stimulus recognition, elicits attenuation of this component, with greater degrees of attenuation depending on the stimulus orientation.

Summary and conclusion

This experiment failed to replicate the orientation effects on the P1 ERP component, but did replicate the effects of orientation on the N1 and the P2 components. However, contrary to the predictions that the orientation effects should only be observed for the task that that required character recognition, effects of orientation were observed for both the category and colour tasks.

In addition to the amplitude effects reported in Chapter 3, this study has provided evidence on the effects on the latencies of the N1 and P2 components. The P2 effects appear to be dependent on the N1 effects, that is, a delay at the N1 stage subsequently affects the timing of the P2 processes. The latency effects showed hemispheric asymmetries, whereby the N1 over the right hemisphere occurred earlier than over the left hemisphere, suggestive perhaps of right hemispheric dominance for processing of alphanumeric characters, which is in contrast to the findings from most neuroimaging studies to date (Garrett *et al.*, 2000; K. H. James & Gauthier, 2006; K. H. James *et al.*, 2005; Joseph *et al.*, 2006; Pernet *et al.*, 2005; Wong, Gauthier, Woroch, De Buse, & Curran, 2005). As the angular departure from upright increased, the latency difference between the hemispheres decreased, and the left hemisphere reacted faster than the right when the stimuli were upside down. This pattern of results may be interpreted as indicating that the right hemisphere function in alphanumeric processing may be based on holistic analysis, while the left hemisphere might be based on analysis of constituent features. The difference in the timing of the effects could then be interpreted as indicative of faster holistic processing when the stimuli are at upright, but larger deficits in holistic processing with misorientation. In contrast, feature-based processing may be slower at the upright orientation, but it is less affected by changes in orientation.

A possibility remains that the participants could not suppress recognition of the highly familiar characters during colour task. Therefore, the role of object recognition on the N1 and the P2 orientation effects remains inconclusive. Nevertheless, comparable effects of orientation on the N1 during both the colour and category tasks are suggestive of stimulus-driven processing. Furthermore, the effects of orientation on the N1 may reflect disruption of the perceptual encoding of the stimulus. If this is the case, then the results of the present study suggest that the effects of orientation precede matching to memory representation.

The mechanism that could account for these results could be perceptual learning. Visual familiarity with a stimulus at a particular orientation may result in plastic changes within the visual system, such as strengthening of synapses and recruitment of larger number of neurons sensitive to a particular view of an object. The plastic changes in the visual system for frequently encountered objects, such as alphanumeric characters, may enable more efficient processing of the stimulus, which would typically lead to recognition. The increase in the N1 amplitude with misorientation may, thus, reflect a need to additional neural processing for structural stimulus encoding of the stimulus – but only relative to the more familiar views.

Chapter 5: General discussion

The experiments reported in this thesis were designed to investigate brain activity underlying category judgements and parity judgements about letters and digits presented in different orientations. The general assumption was that only the parity task would elicit mental rotation, and that the two tasks would otherwise share processing stages, up to and including object recognition. In Experiment 1, brain activity was recorded using fMRI, providing evidence as to the neuroanatomical areas involved in the two tasks. In Experiments 2 and 3, brain activity was recorded using high-density EEG, providing evidence as to the time course of neural events. Experiments 1 and 2 compared category and parity tasks. In Experiment 3 a third task involving judgements of colour was added for comparison with the category task, in an attempt to elucidate the effects of orientation on early visual processing. First, I will examine the functional neuroanatomy of the processing of rotated objects, based initially on fMRI. This will be followed by a focus on the temporal analysis of the different processing stages leading up to mental rotation, mental rotation itself and parity judgements.

Neuroanatomical Correlates: fMRI analysis

In Experiment 1, participants performed parity and category judgements about rotated alphanumeric characters while BOLD signal response was recorded. Three stimulus orientations, 70° apart, were used, ±30°, ±100° and ±170°, and were systematically varied across blocks, which allowed the modulation of BOLD activation to be characterised in terms of linear and quadratic trends. The expectation was that a linear trend would indicate mental rotation, and would be restricted to the parity task. It was also expected that there may be effects of orientation on the BOLD signal common to the two tasks, reflecting orientation-dependent activity involved in stages of processing prior to mental rotation.

Irrespective of the task, the BOLD signal correlates of stimulus orientation were best characterised by a quadratic function restricted to the SMG. The quadratic effect was such that activation was greater for 30° and 170° orientations than for the 100° orientation. Furthermore, an adjacent area within the SMG also showed linear decreases in BOLD signal amplitude with increase in stimulus orientation. Since there was no evidence for an overall difference between tasks in this area, the orientation-dependent activation in the SMG is presumably due to the common process of shape recognition required for both tasks. Previous research has shown that alphanumeric categorisation and recognition elicits activation in this area (Joseph *et al*., 2006) which further supports this interpretation.

RTs increased linearly with stimulus orientation in the parity task but not in the category task, confirming that mental rotation was elicited only by the parity task. Relative to the category task, the parity task also elicited a stronger BOLD signal in both dorsal and ventral streams, lateral and medial pre-SMA, and inferior frontal gyrus. These results replicate previously reported evidenced that parity tasks elicit activation in these areas (e.g. Cohen *et al*., 1996; Jordan *et al*., 2001; Koshino *et al*., 2005; Tagaris *et al*., 1997). However, linear increases in amplitudes for the parity task were confined to a subset of these regions – namely, posterior part of the dorsal IPS, lateral and medial pre-SMA, and the anterior insula. Since linear increases in activation were hypothesised to reflect mental rotation, these results suggest that only a subset of regions that subserve the parity-judgement task are actively involved in mental rotation itself. Other processes distinguishing the two tasks might include the perception of orientation itself, the decision as to which way to mentally rotate, and the final decision as to whether each character was normal or backward.

Experiment 1 revealed no evidence of hemispheric asymmetry in mental rotation, contrary to previous evidence of right-hemispheric specialization (Harris *et al*., 2000; Podzebenko *et al*., 2002). However, the evidence from Experiment 2, discussed below, suggests that hemispheric differences in mental rotation may be evident in the timing of processes rather than in the specific areas involved. Therefore, it is likely that the poor temporal resolution of fMRI was not sensitive to these hemispheric asymmetries in timing.

There was, however, larger activation on the right than the left in a portion of the posterior parietal cortex – the vIPS. This area did not show orientation-specific BOLD responses. Furthermore, larger task differences were observed over the right hemisphere, with larger activation levels for the parity task than the category task within the IFG, lateral and medial pre-SMA, anterior to the areas that showed linear increases with orientation in the parity task. This pattern of results suggests that hemispheric asymmetries may be related to visuospatial processing and attention rather than mental rotation *per se*.

Sequential components: EEG analysis

The fMRI analysis provided an overview of the activated areas, but no information as to the sequence of cortical events in the two tasks. Experiment 2 used event-related potentials from high-density EEG to track the time course of activity. This provided further evidence on the events common to the two tasks that preceded mental rotation, as well as on the components specific to the parity task.

Orientation-specific neural processing preceding mental rotation

In Experiment 2, the letters and digits were presented in their normal and mirror-reversed forms at four orientations: 0°, ±60°, ±120° and 180°, again providing for the computation of linear and quadratic trends, but in this case also a cubic trend. As expected the parity-judgement task elicited mental rotation while category judgement task did not, as indicated by linear trends in response to the parity task for both the RT and ERP measures. Linear increases in ERP negativity as a function of stimulus orientation distributed over the parietal leads are thought to reflect mental rotation and typically occur between 400 and 800 ms after stimulus onset (Heil, 2002; Milivojevic, Johnson *et al*., 2003; Peronnet & Farah, 1989; Wijers *et al*., 1989). In the present experiment, the mental rotation ERP component was evident between 356 and 712 ms after stimulus onset. Therefore, processing leading to mental rotation was accomplished by 356 ms after stimulus onset, by which stage the entire P1-N1-

P2 visual-evoked-potential complex had been completed. I reasoned that since mental rotation of familiar objects should follow object recognition, the preceding VEPs can provide information regarding orientation specificity of neural mechanisms related to lower-level perceptual processing and object recognition. All three VEP components, the P1, the N1 and the P2, were sensitive to stimulus orientation but the pattern of orientation-dependence differed between the three components, and will be discussed in more detail below.

Experiment 3 was designed to test whether the effects of orientation on these early components were related to lower-level perceptual processing or to object recognition. In this experiment the category task was compared to a colour discrimination task involving the same stimuli, on the grounds that colour discrimination does not require the stimuli to be recognised. The EEG sampling rate was increased from 250Hz to 1000Hz to provide a more precise measure of the latency because the results from Experiment 2 indicated that stimulus orientation may also have an effect on the latency of the VEP components[8]. Additionally, the effect of orientation was examined at a more fine-grained orientation resolution by presenting stimuli rotated by 0°, ±30°, ±60°, ±90°, ±120°, ±150° and 180° in either clockwise or counter-clockwise orientations. If orientation effects are related to object recognition, then one might expect them to be present in the category task, but not the colour task.

P1, the oblique effect and orientation perception

The earliest component to be investigated was P1. Somewhat paradoxically, P1 was influenced by orientation in Experiment 2, but not in Experiment 3, even though the category task was used in both experiments, and one might expect early processing to have been the same in both the category task and the colour task. The orientation effect in Experiment 2 was best characterised by a quadratic function with larger P1 amplitudes in response to stimuli presented at oblique orientations (±60° and ±120°) than to stimuli presented at the vertical

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[8] Since sampling rate of 250Hz corresponds to an EEG measurement taken every 4 ms, it is likely to result in temporal smearing of EEG information.

orientations (upright and inverted). Since no difference was observed between upright and inverted stimuli, the effect of orientation on the P1 could be related to the oblique effect described in Chapter 1. W. Li and Westheimer (1997) suggested that perception of shape orientation is based on the principal axis of elongation rather than orientation of the parts of the shape. If this is the case then it follows that both the upright and inverted stimuli would have the same perceived orientation.

This can only be the case if the perception of shape orientation occurs prior to object recognition, since the discrimination between the upright and the inverted orientation would be dependent on identification of the direction of the top and bottom of the stimulus. In order to recognise which part of the stimulus is the top of the object, one must firstly know what the object is. Therefore, one must first recognise an object and then determine its orientation. The same reasoning stands for discrimination between stimuli rotated by 60° and 240° or by 300° and 120° in the clockwise direction from upright. The time to identify orientation is longer than the time to identify object identity (Corballis et al., 1978; DeCaro, 1998; DeCaro & Reeves, 2002). It is conceivable that stimulus orientation is initially extracted based on the orientation of the principal axis of elongation, and then, following object recognition, top-bottom direction can be "superimposed" on the orientation of the shape. If this is the case, then the effect of stimulus orientation on the P1 component may reflect the first instance of orientation perception based on the principal axis of shape elongation.

As mentioned in Chapter 1, the oblique effect is thought to originate in the primary visual cortex. It is unlikely that the striate regions are the sole generators of the P1 component. Some of the earlier attempts to source-localise this component have reported uniquely striate generators (Biersdorf, 1974), or striate and extrastriate generators (Darcey & Arj, 1980; Maier, Dagnelie, Spekreijse, & van Dijk, 1987). However, more recent attempts at source localisation have found that the P1 is generated by extrastriate regions only, primarily within BA18 or 19 (Clark, Fan, & Hillyard, 1995; Di Russo et al., 2002). However, preference for stimuli at cardinal orientations has also been observed in higher-order visual areas in the middle temporal (Xu *et al*., 2006) and inferior temporal (Orban & Vogels, 1998) cortices. Therefore, if the effects are related to stimulus obliqueness, the origin of this effect need not be the primary visual cortex.

It may seem counterintuitive that effects of obliqueness were manifest as increases in amplitudes, given that there are larger numbers of cells tuned to cardinal orientations, compared to any of the oblique orientations. There are two possible explanations for this. The first is that the tuning curves are wider for oblique than for cardinal orientations (B. Li *et al*., 2003), and thus the overall number of cells that respond to any particular orientation may result in a larger combined response. Alternatively, the orientation-sensitivity of the P1 may reflect a flow-on effect from the relatively poorer processing by the primary visual cortex. The increase in amplitude may act as a compensatory mechanism at a later visual processing stage, marked by the P1.

Experiment 3 had the potential to determine whether the effect of orientation on the P1 was related to stimulus obliqueness, since stimuli were presented at both the vertical (upright and inverted) and horizontal (±90°). If the amplitude of the P1 increased in response to oblique stimuli, than the amplitude of P1 would be smaller to stimuli presented at cardinal orientations (0°, ±90°, 180°) than to stimuli presented at oblique orientations (±30°, ±60°, ±120° and ±150°). Unfortunately, no effects of stimulus orientation were observed on either the amplitude or latency of the P1 component.

What is reasonably certain is that the orientation effects on the P1 component are not related to object recognition. Firstly, no difference was observed between upright and inverted stimuli, indicating that the top and the bottom of the stimuli have not been differentiated. Secondly, the P1 component is not sensitive to object type. Rossion *et al*. (2000) showed that, while distinct classes of objects, such as cars, houses and faces evoked different N1 amplitudes, no effect of object class was apparent over the P1. Therefore, the orientation-specificity of the P1 component must reflect perceptual processing preceding object recognition. This may either be related to perception of orientation or a flow-on effect from a disruption of lower-level visual processing related to the oblique effect.

N1, perceptual encoding, and object recognition

The second component investigated in this thesis was the N1. The effect of stimulus orientation on the amplitude of N1 component was observed in both Experiment 2 and 3. In both experiments, the amplitude of the N1 increased with misorientation, but the increase was smaller for inverted stimuli than for most other orientations. These results replicate findings from a previous mental-rotation study by Milivojevic, Johnson *et al.* (2003). Experiment 2 also showed that mirror-reversal and inversion increased the N1 response by about the same amount. Given that alphanumeric characters have a clear canonical orientation both for the left-right and top-bottom axes, these results suggest that mirror-reversal and inversion have a similar effect on neural processing. It is also of note that mirror-reversed characters do not elicit responses that differ from those to normal characters when the characters are presented upside-down, suggesting that parity information is lost with inversion. This observation supports the notion that decisions based on parity information, such as left-right or mirror-normal judgements, would require mental transformation to the upright. Experiment 3 also showed that the amplitude of the N1 increased gradually between 0° and 60°, remained relatively constant between 60° and 150° orientations, and then decreased slightly between 150° and 180° orientations.

Results from Experiment 2 and 3 indicate that the increase in amplitude in response to inversion, and mirror-reversal in Experiment 2, is smaller compared to the increase in amplitude in response to stimuli at other orientations ranging from 60° to 150° from upright, and in Experiment 3 stimuli at 30° orientation elicited N1 amplitudes comparable to those for upside-down stimuli. A possibility that the larger N1 amplitude evoked by the stimuli whose principal axis is not aligned to the upright characters may be related to a flow-on effect of earlier cortical processing was discussed in Chapter 4. This possibility is based on the results from Experiment 2 where obliquely presented stimuli elicited greater P1 amplitudes than the upright or inverted stimuli. This increase in processing may have resulted in increased processing demands at the subsequent processing stage reflected by the N1. However, the results from Experiment 3 do not support this interpretation given that similar pattern of orientation dependence was observed for the N1 amplitude, in absence of the P1 effects and that the stimuli presented at 30° orientation elicit amplitudes similar to those presented at 180°.

In Experiment 3, the enhanced sampling rate revealed latency differences, both as a function of stimulus orientation and hemisphere. The N1 in response to upright stimuli reached peak amplitude earlier on the right than on the left, but when the stimuli were inverted the N1 reached its peak earlier on the left. On the right, its latency increased gradually with increases in orientation up to 120° orientation and then decreased slightly at 150° and 180°. On the left, the latency of the N1 was similar for upright and inverted stimuli and increased up to 90° orientation.

The first thing to note here is that the amplitude of the N1 can be used to differentiate between upright and inverted stimuli, and between normal and mirror-reversed stimuli at upright. As already mentioned, to recognise which part of the stimulus is the top of the object, or whether it is normal or mirror-reversed, one must firstly know what the object is. It then follows that some level of object recognition has occurred by this processing stage.

I say "some level" because N1 amplitude is not always correlated with within-class differentiation; as an example, the N1 does not appear to be sensitive to face familiarity (Rossion *et al.*, 1999). Pernet et al. (2003) suggested that the N1 probably does not mark object recognition in the sense of matching to a long-term memory representation. Rather, it may represent the perceptual encoding processing stage at which a stimulus driven mental representation is generated prior to a match to a memory representation (Pernet *et al.*, 2003). However, Jacques and Rossion (2006) have shown that the N1 responses mark a stage at which individual representations of faces are activated. Therefore, it is possible that the N1 marks a stage immediately prior to a memory matching stage that is nevertheless influenced by object identity.

As K. H. James and colleagues (2005) noted, it seems reasonable that extensive experience with alphanumeric characters would result in plastic changes within the visual system, that would enable efficient recognition of these characters. There is some evidence to support this view. Just as pictures of faces and scenes elicit increased activation in proximal areas within the ventral stream, the fusiform face area and parahippocampal place area respectively, so have alphanumeric characters been shown to elicit activation in specific subregions of the ventral stream (K. H. James & Gauthier, 2006; K. H. James *et al.*, 2005; Polk & Farah, 1998).

Furthermore, Wong, Gauthier, Woroch, De Buse and Curran (2005) showed that alphanumeric characters also elicit an increased N1 amplitude in comparison to either Chinese characters or visually-similar letter-like symbols on the left. They also showed that both the alphanumeric characters and Chinese characters elicit increased N1 amplitudes in comparison to letter-like symbols in Chinese-readers. These results indicate that letter perception has a similar electrophysiological correlate to that of face perception, in the sense that it elicits a clear N1 that can be used to differentiate between known symbols and visually similar symbols.

In this sense, it may be worth comparing the current findings to those reported in the face-perception literature. Evidence indicates that both the amplitude and the latency of the

N1 increase with stimulus inversion. These effects are thought to reflect a disruption of configural object processing (Rebai *et al*., 2001; Rossion *et al*., 2000). Although the effects of stimulus inversion on the amplitude and the latency of the N1 are best documented with face stimuli (e.g. Rossion *et al*., 2000), there some evidence that indicates that the amplitude of the N1 also increases with inversion of complex objects such as cars and words (Rebai *et al*., 2001; Rossion *et al*., 2003).

Few studies have investigated the effects of orientation on ERPs to misoriented objects at larger number of orientations. Jeffreys (1993) did this with faces, and observed that the vertex-positive potential (VPP) is modulated with rotation of the faces from upright. The latency of this potential increased gradually up to 120° point and decreased slightly between 120° and 180° orientations. Although some authors have argued that the VPP is not related to the N1, more recent accounts suggest that the VPP is a polarity-reversed form of the N1 (Joyce & Rossion, 2005). However, in my previous work (unpublished findings), the effect of face rotation on the N1 to faces showed similar pattern to the current results, with larger N1 increases in response to stimuli presented at ±60° and ±120° orientations than for inverted faces.

In a more recent study, Jacques and Rossion (2007) investigated the effects of face orientation on amplitude of the P1 and the N1 components. They also examined correlations between the ERP effects and behavioural performance on a delayed face-matching task. Participants viewed pictures of faces presented at 12 orientations ranging between 0° and 330° at 30° increments. The participants were required to decide whether two sequentially presented faces were the same or different. The faces were always at same orientation as each other, and only the ERPs in response to the first face were examined. The RTs and error rates increased as a function of face orientation between 0° and ±120°, while no further increase was observed between ±120° and 180° orientations.

Jacques and Rossion (2007) found that the amplitudes and the latencies of both the P1 and the N1 components increased as a function of orientation. For the P1 component, both the latencies and the amplitudes were larger at ±90° orientations and smaller for 0° and 180° orientations, with a sharp increase in amplitude between ±30° and ± 60° orientations, and a more gradual increase for the latency measure between 0° and 90° orientations.[9] Furthermore, the effects of orientation on the P1 component did not correlate with the effects of orientation on either RTs or error rates suggesting that the effects of orientation on the P1 component were not related to stimulus recognition or perceptual encoding of the stimulus.

In terms of the N1 component, Jacques and Rossion (2007) observed a sharp increase in both amplitude and latency of the N1 between 0° to 90° on both the left and the right sides. On the left no further increase in either of these measures was observed between 90° to 150° and a small decrease in amplitude only was observed from 150° to 180° orientations, while on the right latencies and amplitudes continued increasing up to the 150° orientation, and were followed by a dip at 180° orientation. Furthermore, both the amplitude and the latency effects were highly correlated with orientation-dependent deficits on delayed-matching task. Despite the correlations between the latency and amplitude measures, and between both of these measures and behavioural effects, Jacques and Rossion (2007) argued that the effects of orientation on the latency and amplitude of these components do not necessarily reflect the same neural processes. They suggested that the latency effects reflect slower accumulation of neural activity. They related the amplitude effects to recruitment of additional cortical regions on processing, as suggested by functional neuroimaging studies (e.g. Haxby *et al*., 1999).

The results from the present thesis also indicate that the effects of orientation on amplitude and latency are not the same. Effects of orientation on the amplitude of the N1 were characterised by a stronger quadratic trend which explained approximately 77-78% of the

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[9] It might be worth noting here that the effect of orientation on the amplitude of the P1 in this study (Jacques & Rossion, 2007) is similar to the pattern observed in Experiment 2 for the amplitude of the P1.

variance in Experiments 2 and 3, and a weaker linear trend which explained approximately 21% of the variance in Experiment 2 and 14% of variance in Experiment 3. Furthermore, the effects of orientation on the amplitude of the N1 did not differ between the hemispheres. In contrast, the effects of orientation on the *latency* of the N1 differed between the hemispheres. On the left, the effect of orientation was characterised by a quadratic trend, which accounted for approximately 85% of variance. On the right, the effect of orientation was characterised by a linear trend, which accounted for approximately 58% of the variance, and a quadratic trend, which accounted for 36% of the variance.

These effects of orientation on the latency of the N1 may bear on hemispheric asymmetries related to holistic and feature-based recognition mechanisms. The right hemisphere is thought to subserve holistic or configural processing, while the left subserves feature-based or piecemeal processing (Bradshaw & Nettleton, 1981). The non-linear increases in N1 latency with rotation from upright on the right can be interpreted as increases in the time needed to recruit sufficient neural activity for recognition of the overall shape. In contrast, increases in N1 latency with rotation away from the orientations in which the top-bottom axis is aligned to the canonical orientation (i.e. upright and inverted) can be interpreted as increases in the time needed to recruit sufficient neural activity for feature-based recognition mechanisms. The orientation-dependence on the left could be related to misalignment between the internal descriptions of feature configurations and the feature configurations of the input image, as suggested by Hummel and Biederman (1992). Feature-based processing may be more similar between the upright and inverted stimuli because the vertical axis is in alignment for stimuli presented at these two orientations. Additionally, the largest disparity occurs if an object is rotated by 90° in either the clockwise or counter-clockwise direction because the vertical axis is maximally misaligned from the canonical orientation. In this situation, information regarding the object-centred descriptions – in terms of locations of individual features relative to each other – would be inconsistent if these descriptions are in terms of above/below and next-to attributes (as per Hummel & Biederman, 1992). Misalignment of 90° between the vertical axes of the internal and the stimulus would results in above/below attributes being perceived as next-to attributes, and the next-to attributes would be perceived as above/below attributes.

Therefore, non-linear increases in N1 latency with rotation from upright on the right can be interpreted as increases in the time needed to recruit sufficient neural activity for recognition of the overall shape. In contrast, increases in N1 latency with rotation toward the ±90° orientation, could be interpreted as increases in time needed to recruit sufficient neural activity for recognition based on feature extraction. This interpretation would then suggest that both feature-based and holistic object recognition mechanisms are recruited and operate in parallel. This provides some support for Jolicoeur's (1990) dual-route hypothesis. However, in contrast to Jolicoeur's hypothesised involvement of mental rotation for whole-shape recognition, the results from this thesis suggest that the right hemisphere is involved in holistic recognition that depends on stimulus orientation away from upright, while the left hemisphere is involved in shape recognition based on feature identification.

The N1 component is thought to be an ERP correlate of neural activity in the inferior temporal cortex (Jacques & Rossion, 2007; Pizzagalli, Lehmann, Hendrick, Pascual-Marqui, & Davidson, 2002; Rossion et al., 2003). Therefore, it may be useful to consider the present results in the context of what is known about orientation-specificity of neurons in the inferior temporal region. Perrett *et al.* (1998) have provided detailed accounts of the response properties of orientation specificity in response to faces and bodies. I have mentioned that these stimulus types are thought to engage configural processing mechanisms more than other classes of objects (e.g. Bruce *et al.*, 1991; Carey, 1992; Farah *et al.*, 1995; Freire *et al.*, 2000; Reed *et al.*, 2003; Tanaka & Farah, 1993). However, work by Logothetis and colleagues (Logothetis, Pauls, Bulthoff, & Poggio, 1994; Logothetis *et al.*, 1995; Logothetis & Sheinberg, 1996) suggests that similar orientation-specificity can be observed for novel three-dimensional shapes. The majority of object-responsive neurons in the inferior temporal cortex are preferentially responsive to a particular viewpoint (or orientation) of that object, although there are neurons that also respond to objects in a viewpoint-invariant manner (Perrett *et al.*, 1998).

The number of neurons that respond to a particular viewpoint of the object is also dependent on experience with the object at that particular viewpoint. Therefore, if an object is most commonly viewed upright, then more orientation-sensitive cells will respond preferentially to that object when it is upright, compared to other orientations. In the case of alphanumeric characters, the largest number of neurons should be responsive to their canonical representations which have a well defined top-bottom and left-right orientation. Furthermore, some neurons also show mirror-image equivalence, whereby an object rotated by 180° in depth will elicit activation of the same neural responses as the one not rotated in depth. In the case of alphanumeric characters, though, where the parity information is critical, one might expect more parity-specific cells than for other classes of objects, where parity is less important. Perrett *et al.* (1998) argued that the RT cost associated with object misorientation arises because a smaller neural population would require more time to elicit sufficient neural activity for object recognition. Therefore, it may be reasonable to suppose that the effects should be observed in terms of latency, rather than in terms of amplitude. The response pattern of the orientation-sensitivity of the N1 observed over the right-hemisphere in Experiment 3 is in line with that prediction.

Somewhat paradoxically, misorientation of the characters elicited an increase of the amplitude of the N1. I say paradoxically because if the above interpretation is correct, then one might expect that a larger neural population would also summate to produce larger amplitude. Given that an increase in amplitude of the N1 is commonly observed with face inversion, the present results could similarly indicate that the increase in amplitude of the N1 is related to an increased difficulty of processing misoriented stimuli or recruitment of additional cortical regions within the ventral stream (Rossion *et al*., 1999).

Alternatively, the amplitude pattern observed for the N1 in Experiments 2 and 3 might be explained by wider tuning curves for neurons selective to non-canonical letter orientations, and for neurons selective to off-vertical orientations. The mechanism I propose here would stem from relatively independent, or at least additive, neural processes. One of these processes would be related to changes in the orientation relative to the canonical upright. The width of the tuning curves would depend on visual familiarity with the particular stimulus at a specific orientation. Orientation-sensitive neurons have relatively broad tuning curves and respond maximally to the middle orientation (Logothetis et al., 1994; Logothetis et al., 1995; Logothetis & Sheinberg, 1996; Perrett et al., 1998). As the object is rotated away from the preferred viewpoint, the neural firing rates decrease. The tuning curves of individual cells may also be dependent on experience with that view. This is based on the finding that perceptual learning of line segments results in narrowing of the tuning curves within the primary visual cortex (Schoups, Vogels, Qian, & Orban, 2001). Thus, the canonical view of a particular object should not only have the maximal number of orientation-specific cells but these neurons should also have the sharpest tuning curves for that orientation. If the tuning curves are narrower at the most commonly observed stimulus orientations, upright normal characters, then only the cell-assemblies responsive to that orientation will fire when that stimulus is presented. In contrast, if they are wider for stimuli at less common orientations, then cell-assemblies responsive stimuli at, say 60° orientation, would also be responsive to objects presented at adjacent orientations, such as 30° and 90°.

The second process I propose would be related to the relative obliqueness of the stimulus, based on the principal axis of elongation. Orban and Vogels (1998) have shown that vertically oriented stimuli have narrower tuning curves than stimuli presented at off-vertical orientations. If tuning curves are narrower for vertically oriented stimuli, then inverted stimuli would automatically have narrower tuning curves than stimuli presented at off-vertical orientations (i.e. orientations other than normal or mirror-reversed characters presented at upright or inverted orientations).

Such a mechanism would explain increases in amplitude of the N1 in response to both mirror-reversal and inversion as reflecting wider tuning curves for non-canonical orientations, but not involve increases in amplitude due to wider tuning curves for off-vertical orientations. Increases in amplitude for stimuli presented at orientations between 30° and 150° would reflect wider tuning curves for stimuli presented at off-vertical orientations *and* wider tuning curves for stimuli presented at non-canonical orientations.

P2 and combining orientation and object information

The effects of orientation on the P2 component were right lateralised for both Experiment 2 and 3, and differed between the tasks in Experiment 2. In Experiment 2, the effects for the parity task were best characterised in terms of linear increases in amplitude with increase in orientation, although a smaller quadratic trend was also apparent, while the effects for the category task were best characterised by a larger quadratic and smaller linear trend. For both tasks, the upright characters elicited the smallest P2 amplitudes, and amplitudes increased with stimulus orientation up to 120° from upright. For the category task, the amplitude of the P2 component decreased for inverted stimuli, while for the parity task the amplitude of the P2 elicited by stimuli presented at 120° and 180° orientations was similar. It is also of note that, in the parity task, the amplitude of the P2 was larger for mirror-reversed than for normal characters at upright and 60° orientation, an effect that was also right lateralised. This observation indicates that the cognitive processes marked by the P2, at least in the parity task, provide information regarding stimulus orientation primarily in reference to the canonical position, i.e. normal, upright characters. It is possible, therefore, that the modulation of the P2 amplitude in the parity task reflects recognition of the degree of stimulus misorientation in reference to the canonical stimulus orientation, which may be a necessary step prior to mental transformation.

If this is the case, then the modulation of P2 amplitude for the category task may also index the recognition of stimulus orientation. Orientation perception in this case may depend on both the top-bottom axis inversion and any additional changes in orientation, such as a tilt away from the canonical orientation of the top-bottom axis. The amplitude increase would be characterised by an increase with inversion in addition to an increase with misalignment of the top-bottom axis from the vertical. Although no behavioural correlates of these effects were observed with the current stimulus set consisting of overlearned alphanumeric characters, this interpretation would fit well with the observation that recognition of stimuli may be easier when the stimuli are inverted than when the stimuli are presented at orientations around the 120° point. Even though no significant task-by-orientation interaction was observed in Experiment 3, the pattern of orientation effects for the category task was similar in Experiments 2 and 3, with increase in amplitude up to 120° orientation and decrease in amplitude for 150° and 180°. For the colour task, peak P2 amplitude was evoked by stimuli at 90° orientation.

Hemispheric asymmetries were observed over the P2 component, with considerably more pronounced orientation effects over the right hemisphere. The orientation effects were best characterised by a quadratic function on the left and a combined linear and quadratic trends over the right. The left-hemispheric effects were not replicated in Experiment 3. The results from Experiment 3 also indicated that the latency of the P2 component is also modulated by changes in orientation over the right hemisphere, but not the left. The effect on latency of the P2 was attributable to the delay in the N1.

As previously discussed, there is some evidence that P2 reflects configural processing (Boutsen et al., 2006; Milivojevic, Clapp et al., 2003), although this evidence is based on face-perception experiments. Nevertheless, if this is an accurate interpretation, then lateralisation of P2 effects could reflect right-hemispheric specialisation for holistic encoding. It seems reasonable to suppose that the processing of holistic information would depend on the orientation of the stimulus, while processing of constituent features may be achieved in an orientation-invariant manner.

For the parity task, the holistic information could be used to assess the degree of misorientation from the canonical position. As noted earlier, object orientation assignment should follow object recognition (Corballis, 1988; Corballis et al., 1978; DeCaro, 1998; DeCaro & Reeves, 2002). I also suggested that an early, pre-recognition sense of orientation might be extracted from the orientation of the principal axis of elongation, and reflected in the P1 component. A full understanding of orientation, following object recognition, might, then, require top and bottom to be "superimposed" on this initial impression. If this is the case, then the effect of stimulus orientation on the P2 component may reflect the second step in orientation perception based on mapping of object identity on the principal axis of shape elongation.

A possibility remains that the quadratic trend within the SMG observed for the fMRI activation in the SMG is related to the P2 effects. The P2 amplitude increase with stimulus orientation was observed for both the parity and the category tasks. If P2 amplitudes at intermediate orientations are interpolated, based on the present results, the orientation functions would appear similar between the ERP and fMRI results. There are problems with this interpretation. Firstly, no lateralisation effects were observed for the fMRI results, while the ERP results were right-hemisphere dominant. Secondly, fMRI results show a decrease in amplitude at intermediate orientations while the ERP results show an increase in amplitude. Finally, a quadratic trend was observed for both the category and the parity tasks in Experiment 1, while the effects of orientation on the parity task in Experiment 2 had a linear component. Additionally, in Experiment 1, a linear *decrease* in amplitude for the parity task was observed in a cluster within the SMG, adjacent to, but not overlapping with, the cluster that showed quadratic modulation.

It is possible that this discrepancy could be resolved by conceptualising the P2 amplitude increase as suppression of a negative-going latent component elicited by stimuli that are presented at the canonical position. The source of this negative component may be the portion of SMG that was identified in Experiment 1. Thus, maximal negativity would be observed for stimuli presented at the canonical upright, or closely aligned with the vertical axis of elongation (i.e. upright or inverted). Reduction of this negativity would correspond to changes in orientation. In Experiment 1, an adjacent portion of the SMG also showed linear decreases in BOLD signal for the parity task. Thus, the effects of orientation on the P2 amplitude for the category and the parity task may not originate from an identical cortical region, but rather, an adjacent one.

Pernet *et al.* (2003) investigated the effect of visual familiarity and discriminability on the posterior N2 defined as a dip following the P2 component. Pernet *et al.* (2003) argued that this component is related to visual categorisation of the stimuli – highly familiar stimuli that were easily categorised, such as faces or letters, elicited greater N2 while unfamiliar stimuli or stimuli that were harder to categorise, such as Chinese characters or "texture" blocks, showed smaller or no N2. Although not specifically investigated as an N2, the P2 component in the current thesis could reflect a negative-going wave, concurrent with the P2. Note also that the amplitude of the P2 for the colour-judgement task was significantly greater than for the category task. The functional contribution of this latent component may signal whether task-relevant information is available. For the category task, the category assignment would be easiest, and elicit the largest negativity when the characters are presented at the upright orientation, and decrease with rotation away from this position up to 120° and then increase when the stimuli are inverted, mimicking the M-shaped function. For the parity task, a match to the memory representation of the characters would be the easiest when normal characters are presented at either 0° or 60°. The reduction in this negative-going wave would signal that the stimulus may need additional processing, i.e. transformation to upright, before it can successfully be matched to a parity-specific memory representation, which may explain why the mirror-reversed characters presented at 0° or 60° would also be transformed.

Mental rotation

Experiment 1 and 2 revealed that only the parity task elicited behavioural, neurophysiological and BOLD signal correlates of mental rotation. These experiments replicate the well established mental-rotation correlates of RTs and ERPs, and extend the neuroimaging literature on mental rotation by providing evidence that BOLD signal amplitude also increases with increased angular departure from upright. The RTs for both Experiment 1 and Experiment 2 show linear increases with stimulus rotation from upright, although the rates of rotation differed somewhat between the two experiments. On average, the rates of rotation in Experiment 1 were approximately 577°/s while in Experiment 2 the rates of rotation were approximately 363°/s. This difference probably reflects the fact that the selection criteria for participants in Experiment 1 were partially based on their ability to perform the parity task within the 2-second trial duration. The time limit in Experiment 2 was considerably longer, 10 seconds, and selection of the participants was largely based on their ability to perform the task accurately.

As described earlier, Experiment 1 showed linear increases in the BOLD signal with stimulus orientation, suggesting mental rotation, in several brain areas. The linear increases in the medial part of the dorsal IPS confirm the well established findings that PPC is involved in mental rotation (e.g. Alivisatos & Petrides, 1997; Cohen *et al*., 1996; Harris *et al*., 2000; Koshino *et al*., 2005; Podzebenko *et al*., 2002; Richter *et al*., 1997; Seurinck *et al*., 2005). The involvement of anterior insula is a novel finding. There is some evidence that alphanumeric categorisation, recognition and discrimination all involve insular regions (Joseph *et al*., 2006; Pernet *et al*., 2004) and it plays a role in speech articulation (Dronkers, 1996).

The involvement of the parietal lobe in mental rotation is largely confirmed in Experiment 2, where the ERP in the parity task was characterised by increases in parietal negativity with larger angular rotations from upright between 356 and 712 ms. This is consistent with previous evidence (Heil, 2002; Heil *et al*., 1998; Johnson *et al*., 2002; Milivojevic, Johnson *et al*., 2003; Peronnet & Farah, 1989; Wijers *et al*., 1989). These increases in negativity, however, coincide with a LP positivity elicited by stimulus recognition, a P3-like component (Wijers *et al*., 1989). Thus the distribution of the ERP waveforms over that time period does not show absolute parietal negativity at any of the stimulus orientations. However, as seen in Experiment 2, the amplitude of the slow parietal negativity increases monotonically as a function of the angular disparity of stimuli from the upright position, mirroring the RT results and suggesting that this ERP component is closely tied to the neurophysiological operations underlying mental rotation (see Heil, 2002 for a review). The problem arises from the fact that the mental-rotation component is identified on the basis of a reduction in P3-related negativity from the baseline condition, usually the ERPs in response to upright stimuli. Therefore, the information subsequent to the response in the baseline condition becomes unusable as an adequate baseline, because the period of mental rotation is now compared to “doing nothing”. Thus, the mental-rotation component will be restricted in time by the baseline condition, and the distribution of the effects is possibly more informative about which areas show a decrease in positivity rather than a net increase in negativity.

Analysis of the BOLD signal in Experiment 1 clearly shows a linear function of orientation in lateral and medial pre-motor areas, whereas there was no evidence for frontal involvement in mental rotation from the analysis of ERPs in Experiment 2. In previous EEG experiments, too, this effect is almost always restricted to the parietal leads (Milivojevic, Clapp *et al*., 2003; Muthukumaraswamy *et al*., 2003; Pegna *et al*., 1997; Yoshino *et al*., 2000). Scalp topography in EEG studies provides little information regarding the anatomical localisation of the underlying cortical generators. The predominantly parietal distribution of the mental rotation effects may reflect both frontal and parietal contribution, depending on the orientation of the generating dipoles.

Nevertheless there are a few exceptions. Lamm and colleagues (Lamm, Fischmeister, & Bauer, 2005; Lamm *et al*., 2001) used a cube-matching paradigm thought to elicit mental rotation and showed increases in negativity over both parietal and frontal leads when recording slow cortical potentials. Furthermore, using a modified version of the Shepard and Metzler task (1971), Silberstein, Danieli, and Nunez (2003) found synchronisation of coherence in the upper alpha range between the frontal and the parietal sites. And in another study, Klimesch, Sauseng, and Gerloff (2003) found that TMS stimulation at subject-specific upper-alpha frequency over both parietal and frontal locations improved mental-rotation performance, which suggests that a fronto-parietal network subserves mental rotation. Therefore, EEG studies employing different methods have found EEG-correlates of mental rotation over the prefrontal regions.

Frontal-lobe involvement, when it occurs, may have more to do with increasing attentional demands than with the mental-rotation process itself. Carpenter *et al*. (1999) have attributed activation within those regions to eye movements or shifts of attention between simultaneously presented stimuli, as is typically the case in paradigms using torus shapes. However, given that our paradigm involved single stimulus displays, it is highly unlikely that the higher order pre-motor activation was due to shifts of attention or eye movements, unless mental rotation is also accompanied by eye-tracking of the imagined motion of the top of the stimulus. Nevertheless, mental rotation has been reported to be impaired following either left (Mehta & Newcombe, 1991) or right (Ditunno & Mann, 1990) damage to the PPC, or by neurodisruptive methods, such as TMS or deep cortical stimulation (Bestmann, Thilo, Sauner, Siebner, & Rothwell, 2002; Feredoes & Sachdev, 2006; Harris & Miniussi, 2003; Zacks et al., 2003) but is apparently unaffected by lobotomy of either the left or the right prefrontal cortex (Alivisatos, 1992). However, to my knowledge, there have been no studies applying TMS to the higher-order premotor regions identified in the current study. Therefore, a possibility remains that impaired mental rotation performance would be observed following stimulation to these areas, and the issue about frontal involvement in mental rotation remains unresolved.

Hemispheric asymmetries in mental rotation

As we have seen, analysis of the BOLD signal in Experiment 1 provided no evidence for any hemispheric asymmetry in mental rotation. This result supports some earlier research showing a lack of cerebral asymmetry in mental rotation tasks (e.g. Carpenter et al., 1999; Cohen et al., 1996; Jordan et al., 2001; Just et al., 2001; Podzebenko et al., 2002), but is contrary to other evidence that mental rotation depends largely on the right (e.g. Harris et al., 2000), or the left hemisphere (e.g. Alivisatos & Petrides, 1997).

Experiment 2 provides a partial reconciliation of conflicting evidence. In that study, the analysis of ERPs suggested that the differences between hemispheres is in terms of the relative durations of mental-rotation processes, rather than in relative amplitudes. Such differences would not be apparent in the BOLD signal, which is relatively impervious to the timing of events. Specifically, the ERP analysis suggested that the right hemisphere may perform mental rotation faster than the left, as indicated by the relatively shorter duration of mental rotation effects over the right hemisphere. Although the right hemisphere appears to be faster than the left, the amplitudes of these effects do not differ between the hemispheres. These results would then indicate that both hemispheres are involved in mental rotation, starting at the same time and recruiting a comparable degree of neural processing, although the operation continues for longer in the left.

This finding might explain at least some of the discrepancies reported in the literature regarding hemispheric asymmetries in mental rotation. For example, in a TMS study, Harris and Miniussi (2003) reported increase in RTs to an alphanumeric parity task following stimulation over the right IPS, but not over the left IPS, or a control, midline parietal, site. They interpreted these results as indicating that the right hemisphere is dominant for mental rotation and that stimulation within the right IPS selectively delays mental rotation performance. However, TMS stimulation did not affect accuracy of responses, implying that participants were still able to perform the task. It is possible, therefore, that the increase in RTs following right IPS stimulation was caused by continued mental rotation by the relatively slower left hemisphere. An alternative may be that mental rotation was disrupted following right hemisphere stimulation, and that the right hemisphere continued the transformation following recovery from TMS stimulation.

Mental rotation and parity discrimination

The results of Experiments 1 and 2 offer continued support for the view that people mentally rotate stimuli to the upright prior to discriminating them from their mirror images. For some stimuli, such as alphanumeric characters, one form is the standard version while its mirror image is anomalous, and is much more rarely seen than its standard counterpart. In these cases there is characteristically an additional delay in responding to the mirror-image version than to the standard version. While this might result simply from the greater familiarity of the standard version, it has also been suggested that mental rotation may play an extra role in identifying the mirror-image. Thus Hamm *et al.* (2004) found that the neurophysiological correlates of mental rotation for mirror-reversed characters were temporally delayed in comparison to the effects observed for normal characters, and that these effects can be attributed to mental rotation of mirror-reversed characters out of the picture plane. That is, participants effectively flip mirrored characters over, presumably to verify that they are indeed mirrored.

Experiment 2 provided some support for this model. RTs to mirror-reversed characters were systematically longer than those to normal characters across all orientations. However, the rate of rotation out of the picture plane, as estimated by the difference in RT between normal and backward characters, was approximately 823°/s, which is considerably faster than the rates of rotation through the picture plane, of about 363°/s. Although Shephard and Metzler (1971) claimed that rotation rates within and out of the picture plane are the same, Murray (1997) showed that rotations out of the picture plane are indeed faster than rotations within the picture plane. Additional support for this claim is the observation that both the effects of increases in stimulus orientation, and difference between normal and mirror-reversed characters elicit increases in parietal negativity which start at about 350 ms after stimulus onset.

It is perhaps not clear why deciding whether a character presented at upright is normal or mirror reversed would require mental rotation to the canonical position. As discussed earlier, Experiment 2 showed that parity-specific neural activation is observed as early as the N1 ERP component. At this stage, the N1 amplitude is larger for mirror-reversed than for normal characters at upright. Subsequently, the P2 amplitude is larger for mirror-reversed than for normal characters at upright and 60° orientations for the parity-judgement task only. These effects are attenuated when the stimuli are rotated from upright, indicating that the characters need to be rotated to upright before parity-discrimination can be made.

Nevertheless, parity-specific neural activity is present prior to onset of mental rotation in the parity task. Therefore, it still remains unclear as to why one would need to rotate a mirror-reversed character out of the picture plane prior to deciding whether it is normal or mirror-reversed. It is possible that the neural activity preceding mental rotation signals that the characters are misoriented, either by mirror-reversal or by rotation in the picture-plane, rather than specifically signalling the specific orientation or parity of the characters. For both the N1 and the P2 components, there is no difference between mirror-reversed upright characters and both versions of inverted characters.

It is possible that the ventral stream, although sensitive to stimulus orientation (and parity), does not code for spatial position of an object in reference to the observer. This function could be coded by the dorsal visual stream (Hummel & Biederman, 1992; Priftis et al., 2003; Turnbull & McCarthy, 1996; Warrington & Davidoff, 2000). Therefore, the dorsal stream may use the information supplied by the ventral stream to decide whether a stimulus needs to be rotated and in which direction. If the dorsal stream codes for parity-specific object-information, then rotation out of the picture plane may be used as a check that the mirror-reversed character indeed matches a memory representation of the known character.

Summary and Conclusion

The main aim of this thesis was to characterise the neural events involved in the processing of rotated objects. Alphanumeric characters were chosen as the objects for study, because they are highly familiar, have a clear canonical orientation and parity, and are two-dimensional. A parity task, in which participants were asked to decide whether the characters were normal or backward, was used to investigate the neural correlates of mental rotation, and a category task and a colour discrimination task were used to investigate the earlier processes of perception and character recognition that precede mental rotation. Functional MRI was used to identify the principal anatomical areas involved, followed by EEG analysis of the successive stages of processing.

The results confirmed that mental rotation was restricted to the parity task, but showed also that visual processing preceding mental rotation is dependent on stimulus orientation at several processing stages. The first processing stage was assessed with the P1 component, and probably reflects lower-level visual processing associated stimulus orientation based on principal axis of elongation. At this stage increased processing demands may be required by obliquely presented stimuli. The second processing stage was assessed by the N1 component and is likely to reflect the initial stages of object recognition. At this stage, object misorientation may result in increased processing demands associated with perceptual encoding of the stimuli, as effects appear to be stimulus-driven. This conclusion is supported by the observation that the effects were elicited by the colour-judgement task – a task that did not require recognition, although it is possible that the participants may have been unable to suppress recognition. The final processing stage preceding mental rotation was marked by the P2 component. This stage may somehow be related to orientation perception in reference to the canonical position. Instead of an increase in amplitude with misorientation, I suggested that the effects of orientation may reflect an increase in a latent negative-going wave originating from the SMG.

With respect to mental rotation itself, there were two main questions of interest. The first question was whether activity associated with mental rotation was restricted to the PPC, or whether other brain areas are involved. In Experiment 1, the BOLD signal revealed activity associated with mental rotation in the anterior insula, which is a new finding. It also showed activity in the lateral and medial premotor areas, but this was not evident in the EEG analyses. Therefore, a possibility remains that the prefrontal activation may be a result of prominent anatomical connections between the PPC and the pre-motor areas, given that in some cases anatomically-connected cortical regions will show co-activation even if only one of those areas is actively involved in the task (Rorden & Karnath, 2004). What seems certain is that, based on the results in the present thesis, it is difficult to attribute activation within the parietal lobe to mental rotation *per se* and within the higher-order pre-motor areas to processes other than mental rotation. Secondly, there has been conflicting evidence over whether mental rotation is accomplished preferentially by one or other hemisphere. In Experiment 1, the BOLD signal revealed no evidence for cerebral asymmetry associated with mental rotation, but EEG analysis in Experiment 2 suggested that mental rotation was accomplished more quickly in the right than in the left hemisphere. This finding might help reconcile some of the earlier conflicting evidence.

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