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The neurobiology of object constancy

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The Neurobiology Of Object Constancy

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This thesis is submitted in part fulfilment of the degree of Doctor of Philosophy,
completed at the Centre for Cognitive Neuroscience,
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Abstract

'Object constancy' is the name given to the brain's ability to overcome the myriad environmental obstacles to visual perception and produce a stable, consistent internal representation of object shape. Changes in object orientation represent one such confound. It can be inferred from the time taken to recognise misoriented objects that we encode specific object views based on our experience of those objects and their typical orientations ('viewpoint-dependent recognition'). Such studies also suggest that we may recognise certain objects in a manner that is not dependent on their orientation ('viewpoint-invariant recognition'). Further studies indicate that the time to resolve two angularly disparate shapes ('mental rotation') increases as a function of their angular disparity. It is hypothesised, based on these findings, that viewpoint-dependent recognition and mental rotation share a common mechanism for transforming the global stimulus percept into alignment, but that viewpoint-invariant recognition is achieved by some other, non-transformational means. This thesis presents studies that examine the cortical correlates of viewpoint-dependent and viewpoint-invariant object recognition using novel objects to eliminate the confounding effects of prior experience. It also presents a study that directly compares the cortical correlates of mental rotation, viewpoint-dependent and viewpoint-invariant recognition. Further comparison of these object constancy processes is then made using electrophysiological markers of visuospatial transformation. The findings of these studies indicate that viewpoint-dependent recognition and mental rotation recruit a bilateral parietal-premotor network for the manipulation of global stimulus percepts, hypothesised to be the same mechanism as that used for physical object manipulation and prehension. Viewpoint-invariant recognition does not appear to recruit such a mechanism, and this process appears to be less expensive in terms of cognitive resources than transformational object constancy mechanisms. Thus, implementation of a viewpoint-invariant mechanism to recognise misoriented objects is preferable, but may not be possible where stimulus features are few or ambiguous. In recognising misoriented objects, viewpoint-dependent and viewpoint-invariant mechanisms initially proceed in parallel, but successful recognition of object invariant features may be sufficient to terminate the viewpoint-dependent mechanism.

General introduction

One of the most basic requirements of the visual system is to perceive objects in a manner that preserves information about those objects - a function essential to a consistent account of our environment and our own progress within it. That we achieve this at all is quite remarkable, since as a result of visual saccades and head or body movement, the pattern of light falling on the retinal surface is in constant flux; yet the visual system successfully interprets it as a stable, consistent, three-dimensional environment. We also manage to extract information from this ever-changing retinal illumination that enables us to recognise objects previously encountered at different orientations (a phenomenon known as object – or shape – constancy) and varying distances (size – or scale – constancy). This problem is illustrated in Figure 1.

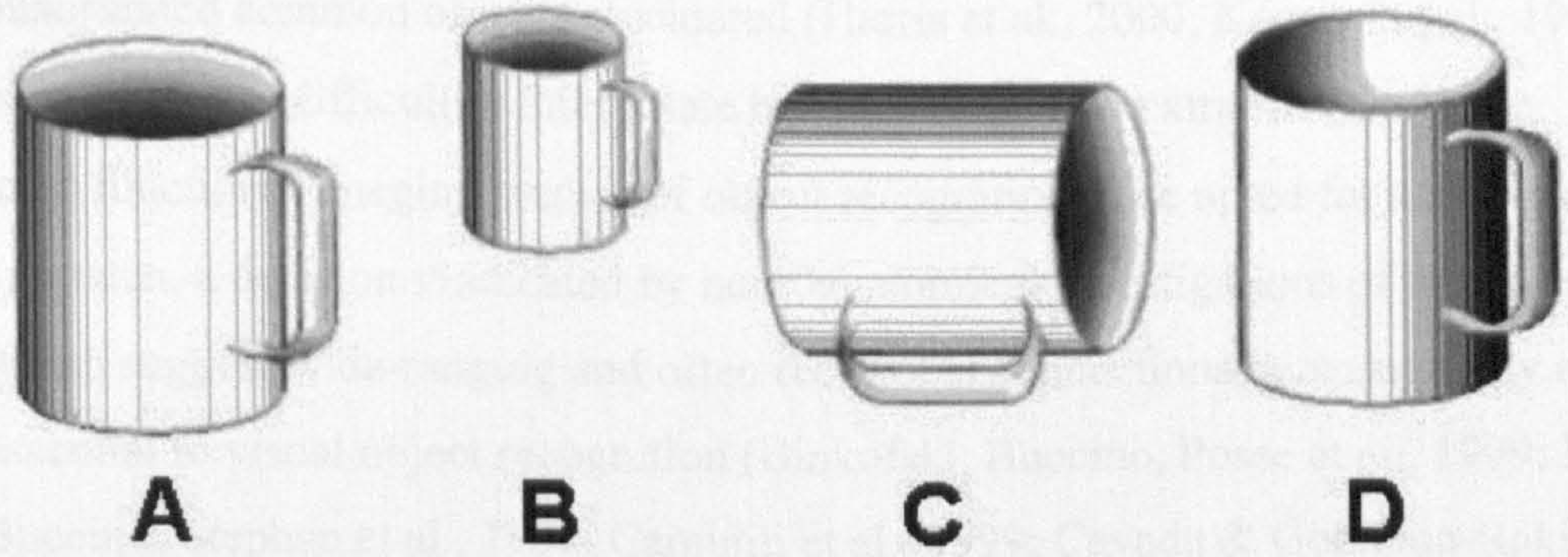

Figure 1. Encounters with object (A) at different distances (B), different orientations (C), and in the presence of different light sources (D). All such changes will affect the retinal image, which must somehow be resolved with the original stored representation (A) for recognition to take place.

The aim of the present thesis is to use functional imaging techniques and behavioural measures to elucidate the cognitive and neuroanatomical bases of visual object constancy, specifically those processes recruited during the perception of misoriented stimuli. One way of determining how the visual system achieves this is to study the time taken to identify misoriented familiar objects or learned novel objects. While there is evidence to suggest that object recognition is dependent on the object's orientation (Cooper & Shepard, 1973; Jolicoeur, 1985, 1990; Tarr & Pinker, 1989, 1990) (so-called 'viewpoint-dependence'), the existence of 'viewpoint-invariant' mechanisms may also be inferred from studies showing that the time taken to identify certain misoriented objects is not dependent upon orientation

(Biederman, 1987; Corballis, Zbrodroff, Shetzer, & Butler, 1978; Tarr & Pinker, 1989, 1990). A second paradigm commonly encountered in the literature is 'mental rotation', in which two novel two- or three-dimensional stimuli presented simultaneously or sequentially must be compared to determine some structural congruency such as whether they are identical or mirror-images of each other (Just & Carpenter, 1985; Koriat & Norman, 1985; Pierret & Peronnet, 1994; Shepard & Metzler, 1971). An overview of the psychometric literature investigating object constancy across changes in stimulus orientation forms the basis of Chapter 1 of the present thesis.

One of the main problems inherent in any study of functional neuroanatomy lies in reconciling empirical observation at microscopic and macroscopic levels. For example, although neuronal encoding of line-orientation has been documented (Hubel & Wiesel, 1959; Kim, Duong, & Kim, 2000) and the main cortical regions involved in the perception of misoriented common objects elucidated (Harris et al., 2000; Kosslyn et al., 1994; Sugio et al., 1999), it is difficult to interpolate between these two extremities of scale. In practice, most functional imaging studies of object recognition have opted for a macroscopic approach, a decision vindicated by neuroanatomical investigations of the macaque brain which suggest wide-ranging and often reciprocal connections between many areas of cortex essential to visual object recognition (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999; Caminiti et al., 1999; Cavada & Goldman-Rakic, 1989; Murata et al., 1997; Ungerleider & Mishkin, 1982; Webster, Bachevalier, & Ungerleider, 1994). Recent developments in functional imaging, and the inherent adaptability of such techniques to resolving issues in cognitive psychology, mean that functional imaging studies form the largest contribution to Chapter 2 of this thesis, which discusses recent attempts to extrapolate the neuroanatomical correlates of misoriented object recognition and mental rotation.

Although there is some evidence to suggest that viewpoint-invariant and viewpoint-dependent visual processes may recruit different areas of cerebral cortex (James, Humphrey, Gati, Menon, & Goodale, 2002), no prior studies have compared directly the cortical correlates of viewpoint-dependent and viewpoint-invariant misoriented novel object recognition[1]. Chapters 3 and 4 of this thesis describe two functional magnetic resonance imaging (fMRI) studies that attempt to clarify and compare the neurobiological and cognitive bases of these two object constancy processes. A second unresolved issue in object constancy is whether the similar pattern of response-times that characterises studies of viewpoint-dependent recognition and mental rotation is indicative of a single visuospatial transformation mechanism common to both processes, or whether these are in fact functionally distinct mechanisms (Lawson & Jolicoeur, 1999). This question is addressed in Chapter 4, which compares the cortical regions recruited by mental rotation, viewpoint-dependent and viewpoint-invariant recognition.

The field of electroencephalography (EEG) has also contributed to our understanding of the neurobiological mechanisms underpinning object constancy. Previous studies, reviewed in Chapter 5 of this thesis, identify temporally-sensitive electrophysiological markers (event-related potentials – ERPs) associated with the visuospatial transformation process believed to underpin mental rotation (Inoue, Yoshino, Suzuki, Ogasawara, & Nomura, 1998; Muthukumaraswamy, Johnson, & Hamm, 2003; Yoshino, Inoue, & Suzuki, 2000). Chapter 5 presents a study that attempts to replicate these ERP markers of visuospatial transformation. This marker is then used to assess the extent to which visuospatial transformation also underpins viewpoint-dependent and viewpoint-invariant object recognition, and so clarify the nature of these object constancy processes.

Chapter 6 reviews the results of each of these studies and then discusses the conclusions that can be drawn from them regarding the neurobiology of object constancy, and the nature of its constituent cognitive processes.

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[1] The use of novel stimuli in misoriented object recognition tasks is an important consideration in any study of object constancy, since the more popular paradigm of misoriented common object recognition may be criticised on the grounds that there is no way of controlling for prior exposure to stimuli, and, by inference, for the manner in which stimulus representations become encoded. This issue is discussed further in subsequent chapters.

Chapter 1

1. A Review Of Psychometric Studies Investigating Mental Rotation And The Perception Of Misoriented Stimuli.

1.1 Introduction

In seeking to understand object constancy, it is necessary to consider the way in which we visually obtain information about objects. Whether for the purposes of recognition or merely determining whether two novel stimuli are identical, object information must be extracted from the current pattern of light falling on the retina and be compared against some other, previously acquired, representation. Marr (1982) proposed that the process of visual perception involved the extraction of 'object primitives' from the raw, grey-scale retinal image, representing a transition from analogue to symbolic object representation. He proposed that acquisition of object primitives would permit the construction of more elaborate, surface-based object representations, ultimately leading to the identification of feature conjunctions and thence entire objects. In fact, the exact nature of the information we extract from the retinal image has been widely debated: it may relate to the identification of global features such as an object's major axis (Humphreys & Riddoch, 1984; Marr, 1982; Marr & Nishihara, 1978; Tarr & Pinker, 1989, 1990), or to local features of the object, such as that first proposed in Selfridge's Pandemonium model (Biederman, 1987; Biederman & Gerhardstein, 1993; Selfridge, 1957; Selfridge & Neisser, 1960; Thacker, Riocreux, & Yates, 1995). The quality and nature of information available, discussed in subsequent sections, may determine the mechanism by which objects are successfully recognised. Regardless of the type of information obtained from the retinal image percept, the process of comparing this information against a stored internal representation is likely to involve transformations of size[2] and/or orientation: at the very least, information about retinocentric coordinates must be integrated with stored structural object descriptions if a comparison is to be made.

Psychometric investigations of how the human brain reconciles object information in the retinal image (or 'percept') with stored information in memory have generally pursued two main avenues – recognition of misoriented familiar objects, and comparisons between two angularly disparate novel objects (mental rotation). This chapter describes key findings in these areas of study and their implications for theories of object constancy.

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[2] A discussion of the computation of size-transformations is beyond the scope of this thesis. Interestingly, there is plenty of evidence to suggest that transformations in size, like transformations in orientation, elicit proportional increases in RT, and that these increases, as for orientation, are dependent not on absolute, but *relative* size (Bundesen & Larsen, 1975; Cave & Kosslyn, 1989; Larsen & Bundesen, 1978). However, evidence of size-invariant recognition mechanisms has also been claimed in one instance (Biederman & Cooper, 1992).

1.2 Transformational object constancy mechanisms

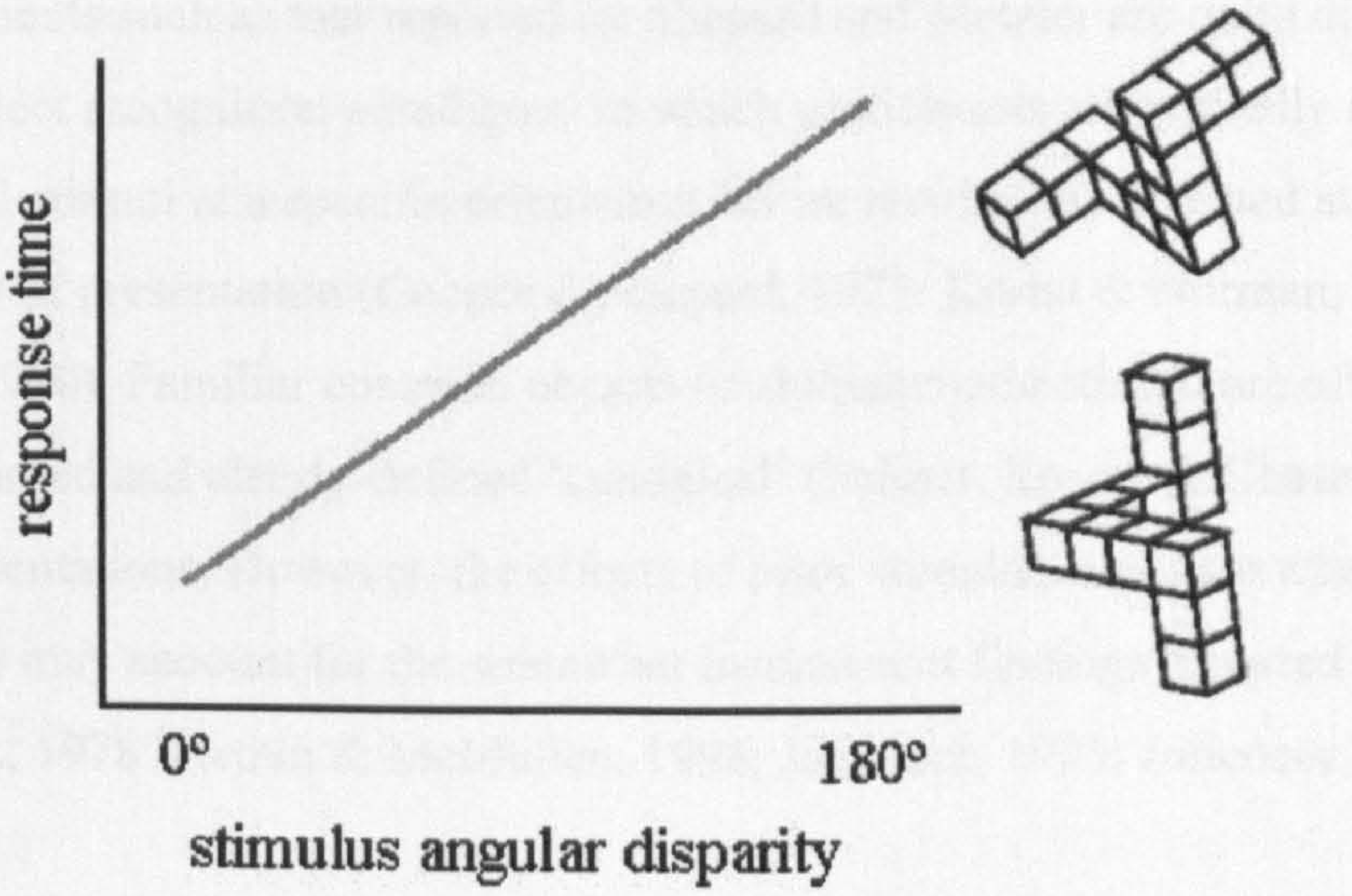

Figure 2. The relationship between stimulus angular disparity and response-time in a mental rotation task. Examples of the type of stimuli used are shown. This relationship was found to persist for angular disparities requiring alignment in the image plane, and those requiring alignment in depth. After Shepard and Metzler (1971).

1.2.1 Mental rotation

'Mental rotation' is best defined in regard to a classic study by Shepard and Metzler, who asked participants to decide whether two line-drawn three-dimensional (3-D) figures were identical or mirror-images (i.e., to make a parity judgement). It was found that mental alignment of two such stimuli into congruence took proportionally longer with greater angular disparity between the figures (to a maximum of 180°), and that this was true of disparities resolved in the picture-plane and those resolved in depth (Shepard & Metzler, 1971). The relationship between angular disparity and response-time (RT) reported by Shepard and Metzler is illustrated in Figure 2 and has since been widely replicated. The effect of stimulus angular disparity on response-time is theorised to reflect a mechanism wherein one or both global stimulus percepts undergo visuospatial transformation until they align (Bartram, 1976; Cook, Fruh, Mehr, Regard, & Landis, 1994; Just & Carpenter, 1985; Koriat & Norman, 1985; Pierret & Peronnet, 1994).

1.2.2 Viewpoint-dependent recognition of misoriented stimuli

Experiments such as that reported by Shepard and Metzler are quite distinct from misoriented object recognition paradigms, in which participants are typically required to memorise novel stimuli at a specific orientation before recognition is tested at several different angles of presentation (Cooper & Shepard, 1973; Koriat & Norman, 1989; Tarr & Pinker, 1989, 1990). Familiar common objects or alphanumeric stimuli are often used, having well-learned and clearly-defined 'canonical' (Palmer, Rosch, & Chase, 1981) – that is, upright – orientations. However, the effects of prior stimulus exposure when using familiar objects may account for the somewhat inconsistent findings reported by such studies (Corballis et al., 1978; Hamm & McMullen, 1998; Jolicoeur, 1985; Jolicoeur, Snow, & Murray, 1987).

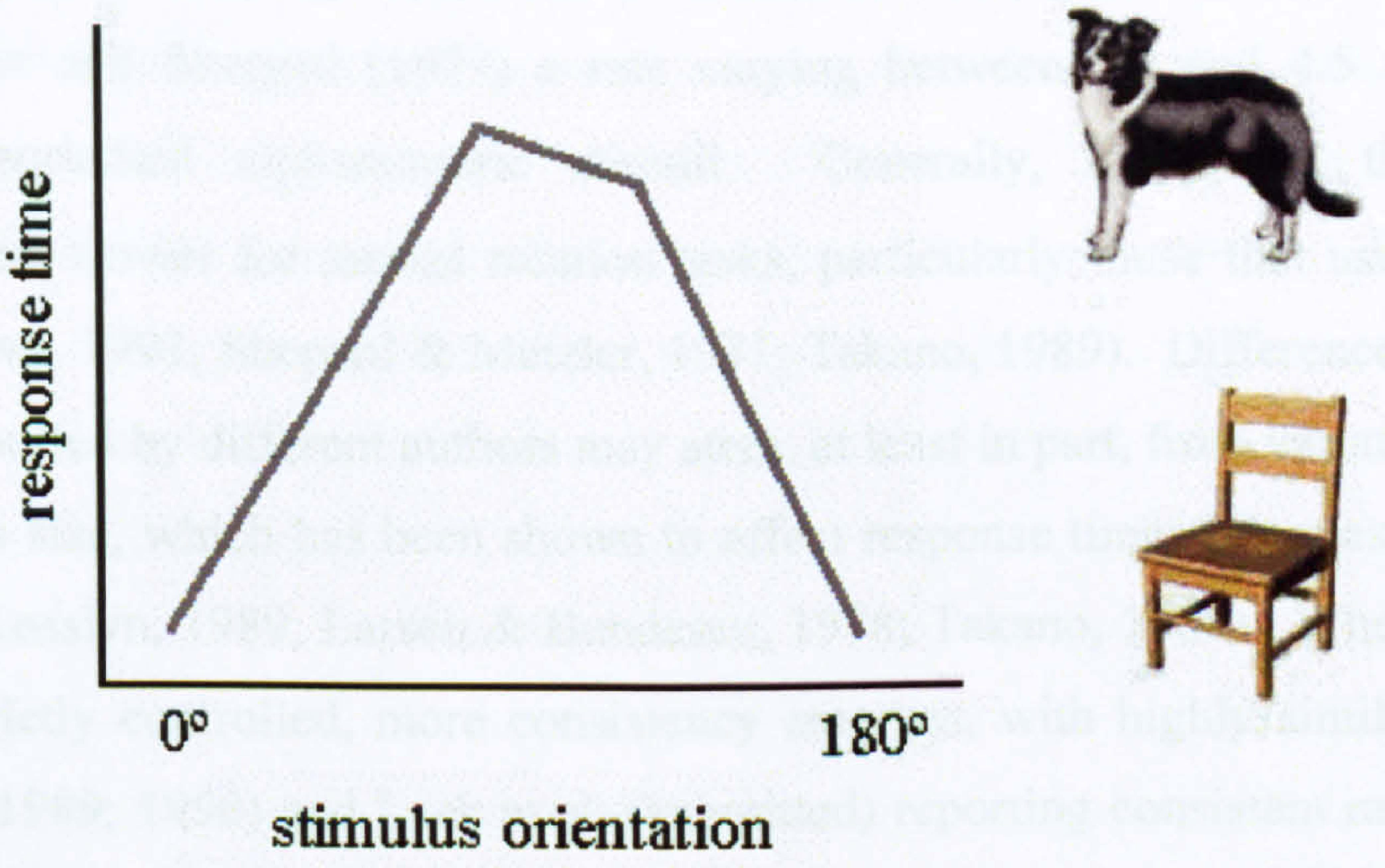

Figure 3. The relationship between the orientation of common objects and the time taken to name them. Examples of the types of stimuli used are shown. After Jolicoeur (1985).

Such studies (see Figure 3 for one example) are often found to evoke a pattern of 'orientation-dependent' recognition times, with RTs greatest when objects are at or near 180° from their normal canonical orientation[3] (Cooper & Shepard, 1973; Hamm & McMullen, 1998; Jolicoeur, 1985; Murray, 1995, 1999; Murray, Jolicoeur, McMullen, & Ingleton, 1993;

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[3] Several authors have noted a tendency for RTs elicited by objects viewed at 180° to be less than would be predicted from RTs to objects at lesser degrees of misorientation (Corballis et al., 1978; Jolicoeur, 1985; Lawson, 1999; Rock, 1973). Rock (1973: cited in Jolicoeur, 1985) posited that the left-right distribution of object features is less perturbed at 180° than at lesser angles, thus rendering the recognition of stimuli that are precisely upside-down more straightforward.

Tarr & Pinker, 1989, 1990). This effect of stimulus orientation on response-time seems likely to reflect global transformation of the stimulus percept in the 'visual buffer' (Kosslyn, 1980) in order to match it against stored shape representations. Misoriented object recognition is thus somewhat different from mental rotation, since the latter does not require access to long-term object representations and is presumed to involve the maintenance of stimulus percepts in the visual buffer strictly on a short-term basis until resolution is achieved.

1.2.3 Distinguishing between mental rotation and viewpoint-dependent recognition

It would appear that mental rotation and viewpoint-dependent recognition tasks evoke at least superficially similar patterns of response-times. However, the rates at which misoriented object recognition and mental rotation are performed may vary considerably – Shepard and Metzler (1971) reported a rate of around 17 ms/degree in their mental rotation task, and Cooper and Shepard (1973) a rate varying between 0.9 and 4.5 ms/degree in recognising misoriented alphanumeric stimuli. Generally, it appears that rates of transformation are slower for mental rotation tasks, particularly those that use 3-D stimuli (Cohen & Kubovy, 1993; Shepard & Metzler, 1971; Takano, 1989). Differences in the rates of resolution reported by different authors may stem, at least in part, from variation in factors such as stimulus size, which has been shown to affect response times (Bundesen & Larsen, 1975; Cave & Kosslyn, 1989; Larsen & Bundesen, 1978; Takano, 1989). When the type of task is more strictly controlled, more consistency emerges, with highly similar studies by Tarr & Pinker (1989; 1990) and Leek et al. (submitted) reporting consistent rates of around 2.4 ms/degree in response to misoriented 2-D novel objects. The exact point at which the regression slope of RT versus angle becomes sufficiently shallow to imply that no transformation of the stimulus percept is taking place has been discussed extensively (Cohen & Kubovy, 1993; Takano, 1989), though a vague consensus emerges that rates of less than 1 ms/degree are too fast to be representative of a transformational process (Cohen & Kubovy, 1993; Corballis et al., 1978; Tarr & Pinker, 1989).

It is therefore important, when comparing mental rotation and misoriented object recognition tasks, to consider whether 2-D or 3-D stimuli are employed. Mental rotation tasks of the Shepard and Metzler type characteristically use line-drawn 3-D objects (which can be rotated in the picture plane or in depth), whereas many studies of misoriented object recognition use 2-D stimuli (which can only be rotated in the picture plane). In fact, it has been established that rotations in the picture plane and those in depth produce very similar RT-curves (Shepard & Metzler, 1971), and there is evidence to suggest that misoriented 2-D and 3-D stimuli are processed by the visual system in a similar manner (Bulthoff, Edelman, & Tarr, 1995; Edelman & Bulthoff, 1992; Leek, 1998a; Tarr & Pinker, 1989). The additional complications presented by depth rotation of 3-D stimuli will be discussed in subsequent sections of this chapter.

There is some evidence to suggest that RTs from mental rotation and viewpoint-dependent recognition tasks reflect the recruitment of two distinct processes. For example, while mental rotation studies typically report a linear relationship between relative angular disparity and RT (Shepard & Metzler, 1971), the relationship between absolute stimulus orientation and recognition time is less clear (Lawson, 1999; Lawson & Jolicoeur, 1999). Support for the neuroanatomical separation of these two functions comes from studies of patients who, following brain damage to visual association cortex, show decrements in their ability to perform either mental rotation tasks of the Shepard and Metzler type or recognition of misoriented objects, but not both (Farah & Hammond, 1988; Turnbull & McCarthy, 1996). The neuroanatomy of both processes is addressed in Chapter 2; the extent to which these object constancy processes recruit a common transformational mechanism is explored in Chapters 4 and 5.

1.3 The internal representation of object shape

1.3.1 Visuospatial manipulation as an analogue of physical object manipulation

The broadly linear effect of orientation or angular disparity on the time taken to make a recognition or congruence decision can be interpreted as evidence of an internal mechanism for visuospatial manipulation that is subject to the same sorts of constraints as its real-world analogue: the greater the angular disparity, the more time required to complete the transformation. Mental rotation has thus previously been described as a smooth analogue function (Cooper, 1976; Shepard & Cooper, 1982), although this claim – somewhat contentious at the time – was never conclusively resolved (Palmer, 1999). Several authors have nonetheless argued that the constraints of object perception are readily transferred to their corresponding internalised representations. For example, size, spatial transformation, and complexity of mental images have all been found to affect the speed at which they are evoked (Cooper, Schacter, Ballesteros, & Moore, 1992; Kosslyn, 1975), and possible and impossible objects have been found to differentially affect priming (Schacter, Cooper, Delaney, Peterson, & Tharan, 1991). Perhaps the most persuasive observation is that the time taken to mentally rotate stimuli is consistent with the *actual* time such a movement would take, and that such RTs are consistent with biomechanical constraints on the hand and arm movements required to perform such an action (Parsons & Fox, 1998). Thus, the storage of internal shape representation may be presumed to conform to a coordinate system analogous to the Cartesian coordinates used to describe 3-D space (Palmer, 1999).

Further support for an internal analogue of physical spatial manipulation can be found in studies that have used blind participants. Studies replicating the Shepard and Metzler mental rotation paradigm with congenitally blind participants, using a tactile rather than visual task, have identified the same linear relationship between angular disparity of stimuli and RT (Carpenter & Eisenberg, 1978; Marmor & Zaback, 1976) as that described by Shepard and Metzler. Visuospatial transformation of the kind required by mental rotation tasks, far from being vision-specific, may therefore be underpinned by a modality-free coordinate reference frame (Marmor & Zaback, 1976). Interestingly, blindfolded, sighted children have been found to perform better on tests of tactile mental rotation than visually impaired children (Millar, 1976). This may constitute additional evidence for a modality-free mechanism of spatial transformation, since sighted children might reasonably be expected to gain more passive experience of visuospatial transformation than non-sighted children absorb passively in the tactile modality. Further evidence for such a non-modality-specific mechanism comes from a similar study comparing blind and sighted (but blindfolded) participants on a tactile mental rotation task (Rosler, Roder, Heil, & Hennighausen, 1993). The authors found similar patterns of electrophysiological activity in both participant groups, and activity was localised to areas of cortex implicated by other studies in the mental rotation of visually-presented stimuli (see Chapters 2 and 5). Most tellingly, Rosler et al. found no significant differences between results from congenitally and adventitiously blind participants, functional differences between whom might be expected if mental rotation was modality-specific. However, although the parsimony of a modality-free system for object manipulation is attractive, it has been demonstrated that estimations of the relationships between objects in space is considerably restricted among congenitally blind, relative to sighted, individuals (Arditi, Holtzmann, & Kosslyn, 1988), suggesting that the results of studies using blind participants to elucidate the nature of internalised spatial representations may not necessarily generalise to the general population.

1.3.2 Frames of reference and the viewpoint-dependent nature of stored representations

A stored object description, whether in long-term memory or in the visual buffer, must necessarily occupy some coordinate reference frame (or 'frame of reference') if its component features are to be locatable with reference to each other –otherwise, objects with identical features in different configurations would be indistinguishable. Stored object descriptions therefore also need to encode the relative orientation of object features. One way for the visual system to achieve this might be through an egocentric, viewpoint-centred reference frame in which information about an object's spatial characteristics is stored with respect to the observer's point of view – for example, a mug is judged to be 'upright' when its major axis of symmetry is aligned perpendicular to the horizon (the horizon itself being stable relative to the observer). This system of representation could be said to be 'viewpoint-dependent'. Rock described such a framework, based on the retinal coordinates of objects, as the 'retinal factor', suggesting that internal representation of shape is made with reference to an external (i.e., environmental) reference frame: specifically, one that aligns 'frame of reference' vertical with 'environmental' vertical, such that the force of gravity pulls directly downwards (Rock, 1973, 1974).

Evidence that we store viewpoint-dependent object representations comes from studies of misoriented object recognition. A classic study by Jolicoeur showed that the time taken to classify line-drawings of familiar objects (for example, different types of dogs: e.g., collies, retrievers, dachshunds, etc) increased as a factor of their misorientation (Jolicoeur, 1985). This finding is interpreted as providing strong evidence that internal stored representations of objects are viewpoint-dependent: that is, information about objects is encoded according to their canonical orientation relative to the observer, and identification of misoriented objects thus necessitates some time-dependent transformation of the stimulus percept to match the canonical stored representation (a viewpoint-dependent mechanism). Studies of misoriented object recognition positing the existence of such mechanisms point to the mainly linear correspondence between RTs and object misorientation, a finding that appears to be consistent for two- and three-dimensional stimuli (Bulthoff & Edelman, 1992; Cooper & Shepard, 1973; Edelman & Bulthoff, 1992; Leek, 1998b; Tarr & Pinker, 1989, 1990). However, there is a paradox inherent in transforming the percept of an as-yet unrecognised object to a more familiar orientation in order to recognise it, in that one cannot know the object's correct orientation until it has been recognised. Tarr and Pinker (1989) have suggested that this is not necessarily paradoxical, proposing that identification of a small number of orientation-invariant object features, prior to performing visuospatial transformation of the stimulus percept, may indicate the direction in which such transformation may most usefully proceed. However, this explanation does not address why, if orientation-invariant features are available, viewpoint-invariant recognition does not then take place.

1.3.3 Canonical object views

As well as studies of the time taken to recognise misoriented objects, evidence that we store specific, viewpoint-dependent views of objects can also be found in the clinical neuropsychology literature. For example, it has been demonstrated that patients with parieto-occipital lesions frequently lack the ability to match pictures of everyday objects at their canonical orientations with pictures of those same objects encountered from unusual viewpoints, a condition known as the 'unusual views deficit' (Warrington & Taylor, 1973). One interpretation of these findings is that neurones encoding viewpoint-dependent representations of objects at non-canonical orientations (see section 1.5) have been damaged in some way, resulting in failure to recognise non-canonically-oriented objects. An alternative explanation is that while viewpoint-dependent processing itself is intact, the area of the brain mediating the transformation between the object's 'unusual view' and its canonical view has been damaged, leaving the patients unable to resolve these two angularly disparate representations. (The results of a later study, which described patients with deficits in matching different object views *and* who suffered from impaired recognition of canonically-oriented objects, are rather more ambiguous (Warrington & Taylor, 1978).)

Our tendency to encode specific object views seems likely to derive from ecological experience. Objects in our environment are subject to the laws of gravity, which dictate that only certain positions and orientations are stable (continuing the example of the mug, this clearly cannot balance on its handle but must be either upright, upside-down, or on its side). We therefore view many of the objects we encounter at relatively few orientations, with some of those orientations being particularly likely. Repeated exposure to the most common views of an object may increase the probability of encoding that object's stored representation in a viewpoint-dependent manner (Leek, 1998b). Studies investigating what constitutes a good 'canonical' object view tend to show high consistency among participants, supporting the idea that frequently-encountered object views have a higher probability of being regarded as canonical (Palmer et al., 1981; Perrett, Harries, & Looker, 1992). It has also been proposed that the visual system retains a certain flexibility for the interpretation of familiar objects at near-canonical orientations (Koriat & Norman, 1985). This would be a sensible strategy if the mental transformation of misoriented stimuli is as computationally expensive as has been suggested (Thacker et al., 1995). However, an alternative perspective comes from a study which described the case of a brain-damaged patient able to determine when stimuli were upright, but unable to relate their orientation when they were not – despite suffering no deficit in identifying the stimuli, which included letters, objects, and faces. The authors interpreted this as evidence that we store canonical (viewpoint-dependent) representations, positing that as we typically encounter most objects at very specific (canonical) orientations, a greater number of neurons become tuned to the object features visible at those orientations (Karnath, Ferber, & Bulthoff, 2000).

1.3.4 Multiple stored views and the recognition of depth-rotated objects

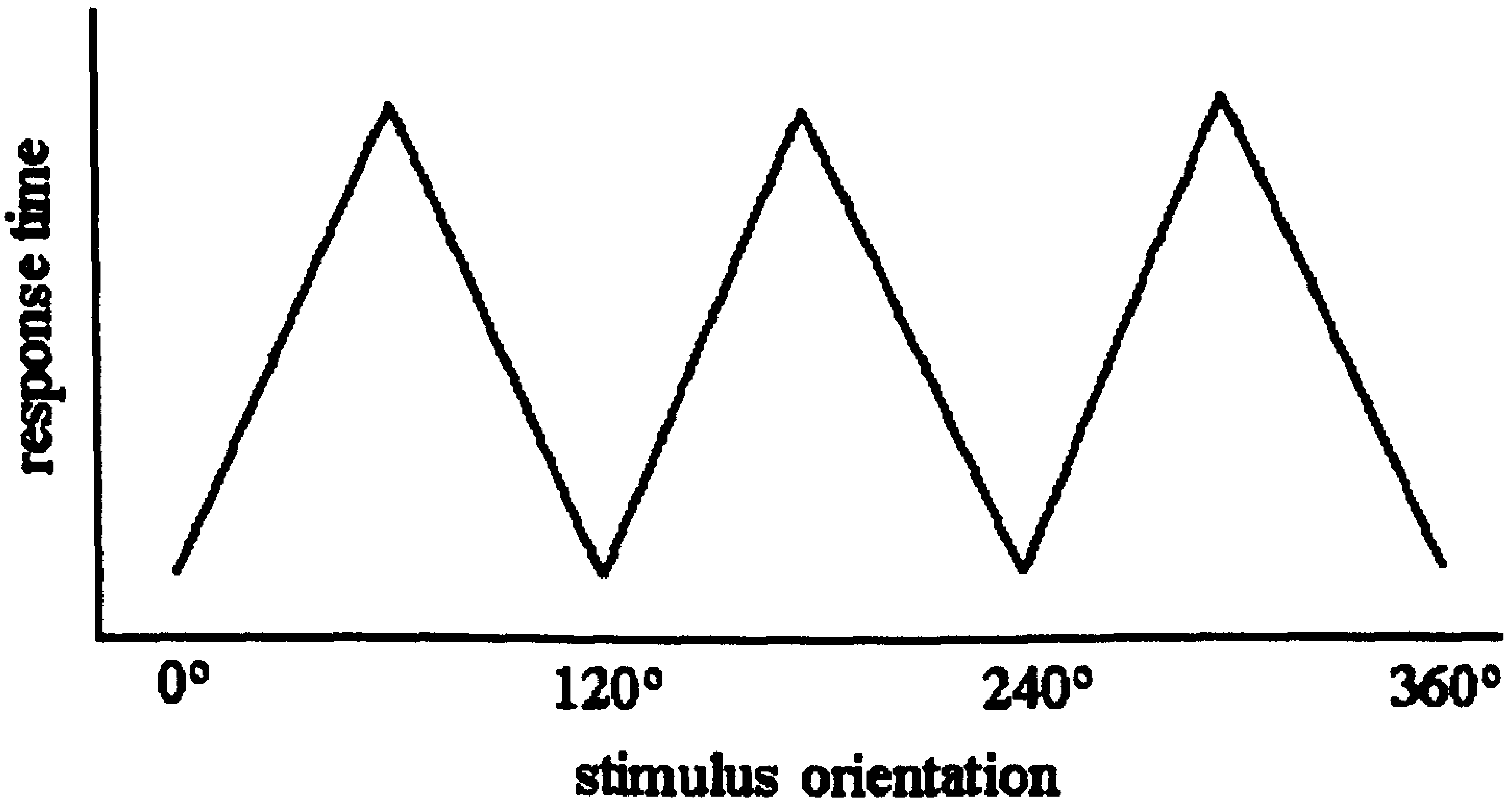

Figure 4. Hypothetical data illustrating the relationship between RT and stored object orientations (in this case at 0°/360°, 120° and 240°). After Leek, 1998.

Related to storage of canonical object views is the idea that we may store multiple object representations, where several differently-oriented object views are stored and the observer transforms the visual percept to that which is most closely aligned (Bulthoff et al., 1995; Leek, 1998a; Tarr & Pinker, 1989). Figure 4 illustrates the type of behavioural data (as outlined by Leek, 1998a) that have led to the formation of this model. Lawson (1999) observes that empirically separating the multiple viewpoints and transformational (or mental rotation) approaches is extremely difficult, since the former relates to storage issues but the latter concerns a dynamic cognitive process, and most experiments must necessarily test both simultaneously.

The idea that the visual system would naturally store multiple representations of an object from different viewpoints becomes more appealing when considering 3-D objects, which constitute a more ecologically valid type of stimulus. The selection of isometric canonical views in the identification of 3-D objects makes sense when one considers the variation in information content as an object rotates out of the picture-plane. While object rotation within the picture-plane results in no loss but merely a spatial transformation of the available information, any rotation in depth will result in significant loss of feature-information and corresponding acquisition of new object information from a previously unseen view. Thus, selection of an isometric view enables us to retain known information about the front of a shape while hedging our bets from a second angle too.

Empirical evidence suggests that three-dimensional objects may be internally represented as several overlapping views. Interpolation between previously encountered views of three-dimensional novel objects has been found to be possible within a practiced range, although this interpolation apparently fails when objects are viewed at orientations outside that range (Edelman & Bulthoff, 1992; Humphrey & Khan, 1992). This observation led to the proposal that three-dimensional objects may be represented as a collection of two-dimensional 'aspect graphs', with similar object views linked by their common (overlapping) features (Bulthoff & Edelman, 1992; Bulthoff et al., 1995). This would be consistent with speculation by computational theorists that a neural network would require many object views – of the order of tens – to successfully interpolate between them and achieve recognition (Ashbrook, 1996). Thus, at least superficially, the internal representation of 3-D shapes appears to be similar to the manner in which 2-D objects are represented.

1.4 Non-transformational object constancy mechanisms

1.4.1 Viewpoint-invariance

Response-time studies implicate an alternative object constancy process, distinct from the viewpoint-centred reference frames implicit in canonical or multiple-views approaches. It can be shown that, under certain conditions, response-times to line-drawn objects do not increase proportional to the shapes' misorientation, but remain constant (Biederman, 1987; Biederman & Gerhardstein, 1993; Cave & Kosslyn, 1993; Corballis et al., 1978; Tarr & Pinker, 1989, 1990). One such finding is illustrated in Figure 5.

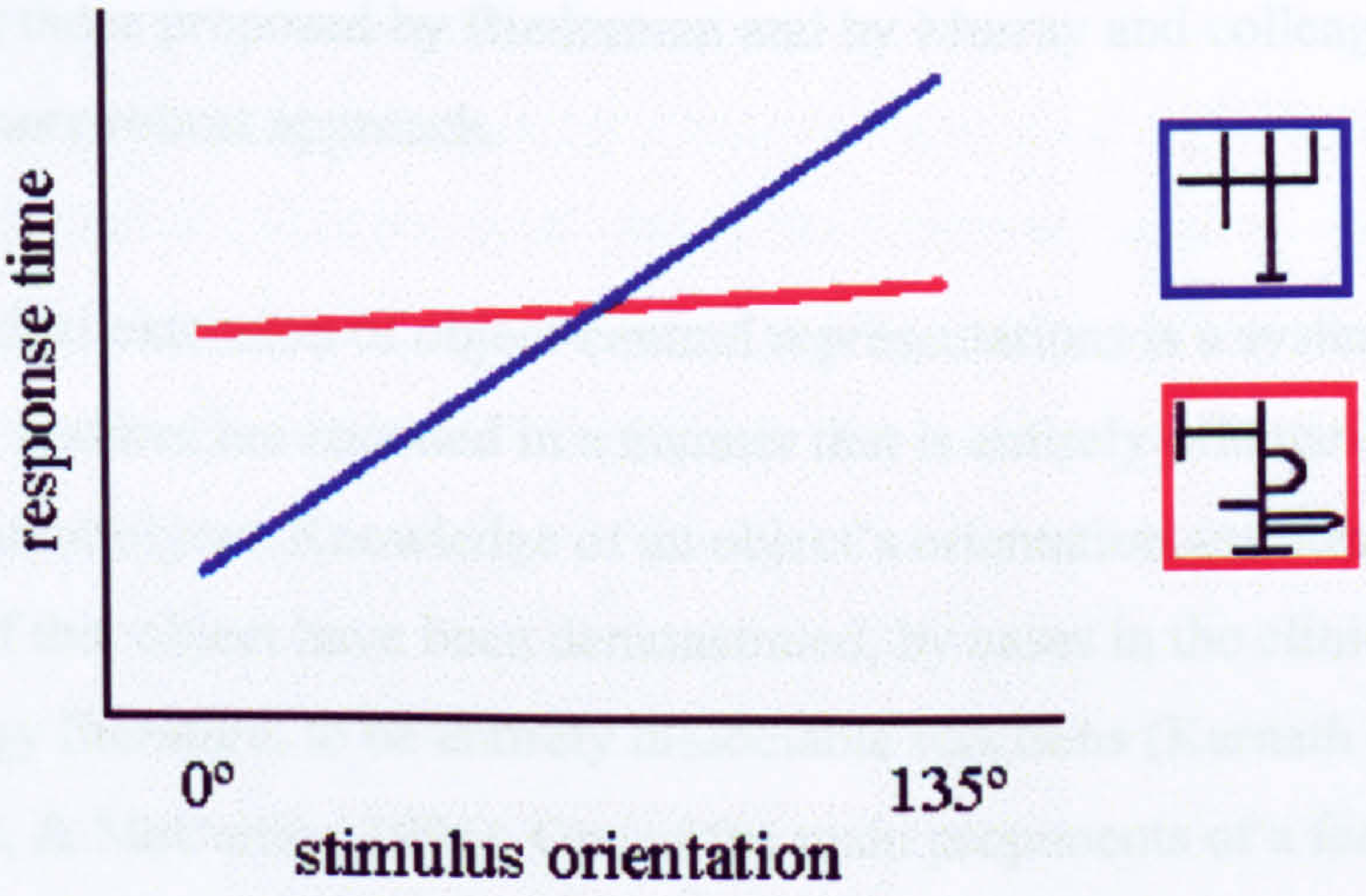

Figure 5. It is possible to infer the existence of viewpoint-dependent and viewpoint-invariant recognition mechanisms from response-times (RTs) to learned novel objects with different feature characteristics. Here, 'orientation-dependent' RTs are elicited by the blue class of shapes, whereas misorientation of the red class of shapes results in RTs that can be described as near-'orientation-invariant'. After Tarr and Pinker (1990).

Studies such as these infer the existence of a mechanism that extracts viewpoint-invariant information about objects, obviating the need to transform the global stimulus percept to match a stored canonical representation. Such mechanisms may require the encoding of an object-based representation, in which object features are represented only with reference to the object itself (for instance, the mug from our earlier example is cylindrical about its own major axis), and with no external reference to the observer or the immediate environment. This frame of reference can be described as viewpoint-invariant, since object recognition is unaffected by changes in the object's or the observer's orientation.

Marr and Nishihara proposed that object-centred representations form a plausible basis for viewpoint-invariant recognition, proposing that an object's principal axis may be identified based on maximal elongation and symmetry (Marr, 1982; Marr & Nishihara, 1978). It has subsequently been demonstrated that ambiguity in identifying an object's principal axis, resulting in failure to access object-centred representations, may be associated with reliance on viewpoint-dependent recognition mechanisms (Humphreys & Riddoch, 1984; Tarr & Pinker, 1989, 1990). However, visual recovery of global features such as major axes, though frequently used to account for empirical findings (Humphreys & Riddoch, 1984; McMullen & Farah, 1991; Tarr & Pinker, 1989, 1990) has been criticised by computational vision theorists (Thacker et al., 1995) as being infeasible, since they fail to take account of real-world visual problems such as image fragmentation and clutter[4]. Local feature-detection models, such as those proposed by Biederman and by Murray and colleagues (Murray et al., 1993), offer a more robust approach.

The logical extension of object-centred representations is a system of representation in which object features are encoded in a manner that is entirely orientation-free, even with regard to the parent object. Knowledge of an object's orientation and successful identification of that object have been demonstrated, by cases in the clinical neuropsychology literature, to be entirely dissociable functions (Karnath et al., 2000; Turnbull, Laws, & McCarthy, 1995). One of the main proponents of a feature-based approach is Biederman (1987), whose 'recognition by components' theory states that object descriptions can be stored in terms of orientation-invariant object primitives ('geons'), and that successful identification of these primitives by the visual system, within certain constraints regarding the visual availability of feature information (Hummel & Biederman, 1992), precludes the need for any kind of angular transformation in depth (though this may not be true of stimuli rotated in the image plane). Support for the encoding of feature-based, rather than object-based, viewpoint-invariant representations comes from a study showing that when spatial relations between the elements of an object are crucial to successful identification, RTs are more likely to be viewpoint-dependent (Koriat & Norman, 1989). It has also been found that when individual object features are sufficient to recognise or

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[4] From a machine vision perspective, if object recognition is dependent on the detection of a global object feature (e.g., a major axis), then this renders the entire recognition processes vulnerable to scene-noise and the effects of perspective (e.g., image fragmentation, scene clutter, and axis foreshortening). Local feature detection is therefore preferable, as it permits the contribution of all features (including major axis fragments) that are detectable.

distinguish a shape, a viewpoint-invariant strategy may suffice (Takano, 1989; Tarr & Pinker, 1989).

1.4.2 Acquisition of orientation-invariance through repeated exposure

Several authors of papers investigating the perception of misoriented stimuli have noted a gradual shift in the nature of RTs elicited throughout the course of such experiments, from orientation-dependent to orientation-invariant (Eley, 1982; Jolicoeur, 1985, 1990; Leek et al., submitted; McKone & Grenfell, 1999; Murray, 1995, 1999; Murray et al., 1993; Tarr & Pinker, 1989). Jolicoeur (1990) noted that repeated exposure to a specific misoriented stimulus decreased the orientation-dependent nature of the resulting RTs, and that this effect did not generalise to other members of the stimulus class. It has been theorised that with repeated stimulus exposure in misoriented object recognition tasks, orientation-invariant features are progressively acquired until viewpoint-invariant recognition of the stimulus object is achievable (Eley, 1982; Jolicoeur, 1985, 1990; Murray et al., 1993). Jolicoeur also proposed an alternative theory to account for this effect –namely, that multiple, viewpoint-dependent object views are acquired over the course of the experiment, thus lessening the closest transformational distance to a stored representation (as in Figure 4) and, in doing so, shortening the – still viewpoint-dependent – RT (Jolicoeur, 1990). This hypothesis is supported by the observation that participants in such experiments may store several viewpoint-specific representations of stimulus shapes, particularly at more extreme stimulus orientations and when those orientations are highly predictable within a given experimental block (Gauthier & Tarr, 1997; Tarr & Pinker, 1989). No such effect of repeated exposure is observed in matching tasks, suggesting that learning orientation-invariant features may not serve to distinguish objects from their mirror-images (Lawson, 1999; Tarr & Pinker, 1989).

Supporting evidence for the gradual acquisition of viewpoint-invariant object representations with increasing exposure also comes from a study by Leek (1998) that compared response-times to 'mono-oriented' objects (those with obvious canonical orientations, such as houses and cars) and 'poly-oriented' objects (those with no definitive canonical orientation: typically small, readily manipulable objects like pencils or keys) (Leek, 1998b). Poly-oriented objects presented at several orientations were found to elicit orientation-invariant RTs, whereas mono-oriented stimuli elicited orientation-dependent RTs. It might reasonably be deduced from this that viewpoint-invariant recognition of poly-oriented shapes is achieved ecologically through repeated exposure, whereas exposure to mono-oriented objects is by definition always canonical, and does not promote the acquisition of viewpoint-invariant features.

1.5 Multiple routes to object constancy

1.5.1 The relationship between transformational and non-transformational object constancy mechanisms

Empirical evidence for the existence of both a viewpoint-dependent transformational mechanism and a viewpoint-invariant mechanism of object recognition (which may rely on global or local object-centred representations) is well established (Biederman & Gerhardstein, 1993; Humphreys & Riddoch, 1984; Jolicoeur, 1985, 1990; Leek et al., submitted; Tarr & Pinker, 1989, 1990). Functional separation of these two mechanisms, which may be inferred from the clinical neurobiology literature (Humphreys & Riddoch, 1984; Karnath et al., 2000; Turnbull, Della Sala, & Beschin, 2002), is discussed in Chapter 2. The extent to which these mechanisms interact has attracted some attention: based on the observation that characteristic RTs for 180°-misoriented stimuli are often less than the regression line would predict – that is, the relationship between RT and orientation is not entirely linear – it has been proposed that the two processes were operating in parallel (Jolicoeur, 1990). It has also been suggested that viewpoint-dependent recognition of misoriented shape may function as a means of double-checking information acquired through other mechanisms, rather than as a fully independent system (Corballis, 1988). Indeed, selection of a particular recognition mechanism cannot proceed *a priori* since any such preferential selection would imply that the object had already been recognised! Therefore, it may be more helpful to reframe the debate about viewpoint-dependent or viewpoint-invariant recognition as a matter of the extent to which each mechanism is involved.

1.5.2 Reference frames and context in the selection of an appropriate object constancy mechanism

Visual reference frames have generally been categorised as either object-centred or viewpoint-centred coordinate systems (e.g., Marr & Nishihara, 1978). In fact, there is no reason why additional coordinate systems might not exist: Hinton's connectionist model of object recognition proposed that object representations in several different reference-frames would compete, with the winning representation being the most apposite (Hinton & Parsons, 1981). There is some evidence that the brain encodes body-centred coordinate-frames as well as viewpoint- and object- based perspectives (Parsons, Gabrieli, Phelps, & Gazzaniga, 1998), and the existence of distinct retinocentric and body-centric coordinate reference frames has been inferred from studies of patients suffering from mirror ataxia and mirror agnosia (Binkofski, Buccino, Dohle, Seitz, & Freund, 1999).

Visual context may influence the selection of a particular reference frame or stored object view. For example, consecutive presentations of an otherwise identical stimulus object, orientation of which has altered from one presentation to the next, have been found to elicit orientation-dependent RTs which suggest that respondents' frame of reference is set relative to the first stimulus (Koriat & Norman, 1988, 1989; Koriat, Norman, & Kimchi, 1991). When a participant's own bodily reference-frame is tilted relative to the environment, object recognition performance indicates that the environmental reference frame is adopted (Rock & Heimer, 1957). However, if that reference frame is not available, performance reflects the adoption of an egocentric frame of reference (ibid.). It has also been posited that the adoption of particular reference frames depends on the visual availability of a major axis (Humphreys, 1983; Humphreys & Riddoch, 1984; Tarr & Pinker, 1989, 1990).

1.6 Summary

Response-time studies indicate that the time taken to match two angularly disparate novel shapes (the classic 'mental rotation task') increases in proportion to the size of the angle between them. It is hypothesised that such disparities are resolved by visuospatial transformation of the two global stimulus percepts into alignment. The results of other studies indicate that response-times to misoriented familiar objects that have clearly-defined canonical orientations increase proportional to the extent of their misorientation. These findings support the existence of a viewpoint-dependent mechanism for object recognition that compares the stimulus percept against a canonical stored representation. Such data are frequently used to argue that the transformation process underpinning viewpoint-dependent recognition is the same mechanism as that recruited during the mental alignment of angularly disparate stimuli.

In some cases, response-times to certain misoriented objects have been shown to be largely invariant to changes in stimulus orientation, providing support for the existence of a second, non-transformational, type of object constancy mechanism known as viewpoint-invariant recognition, in which orientation-invariant object features are compared against a stored, object-centred or feature-based representation, without the need for wholesale transformation of the stimulus percept. Response-time studies indicate that acquisition of orientation-invariant object representations may be achieved through repeated stimulus exposure. Orientation-dependent response-times may also be reduced by the acquisition of multiple stored representations representing different object views. Orientational context may also influence the frame of reference in which objects are perceived, and consequently affect the extent to which the stimulus percept requires transformation.

Preferential recruitment of a transformational or non-transformational recognition mechanism *a priori* would be paradoxical. It therefore appears likely that these two processes proceed in parallel, at least initially, in misoriented object recognition – though this is impossible to determine conclusively by response-time data alone.

This chapter therefore raises the following questions:

- To what extent do viewpoint-dependent and viewpoint-invariant recognition processes operate in parallel?

- How are these recognition strategies implemented? Does viewpoint-dependent recognition involve manipulation of a global stimulus percept?

- Do viewpoint-invariant processes involve global or local stored representations, and is there evidence for global stimulus percept transformation in the former case?

- To what extent do mental rotation and viewpoint-dependent recognition recruit the same visuospatial transformation mechanism?

The following chapter reviews studies investigating the neurobiological correlates of mental rotation, viewpoint-dependent and viewpoint-invariant recognition task performance, with a view to clarifying the natures of these processes and the manner in which they are implemented in the brain.

Chapter Two

2. A Review Of Studies Investigating The Cortical Correlates Of Object Constancy Processes

2.1 Introduction

Viewpoint-dependent and viewpoint-invariant strategies for misoriented object recognition can be inferred from the psychometric literature reviewed in Chapter 1. The existence of a visuospatial transformation mechanism can likewise be inferred from response-time studies. Psychometric investigations cannot adequately determine whether visuospatial transformation and viewpoint-dependent mechanisms constitute a single object constancy process, and do not indicate the extent to which viewpoint-dependent and viewpoint-invariant recognition mechanisms proceed in parallel. Investigation of the cortical regions recruited by all three object constancy mechanisms may elucidate these issues, and clarify the manner in which each proceeds. The present chapter thus reviews the literature concerning object constancy processes in the brain.

2.2 Two cortical routes to visual perception

2.2.1 The dorsal and ventral pathways

Ungerleider and Mishkin (1982) described two distinct pathways subserving object recognition in the macaque. The authors described a 'dorsal' pathway, dedicated to the control of visuospatial manipulation such as reaching and grasping, extending from primary visual cortex in the occipital lobe into the parietal cortex. The homologue of this pathway in humans can be described in terms of the cortical 'Brodmann areas' (Brodmann, 1909): it begins in Brodmann area (BA) 17 (the primary visual cortex, located at the posterior pole of the occipital cortex – see Figure 6) and projects dorsally and rostrally through BA18 and BA19 into BA7 and BA40 in the parietal lobe.

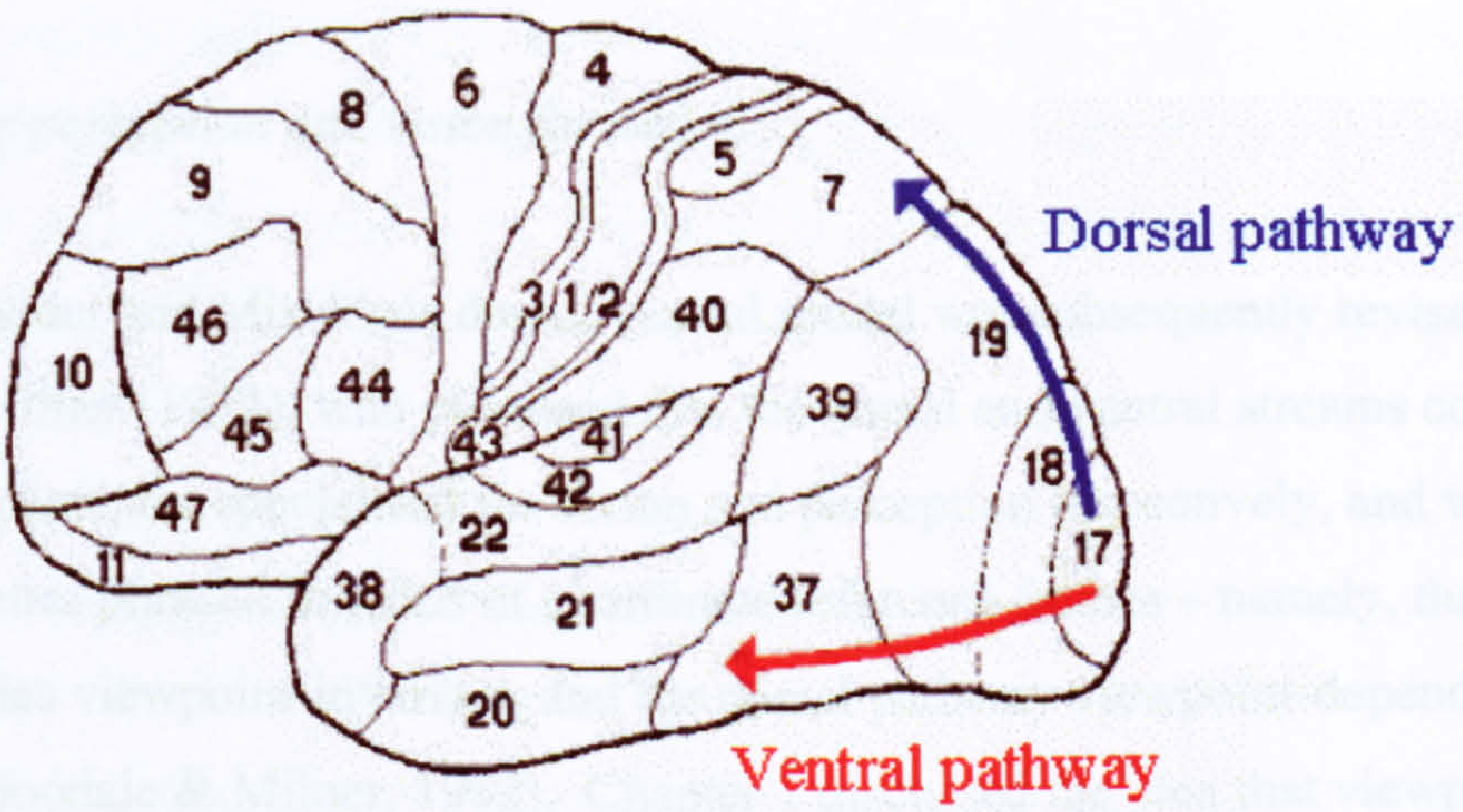

Figure 5. The brain's dorsal and ventral visual pathways, forming occipitoparietal and occipitotemporal streams, respectively. Numbers denote Brodmann cortical areas.

Ungerleider and Mishkin also described a 'ventral' pathway (Figure 6) connecting primary visual cortex with the inferior temporal lobe (in human cortical terms, connecting BA17, BA18, BA19 and BA37), which they believed to encode object-based information such as colour and texture (Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982). This distinction between ventral and dorsal streams has subsequently been characterised as the 'what' and 'where' of objects, respectively (Ungerleider & Haxby, 1994). Evidence supporting Ungerleider and Mishkin's description of the dorsal stream as underpinning visuospatial processes can be seen in studies utilising single-cell recordings, which demonstrate the existence of neurones in the dorsal pathway that respond selectively to spatial information about objects (Andersen, Essick, & Siegel, 1985; Grezes, Armony, Rowe, & Passingham, 2003). Ungerleider and Mishkin's assertion that featural information is encoded in the ventral stream is supported by the finding that some cells in inferotemporal cortex code specifically for stimulus attributes such as colour and texture (Gross, Rocha-Miranda, & Bender, 1972; Logothetis, Pauls, & Poggio, 1995). Areas in the fusiform gyrus have been shown to respond selectively to faces and other objects (Kanwisher, McDermott, & Chun, 1997), and it has been demonstrated that this response increases with visual expertise (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Following the proposal that the ventral pathway contains neurones coding for orientation-invariant aspects of objects (Logothetis et al., 1995), recent functional imaging studies appears to confirm the functional distinction between dorsal and ventral pathways posited by Ungerleider and Mishkin (Haxby et al., 1991; James et al., 2002; Passingham & Toni, 2001).

2.2.2 Vision for perception and vision for action

Ungerleider and Mishkin's dorsal/ventral model was subsequently revised by Goodale and Milner (1992), who proposed that the dorsal and ventral streams constituted segregated mechanisms specialised for action and perception respectively, and would therefore be better phrased in terms of coordinate reference frames – namely, that the ventral pathway encodes viewpoint-invariant, and the dorsal pathway viewpoint-dependent, information (Goodale & Milner, 1992). Chapter 1 discussed the idea that viewpoint-invariant processing is likely to hinge on the recognition of object features, so the finding that object feature information is encoded in inferotemporal cortex, part of the ventral pathway (Gross et al., 1972; Kanwisher, McDermott et al., 1997; Logothetis et al., 1995) is consistent with the model proposed by Goodale and Milner. Another idea discussed in Chapter 1 was that the process of mental rotation or viewpoint-dependent recognition may be analogous to the physical movement of reconciling two misaligned objects; the idea that the dorsal pathway, believed to mediate object manipulation, may be involved in such cognitions is therefore appealing.

The corollary of the functional distinction between dorsal and ventral pathways can be found in the clinical neuropsychology literature, where double-dissociation can be seen between selective dorsal or ventral brain injury and the type of object recognition deficit that results. If viewpoint-dependent processes are mediated by the dorsal stream, then object recognition requiring stimulus percept transformation should be affected when the dorsal stream is damaged. Deficits in the ability to perform mental rotation (Farah & Hammond, 1988; Turnbull et al., 1995; Warrington & Taylor, 1973), and in perception of misoriented objects, (Humphreys & Riddoch, 1984; Turnbull & McCarthy, 1996; Vaina, 1994) have indeed been reported following dorsal lesion. The majority of studies appear to support functional segregation of these two processes, reporting that either mental rotation or misoriented object recognition is affected, and the other process preserved; though occasionally, both mechanisms have been found to be damaged (e.g., Warrington & Taylor, 1978)[5]. Likewise, if viewpoint-invariant information is encoded in the ventral pathway, then

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[5] The potentially conflicting case studies described by Farah and Hammond and by Turnbull and McCarthy, where patients are able to perform either mental rotation or misoriented object recognition, but not both, offer evidence that two such apparently similar processes need not recruit exactly the same neuroanatomical

damage to this region might be expected to result in an inability to encode featural information. Patients with inferotemporal lesions are indeed reported to suffer specific visual agnosias or deficits in object recognition relating to featural information such as colour and texture (Damasio, Tranel, & Damasio, 1989; Le et al., 2002; Vaina, 1994).

2.3 Functional imaging studies of transformational object constancy processes

2.3.1 Introduction to functional imaging of object constancy processes

Recent advances in functional imaging mean that it is now possible to investigate empirically the involvement of cortical regions, such as the dorsal and ventral pathways, in a variety of tasks believed to recruit object constancy. Such methods offer two chief advantages over the literature presented thus far. The benefits – scientific and ethical – of investigating human brains in preference to using animal models are self-evident. Functional imaging also allows us to examine cognitive processes in the normally functioning brain; prior to the advent of these techniques, most neuroanatomical evidence about object recognition in the human brain came from case studies following brain damage, in which the some aspect of the visual process had been disrupted. While individual clinical case studies may be useful in supporting or disproving hypotheses, it is surely preferable to derive a model of object constancy from observation of normal, uninterrupted brain function.

Functional imaging studies investigating the neural correlates of mental rotation tasks (such as those described by Shepard and Metzler, 1971) and tasks of misoriented object recognition are reviewed below. For a detailed explanation of the methodology of functional magnetic resonance imaging (fMRI), including the requirement for a baseline or contrast condition, see Chapter 3; the methodology of electroencephalography (EEG) is described in Chapter 5. The techniques of positron emission tomography (PET) and magnetoencephalography (MEG) are not discussed in this thesis; the reader is referred to any reasonably current neuropsychology textbook, such as Neil Martin's *Human Neuropsychology* (Martin, 1998).

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mechanisms (as might be supposed from examination of the psychometric literature). This finding that the identification of misoriented shape does not necessarily depend on the same mechanism as mental rotation thus supports Goodale and Milner's proposal that there is more than one pathway to object constancy.

2.3.2 Functional imaging studies of mental rotation

Cohen et al. (1996) used fMRI to examine functional activation in a mental rotation study based on the Shepard and Metzler task. Participants were required to decide whether two misaligned shapes were identical or mirror-image opposites, in contrast with a control condition in which shapes appeared at identical orientations and no alignment was required. Areas recruited most during misaligned, relative to aligned, stimulus presentations included parietal areas BA 7 (and in some participants, BA40), BA 39 and 19, offering clear support for dorsal involvement in visuospatial transformation. Harris et al. conducted a study in which they manipulated the orientation of alphanumeric stimuli while participants judged them to be either mirror-reversed or normal. Significant PET activation correlating with transformation of the stimuli was found in the BA7 in the superior parietal lobe (Harris et al., 2000). PET study by Alivisatos and Petrides found preferential activation of left inferior parietal cortex during a similar mental rotation task (Alivisatos & Petrides, 1997). A study of error rates in a mental rotation task by Tagaris et al. found, using fMRI, that increased error rates were associated with increased blood oxygen level-dependent (BOLD) signal (see Chapter 3) activity in the superior parietal lobule. The authors posited that this correspondence between error rates and cortical blood-flow was indicative of increased cognitive demands during mental rotation (Tagaris et al., 1996). Several other studies utilising similar mental rotation paradigms have also identified the parietal region as a plausible locus of visuospatial transformation (Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Pierret & Peronnet, 1994; Pierret, Peronnet, & Thevenet, 1994; Tagaris et al., 1997; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989; Yoshino et al., 2000).

Preferential recruitment of an occipitotemporal region (Brodmann areas 19, 37 and 39) and the intraparietal sulcus has been found in a mental rotation task using novel objects (Faillenot, Decety, & Jeannerod, 1999). The authors postulated that the observed activity in the occipitotemporal region was likely to reflect a process of comparison between the spatial properties of objects rather than visuospatial transformation as such, since previous studies suggest just such a role for this region. However, since both of the areas identified by Faillenot et al. showed increased BOLD signal in response to angularly disparate stimuli rotated in depth, this is by no means certain. In fact, occipitotemporal and intraparietal areas consistent with those reported by Faillenot et al. have also been found to be active in an fMRI study of mirror-reversed and inverted letter-string reading (Goebel, Linden, Lanfermann, Zanella, & Singer, 1998).

2.3.3 Functional imaging studies of misoriented object recognition

Fewer studies have addressed the cortical regions involved in the perception of misoriented familiar objects. Kosslyn et al. used positron emission tomography (PET) to investigate cortical activity while participants identified pictures of familiar common objects depicted from canonical or non-canonical views. Identification of non-canonically-oriented pictures was found to elicit increased bilateral activation in several areas including the parietal lobe (Kosslyn et al., 1994). Just et al. (2001) found that imagined rotation of a memorised object elicited a greater BOLD signal throughout a parietal region of interest (ROI) when stimulus rotation in depth and in the picture plane was made, relative to rotation in the picture plane only. The authors compared these BOLD results with those obtained during a conventional Shepard and Metzler mental rotation task, and found the regions involved to be highly similar, particularly within the ROI (Just, Carpenter, Maguire, Diwadkar, & McMains, 2001). Recognition of non-canonical object views has also been found to preferentially recruit posterior parietal cortex (Sugio et al., 1999).

2.4 Parietal cortex as a locus of reference-frame transformation

2.4.1 A region common to viewpoint-dependent recognition and mental rotation

Visual reference frames for perception and recognition of objects were discussed in Chapter 1. In order for visual perception to proceed successfully, transformations of stimulus information from one reference-frame to another (e.g., from a retinal coordinate-frame to a viewpoint- or object-centred representation) must be computed. Although there is no explicit evidence that mental rotation tasks such as the Shepard and Metzler paradigm invoke the same visuospatial transformation mechanism as that believed to mediate misoriented object recognition (since the observed RTs in mental rotation tasks may simply reflect a transformation between two object-based [viewpoint-invariant] coordinate systems), the functional imaging evidence reviewed appears to suggest that parietal cortex is involved in both processes. This region is thus implicated in the transformation of object information between discrete coordinate reference-frames.

2.4.2 Posterior parietal cortex and the intraparietal sulcus as a site for perceptual reference-frame integration

Support for the involvement of parietal cortex in the integration of reference-frame information may also be obtained from studies of single-cell recordings. Cells in the posterior parietal cortex (PPC, which includes the area homologous to the human superior parietal lobule) of the primate brain have been identified as being preferentially tuned to motor and visual tasks (Andersen et al., 1985). Anderson et al. propose that PPC is involved in visuomotor integration, and that it encodes the coordinate transformation between sensory input and motor output (Andersen, Snyder, Bradley, & Xing, 1997). They also nominate PPC as a likely locus of coordinate transformation between *all* sensory reference-frames, which they list as eye-centred, head-centred, body-centred, limb-centred and world-centred (Andersen, 1995; Andersen, Batista, Snyder, Buneo, & Cohen, 2000). The inferior parietal lobule (LIP), caudal to the intraparietal sulcus (IPS), has been proposed as the locus in humans for the integration of visual information from dorsal and ventral streams (Watson, Valenstein, Day, & Heilman, 1994). The LIP has been identified in at least one study as a possible area for the computation of mental rotation (Alivisatos & Petrides, 1997).

Luppino et al. (1999) propose that the transformation of sensorimotor information between reference-frames in the macaque brain is sited in the IPS (Luppino, Murata, Govoni, & Matelli, 1999). It is likely that this area in the macaque is homologous with the human IPS, which separates the superior and inferior parietal lobules (Rushworth, Paus, & Sipila, 2001). It has been demonstrated that human IPS is recruited during tactile exploration of complex objects (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999), in the transformation of body-centred coordinate frames (Bonda, Petrides, Frey, & Evans, 1995), and during object comparisons across orientation (Carpenter et al., 1999; Faillenot et al., 1999; Harris et al., 2000; Vanrie, Willems, & Wagemans, 2001) and size (Faillenot et al., 1999). Increased recruitment of IPS has been found in response to larger angular disparity between stimuli during matching tasks (Carpenter et al., 1999) and when stimuli are rotated in depth (Faillenot et al., 1999), as well as with greater stimulus misorientation in a recognition task (Harris et al., 2000). Greater IPS involvement in all of these tasks seems likely to reflect their increased cognitive demands. Lastly, an area of IPS has been identified as responding selectively to identical stimulus views in a matching task (James et al., 2002).

2.4.3 Reference-frames and the perception of body-related stimuli

As discussed in Chapter 1, there may exist several different reference-frames for the perception and recognition of visual stimuli. Evidence that parietal cortex may be involved in computing reference-frame transformations comes from several functional imaging studies that have investigated the cortical regions associated with decisions about the laterality of body parts (usually hands). One such study, by Parsons et al., used a mental rotation task in which participants determined whether the pictures viewed were of left or right hands. PET data revealed increased functional activation of the parietal area correlating with the handedness decision (Parsons et al., 1995). An MEG study by Kawamichi et al. (1998), using an identical task, also found evidence of inferior parietal lobe recruitment during handedness decisions (Kawamichi, Kikuchi, Endo, Takeda, & Yoshizawa, 1998), as did a study by Kosslyn et al. which examined both mental rotation tasks of abstract figures and a handedness decision task (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998). Activation of superior, intraparietal and inferior parietal regions during a task requiring mental rotation of the hand has also been found in a PET study (Bonda et al., 1995). Kosslyn et al. (1998) found parietal recruitment during a matching task and in a hand laterality decision task. Regardless of the nature of the transformations underpinning handedness decisions (the possibility of body-part stimuli recruiting body-centric reference frames is addressed later in this chapter), they appear to be recruiting areas in parietal cortex.

It would therefore appear likely that reference-frame transformation occurs at some point in the dorsal pathway; posterior parietal cortex or the intraparietal sulcus seem the most plausible candidate areas, although primate and human studies do not always concur as to the precise location of such a region. Thus, there would appear to be persuasive evidence that the dorsal stream is involved in the visuospatial transformation process common to viewpoint-dependent recognition and mental rotation.

2.5 The ventral stream as an alternative locus of viewpoint-dependent recognition

2.5.1 Inferotemporal cortex may mediate viewpoint-dependent recognition (but not mental rotation)

Although there is comparatively little evidence (particularly from functional imaging studies) to suggest that the ventral stream may be capable of computing visuospatial transformation, the results of some studies do suggest that viewpoint-dependent processing may take place there. Walsh and Butler proposed, based on studies of the primate brain, that inferotemporal cortex may underpin misoriented object recognition, but that the process of discriminating between the handedness (or mirror-inversion) of stimuli can only be computed by parietal cortex (Walsh & Butler, 1996). This is consistent with a study by Gauthier et al. (2002) which used fMRI to compare cortical recruitment during two different matching tasks: a mental rotation task, in which participants had to state whether stimuli were identical or mirror-images, and an object recognition task in which they were merely required to identify whether or not stimuli were the same shape. In the mental rotation task, greater BOLD signal in superior parietal cortex correlated with greater angular disparity between stimuli, while the misoriented object recognition task elicited greater BOLD signal in the fusiform gyrus with greater stimulus misorientation (Gauthier et al., 2002). Gauthier et al. concluded that these two tasks recruit distinctly separate pathways synonymous with dorsal and ventral streams, albeit not in the way originally envisaged by Goodale and Milner.

2.5.2 Evidence from neuropsychology case studies

Thus, it would appear that there is an alternative route for recognition of misoriented shape, and that it may involve the ventral pathway. However, when the ventral stream is damaged, object constancy may proceed via the dorsal stream. Several clinical studies describe cases in which patients with brain damage have lost the ability to encode, process, or perhaps integrate, viewpoint-dependent information, and are instead reliant on orientation-invariant object identification, or describe patients who are able to perform mental rotation, but not misoriented object recognition. A study by Turnbull et al. (2002) described a patient with anterior parietal lobe damage, apparently unable to encode stimulus orientation, who showed orientation-invariant responses to misoriented stimuli, but normal RTs in a mental rotation task (Turnbull et al., 2002). In another case study (Turnbull & McCarthy, 1996), a patient who had sustained occipital damage bilaterally was found to be unable to recognise misoriented objects but was able to perform mental rotation normally. Another investigation, by Cooper and Humphreys, found that a patient with a frontotemporoparietal lesion, including damage to inferior parietal cortex, was able to recognise misoriented objects without incurring orientation-dependent time-costs, but whose performance on a mental rotation task elicited the characteristic increase in RTs with greater stimulus disparity (Cooper & Humphreys, 2000). This last case is particularly tricky to interpret in view of the extent of the damage sustained, and the consequent breadth of functional deficits, including some evidence of spatial neglect in the patient.

Attempting to interpret these cases in the framework of Walsh and Butler's theory, we might infer that (at least in those patients described by Turnbull and colleagues) damage had been done to that part of the ventral pathway that would ordinarily have performed viewpoint-dependent recognition, but that the dorsal pathway, mediating mental rotation, was still intact. By way of double dissociation, Farah and Hammond (1998) describe the case of a patient with a middle cerebral artery infarct – apparently affecting dorsal pathway function – who was unable to perform mental rotation, but who was perfectly capable of recognising misoriented objects. However, Walsh and Butler's proposal that viewpoint-dependent processing may proceed via the ventral stream is difficult to resolve with studies that describe patients with purely parietal lesions suffering from the classic 'unusual views deficit', such as the case reported by Vaina (1994).

2.5.3 The perception of rotational motion in the ventral pathway

Although it has classically been viewed as the locus of viewpoint-invariant object recognition, there is indeed no reason why the ventral stream might not process viewpoint-dependent object recognition. Some support for this idea can be inferred from a study showing that some neurones in the ventral stream may be specialised for the perception of rotational motion. Barnes et al. reported preferential recruitment of an area in inferior temporal cortex when participants passively viewed rotationally-moving 3-D novel stimuli (like those used by Shepard and Metzler) and when they were asked to mentally rotate those same stimuli in a matching task (Barnes et al., 2000). This finding is consistent with the common subjective observation by participants in mental rotation and misoriented object recognition studies that they actually visualise the stimuli rotating. The area reported by

Barnes et al., described as 'an inferior satellite area of V5', did not appear to be recruited during tasks involving non-rotational (i.e., linear) motion perception (real or imaginary). Having previously established that cells in cortical area V5, at the junction of occipital and temporal cortex in BA19, are tuned preferentially for the perception of motion (Anderson, Holliday, Singh, & Harding, 1996; Zeki, Watson, & Frackowiack, 1993), and that V5 itself has been implicated in several studies of mental rotation (Alivisatos & Petrides, 1997; Cohen et al., 1996; Pegna et al., 1997; Vanrie, Beatse, Wagemans, Sunaert, & Van Hecke, 2002), it seems quite plausible that cells in the ventral stream identified by Barnes et al. may be further specialised for the perception of rotational motion. Furthermore, findings from an eye-movement study by Just and Carpenter indicate that the resolution of angularly disparate object views may proceed via a process of featural segmentation, followed by rotational transformation, of each individual feature (Just & Carpenter, 1985) This proposal was lent support in a later study by Carpenter et al. (1999), who found that fusiform and inferotemporal regions of the ventral stream, as well as dorsal regions, were recruited during a classic Shepard and Metzler mental rotation task.

2.5.4 Global stimulus perception and representation in the ventral pathway

If viewpoint-dependent processing may be mediated by the ventral pathway, then it might be anticipated that global shape representations of misoriented objects (the percepts of which are presumed to be transformed wholesale during viewpoint-dependent recognition) would involve this area[6]. Inferior temporal gyrus and inferior fusiform gyrus have been found to be preferentially recruited by tasks relating to the perception of possible (but not impossible) objects (Schacter et al., 1995), suggesting a role for the ventral pathway in determining an object's global 'structural coherence' (a finding somewhat at odds with the classic depiction of the ventral pathway as supporting piecemeal feature detection). These findings are supported by Kanwisher et al. (1997), who compared cortical responses to scrambled and normal stimuli and proposed that an area at the occipitotemporal junction – possibly the same region as that identified by Faillenot et al. (1999) – is responsible for the processing of global object shape (Kanwisher, Woods, Ioacoboni, & Mazziotta, 1997). It has also been suggested that the topography of areas in inferotemporal cortex that are specialised

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[6] Although global shape representation is not necessarily limited to viewpoint-dependent object recognition (e.g., Humphreys & Riddoch, 1984), it would be difficult to demonstrate the extent to which it underpins viewpoint-invariant recognition without identifying functional markers of global and local feature encoding, the presence of each of which could then be tested during misoriented object recognition.

for object recognition is organised by visual field eccentricity (Malach, Levy, & Hasson, 2002). This may account for findings such as those reported by Humphreys and Riddoch (1984), in which patients' ability to process global or local object features apparently depended on the focus of structural damage.

2.6 Viewpoint invariant object recognition

None of the studies mentioned above have attempted to elucidate the neuroanatomy of viewpoint-invariant processing. Vanrie et al. (2002) used fMRI to contrast the cortical areas recruited by a mental rotation task (orientation-dependent RTs) against those recruited during misoriented object recognition (feature-detection; orientation-invariant RTs) task. The authors noted that all areas found to be preferentially recruited during the viewpoint-invariant condition (areas which included regions in dorsal and ventral pathways) were also present during the mental rotation task, and concluded that no specific region was preferentially recruited by viewpoint-invariant (relative to viewpoint-dependent) processing (Vanrie et al., 2002). However, the authors did note that a larger volume of suprathreshold voxels was observed in inferior occipital cortex in the viewpoint-invariant condition, consistent with other accounts proposing that object feature information is processed in this region (Carpenter et al., 1999; James et al., 2002; Logothetis et al., 1995). There is thus currently no functional imaging evidence to support preferential recruitment of the ventral pathway during viewpoint-invariant object recognition.

To conclude our brief tour of the dorsal and ventral streams, the classic description of dorsal and ventral pathways as mediating viewpoint-dependent and viewpoint-invariant object recognition may be insufficient: while the majority of functional imaging studies implicate the parietal lobe as the locus of mental rotation and misoriented object recognition, there is evidence that viewpoint-dependent processing of the kind required in misoriented object recognition may also proceed in the ventral stream. Thus, the model put forward by Goodale and Milner (1992) may be not so much inaccurate as incomplete, and may yet be subject to modification in light of suggestions by Gauthier et al. (2002) and Walsh and Butler (1996).

The remainder of this chapter will focus on the other regions implicated in tasks of mental rotation and misoriented object recognition, and outline their functional importance.

2.7 A role for prefrontal cortex in visuospatial transformation

2.7.1 Prefrontal lobe connectivity with dorsal and ventral pathways

Several studies investigating the cortical correlates of visuospatial transformation during mental rotation tasks report increased prefrontal activity in dorsolateral prefrontal cortex (DLPFC) (Cohen et al., 1996; Just et al., 2001; Vanrie et al., 2002). Recruitment of DLPFC has also been reported during misoriented object recognition (Kosslyn et al., 1994). Studies of the macaque brain indicate the existence of strong reciprocal connections between parietal cortex and DLPFC (Cavada & Goldman-Rakic, 1989; Ungerleider & Mishkin, 1982). FMRI investigation of human subjects reveals that physical manipulation of complex novel objects correlates with increased activity in the intraparietal region, ventral premotor cortex, superior parietal lobule, and opercular parietal cortex (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999). This led Binkofski et al. to propose the existence of a fronto-parietal system in the human brain that had evolved specifically for the spatial manipulation of objects. This pathway, connecting the region around the intraparietal sulcus with prefrontal cortex (and DLPFC in particular), may therefore be viewed as an extension of the dorsal system originally proposed by Ungerleider and Mishkin; its importance in physical object manipulation is perhaps unsurprising given the apparent involvement of IPS in reference-frame transformation, discussed earlier.

Interestingly, projection of the ventral stream into the prefrontal lobes has also been identified in the form of a pathway connecting ventrolateral prefrontal cortex (VLPFC) with inferotemporal cortex (Carmichael & Price, 1995; Webster et al., 1994). Area TE (the anterior region of inferotemporal cortex (Von Bonin & Bailey, 1950)) has also been demonstrated to project to area 46 in the DLPFC (Shiwa, 1987). Reciprocal connections between the intraparietal sulcus and ventral premotor cortex have also been identified (Luppino et al., 1999). The exact role of such pathways in either mental rotation or misoriented object recognition is rather less clear than those involving DLPFC.

2.7.2 DLPFC recruitment may reflect working memory function during visuospatial transformation

Recruitment of DLPFC has been found during demanding object-based tasks recruiting working memory (Stern et al., 2000) and those requiring both spatial and object-based working memory (Mottaghy, Gangitano, Sparing, Krause, & Pascual-Leone, 2002). Tasks of both types have also been found to correlate with increased BOLD signal in the IPS (Belger et al., 1998), consistent with the findings of Binkofski and colleagues that DLPFC and IPS share functional and anatomical connectivity. A study by Jonides et al. (1993), examining the cortical correlates of working memory, found PET activation of prefrontal, premotor, parietal and occipital cortex[7]. It would therefore appear that the cortical areas subserving visuospatial transformation of the type required by mental rotation tasks overlap substantially with those identified in functional imaging studies of working memory, with only one study finding these areas recruited during misoriented object recognition (Kosslyn et al., 1994). These results are not necessarily unexpected when one considers the differing demands on working memory of mental rotation and misoriented object recognition tasks: working memory load in maintaining and resolving two discrete, non-aligned shape representations in a mental rotation task is likely to be larger than during recognition task, when only one such stimulus percept must be maintained and matched against a long-term representation in memory. The idea that mental rotation tasks place a demand on spatial working memory is supported by the finding that recruitment of DLPFC is more extensive when mental rotation is performed in depth and in the picture plane (i.e., rotation in two separate dimensions) than when it is performed in just the picture plane (Just et al., 2001).

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[7] In fact, the results reported by Jonides et al. are remarkably consistent with the cortical recruitment observed in many of the functional imaging studies of mental rotation already described, which typically report recruitment of precisely these areas. This substantial overlap in functional anatomy has been addressed by Carpenter et al., who conclude that a reappraisal of the traditional approach to cortical mapping (one function = one area) is necessary (Carpenter, Just, & Reichle, 2000).

2.8 A role for premotor cortex in visual perception for action

2.8.1 Premotor cortex involvement in tasks requiring motor imagery

Like prefrontal cortex, recruitment of premotor cortex (Brodmann areas 6/8 and 44) has been widely reported in tasks of mental rotation (Cohen et al., 1996; Kawamichi et al., 1998; Kosslyn et al., 1998; Parsons et al., 1995; Richter, Somorjai, Summers, & Jarmasz, 2000; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Tagaris et al., 1998; Vanrie et al., 2002). Two further studies indicate that this region is preferentially recruited during the perception of non-canonical object views (Gauthier et al., 2002; Sugio et al., 1999) suggesting a role for premotor cortex in both types of transformational process .

Primary and premotor cortical recruitment has previously been reported in tasks of motor imagery (Leonardo et al., 1995; Porro et al., 1996), a phenomenon that has been described as 'subliminal activation of the motor system' (Jeannerod & Frak, 1999). Primary motor cortex has also been implicated in mental rotation: a study by Ganis et al. (2000) found that delivering transcranial magnetic stimulation to primary motor cortex during a misoriented object and handedness decision task disrupted task performance (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000). If the speed and analogue nature of mental rotation are indeed biomechanically plausible (Parsons & Fox, 1998), then it is tempting to envisage mental rotation as necessarily recruiting motor preparation (if not primary motor) areas (Parsons et al., 1995). However, the paradigm utilised by Cohen et al. (1996) was designed to 'subtract out' functional activation due to motor planning by virtue of including it in the control task. The authors concluded that the resulting observed premotor recruitment must be due to increased attentional demands of the task, although this does not adequately explain the discovery by Cohen et al. that the hand somatosensory cortex was also apparently recruited, an observation consistent with imagined stimulus manipulation and which has also previously been reported during imagined motor function (Leonardo et al., 1995).

2.8.2 Premotor cortical involvement in body-centred reference-frame decisions

One possible explanation for premotor activity in some studies of mental rotation arises from the putative involvement of body-centred reference-frames in tasks where participants must judge whether a pictures is of a left or right hand. For example, it has been demonstrated using MEG that the time-course of activation of a handedness-judgement involves sequential recruitment of parietal cortex, premotor cortex, then parietal cortex again (Kawamichi et al., 1998). A similar study also implicated premotor and parietal activity in handedness judgements (Parsons & Fox, 1998)). This topographic sequence of cortical recruitment may reflect successive updating of coordinate transforms during the mental rotation process (Duhamel, Colby, & Goldberg, 1992). Kawamichi et al. proposed that their results were indicative of a transformation between retinotopically-referenced information and a body-centred reference-frame. Evidence from split-brain patients suggests that handedness decision tasks of the type used by Kawamichi et al. do rely on the involvement of the hand's controlling, contralateral hemisphere, implying the recruitment of a body-part centred reference frame (Parsons et al., 1998). Support for this proposal also comes from the finding that premotor recruitment was detected during a mental rotation task requiring participants to make a handedness decision, but not during an equivalent task using abstract (non-body-part) stimuli (Kosslyn et al., 1998). However, these findings cannot account for other studies reporting the apparent involvement of premotor cortex in tasks that do not use or directly imply the involvement of body parts (Cohen et al., 1996; Richter et al., 2000; Sugio et al., 1999).

2.8.3 The role of canonical and mirror neurones in stimulus percept manipulation

An alternative explanation for the involvement of premotor cortex in visuospatial transformation may be found in single-cell recording studies of the primate brain. Cells in primate primary motor cortex have been shown to be selectively tuned to movement in particular directions (Georgopoulos, Kalaska, Caminiti, & Massey, 1982; Lurito, Georgakopoulos, & Georgopoulos, 1991), with populations of cells theorised to underpin internalised visuospatial transformation processes ('population vector transforms') (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989; Pellizzer, 1996). The existence of 'canonical' neurones (cells apparently specialised in monkeys for observation and manipulation of objects) and 'mirror-neurones' (cells specialised for the observation of another person or monkey performing some object-based motor action such as grasping an object) in primate and human premotor cortex and IPS has also been established (Grezes et al., 2003; Rizzolatti et al., 1996), leading to the proposal that these two areas form a parietopremotor pathway specialised for the observation and manipulation of graspable objects, and motor planning (Grezes et al., 2003). The study by Grezes et al. is particularly important, as it offers precedent for the existence of mirror neurones in premotor and parietal, rather than solely primary motor, regions. These findings could therefore be used to account for the premotor activity often observed in studies recruiting object constancy mechanisms, if one acknowledges that all objects of suitable size may afford a certain degree of graspability.

2.9 Hemispheric lateralisation of object constancy mechanisms

2.9.1 Evidence from clinical case studies

The extent to which the cortical networks subserving object constancy are lateralised in the brain has been extensively debated. The greater affinity of the right hemisphere for tasks requiring spatial perception is generally well established, for example by investigations of 'split-brain' patients who have undergone surgery (commissurotomy) to separate the two halves of the brain to prevent the spread of electrical seizures during epilepsy (Gazzaniga, Bogen, & Sperry, 1965). Patients who are unable to reconcile canonical and non-canonical object views or recognise non-canonically-oriented stimuli (the 'unusual views deficit') following brain damage are often found to have suffered damage to the right hemisphere (Warrington & Taylor, 1973, 1978), and the failure to compare structural aspects of objects has been associated with right-hemispheric damage (DeRenzi, Scotti, & Spinnler, 1969). Evidence of right-hemispheric involvement in mental rotation comes from a clinical case study describing a patient who had suffered a stroke in the right middle cerebral artery and consequently was unable to perform Shepard and Metzler-like tasks of mental rotation, but who had no difficulty in recognising misoriented objects (Farah & Hammond, 1988). However, there is also evidence to suggest that the left hemisphere is important in executing visuospatial transformation – Mehta and colleagues have shown that the ability of patients with left-hemispheric damage to perform mental rotation tasks was significantly poorer than those with right hemispheric damage (Mehta & Newcombe, 1991; Mehta, Newcombe, & Damasio, 1987). Another study reported a patient with right parietal damage who showed normal performance in a mental rotation task (Turnbull et al., 2002). And in a study of normal participants, tachistoscopic presentation of matching task stimuli to individual visual hemifields was used to demonstrate that the left hemisphere may be superior in tasks of mental rotation (Cook et al., 1994).

2.9.2 Functional imaging evidence

Functional imaging studies have also made a substantial contribution to the hemispheric lateralisation debate. Deutsch et al. (1988) compared the distribution of cortical blood-flow during a task requiring participants to judge line orientations, and a task recruiting mental rotation, and found that both elicited increases in activity of the right hemisphere, and that, of these two tasks, mental rotation induced a greater increase in right-hemispheric blood flow (Deutsch, Bourbon, Papanicolaou, & Eisenberg, 1988). A parametric PET study by Harris et al. (2000) found that blood flow to right parietal cortex increased with greater stimulus misorientation in a mental rotation task. EEG studies, although harder to interpret with regard to functional anatomy, also appear to confer a principal role for the right hemisphere in mental rotation (Inoue et al., 1998; Yoshino et al., 2000). More unusually, Cohen et al. reported bilaterally identical results in an fMRI study examining cortical recruitment during the Shepard and Metzler task, and Alivisatos and Petrides (1997) demonstrated preferential recruitment of left inferior parietal cortex during mental rotation.

2.9.3 Task demands may influence hemispheric recruitment

Although the majority of the studies report right hemispheric parietal dominance in tasks recruiting object constancy processes, it has been proposed that the involvement of right parietal cortex may relate to a process of comparison between stimuli and/or stored stimulus representations, whereas visuospatial transformation itself may be mediated by the parietal and/or temporal regions of the left hemisphere (Gill, O'Boyle, & Hathaway, 1998). There is some evidence to suggest that the relative hemispheric involvement in tasks recruiting object constancy depends on the cognitive complexity of the task at hand: Kosslyn et al. (1994) and Sugio et al. (1999) both report evidence for bilateral cortical involvement in tasks of misoriented stimulus recognition, relative to right hemispheric involvement only when viewing canonically-oriented objects. Bilateral parietal recruitment may also result from increased task difficulty in such studies (Just et al., 2001; Milivojevic, Johnson, Hamm, & Corballis, 2003; Tagaris et al., 1996). The conditions in which parietal cortex may be recruited bilaterally are discussed further in Chapters 3 and 4.

The type of object constancy mechanism recruited may also affect the extent to which each hemisphere is involved: object-oriented memory tasks have been found to preferentially recruit inferior frontal and inferotemporal cortex in the left hemisphere, compared to spatial tasks, which appear to increase recruitment of right prefrontal and right parietal cortex (Belger et al., 1998). Left inferotemporal cortex has also been implicated in the construction of viewpoint-invariant object representations (Alain, Bernstein, He, Cortese, & Zipursky, 2002). Thus, although the weight of evidence appears to favour the right hemisphere as underpinning aspects of object constancy during mental rotation and viewpoint-dependent recognition, the left hemisphere may play a greater role in viewpoint-invariant object recognition.

2.10 Summary

Visual pathways in the brain may broadly be classified as those specialised for either perception (the ventral pathway, connecting primary visual cortex with the inferior temporal lobe) or action (the dorsal pathway, connecting primary visual cortex with the parietal lobe). Neurones in the ventral pathway are specialised for local feature detection and appear to encode object information in an orientation-free manner. The ventral pathway has, therefore, been proposed to mediate viewpoint-invariant recognition – though to date there is little functional imaging data to support this assertion. It is hypothesised that the dorsal pathway, which is involved in spatial perception and object prehension, mediates viewpoint-dependent recognition. Support for this comes from a handful of functional imaging studies investigating recognition of misoriented familiar objects, all of which implicate superior parietal cortex in viewpoint-dependent recognition. Studies of the primate brain implicate superior parietal cortex as the most likely site for integration of sensory information encoded in discrete reference-frames (for example, the retinal stimulus percept and stored canonical representations). Superior parietal recruitment has also been found in several studies investigating mental rotation, providing strong evidence that visuospatial transformation is likewise mediated by the dorsal pathway. This supports the theory that mental rotation and viewpoint-dependent recognition depend on the same dorsally-mediated transformational mechanism, though this has not previously been tested directly. Studies investigating both perceptual processes also implicate – though with less consistency – DLPFC and premotor cortex in object constancy. The former area is theorised to underpin maintenance of the stimulus percept in working memory during its mental transformation (either in comparison to stored shape representations or to a second, angularly disparate stimulus). Involvement of premotor cortex seems likely to reflect the engagement of neuronal population vector transforms, believed to be important in integrating visual and motor information for prehension. Transformational object constancy processes may thus be somewhat analogous to physical object manipulation. This chapter therefore raises the following questions:

- What are the cortical correlates of viewpoint-dependent recognition of novel objects? Is this process mediated by the dorsal pathway?
- What are the cortical correlates of viewpoint-invariant recognition of novel objects? Is it mediated by the ventral pathway?
- Are the same regions recruited during mental rotation as during viewpoint-dependent recognition?
- To what extent is there concurrent functional imaging evidence of transformational object constancy processes during viewpoint-invariant recognition?
- To what extent is there concurrent functional imaging evidence of viewpoint-invariant processes during viewpoint-dependent recognition and mental rotation?
- What do the cortical regions recruited by each of these processes indicate about the manner in which each is implemented? That is, to what extent do they operate in parallel, and is there evidence to support the idea that transformational processes involve internalised manipulation of a global stimulus percept, while viewpoint-invariant processes rely on local feature identification?

Chapters 3, 4 and 5 use functional imaging techniques to address these questions as well as those posed at the end of Chapter 1.

Chapter Three

3. The Cortical Correlates Of Viewpoint-Dependent And Viewpoint-Invariant Object Recognition

3.1 Introduction to functional magnetic resonance imaging

3.1.1 MRI and BOLD fMRI

The principles of magnetic resonance imaging (MRI) are concisely described by Cohen and Bookheimer as follows (Cohen & Bookheimer, 1994):

> *The subject is placed into a strong and homogeneous magnetic field. Various atomic nuclei ... align themselves with this field and reach a thermal equilibrium. The subject is thereby 'magnetized'.*
>
> *The [particles] precess about the applied field at a characteristic frequency but at a random phase (or orientation) with respect to one another.*
>
> *Application of a brief radio frequency electromagnetic pulse disturbs the equilibrium, and induces a transient phase coherence to the nuclear magnetization that can, in turn, be detected as a radio signal, and formed into an image.* (p. 269)

Blood Oxygen-Level Dependent (BOLD) imaging is a functional variant of MRI first described by Ogawa and Lee (Ogawa & Lee, 1990). BOLD is based on the premise that neuronal activation in the brain (for example during a cognitive task) induces increased blood flow to the active area to meet metabolic demand. During this period of increased local metabolism, oxygen in the blood, which is ordinarily bound to haemoglobin, is taken up by the brain's cells, leaving blood haemoglobin 'deoxygenated'. However, it has been shown that the circulatory system overcompensates for this deoxygenation, such that more oxygenated blood is diverted to the active region than is actually absorbed by the surrounding cells (Fox & Raichle, 1986). Thus, the proportion of oxyhaemoglobin to deoxyhaemoglobin is increased in metabolically active areas. This alters the local magnetic resonance signal and so can be used to establish areas of increased cerebral blood flow while the patient is in a particular cognitive state. This method is known as functional magnetic resonance imaging (fMRI).

3.1.2 Constraints and limitations of BOLD fMRI

BOLD fMRI compares the pattern of oxygenated/deoxygenated haemoglobin ratios in two or more experimental conditions (one of which may be a baseline condition reflecting the participant's cerebral blood-flow at rest). A good experimental design manipulates these conditions as subtly as possible in order to reduce the number of cognitive and confounding variables to a minimum, such that any areas of differential recruitment between conditions reflect the differences in the task. To some extent, a trade-off must be made between creating a detectable (and statistically significant) BOLD signal and ensuring that any differences observed between experimental conditions are only attributable to the different cognitions experienced. However, one of the implicit assumptions in using such a technique is that cerebral activation *will* alter between experimental conditions. FMRI cannot identify regions where blood flow is consistent across all conditions, since the nature of the technique is essentially subtractive and can be thought of as the distribution of blood flow in one condition minus the distribution of blood flow in the other[8]. The value of techniques such as positron emission tomography (PET), which measure absolute rather than relative activity, should therefore not be underestimated.

Studies utilising fMRI are constrained by the speed at which blood is redirected to newly-active parts of the brain, a delay of 3-4 seconds known as the 'haemodynamic response'. This is a sigmoid function which saturates following concentrated periods of stimulus presentation and decays approximately in reverse (Friston, Josephs, Rees, & Turner, 1998; Stephan, Harrison, Penny, & Friston, 2004). This limited temporal resolution means that fMRI is unlikely to reflect the brain's most transient changes (Richter et al., 2000; Richter, Ugurbil, Georgopoulos, & Kim, 1997), to which other methodologies such as electroencephalography (EEG – see Chapter 5) are better suited. The approach taken by most fMRI studies is to construct a 'block paradigm' in which relatively long periods of each experimental condition are alternated, such that each condition of the experimental task allows the BOLD signal (in those regions involved in each condition) to become saturated. In obtaining repeated samples to increase the likelihood of saturating the BOLD signal, this method also serves to maximise the signal-to-noise ratio. However, it is important to consider that the BOLD signal tends to attenuate over time, so that the first block of trials in any given scan may naturally return a 'better' result, thus posing a potential experimental confound. This tendency is addressed in the present study by counterbalancing the order in which participants completed the two functional scans.

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[8] Strictly speaking, it is more correct to describe this process as a correlation between BOLD signal and a square-wave function representing alternating experimental conditions.

Some controversy exists as to the appropriateness of directly subtracting image data, since this may result in an artifactual BOLD signal (Friston, Holmes, Poline, Price, & Frith, 1996). For example: in a group of n participants, if one participant were to perform both experimental conditions identically, or differently from the other participants, this would only appear as a small trend, at most 1/n, of the averaged group result. However, if averaged group data from one condition was then subtracted from averaged group data in a second condition, the order of magnitude of that result would also be in the region of 1/n, rendering it entirely possible that any result obtained would reflect the rogue participant's data – in other words, that it would be an artifact of the analysis.

3.1.3 Design of the present study to accommodate the limitations of fMRI

In the present chapter, participants' BOLD signal data was compared (subtracted) between one experimental condition and a 'baseline' (control) condition, rather than directly subtracting the BOLD signal between two fundamentally very similar experimental conditions. As this work constituted a pilot study, it was felt that this was the optimal way of discerning whether the two experimental conditions were sufficiently functionally distinct to produce a differential BOLD signal (but see Chapter 4 for further discussion of this topic). Another issue related to the use of a correlational design is the inability of fMRI to detect activity in any region that is active throughout all conditions of an experiment: when comparing BOLD signal in two or more conditions, any region consistently active throughout (and therefore receiving a consistent blood supply) will not be evident when comparing the BOLD signal during any two periods within that time. Unfortunately, there is no way of ensuring that a region of the brain will 'turn off' when its involvement in a cognitive task ceases. Thus, it is effectively impossible to disprove the involvement of a given region of the brain in a BOLD fMRI experiment. In the present study, it was decided to contrast each experimental condition against a baseline level involving minimal, passive visual fixation was made in order to reduce the likelihood of overlooking constantly recruited regions in this manner.

A final issue in the analysis of BOLD fMRI data is the signal-to-noise ratio, which is generally around 1:1. Some kind of compensatory amplification is therefore necessary if significant changes in blood flow due to the experimental task are to be detected. One method is to use a stronger magnet, although higher field strengths can introduce problems such as increased signal artefacts and spatial distortion. A less controversial solution is to increase the number of samples taken, which has the effect of amplifying the signal by $1/\sqrt{\text{no. of samples}}$ (thus sampling 100 times will improve the signal by 10%). Repetitive sampling of each participant's BOLD signal is also likely to introduce less variance in the data than the alternative strategy of acquiring data from a great number of participants, since variations in structural and functional neuroanatomy between individuals may dilute the BOLD signal in a given voxel when many participants' data is averaged together, even after spatial normalisation. However, there is also an important trade-off to consider between reducing between-subjects variance and ensuring that an individual participant's time in the scanner does not exceed the time taken for them to habituate to the experimental task. This trade-off impacts directly on the usefulness of the resulting BOLD data, which, as noted previously, already attenuates over time, irrespective of cognitive demand. The fMRI study reported here attempts to strike a compromise between these two demands.

3.2 Background and rationale for the present study

3.2.1 Viewpoint-dependent and viewpoint-invariant object recognition

The existence of viewpoint-dependent and viewpoint-invariant recognition mechanisms, reviewed in Chapter 1, can be inferred from psychometric studies (Biederman, 1987; Biederman & Gerhardstein, 1993; Shepard & Metzler, 1971; Tarr & Pinker, 1990). Viewpoint-dependent recognition is thought to require some global transformation of the stimulus percept to match a stored canonical orientation, whereas viewpoint-invariant recognition is not thought to recruit such a mechanism, but rely instead on the detection of orientation-invariant object features. It can be inferred from the literature reviewed in Chapter 2 that some functional separation of these two processes may be inferred, and that this is likely to differentially recruit the brain's dorsal and ventral streams, respectively. The following sections review the findings from previous investigations in this area and explain the motivations for the study described in the present chapter.

3.2.2 Functional imaging studies of viewpoint-dependent recognition

Functional imaging studies, reviewed in Chapter 2, indicate that viewpoint-dependent recognition is very likely to proceed via the dorsal stream, with parietal cortex (inferior and superior parietal lobules, and the intraparietal sulcus, which separates them) being the most common areas implicated in transformation of the misoriented stimulus percept (Alivisatos & Petrides, 1997; Carpenter et al., 1999; Just et al., 2001; Kosslyn et al., 1994; Sugio et al., 1999). Several of these studies also report the recruitment of additional regions of premotor and prefrontal cortex during misoriented object recognition. There is also some functional imaging evidence that the ventral stream may be involved in misoriented object recognition (Gauthier et al., 2002). This section will describe the contribution of some of these studies in more detail.

Kosslyn et al. (1994) used positron emission tomography (PET) to measure regional cerebral blood flow while participants identified whether pictures of familiar common objects at canonical or non-canonical orientations matched a spoken word, presented simultaneously. Increased blood flow was observed in left superior parietal cortex (BA7), bilateral dorsolateral prefrontal cortex (DLPFC), left middle temporal and right inferior temporal cortex, and right inferior parietal cortex in the non-canonical condition relative to the canonical condition. Participants in an fMRI study by Sugio et al. (1999) passively viewed canonical and non-canonical views of common objects. It was found that relative to the canonical condition, non-canonical viewing elicited significantly greater BOLD signal in premotor cortex (BA 4/6,44; bilaterally) and the left superior parietal lobule. Just et al. (2001) asked participants to memorise a picture of an old-fashioned alarm clock, then used fMRI to monitor cortical activity while participants mentally manipulated the clock in response to spoken commands[9]. Just et al. observed significant increases in BOLD signal bilaterally in superior and inferior parietal regions, inferior frontal gyrus, DLPFC, posterior temporal lobe and the frontal eye fields (FEFs), with increased BOLD signal correlation in the parietal, inferior frontal and DLPFC regions when objects were mentally rotated in the picture plane and in depth.

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[9] Although the task used by Just et al. (1999) was described as 'mental rotation', it depended upon the manipulation of an internalised representation of an object (an old-style alarm clock) committed to memory. This paradigm might therefore be considered to inhabit a region somewhere between classic mental rotation studies of novel figures as per Shepard and Metzler, and studies investigating viewpoint-dependent recognition of familiar shapes such as those described by Kosslyn et al (1994). and Sugio et al. (1999).

The apparent differing involvement of premotor cortex (identified by Sugio et al. but not by Kosslyn et al.) and DLPFC (vice versa) in these otherwise similar studies may reflect the relative task demands of each study[10]. Participants recruited by Kosslyn et al. had already been primed with a word when they viewed each picture and attempted to make a match/non-match decision; thus, it seems likely that a top-down visual search process was employed to confirm or disprove that the picture represented the prime word, and that the recruitment of DLPFC (discussed in Chapter 2) in this process may reflect greater demands on working memory in this task, rather than in viewpoint-dependent recognition generally. In contrast, participants in the study by Sugio et al. had no such prior information when viewing stimuli. The regions found to be active in the latter study seem likely to reflect more accurately the neural substrate of bottom-up misoriented object recognition, and premotor cortical activity (discussed in Chapter 2) the possible recruitment of canonical neurones (Grezes et al., 2003) in anticipation of object prehension.

What these studies of misoriented common object recognition (Just et al., 2001; Kosslyn et al., 1994; and Sugio et al., 1999) do have in common is apparent preferential recruitment of parietal cortex during viewpoint-dependent recognition. Parietal recruitment was reported bilaterally in the study by Just et al., and in the left hemisphere only by Kosslyn et al. and Sugio et al. As related in Chapter 2, parietal cortex seems likely to be the locus of the visuospatial transformation process believed to underpin viewpoint-dependent recognition, and possibly also mental rotation.

3.2.3 Functional imaging studies of viewpoint-invariant recognition

On the basis of primate research and clinical case studies, viewpoint-invariant, feature-based recognition seems most likely to be encoded in the ventral pathway (e.g. Logothetis et al., 1995). However, the functional anatomy of viewpoint-invariant recognition has only been addressed in a single functional imaging study. Vanrie and colleagues attempted to differentiate between the cortical regions underpinning mental rotation and those responsible for viewpoint-invariant object recognition (Vanrie et al., 2002). The

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[10] In fact, Sugio et al. (1999) did observe significant bilateral correlation of the BOLD signal in DLPFC during non-canonical view presentation when compared against a baseline condition, but differential BOLD signal in DLPFC was not evident when contrasting non-canonical with canonical conditions –the latter equating to the experimental comparison made by Kosslyn et al (1994).

authors used three-dimensional abstract stimuli similar to those used in many other mental rotation studies. In the mental rotation condition, participants determined whether two such shapes presented simultaneously were identical or mirror-images, whereas in the viewpoint-invariant condition, participants determined whether or not the features of one object were skewed (non-perpendicular to the object's major axis) relative to those on the other object. Response-times in each of these conditions were found to be viewpoint-dependent and viewpoint-invariant, respectively. Relative to a control condition, viewpoint-invariant processing was found by Vanrie et al. to recruit occipital (Brodmann areas (BA) 18 and 19), fusiform (BA 19 and 37) and superior parietal (BA7) regions. Viewpoint-invariant processing did not appear to recruit preferentially any area not also involved in the mental rotation condition, although the authors did observe a larger region of significant BOLD signal in the right inferior occipital gyrus, leading them to propose that this area is integral to recognition of basic object feature-fragments such as angles, a proposal consistent with previously-established ventral stream involvement in feature detection (Gross et al., 1972; Haxby et al., 1991; Logothetis et al., 1995; Ungerleider & Mishkin, 1982).

One possible explanation for the failure by Vanrie et al. to identify a cortical region specialised for viewpoint-invariant recognition relates to the manner in which BOLD fMRI works. Any such cortical regions that were recruited throughout the experiment would have been undetectable. The authors' finding that superior parietal cortex (generally associated with transformational object constancy processes, as discussed in Chapter 2) was apparently involved in viewpoint-invariant processing may relate to the experimental task demands. Participants in the study reported by Vanrie et al. were required to compare two objects to determine whether their constituent features were equal. This may actually constitute a mental rotation task (that is, making a match/mismatch decision when stimuli are angularly disparate) of the kind employed in similar previous studies (e.g., Alivisatos and Petrides, 1997). Contribution of parietal cortex to the computation of viewpoint-invariant object recognition is thus somewhat uncertain. The study by Vanrie et al. is given further consideration in Chapter 4.

Nevertheless, the discovery that viewpoint-invariant recognition may involve a larger region of the ventral pathway than viewpoint-dependent processing invites further study. Additional, though indirect, support for ventral encoding of viewpoint-invariant representations comes from a study that used fMRI to demonstrate that cortical areas in ventral and dorsal pathways displayed different responses to misoriented objects in a priming study (James et al., 2002). It was found that repeat presentation of stimuli led to a reduction in BOLD signal in a ventral region of occipitotemporal cortex (ventral pathway), and that this effect was maintained even when objects appeared at different orientations. BOLD signal in an anterior region of the IPS (dorsal pathway) was also monitored, and this was found to be reduced only when identical object views were presented, but not when misoriented objects were shown. James et al. interpreted these results as evidence that the dorsal pathway regards non-identically-oriented object representations as separate objects. The authors also proposed that it is important for viewpoint-dependent object representations to be encoded separately in the dorsal pathway, since proficient grasping of objects will necessarily be determined by their orientation.

3.2.4 The use of novel stimuli in misoriented object recognition tasks

As noted in Chapter 1, the vast majority of studies investigating misoriented object recognition utilise familiar common objects as stimuli. Chapter 1 also discussed the idea that experience dictates the extent to which particular object views are encoded, and also considered the effects of inherent stimulus characteristics and viewing experience on the type of object representations encoded (e.g., the 'mono-oriented' and 'poly-oriented' objects, described by Leek, 1998). An important consideration, therefore, in any exploration of the relationship between viewpoint-dependent and viewpoint-invariant recognition, is that participants' prior exposure to stimuli is strictly controlled. By using entirely novel, abstract stimuli with strictly implicit canonical orientations, and thus controlling for prior orientation-specific exposure in a way that studies using familiar common objects cannot, it should be possible in this study to compare directly the cortical regions subserving viewpoint-dependent and viewpoint-invariant recognition in a way that minimises the potentially confounding effects of prior experience.

The present chapter therefore uses stimuli from a study of misoriented novel object recognition by Tarr & Pinker, who found that novel abstract shapes with ambiguous axes of symmetry (see Figure 7) elicited viewpoint-dependent RTs, whereas those with unambiguous axes of symmetry elicited viewpoint-invariant RTs (Tarr & Pinker, 1990) (theories accounting for such results were discussed in Chapter 1). Use of these stimuli in a misoriented recognition task can thus elicit preferential recruitment of viewpoint-dependent and viewpoint-invariant recognition processes to enable their cortical correlates to be studied, with the additional advantage that the stimuli are novel and thus insensitive to participants' prior experience.

3.2.5 Aims and hypotheses of the present chapter

The aim of the work presented in this chapter was to replicate the psychometric findings of Tarr and Pinker (1990) and use fMRI to elucidate the cortical regions mediating viewpoint-dependent and viewpoint-invariant object recognition. The aims of the present study were:

- To elucidate the cortical correlates of viewpoint-dependent recognition of misoriented novel objects. It was hypothesised that viewpoint-dependent recognition would recruit parietal cortex and premotor cortex, indicative of dorsal pathway involvement in this process. It was tentatively hypothesised that DLPFC might also be recruited, since demands on spatial working memory during global transformation of a stimulus percept might be expected to exceed those required during recognition of orientation-invariant object features.

- To elucidate the cortical correlates of viewpoint-invariant misoriented novel object recognition. It was hypothesised that viewpoint-invariant recognition would principally recruit inferotemporal cortex, indicative of ventral pathway mediation of this process. It was predicted that viewpoint-invariant recognition would not recruit premotor or parietal cortex, as involvement of these regions is believed to underpin transformational processes that are unlikely to be required by a viewpoint-invariant recognition mechanism.

- To establish the nature of both object constancy processes by considering the cortical correlates mediating each. Involvement of premotor cortex in viewpoint-dependent recognition may indicate that this object constancy process is analogous to physical manipulation of objects. Parietal recruitment would suggest implementation of reference-frame transformations. DLPFC recruitment may indicate increased demand on working memory, particularly during global stimulus percept transformation. Recruitment of both dorsal and ventral areas during either process might be interpreted as indicating the parallel recruitment of viewpoint-dependent and viewpoint-invariant mechanisms.

3.3 Method

3.3.1 Design

A two-factor repeated measures design was used, manipulating stimulus type on two levels (orientation-dependent or orientation-invariant) and stimulus orientation on three (+/- 45°, +/- 90° or +/- 135°) while participants assessed whether the stimulus presented was one they had previously memorised. Response-time (RT) measures were obtained for participants in the behavioural study, but were not acquired during scanning for the technical reasons explained in the following section.

In order to control for practice effects arising from the use of a repeated measures design, task order was counterbalanced: half of the participants completed learning and test phases with Set A stimuli prior to repeating the experiment with Set B stimuli [Group 1]. The other half completed the task in the reverse order [Group 2]. Participants' practice and testing proceeded in the specified counterbalanced order for their group throughout.

3.3.2 Participants

No equipment was available at the time of scanning to permit participants' psychometric data to be collected while in the scanner. Therefore, two groups of participants were recruited: one group to undergo scanning and a second group to provide behavioural data to indicate whether the two conditions in the experimental task were likely to be eliciting appropriate patterns of response-times.

Behavioural study participants

Fourteen participants (seven male and seven female, all undergraduates at the University of Wales, Bangor, between 18 – 35 years of age) performed the behavioural task. Participants were right-handed and had normal or corrected-to-normal vision. All participants were unpaid volunteers who had given written informed consent. Ethical approval of the behavioural study was granted by the University of Wales.

fMRI study participants.

Twelve participants (four female and eight male, between 22-34 years of age) volunteered for the fMRI study. All were right-handed non-smokers and had normal or corrected-to-normal vision. One participant had suffered from epilepsy 15 years previously but had had no recurrence of episodes since. The others had no known history of neurological illness. Participants' written consent to participate was obtained prior to commencement of the study. Ethical approval for the fMRI study was granted by the University of Manchester. Only participants achieving a minimum of 95% correct responses in this final practice session were permitted to complete the test phase trials; all participants recruited for both RT and fMRI studies achieved this criterion.

3.3.3 Apparatus and stimuli

Stimuli consisted of line drawings of two sets of novel objects and were taken from the original stimuli developed by Tarr and Pinker (1990). Set A contained seven line-drawn shapes that had previously been found to elicit orientation-dependent RTs. Set B contained seven different stimuli that the same study had shown to elicit an orientation-invariant response-pattern. Stimuli are illustrated in Figure 7. Stimuli for the behavioural study were presented using PsycLab software (Gum, 1995) run on a Macintosh LC7200 computer. PsycLab also monitored and collated participants' response-time data in the test-phase of the behavioural study.

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Figure 7. Stimuli previously found to elicit (A) orientation-dependent and (B) orientation-invariant RTs. After Tarr and Pinker (1990).

Stimuli for the fMRI study were presented using TINA software (Pollard, Porrill, & Thacker, 1989) run on an IBM ThinkPad T21 portable computer. Responses during practice trials and in the test-phase of the behavioural study were made by pressing a mouse-button. During the test phase of the fMRI study, participants pressed a hydraulic bulb, and results were recorded manually. Projection of images from the computer onto a screen inside the scanning room allowed participants to view stimuli reflected in a mirror positioned at 45° directly above their head. Stimuli presented in this way subtended approximately 19° of visual angle. Scanning was performed using a 1.5 tesla Philips MR scanner (ACS –NT PT6000, Philips Medical Systems, Best, NL) at the Division of Imaging Science and Biomedical Engineering at the University of Manchester.

3.3.4 Procedure

Learning phase: participants memorised one stimulus from Set A and one from Set B by copying them with paper and pen. Participants viewed stimuli at a 'canonical' (zero-degree: at which the principal axis of the stimulus was aligned vertically, as shown in Figure 7) orientation.

Training phase: Recognition of the learned stimulus was then tested against distracter stimuli at canonical orientations only, over a single blocks of 40 trials in which the target (learned) stimulus was presented 16 times at its canonical orientation. On the remaining trials, six distracter stimuli (the remaining unlearned shapes from each object type) were each presented four times at their canonical orientations. Each trial (see Figure 8) began with a 500 ms fixation-point in the centre of the screen, which was replaced by either a target or distracter stimulus shown at one of the tested stimulus orientations (inter stimulus interval = 750 ms). Participants indicated with a right-handed key-press whether the stimulus was the previously-memorised shape. The stimulus remained on the screen until participants responded, or RT exceeded 2500 ms. Feedback about the stimulus (target; non-target) was then presented for 1000 ms. In the behavioural study, when participants made an incorrect response, or did not respond before 2500 ms, an error message was displayed, accompanied by a short beep. Trial order was randomised. Participants in the fMRI study undertook two additional training sessions prior to the scanning phase to ensure an acceptable level of performance in the scanner. These additional computerised sessions, in which stimuli were presented at non-canonical orientations only, were identical to the test phase performed during scanning, except that the rate of trial presentation was slower.

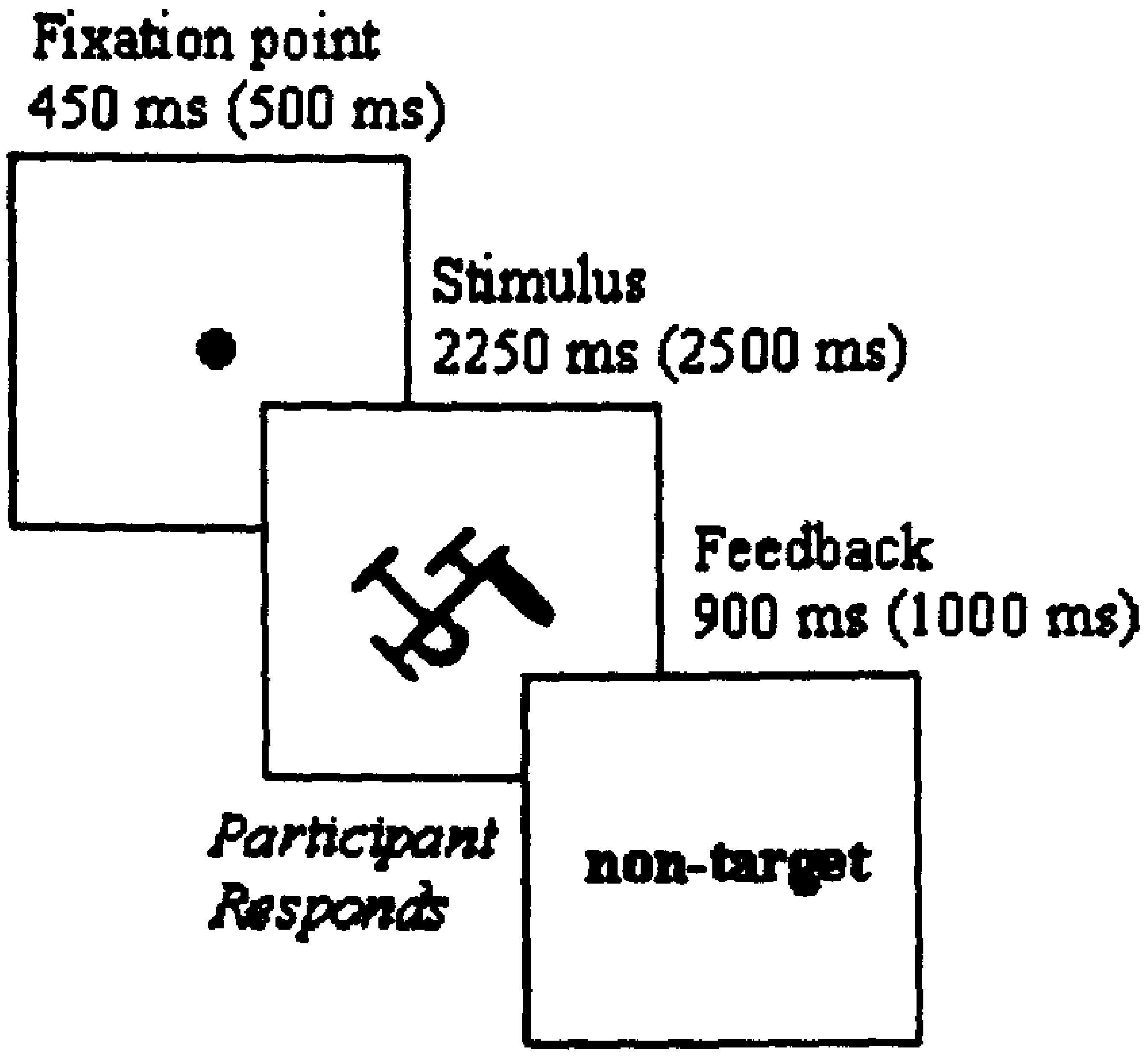

Figure 8. A single test trial. The slower presentation times used during training sessions are shown in parentheses. Total trial time = 3600 ms (4000 ms)

Test phase: Participants completed two 40-trial test blocks in which targets were shown 14 times at the zero-degree orientation, and 14 times each at +/- 45°, +/- 90° and +/- 135° (total = 56 trials). Each distracter was shown four times, with the number of distracter presentations equal for each orientation (total = 24 trials). Trial presentation was speeded up by 10% such that each trial lasted 3.6 s. The 40-trial blocks for each stimulus type were divided into four sub-blocks, each consisting of ten trials and followed by a rest period of equal length (36 s) during which participants were instructed to focus on a fixation point at the centre of the presentation screen. In this way, eight alternating sub-blocks (four of task performance and four at rest) were completed during scanning. Participants' performance during scanning was monitored (all participants performed at greater than 90% accuracy), but as noted earlier, RT measures were only obtained from participants in the behavioural study. During training and scanning, participants were instructed to respond *only* when a non-target shape was presented; the proportion of non-target presentations was set deliberately low (30% of the total) to reduce the number of trials in which participants made any physical movement in the scanner, in order to minimise motion artifact.

3.3.5 FMRI data acquisition and processing

Data acquisition

Anatomical reference scans were obtained using an inversion recovery sequence (TR/TE/TI/matrix: 3000 ms/50 ms/300 ms/256^2; slice thickness 3 mm; interslice spacing 0.3 mm; FOV 23 cm^2). Functional imaging was performed using a single shot echo planar acquisition consisting of 25 slices (TR/TE/matrix: 3000 ms/550 ms/64^2; slice thickness 3.5 mm; interslice spacing 0.5 mm; FOV 23 cm^2). Each set of blood oxygen level-dependent (BOLD) images was acquired in 3.6 s and the sequence repeated to obtain 100 contiguous data sets with total acquisition duration 360s. Anatomical coverage was selected by an experienced radiographer to include the entire prosencephalon with the exception of the base of the temporal lobe. All images were obtained in an anatomical plane parallel to a line joining the midpoint of the lower border of the splenium and the genu of the corpus callosum.

Data processing

Image analysis was performed using TINA image analysis software. Image data was coregistered to the baseline images and resliced using SINC interpolation (Thacker, Jackson, Moriarty, & Vokurka, 1998) to minimise motion artefact (Friston, Williams, Howard, Frackowiack, & Turner, 1996). An initial correction was made for time varying gain artefacts (Vokurka, Thacker, & Jackson, 1999) and a correlation analysis, equivalent to a subtraction of the BOLD signal between task performance and rest, was then performed. Correlation analysis included a variable (restricted) phase offset in the time domain so that the largest correlation between the experimental paradigm and the test data was identified. Tests were made for residual motion artefacts (Thacker, Burton, Lacey, & Jackson, 1999). A Monte Carlo technique was used to correct the z-score values for the effects of the phase offset. During this process, the probability of finding a statistically significant result purely by chance was assessed as $p < 10^{-8}$. The presence of spatial correlation within the data resulting from processes such as image smoothing, and which has been observed by other authors (Friston, Holmes et al., 1996), was tested by examining a scatter plot of adjacent pixel values in TINA. As scattergram data were centrally distributed, with no diagonal structure, this was interpreted as indicating the desired lack of spatial correlation between adjacent voxels in the image data.

After image processing, fMRI data from each participant was aligned with a 64 x 64 volume-element (voxel) 'fuzzy' brain in Talairach space using a combination of manual realignment and an automated least squares method embedded in TINA. After realignment, each participant's fMRI data were re-sliced to conform to axial slices as per the Talairach and Tournoux stereotaxic coordinate system (Talairach & Tournoux, 1988). Finally, data from all participants was averaged by participant group and experimental task to give four sets of BOLD data (1A, 1B, 2A and 2B) representing BOLD activation relative to rest for that group and condition. Each set of results comprised 21 slices, each slice a 64 x 64 array of z-scores representing BOLD signal activation in the axial plane.

An a priori significance level corresponding to $z = 6.0$ standard deviations from the mean ($p < 10^{-8}$) was adopted as the criterion for assessing significant activation in each averaged data set. An automated assessment tool in TINA allowed all voxels exceeding the significance threshold to be logged, and their Talairach coordinates determined with reference to the Talairach Daemon client application (Lancaster, Summerln, Rainey, Freitas, & Fox, 1997; Lancaster et al., 2000). All such voxels centred on Talairach coordinates within cerebral cortex and the immediately underlying white matter were recorded.

3.4 Results

3.4.1 Behavioural data

Response-time (RT) data from the fourteen participants who completed the behavioural experiment only was collated, and data from incorrect trials (accounting for around 4% of the total data) discarded. RT data were analysed in two batches: the first from the group of seven participants performing the orientation-dependent task first (Group 1), and the second batch of data from the seven participants who performed the tasks in the reverse order (Group 2). Mean RT data for each participant group and condition, and their corresponding regression slopes, are listed in Table 1 and illustrated in Figure 9.

Table 1: Mean RTs for each participant group for each stimulus type and orientation in the behavioural task. Regression slopes are in milliseconds per degree (ms/deg).

		Stimulus orientation			*Row*	**Regression**
Stimulus type	***0°***	***45°***	***90°***	***135°***	*mean*	**slope**
Group 1: Orientation-dependent	702	807	848	930	*821*	***1.61***
Group 2: Orientation-dependent	624	676	840	979	*780*	***2.73***
Column mean	*663*	*742*	*844*	*954*	*801*	**2.17**
Group 1: Orientation-invariant	790	1066	1031	1167	*1014*	***2.45***
Group 2: Orientation-invariant	802	820	882	877	*845*	***0.64***
Column mean	*796*	*943*	*956*	*1023*	*929*	**1.54**

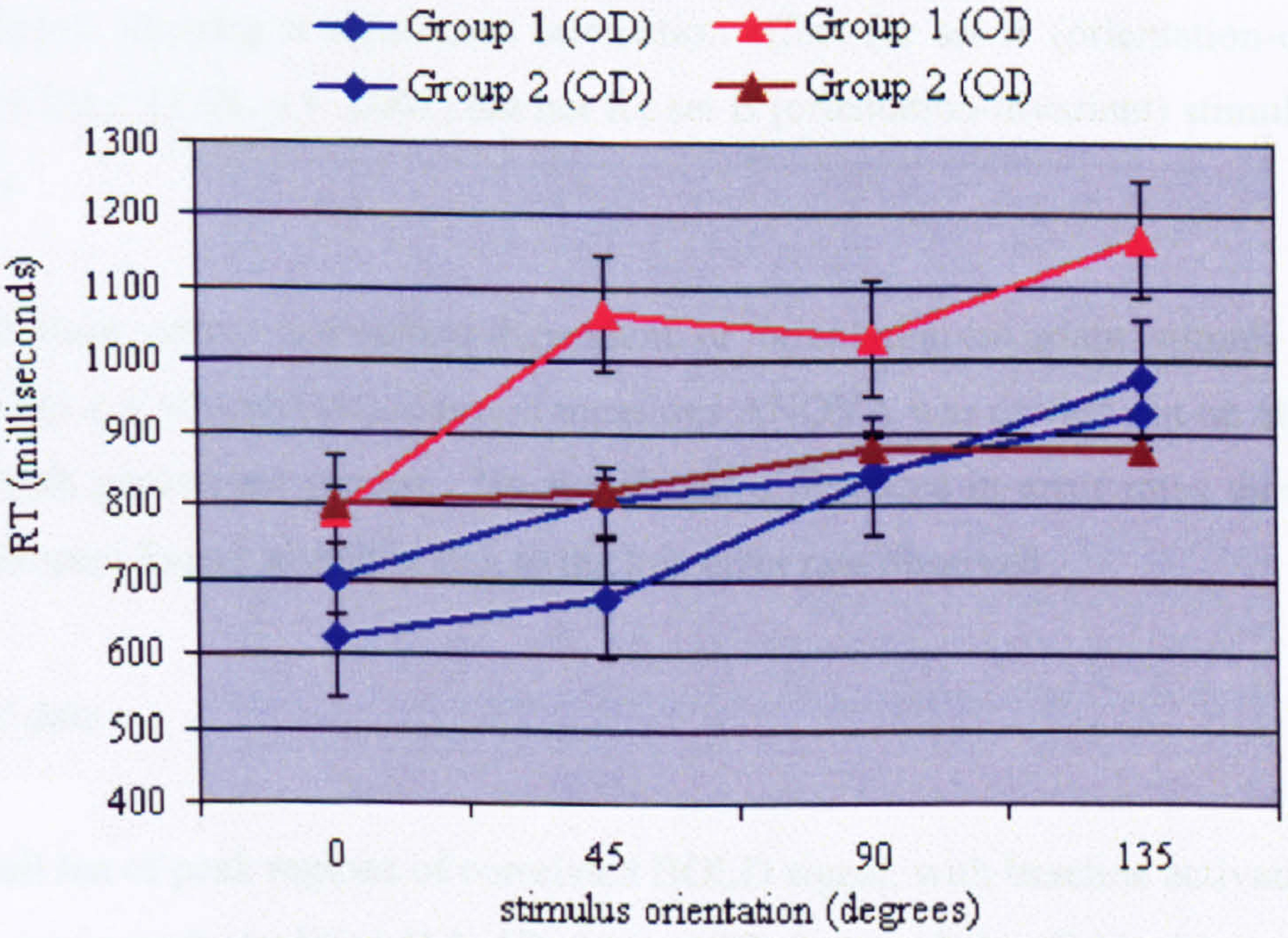

Figure 9. RT data from the behavioural study. Participants in Group 1 performed the task with the orientation-dependent (OD) stimulus type first; those in group 2 with the orientation-invariant (OI) stimuli first.

A 2 (stimulus type) x 4 (orientation) repeated measures ANOVA was carried out on RT data from each group.

Group 1

A significant main effect of orientation (F (3,18) = 4.32, p < .01) was found, with larger RTs recorded for greater stimulus misorientations. No significant effect of stimulus type (F (1, 6) = 0.76, n.s.) or significant interaction between stimulus type and orientation (F (3, 18) = 0.54, n.s.) were observed.

Group 2

A significant main effect of orientation (F (3,18) = 9.96, p < .001) was found, with larger RTs recorded in response to greater stimulus misorientations. No significant main effect of stimulus type (F (1,6) = 0.29, n.s.). A significant interaction between stimulus type and orientation (F (3,18) = 4.40, p <.01) was observed, reflected in the very different regression slopes obtained in Group 2, in which orientation-dependent stimuli elicited larger regression slopes than orientation-invariant stimuli. This interaction was further examined using simple effects analyses, showing a significant orientation effect for set A (orientation-dependent) stimuli (F (3,18) = 12.98, p < .0001) but not for set B (orientation-invariant) stimuli (F (3,18) = 0.91, n.s.).

A 2 (task order: orientation-dependent or orientation-invariant stimuli first) x 2 (stimulus type) x 4 (orientation) repeated measures ANOVA was carried out on all error rate data from both participant groups. No significant differences in error rates due to any of these factors were found, probably due to the low error rate observed.

3.4.2 FMRI data

A full list of peak regions of correlated BOLD signal, with baseline activation subtracted out, in each condition (1A, 1B, 2A and 2B) is provided in Table A1 (see Appendix A). Task performance in each condition was associated with widespread cortical and sub-cortical activation in prefrontal, premotor, parietal, occipital, temporal and cerebellar regions. A summary of the regions differing between conditions is given in Table 2.

Table 2. Cortical regions of interest where significant BOLD signal differed between groups and conditions. Brodmann areas (BA) are listed in approximate anteriority in the axial plane from rostral to caudal; anatomical features where significant BOLD signal was recorded are listed in order of *z*-score.

Cu = Cuneus; GFd = medial frontal gyrus; GFi = inferior frontal gyrus; GFm = middle frontal gyrus; GPrC = precentral gyrus; GFs = superior frontal gyrus; LPi = inferior parietal lobule; LPs = superior parietal lobule; PreCu = precuneus.

Group/task	*1A*		*1B*		*2A*		*2B*	
Hemisphere	R	L	R	L	R	L	R	L
Region								
BA10	GFm		GFs, GFm		GFs, GFm			
BA9	GFm, GFi	GFi, GFm, GPrC	GFi, GFm, GPrC, GFs	GFi	GFi, GFm	GFm		
BA46	GFm		GFm		GFm			
BA6	GFi, GFm, GPrC, GFd, GFs	GPrC, GFm, GFd, GFs	GPrC, GFd, GFs, GFm	GFd, GPrC, GFs, GFm	GPrC	GPrC	GFm	
BA7	LPs, PreCu	PreCu, LPs, Cu, LPi	LPs, PreCu, LPi, Cu	PreCu, LPi, LPs	PreCu, LPs, Cu, LPi	PreCu, LPi, LPs	PreCu, LPs, Cu, LPi	PreCu, LPi

Selected axial anatomical slices showing superimposed regions of suprathreshold correlated BOLD signal are shown in Figure 10.

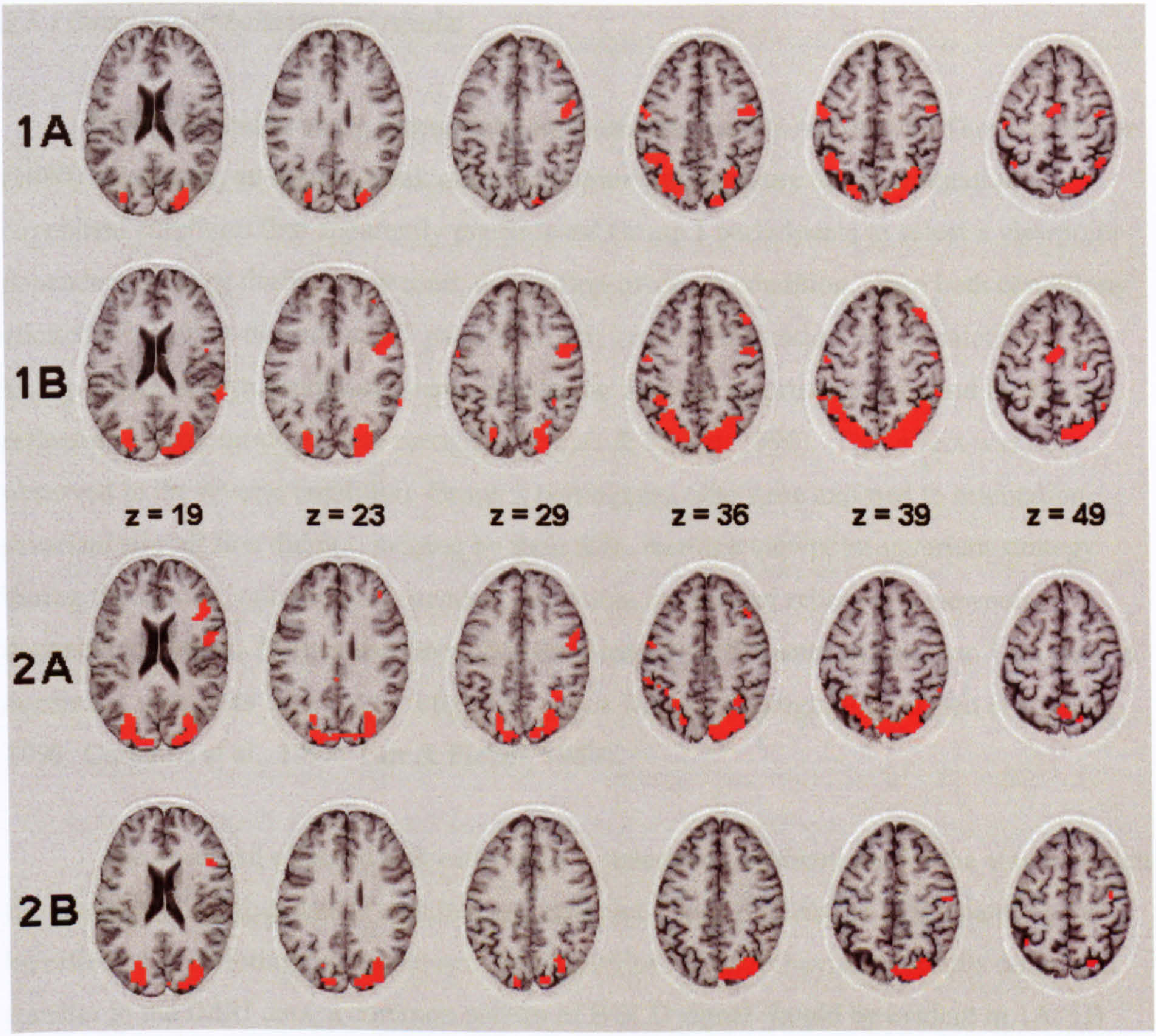

Figure 10. Selected axial slices showing areas of suprathreshold ($z > 6.0$) BOLD signal for Groups 1 and 2 in orientation-dependent (A) and orientation-invariant (B) stimulus conditions, respectively. z represents slice height, in mm, above a line passing through anterior and posterior commissures. Left and right are as shown. Visible regions of significant BOLD signal include prefrontal, precentral, parietal and occipital cortex. Not all identified regions of significant activation are discernible on the slices shown.

3.5 Discussion

3.5.1 Summary of behavioural results

The behavioural study successfully replicated the results reported by Tarr and Pinker (1990). However, an effect of task order was observed: exposure to the orientation-dependent condition first apparently predisposed Group 1 participants to select a viewpoint-dependent strategy during the second, orientation-invariant condition, since both conditions elicited orientation-dependent RT patterns in this group. Regression slopes calculated for Group 1 data in both conditions were very similar to those reported by Tarr and Pinker as reflecting viewpoint-dependent recognition (Tarr & Pinker, 1990). This effect was not observed in the reverse condition: Group 2 participants who were exposed to orientation-invariant stimuli first did not, judging by their RTs, recruit a viewpoint-invariant strategy during the second, orientation-dependent condition, but instead relied on a viewpoint-dependent strategy. Regression slope data for Group 2 participants, at less than 1 ms/deg, is consistent with rates believed to reflect viewpoint-invariant recognition (Cohen & Kubovy, 1993; Corballis et al., 1978; Tarr & Pinker, 1989).

The observed effect of task order on RT pattern has implications for the way in which the functional imaging data is acquired and analysed, since differences in RT patterns may be reflected in differing functional activation profiles. If the behavioural results do indeed transfer to the fMRI data, a common pattern of BOLD signal should be evident in 1A, 1B and 2A, whereas condition 2B should elicit quite a different pattern of results (this last group equating to the orientation-invariant responses observed in Group 2 in the behavioural task).

3.5.2 Summary of fMRI results

A wide range of cortical regions were found to be recruited in both participant groups and both experimental conditions. Significant BOLD signal was recorded in cortical areas of the dorsal and ventral pathways in both conditions. A consistent pattern of functional activation was found for Group 1 in both viewpoint-dependent (1A) and viewpoint-invariant (1B) conditions (corresponding to the orientation-dependent RTs observed in Group 1 participants during both conditions of the behavioural task). The profile of cortical recruitment thus inferred to be specific to viewpoint-dependent recognition in Group 1 consisted of bilateral superior parietal cortex, bilateral dorsolateral prefrontal cortex, right-hemispheric BA10 (middle/inferior frontal gyri)[11], and bilateral premotor area BA6 (principally in the precentral gyrus but also spreading to middle, medial and inferior frontal gyri).

The same regions as those observed in Group 1 participants in both conditions were found to be recruited in Group 2 participants during the viewpoint-dependent condition (2A). However, for Group 2 participants in the viewpoint-invariant condition (2B), significant recruitment of premotor cortex was only observed in the middle frontal gyrus of the right hemisphere. Superior parietal area BA7, implicated bilaterally in viewpoint-dependent recognition in data-sets 1A and 1B, was likewise found to be recruited bilaterally in 2A, but in the right hemisphere only in 2B. The number of suprathreshold voxels in superior parietal cortex in 2B was also much reduced, relative to the equivalent volume observed in 2A. No cortical regions were found to be recruited exclusively during condition 2B (viewpoint-invariant recognition).

As predicted by the results of the behavioural study, conditions 1A, 1B and 2A do indeed show a common profile of functional recruitment not found in condition 2B. The effect of task order found in the behavioural study therefore appears to be replicated in the functional imaging data, suggesting that the patterns of cortical activity observed in three of the four data-sets in the imaging study similarly represent viewpoint-dependent object recognition, with the remaining set reflecting the functional profile of viewpoint-invariant recognition.

Recruitment of superior parietal cortex, the putative marker of visuospatial transformation, was observed bilaterally in three of the four data-sets (1A, 1B and 2A), but only in the right hemisphere in condition 2B. This indicates that bilateral involvement of superior parietal cortex may be necessary for the computation of viewpoint-dependent recognition, but that it is apparently unnecessary for viewpoint-invariant recognition. The more widespread (and bilateral) recruitment of premotor cortex during viewpoint-dependent, relative to viewpoint-invariant, recognition was also consistent with predictions, although a

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[11] Fletcher and Henson (2001) distinguish between prefrontal recruitment of in Brodmann areas 9/46 and that in BA10, based on a review of the literature showing consistent functional dissociation between the two regions. In the present study, the foci of activation observed in BA9 and BA46 are actually quite distinct, with peak activation in BA46 around 40 mm anterior to the peak activation observed in BA9.

small region of the right middle frontal gyrus in BA6 was found to be recruited by viewpoint-invariant recognition. Viewpoint-dependent recognition also preferentially recruited several regions of prefrontal and DLPF cortex. Significant BOLD signal specific to viewpoint-invariant object recognition was not found in any region; this may reflect the large extent to which extrastriate areas in ventral pathway were recruited by both experimental conditions relative to the baseline condition, the scale of which was not anticipated *a priori*. Thus, no double-dissociation was observed between dorsal and ventral recruitment and viewpoint-dependent and viewpoint-invariant recognition. The implications of these findings are addressed in the following sections.

3.5.3 Bilateral recruitment of superior parietal cortex may indicate visuospatial transformation

The significant bilateral recruitment seen in superior parietal cortex exclusively during viewpoint-dependent recognition supports the findings of Kosslyn et al. (1994) and Sugio et al. (1999), both of which studies also reported bilateral engagement of superior parietal cortex in response to non-canonical object views. Bilateral superior parietal recruitment would thus appear to be necessary for the computation of viewpoint-dependent object recognition. Recruitment of right-hemispheric parietal cortex has been found to extend to bilateral involvement when the dimensional complexity of a mental rotation task increases (Milivojevic et al., 2003). It might thus reasonably be inferred that the present experimental design requires the allocation of substantial cognitive resources during viewpoint-dependent recognition, and fewer such resources for viewpoint-invariant recognition. This is consistent with machine vision accounts which describing a global (template-matching) solution such as that inferred by Tarr and Pinker as 'computationally expensive' (Ashbrook, 1996; Thacker et al., 1995).

In tasks recruiting object constancy processes, the superior parietal lobule would appear to be sensitive to the cognitive complexity of the task. This may account for the finding by Harris et al. (2000) that activation of right posterior parietal cortex (around the IPS) was greater when a greater proportion of stimuli in a mental rotation task were angularly disparate. Increased involvement of the superior parietal lobule has previously been shown to correspond with greater cognitive demands in a mental rotation task (Tagaris et al., 1996), and proportionally greater recruitment of this area has been found when participants were required to mentally rotate a shape about two axes than when rotation about one axis was performed (Just et al., 2001). Superior parietal activity has also been linked to the computation of coordinate transformations (Andersen, 1995; Andersen et al., 2000; Andersen et al., 1997; Yoshino et al., 2000). Related to this are findings indicating that selective recruitment of superior parietal cortex during matching tasks is associated with the focusing of spatial attention (Cohen et al., 1996; Corbetta, Miezin, Shulman, & Petersen, 1993), spatial working memory function, (Postle & D'Esposito, 1999), and high levels of saccadic activity (Kimmig et al., 2001). The extensively documented involvement of parietal cortex, and superior parietal cortex in particular, in mental rotation was discussed in Chapter 2; the results presented here, and those from previous studies of misoriented object recognition, may provide evidence that a similar visuospatial mechanism for stimulus percept transformation may underpin both processes – this hypothesis will be tested directly in Chapter 4.

3.5.4 DLPFC may reflect spatial working memory load during visuospatial transformation

The fMRI results reported here would appear to corroborate the results reported by Kosslyn et al. (1994) and Sugio et al. (1999), both of which studies reported bilateral activation in DLPFC in response to non-canonical object views, and those described by Just et al. (2001), who reported bilateral DLPFC involvement during mental rotation of a memorised object. The focus of DLPFC recruitment in each of these studies varies somewhat; a summary is given in Table 3. It can be seen that there is reasonable variation between studies, with the coordinates reported by Sugio et al. apparently closest to those presented here – as noted earlier, the task demands of that study most closely resemble those of the Tarr and Pinker task.

Table 3. Loci of DLPFC activity in the present study and related publications

Study	Task	Max/centroid DLPFC *x, y, z* coordinates	
		Right	*Left*
Present chapter	Misoriented object recognition, relative to baseline	49,40, 23 (BA46) 49,5,26 (BA9)	-53,5,36 (BA9)
Sugio et al. (1999)	Non-canonical object views, relative to baseline	48,10,34 (BA6/9)	-46,10,38 (BA9)
Kosslyn et al. (1994)	Non-canonical object views, relative to canonical views	35,15,28 (BA9/46)	-22,40,-8 (BA47)
Just et al. (2001)	Mental rotation of a memorised real object, relative to baseline	32,24,42 (BA8)*	-36,27,34 (BA9)*

* Just et al do not provide information on Brodmann areas; the cortical regions shown are those listed in the Talairach Daemon database for the coordinates they reported.

The finding that DLPFC and anterior frontal recruitment are associated exclusively with viewpoint-dependent object recognition suggests that these areas contribute to global stimulus percept transformation. One possibility is that this pattern of functional activation reflects the recruitment of short-term working memory resources during the transformation of the image percept; it has been proposed that increased activation in BA9/46 reflects proportionally greater recruitment of the neural systems subserving working memory (Braver et al., 1997; Stern et al., 2000). Prefrontal activation, particularly in the DLPFC, has been shown to correlate specifically with tasks thought to recruit spatial working memory (Jonides, Smith, Koeppe, Minoshima, & Mintun, 1993; Stern et al., 2000), and DLPFC has been proposed as the locus for manipulation of spatio-temporal information in working memory (Postle, Berger, Taich, & D'Esposito, 2000). Bilateral recruitment of DLPFC has been associated with the performance of object-based working memory (Belger et al., 1998), and the involvement of DLPFC in monitoring aspects of the stimulus percept in terms of how they relate to a hypothetical match for that stimulus in memory has been inferred (Kosslyn et al., 1994). DLPFC recruitment has also been found to correlate explicitly with tasks of misoriented shape-matching (Cohen et al., 1996; Vanrie et al., 2002). Premotor recruitment, found in the present study, has also previously been reported in a task explicitly recruiting spatial (but not object) working memory (Smith, Jonides, Koeppe, Schumacher, & Minoshima, 1995). However, in a meta-analysis of studies reporting consistent loci of prefrontal activity, including regions in dorsolateral and ventrolateral prefrontal cortex and a medial anterior cingulate region (which could include posterior regions of BA10 – see section 3.5.5), the authors concluded that this pattern of functional activation appeared to be common to a cognitively diverse range of tasks, which included, but were not limited to, tasks manipulating working memory load and perceptual difficulty (Duncan & Owen, 2000). Speculation about the functional involvement of these areas in the perception of misoriented shape should therefore proceed cautiously.

3.5.5 BA10 recruitment may reflect increased demands on decision-making and retrieval during viewpoint-dependent recognition

A possible role for Brodmann area 10 in viewpoint-dependent recognition may be in the executive control of working memory subsystems to allow comparison between long term memory and perceptual stimulus representations (Fletcher & Henson, 2001; Gill et al., 1998). Increased recruitment of this area has also been associated with increasing degrees of memory retrieval (McIntosh, Nyberg, Bookstein, & Tulving, 1997); McIntosh et al. also implicate inferior frontal region BA45, found to be recruited in all four conditions of the present study, in the retrieval process – thus, concurrent recruitment of BA10 and 45 during viewpoint-dependent recognition may reflect increased demands on retrieval of stored stimulus representations during this process. The exclusive involvement of BA10 in viewpoint-dependent object recognition implies greater decision-making demands imposed by those experimental conditions: Brodmann area 10 has been shown (Rogers et al., 1999) to receive signals from several parts of the cortex and limbic system that are instrumental in forming a decision where a choice must be made between two or more options in a task. The apparent relevance of BA10 to decision-making and retrieval processes supports the earlier assertion that viewpoint-dependent recognition may be more cognitively expensive than viewpoint-invariant recognition.

3.5.6 Premotor cortical recruitment may reflect the computation of population vector transforms during viewpoint-dependent recognition

Significant, bilateral BOLD signal in premotor cortex was found to correlate with conditions believed to be recruiting viewpoint-dependent recognition, whereas right-sided premotor involvement was only inferred during viewpoint-invariant recognition, and across relatively few voxels. Although the results from Group 2 (2A and 2B) showed less widespread premotor activity than the results from Group 1, significant BOLD signal in the precentral gyrus was observed bilaterally in 1A, 1B and 2A, whereas in 2B there was only one suprathreshold voxel in this region, located in the right middle frontal gyrus. This finding is in agreement with results reported by Sugio et al. (1999), who found greater recruitment of premotor cortex when participants viewed non-canonically oriented, relative to canonically oriented, objects. The suggestion that greater premotor recruitment might be due to longer response-times arising through the recruitment of a viewpoint-dependent recognition strategy (leading to a larger haemodynamic response in motor preparation areas during each such trial) may be dismissed by examining the behavioural data, which shows no significant difference in mean RTs for each condition.

Recruitment of premotor cortical areas has also been reported in studies of mental rotation (Parsons et al., 1995; Richter et al., 2000), and mental rotation of hand-shapes into congruence has been found to be disrupted by the application of transcranial magnetic stimulation to primary motor cortex (Ganis et al., 2000). Premotor cortex is also believed to be involved in the computation of population vector transforms for visuomotor control (Grezes et al., 2003). Such correspondence raises the possibility that the visuospatial transformation mechanisms which permit misoriented object recognition and visuomotor control involve the computation of similar kinds of population vector transform. Premotor cortex has also been shown to correlate with imagined motor task performance (Leonardo et al., 1995) and BA10 (right hemispheric recruitment of which was observed in all three conditions of the present study believed to have invoked viewpoint-dependent recognition) is also known to be critical for the coordination of intended movement (Terry & Rosenberg, 1995). Extensive premotor cortical recruitment during viewpoint-dependent recognition may thus signify some internalised spatial manipulation of the stimuli analogous to righting an upturned object, although in the absence of more robust evidence this must remain conjectural.

3.5.7 Viewpoint-invariant recognition

Although several regions of ventral cortex were found to be recruited during viewpoint-invariant recognition, these were also found to correlate with viewpoint-dependent recognition. No region of cortex was identified as being preferentially recruited during viewpoint-invariant recognition. This was, however, consistent with the result obtained by Vanrie et al. (2002), who sought to elucidate the cortical areas computing viewpoint-invariant object perception and found that the areas recruited represented a subset of those recruited during mental rotation. As already mentioned, the possibility of identifying a cortical region in the ventral pathway (or indeed anywhere in extrastriate cortex) specific to viewpoint-invariant recognition was greatly reduced by the extent to which these regions were found to be recruited during both viewpoint-dependent and viewpoint-invariant recognition. This finding may provide evidence for parallel engagement of viewpoint-dependent and viewpoint-invariant mechanisms during misoriented object recognition, a theory which is discussed below. A more subtle experimental design (specifically, one in which the baseline condition involves canonically-oriented stimuli, such as that conducted by Sugio et al., 1999) might be expected to reveal differences in the functional activation profile of viewpoint-dependent and viewpoint-invariant recognition; such an experiment is described in Chapter 4.

The finding that regions of prefrontal and superior parietal cortex, which were recruited bilaterally during viewpoint-dependent object recognition, were also recruited in the right hemisphere during viewpoint-invariant recognition, invites speculation. Although it is impossible to make any kind of quantitative assessment about the relative extent to which cortical recruitment was engaged by each condition, it is possible that the minimal pattern of significant premotor and superior parietal cortical recruitment in viewpoint-invariant recognition may reflect extant but less widespread engagement of neuronal population vector transformations, and/or reference-frame transformations, respectively, in that process. One explanation for these results is that such computations are essential to viewpoint-invariant object recognition, for example, in transforming a viewpoint-dependent stimulus percept into alignment with a stored, global, object-centred representation (Humphreys & Riddoch, 1984; Marr & Nishihara, 1978). A second interpretation is that the types of reference-frame transformations believed to be carried out in premotor and superior parietal cortex are – as appears more likely – integral to viewpoint-dependent recognition, and that their diminished presence during viewpoint-invariant recognition reflects transient engagement of a parallel viewpoint-dependent mechanism prior to solution of the task by viewpoint-invariant means. The latter model has previously been used to account for the non-linearity of orientation-dependent RT patterns (Jolicoeur, 1990). Support for this view also arises from the observation that, in the present study, significant recruitment of inferior parietal cortex was observed in all conditions: inferior parietal cortex has been implicated (Milner, 1995; cited in Turnbull et al., 1997) as the locus of integration between viewpoint-dependent and viewpoint-invariant representations. However, since no significant BOLD signal was observed in BA10 or DLPFC (areas found to be preferentially recruited during viewpoint-dependent recognition) was observed during viewpoint-invariant recognition in the present study, this proposition remains somewhat speculative. The putatively concurrent recruitment of viewpoint-dependent and -invariant processes is addressed further in Chapters 4 and 5.

3.5.8 A common visuospatial transformation mechanism for object constancy?

Areas found in the present study to be recruited during viewpoint-dependent recognition appear to overlap substantially with those regions previously implicated in mental rotation tasks. It appears on the basis of these results that the visuospatial transformation mechanisms underlying these two processes may be similar, if not synonymous, appearing to be underpinned by a common neural substrate. For example, it has been demonstrated that performance of the Shepard and Metzler task also evokes recruitment of parietal (Carpenter et al., 1999; Cohen et al., 1996), premotor (Cohen et al., 1996; Richter et al., 2000) and DLPF (Cohen et al., 1996) cortex.

However, it has also been proposed by Kosslyn et al. (1998) that 'mental rotation' (visuospatial transformation) may take at least two forms. The first kind, inferred from a PET study of the cortical regions involved in mentally rotating Shepard and Metzler-style novel stimuli, is proposed to function solely for the purpose of object recognition. This process was found by Kosslyn et al. to recruit superior and inferior parietal cortex (BA7 and 19) bilaterally, and may account for similar results obtained in previous mental rotation studies, such as those reported by Alivisatos and Petrides (1997). The second kind of mental rotation process proposed by Kosslyn et al. was hypothesised to recruit a network of cortical areas specifically for the purpose of object manipulation: mental rotation of line-drawn pictures of hands was found to recruit entirely left-hemispheric regions in premotor and primary motor cortex, superior and inferior premotor cortex, insula and a dorsal region of BA9. To paraphrase Goodale and Milner (1992), Kosslyn et al. thus proposed the existence of 'visuospatial transformation for perception, and visuospatial transformation for action'. Based on their respective functional activation profiles, the latter action-oriented mechanism proposed by Kosslyn et al. would appear to be very similar to the viewpoint-dependent mechanism employed by participants in the present study, despite the use of novel, non-hand shaped stimuli. In particular, the finding by Kosslyn et al. that left-hemispheric regions were activated during this process resonates with the discovery in the present chapter that viewpoint-dependent recognition correlated with peferential recruitment of left-hemispheric premotor, DLPF and superior parietal cortex (though the region of DLPFC recruited in the present study was not close to the superior region of BA9 identified by Kosslyn et al., and as such is probably representative of a different function). Since the study reported by Kosslyn et al. used a mental rotation task and not misoriented viewpoint-recognition, this provides additional support for the recruitment of a common visuospatial transformation mechanism in both processes.

The discovery of several distinct and widely-distributed foci of cortical recruitment in many other functional imaging studies of object constancy suggests that visuospatial transformation is not just computed within the occipitoparietal pathway, but rather, that this dorsal stream may extend into areas of the frontal lobe. DLPFC has been shown to share a large number of reciprocal connections with the parietal lobe (Cavada & Goldman-Rakic, 1989), while premotor cortex has been implicated as part of a 'fronto-parietal circuit', evolved for the physical manipulation of objects in space and analogous to a network thought to exist in the monkey (Binkofski, Buccino, Posse et al., 1999; Rizzolatti et al., 1996). It is possible that other regions in the occipital, inferior parietal and inferior temporal lobes also form part of this network (Carpenter et al., 1999; Gauthier et al., 2002), but any such recruitment in the present study may have been masked by the substantial BOLD signal observed in those regions in all conditions.

3.5.9 Computational implications of this chapter

The computational implications of the behavioural results in the present study are twofold. Firstly, they indicate that Tarr and Pinker's so-called 'orientation-invariant' stimuli can be recognised using either viewpoint-invariant or viewpoint-dependent processes.

Second, it appears that Tarr and Pinker's 'orientation-dependent' stimuli can only be recognised using a viewpoint-dependent process. The effects of task order on response-time from which these conclusions are inferred were also seen in the functional imaging data, supporting correspondence between the cognitive and physiological processes being measured.

It would appear that, regardless of the manner in which the orientation-invariant stimuli encountered by participants in condition 1B were initially encoded in the learning phase, the process by which these stimuli were later compared against their stored representations was viewpoint-dependent. Since it is unlikely that one would encode a stimulus in a viewpoint-invariant manner, only to employ a viewpoint-dependent recognition strategy later, a more plausible interpretation might be that when an object is repeatedly encountered at a single, canonical orientation (such as in the learning and training phases of the study), viewpoint-dependent encoding is likely to result (Jolicoeur, 1985, 1990; Leek, 1998b; Tarr & Pinker, 1989, 1990). However, context may modulate the manner in which stored object representations are encoded and accessed. For example, in condition 1B, participants had already established in condition 1A the efficacy of applying a viewpoint-dependent strategy in the context of this experiment; therefore, a statistically-based decision process about which strategy to use in condition 1B might be heavily weighted towards selection of a viewpoint-dependent strategy. Although evidence from behavioural studies suggests that orientation-invariant features of misoriented objects are accumulated with repeated exposure, something that may permit participants to recruit viewpoint-invariant recognition strategies in later experimental trials (Eley, 1982; Jolicoeur, 1985, 1990; Leek et al., unpublished; McKone & Grenfell, 1999; Murray, 1995, 1999; Murray et al., 1993), it does not necessarily follow that participants would abandon a successful viewpoint-dependent strategy.

Another reason why the task order effect was observed for Group 1, but not Group 2, participants may relate to the stimuli themselves. It may be that the relative featural sparseness of the orientation-dependent stimuli (or ambiguity regarding the object's major axis, as proposed by Tarr & Pinker, 1990) did not permit the extraction of unambiguous orientation-invariant features, leading to reliance on a viewpoint-dependent solution. Orientation-invariant stimuli, by contrast, had many more distinctive features (and unambiguous major axes), which may have assisted the identification of orientation-invariant features, but would not prohibit viewpoint-dependent recognition. The work presented in Chapter 4 attempts to eradicate the potentially confounding effect of radically different stimulus features and their potentially biasing effect on preferential selection of a specific object constancy mechanism.

3.6 Summary

Previous studies have not directly compared the cortical correlates of viewpoint-dependent and viewpoint-invariant misoriented object recognition. Additionally, functional imaging studies investigating misoriented object recognition have used familiar objects, which have well-learned canonical orientations and features. This chapter described an fMRI study designed to establish the cortical correlates of viewpoint-dependent and viewpoint-invariant misoriented novel object recognition and assess the extent of differential dorsal and ventral involvement in these processes. Areas found to correlate with viewpoint-dependent recognition included bilateral superior parietal, premotor and DLPF cortex, all previously implicated in the recognition of misoriented familiar objects. These findings support dorsal pathway mediation of viewpoint-dependent recognition. Parietal, prefrontal and premotor cortex have previously been proposed to form a network specialised for physical object manipulation; the study reported in Chapter 3 provides evidence to suggest that this network may also underpin the internalised manipulation of object percepts. Previous imaging studies indicate that increases in difficulty during tasks recruiting object constancy mechanisms lead to bilateral recruitment of the cortical areas involved; on this basis, viewpoint-dependent recognition appears to be more effortful than viewpoint-invariant recognition. Additional support for this view comes from the observation that right Brodmann area 10, an area associated with decision-making and retrieval of stored information, was also preferentially-recruited during viewpoint-dependent recognition: it appears that recruitment of a transformational recognition mechanism may be more effortful than a viewpoint-invariant one, an assertion consistent with machine vision accounts of object recognition.

A subset of the areas recruited during viewpoint-dependent recognition were found to be recruited during viewpoint-invariant recognition, relative to the control condition, but no cortical areas appeared to be specific to viewpoint-invariant recognition of misoriented objects. Thus, no evidence was found to support ventral pathway mediation of viewpoint-invariant recognition. Contrary to the experimental hypotheses, recruitment of both premotor and parietal cortex was found during viewpoint-invariant recognition. One possible interpretation of these findings is that parallel viewpoint-dependent and viewpoint-invariant recognition mechanisms operate for a short time before one is selected, and that transient recruitment of the non-successful mechanism is sufficient to generate a BOLD signal in the regions involved. An alternative interpretation is that viewpoint-invariant recognition requires transformation of the global stimulus percept from a viewpoint-centred to an object-centred reference-frame. This study also identified a unidirectional effect of task order in which participants were able to generalise a successful viewpoint-dependent strategy to recognition of orientation-invariant stimuli, but were not able to use a previously successful viewpoint-invariant strategy to recognise orientation-dependent stimuli. The latter effect may have been due to the relative featural sparseness of the orientation-dependent stimuli, with the lack of invariant features necessitating recognition by viewpoint-dependent means.

Failure of the present study to identify a cortical region specialised for viewpoint-invariant recognition, and lack of an explicit comparison between the regions subserving viewpoint-dependent and viewpoint-invariant recognition in the experimental design, promote the adoption of a more subtle design for future study. Such an investigation is described in Chapter 4. The regions in superior parietal, prefrontal, and premotor cortex believed to mediate viewpoint-dependent recognition correspond closely to those areas inferred by previous studies to be involved in misoriented common object recognition and mental rotation. Such similarity suggests the recruitment of a common visuospatial transformation mechanism in both object constancy processes. Chapter 4 also compares directly these two processes and their respective cortical correlates.

Chapter Four

4. Cortical Correlates Of Viewpoint-Dependent and Viewpoint-Invariant Object Recognition, And Visuospatial Transformation

4.1 Reassessing fMRI experimental design

4.1.1 Summary of methodological benefits of the previous fMRI study

Chapter 3 described an fMRI study wherein two experimental conditions were each contrasted against the baseline in separate scans, and the results of those two subtractions were compared (though not contrasted directly within the same functional scan). The advantages of such a design were twofold: firstly, that in what was essentially a pilot study, sufficient signal-to-noise ratio for a statistically significant BOLD signal was obtained; second, that an assessment could be made of all regions involved in viewpoint-invariant misoriented object recognition. The latter point is particularly relevant to the aims of the present thesis since the only previous study that has attempted to image viewpoint-invariant recognition did so as part of a subtractive paradigm (comparing the resolution of orientation-invariant and orientation-dependent stimuli in a matching task (Vanrie et al., 2002)). Such an approach can reveal those areas that differ between the two conditions, but not the full extent of the regions involved in each. The study described in Chapter 3 was able to catalogue a number of regions of significant BOLD signal recruited during viewpoint-dependent and viewpoint-invariant object recognition relative to a control (fixation) condition.

Another way in which the design employed in the previous chapter represents an improvement on previous investigations concerns the degree to which the BOLD signal is saturated during a block paradigm design. Vanrie et al. (2002) reported that viewpoint-invariant resolution of the matching task stimuli apparently recruited a subset of those regions recruited during mental rotation of the orientation-dependent shapes. Response-times in the orientation-invariant task reported by Vanrie et al. were significantly faster than those recorded during the mental rotation task (consistent with the finding, discussed in Chapter 1, that mental rotation tasks typically take longer to perform than misoriented object recognition tasks). This reveals a potential flaw in the results obtained by that study: namely, that longer RTs in the mental rotation task (presumably reflecting longer cognitive deliberation per experimental trial than during the orientation-invariant matching task) may account, at least in part, for the greater BOLD signal found by Vanrie et al. in that condition. In other words, if there is a longer period between successive trials in one experimental condition, in which the BOLD response has more time to peak, this is likely to result in greater BOLD signal in that condition. By contrast, the study described in the previous chapter of this thesis utilised stimuli that, serendipitously, elicited very similar mean response times, and thus, such an explanation is unlikely to account for the results reported there.

4.1.2 Constraints of the previous fMRI study

However, there were also disadvantages to the experimental design employed in Chapter 3. The first was that the BOLD response in all areas of primary visual and extrastriate cortex was unexpectedly large in both experimental conditions relative to the baseline. The main consequence of this result was to mask any preferential recruitment of smaller cortical areas in striate and extrastriate cortex in a single condition. This may also have been why no region specific to viewpoint-invariant object recognition was identified, particularly if this process is rooted in the ventral pathway, as has previously been suggested (e.g., Logothetis et al., 1995; James et al., 2002). A second problem with the experimental design of the study reported in the previous chapter was that the cortical regions recruited during viewpoint-dependent and viewpoint-invariant recognition could not be compared by direct subtraction; in fact, it is debatable whether they should, strictly, be compared at all. Since scanners of the type used for fMRI are recalibrated at the beginning of each scan, there can be no assumption of parity between any two functional scans, regardless of how closely in time these are carried out[12]. Thus it cannot categorically be claimed that the two functional activation profiles identified by the study are an accurate reflection of the relative differential substrates of viewpoint-dependent and -invariant object recognition.

The study described in the present chapter attempts to compensate for the limitations of the last by introducing a more refined subtractive fMRI design to compare directly the differences in cortical activation during viewpoint-dependent and viewpoint-invariant processing by alternating between these two conditions in a single scanning session, thus addressing a methodological weakness of the previous study.

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[12] Other factors such as ambient room temperature, recent ingestion of caffeine (a vasodilator) and so on, which may affect the dynamics of the BOLD signal within a single scan lasting for several minutes, can thus also affect comparisons between BOLD data obtained over two separate scans. Such variations also constitute a potential confound when averaging fMRI data across several participants.

4.1.3 Non-fMRI-related constraints of the previous study

One criticism of the study presented in Chapter 3 relates to the nature of the stimuli employed. Orientation-dependent and orientation-invariant stimuli were quite distinct in their featural characteristics. Orientation-dependent stimuli were composed entirely of straight lines bisecting at 90° angles, whereas orientation-invariant stimuli presented a variety of distinctive feature fragments such as curves and straight-line fragments. Such features may have presented sufficient detail to enable recognition based on the extraction of viewpoint-invariant characteristics (Biederman, 1987; Biederman & Gerhardstein, 1993). Orientation-dependent stimuli were rather more featurally sparse, a quality that may have precluded recognition by a viewpoint-invariant mechanism dependent on the identification of unique feature fragments (Thacker et al., 1995). The constraints imposed by such featural sparseness may thus have necessitated selection of a viewpoint-dependent mechanism such as global template-matching. Evidence from the original study by Tarr and Pinker (1990) indicates that even basic differences in stimulus symmetry may result in the preferential selection of a particular recruitment mechanism. The present chapter will therefore use more featurally-similar stimulus types to minimise any such confounding effects of stimulus feature variation.

An apparent effect of task order in the Tarr and Pinker (1990) object recognition task was also uncovered in the behavioural and functional imaging results presented in the previous chapter. This effect was only evident when participants performed the conditions in the order 'orientation-dependent task first, orientation-invariant task second'. Thus, in the present chapter, the opposite task order (orientation-invariant task first) will be employed for all participants, to try to ensure behavioural and functional activation profiles consistent with viewpoint-dependent and viewpoint-invariant task performance. This will also ensure that BOLD data from all participants can be averaged together, thus improving the fMRI signal-to-noise ratio as discussed in Chapter 3.

4.2 Motivations for the present study

4.2.1 Functional imaging of misoriented object recognition tasks

The review of past research into the cortical correlates of object constancy processes conducted in Chapter 2 demonstrated that no studies have investigated misoriented novel object recognition. The previous chapter attempted to elucidate those regions of the brain underpinning viewpoint-dependent and viewpoint-invariant recognition of misoriented novel objects by using functional magnetic resonance imaging (fMRI) to measure the distribution of blood flow during tasks understood to recruit these two mechanisms (Tarr & Pinker, 1990). Viewpoint-dependent recognition was found to preferentially recruit superior parietal, dorsolateral prefrontal (DLPF), and premotor cortex (all bilaterally), and right anterior prefrontal cortex. These results presented a functional activation profile similar to previous studies of misoriented familiar object recognition (e.g., Kosslyn et al., 1994; Sugio et al., 1999). Viewpoint-invariant recognition correlated with recruitment of bilateral parietal (but not superior parietal) cortex and a small region of right-hemispheric premotor cortex. This process did not preferentially recruit any area that was not also involved in viewpoint-dependent recognition. Preferential recruitment of cortical areas in the ventral pathway, thought to mediate viewpoint-invariant recognition, may have been undetectable due to the large BOLD signal identified in this region during both experimental conditions.

Viewpoint-dependent recognition thus appears to involve several regions of cortex. Recruitment of superior parietal cortex may reflect the computation of coordinate-frame transformations between different perceptual reference-frames (Andersen, 1995; Andersen et al., 2000; Andersen et al., 1997; Yoshino et al., 2000) and seems to be the most consistently-reported region in studies of the cortical basis of object constancy processes (see Chapter 2 for a review). Widespread involvement of premotor cortex in viewpoint-dependent, relative to viewpoint-invariant, recognition may reflect greater reliance on computation of neuronal population vector transformations analogous to those used in the performance of physical movements (Georgopoulos, 1995; Grezes et al., 2003; Rizzolatti et al., 1996), supporting some correspondence between the real and imagined manipulation of stimuli. The involvement of DLPFC seems most likely to reflect working memory demand during visuospatial transformation of the stimulus percept (Jonides et al., 1993; Postle et al., 2000; Stern et al., 2000), although it has been noted that this region of cortex is implicated in a wide array of cognitive tasks (Duncan & Owen, 2000); therefore, interpretation of this region's involvement should be made with care. Recruitment of anterior frontal cortex in viewpoint-dependent recognition may reflect increased difficulty in making a decision during a forced-choice recognition task (Rogers et al., 1999) or increasingly effortful retrieval of the canonical stimulus percept (Fletcher & Henson, 2001; McIntosh et al., 1997).

4.2.2 Functional imaging of mental rotation tasks

The same regions as those identified in Chapter 3 as underpinning viewpoint-dependent object recognition have been demonstrated by previous functional imaging studies to be involved in mental rotation (Cohen et al., 1996; Just et al., 2001; Milivojevic et al., 2003; Parsons et al., 1995; Richter et al., 2000; Tagaris et al., 1996). This apparent overlap in the functional anatomy profile of viewpoint-dependent recognition and mental rotation tasks provides evidence for a common visuospatial transformation mechanism underpinning the performance of both tasks. In this chapter, the cortical regions recruited during viewpoint-dependent misoriented, relative to canonical, object recognition are compared against those found to be recruited by the matching of angularly disparate, relative to aligned, stimuli in a mental rotation task. If the same functional activation profile is observed in both tasks, it may be concluded that these two processes are likely to recruit the same transformational mechanism. Comparison of the regions involved in mental rotation against those involved in viewpoint-invariant recognition of misoriented stimuli will also serve to demonstrate whether the latter object constancy process relies on visuospatial transformation.

4.2.3 Aims and hypotheses of the present chapter

The aims of the present chapter are to improve and build on the previous fMRI study in three distinct ways: first, to refine the design by changing the experimental contrast to a comparison of the cortical areas recruited during misoriented versus upright stimulus perception; second, to permit direct comparison of viewpoint-dependent versus viewpoint-invariant recognition within a single scanning period; and third, to ascertain the regions involved in the matching of angularly disparate versus aligned stimuli in a mental rotation task, thus determining the functional recruitment profile of visuospatial transformation. It is therefore hypothesised that:

- The regions preferentially recruited during viewpoint-dependent recognition of misoriented, relative to canonical, objects will be superior parietal cortex, premotor cortex, and dorsolateral and anterior prefrontal cortex, as these areas were implicated by the previous study in viewpoint-dependent recognition.

- Cortical regions in the ventral pathway will be selectively implicated in viewpoint-invariant recognition of misoriented, relative to upright, stimuli.

- Dorsal pathway (including premotor) recruitment during viewpoint-invariant recognition, and/or ventral pathway recruitment during viewpoint-dependent recognition, may be interpreted as evidence for parallel recruitment of object constancy mechanisms.

- The regions recruited by the matching of angular-disparate, relative to aligned, stimuli in the mental rotation task will closely correspond to those recruited during viewpoint-dependent recognition, providing evidence that the same visuospatial transformation mechanism underpins both processes. However, it seems likely that BA10 will not be recruited by the mental rotation task, since involvement of this area in viewpoint-dependent recognition is thought to relate to retrieval of shape representations from memory, a process not required by the mental rotation task.

- Regions involved in the mental rotation task are not anticipated to be recruited during viewpoint-invariant recognition, since the latter is not believed to rely on transformational mechanisms.

4.3 Methods

4.3.1 Design

Object recognition task

A repeated measures design manipulated stimulus type on two levels (orientation-dependent or orientation-invariant) and stimulus orientation on two levels (canonical (0°) or misoriented (+/- 60° or +/- 120°)).

Mental rotation task

A repeated measures design manipulated stimulus angular disparity on two levels – aligned (0° disparity) and angularly disparate (+/- 60° or +/- 120°). Response-time (RT) and BOLD fMRI measures were acquired simultaneously throughout both object recognition and mental rotation tasks. All participants undertook the object recognition task first, followed by the mental rotation task.

4.3.2 Participants

Twelve right-handed participants from the School of Biological Sciences at the University of Manchester volunteered to take part in the study: five were male and seven female, with a mean age of 25.8 years (age range 19.3 – 31.8 years). All participants had normal or corrected-to-normal vision and gave written consent to participate. Ethical approval for the study was granted by Central Manchester Healthcare Trust.

4.3.3 Apparatus and stimuli

In the object recognition task, two sets of two-dimensional, line-drawn stimuli were used, acquired from a previous study by Tarr and Pinker (1990). Stimuli are shown in Figure 11. Stimuli had previously been found to elicit orientation-dependent (set A - asymmetrical), and orientation-invariant (set B - symmetrical), response-times (RTs) (Tarr & Pinker, 1990). In the object recognition task, distracter stimuli were the six unlearned stimuli from each set. Mental rotation task stimuli were matched and mismatched pairs of orientation-dependent (set A) shapes. Stimuli were presented, and responses collected, using E-Prime experimental generator software ("E-Prime," 1995). Responses were made during practice trials by pressing a key and during scanning via a fibreoptic response pad ("Response Pad," 2002) connected to the computer. During practice, stimuli were displayed as 8 cm high by 8 cm wide and viewed from a distance of 60cm (thus subtending a visual angle of 8°). During scanning, due to the need to compromise between limited display space and visibility requirements, stimuli necessarily subtended a somewhat larger angle of 18°.

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Figure 11. Orientation-dependent (A) and orientation-invariant (B) shapes used by Tarr & Pinker (1990)

Imaging was performed using a Philips 1.5-tesla Magnetic Resonance Imaging scanner (ACS –NT PT6000, Philips Medical Systems, Best, NL) in the Division of Imaging Science and Biomedical Engineering at the University of Manchester.

4.3.4 Procedure

Object recognition task

Learning phase: participants were shown one canonically-oriented (0°, with the major axis vertical as shown in Figure 11) shape from each of the stimulus sets A (asymmetrical) and B (symmetrical), and asked to memorise them by copying them with pen and paper. *Practice phase:* recognition of each shape was tested in a computerised practice session consisting of 18 trials with all stimuli canonically oriented. Separate practice trials were undertaken to test each shape, with set B stimuli always presented and tested first, including during the scanning phase (practice effects in the Tarr and Pinker (1990) task were discussed in Chapter 3).

Test phase: participants completed four major blocks of trials, each major block comprising eight sub-blocks of 12 experimental trials (total number of trials = 384). Within each major block, sub-blocks alternated between canonical and misoriented (+/- 60° or +/- 120°, with equal numbers of presentations at each angle) stimulus presentation, such that sub-blocks 1,3,5 and 7 presented stimuli canonically (total number of canonical presentation trials = 192) and sub-blocks 2,4,6 and 8 presented misoriented stimuli (total number of misoriented presentation trials = 192). Major blocks alternated between presentations of orientation-invariant (blocks 1 and 3) and orientation-dependent (blocks 2 and 4) stimuli. A ratio of two target (learned) stimuli to one distracter stimulus was maintained throughout practice and testing to ensure that the majority of trials during scanning recruited the desired cognitive – and neuroanatomical – mechanisms (since it is distinctly possible that participants might arrive at 'non-match' decisions in distracter trials via some means other than the viewpoint-dependent or viewpoint-invariant mechanisms anticipated to be invoked by target stimuli). Trials in which the target stimulus was presented thus comprised 256 of the total number, and distracter trials 128.

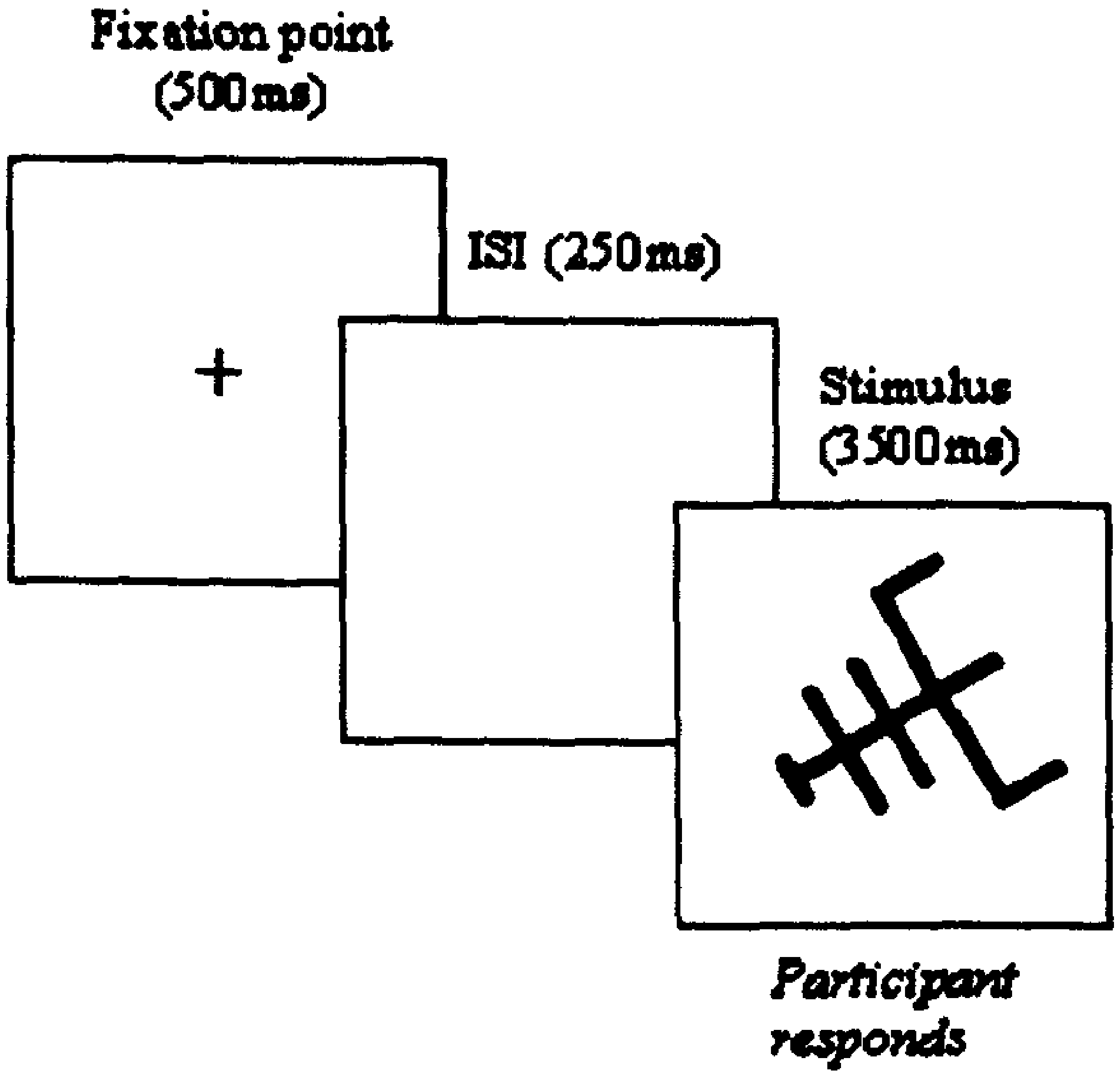

Figure 12. Progression of a single trial in the object recognition task. Total trial time = 4025 ms.

Each trial began with a 500 ms ready-prompt at the centre of the screen. This was replaced by a target or distracter stimulus at one of the test orientations (inter stimulus interval = 250 ms). Stimuli remained visible for a maximum of 3500 ms or until participants indicated by a key-press (target, non-target) whether the stimulus was the previously-memorised target. Response-times were recorded automatically. The format of a single experimental trial is illustrated in Figure 12.

Mental rotation task

No learning of stimuli was required for the mental rotation task. *Practice phase:* 18 practice trials presenting stimuli at identical or angularly disparate orientations was undertaken prior to testing. *Test phase:* participants completed one major block of trials, comprising eight sub-blocks, each comprising 12 experimental trials. Sub-blocks 1,3,5 and 7 (total = 48 trials) presented trials in which stimuli were aligned, and sub-blocks 2,4,6 and 8 (total = 48 trials) presented trials in which stimuli were angularly disparate. Relative stimulus orientation was manipulated such that the number of presentations of first (prime) and second (target) stimuli at each orientation was equally distributed across 0°, +/- 60° and +/-120°, while varying the angular disparity between prime and target stimuli to give equal numbers of trials with 0° and 60° or 120° stimulus disparities (total trials at each angular disparity = 32). As with the design of the object recognition task, a 2:1 ratio of 'mirror-image' to 'non-mirror-image' trials was preserved.

Each trial began with a 500 ms ready-prompt at the centre of the screen. This was replaced by a prime stimulus at one of the test orientations (inter stimulus interval = 250 ms). The prime stimuli were presented for 1000 and followed by the target stimulus (inter-stimulus interval = 250 ms). Target stimuli remained on the screen for a maximum of 4250 seconds, or until participants indicated by a key-press (mirror, non-mirror) whether stimuli were mirror-reflections of each other. Response-times were recorded automatically. The progression of a single experimental trial is shown in Figure 13.

Participants were required to respond to a minimum 80% of trials correctly for both object recognition and mental rotation tasks in the practice phase; this criterion was achieved by all.

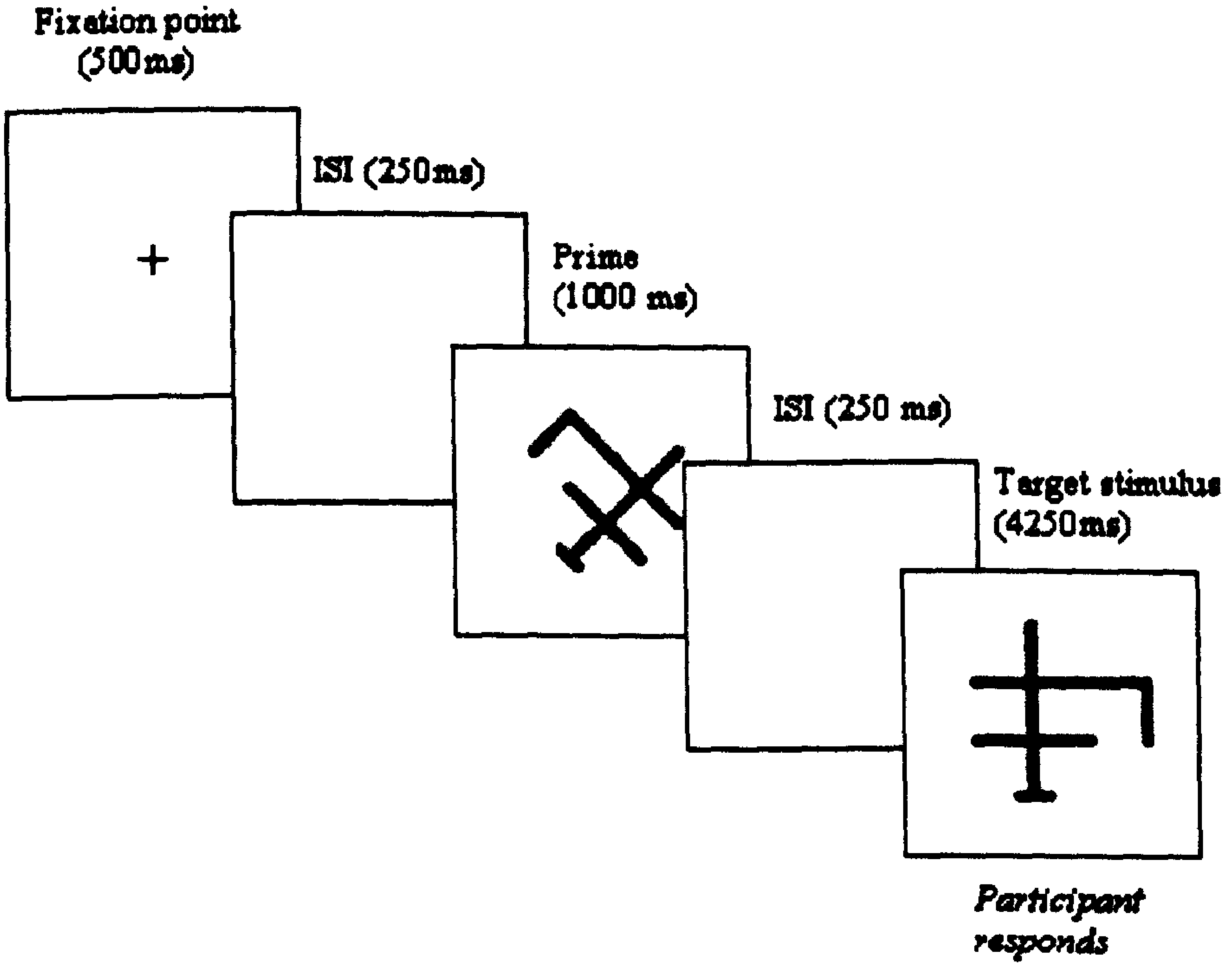

Figure 13. Progression of a single trial in the mental rotation task. Total trial time = 6025 ms.

4.3.5 FMRI data acquisition and processing

Data acquisition

Separate functional MRI scans were employed during object recognition and mental rotation tasks. Functional imaging was performed using a single shot echo planar sequence consisting of 40 slices (TR/TE/matrix: 3150 ms/40 ms/64^2; slice thickness 3.5 mm; interslice spacing 0.5 mm; FOV 23 cm^2). Anatomical reference scans were also obtained for each participant. Anatomical coverage for functional images was selected by an experienced radiographer to include the entire prosencephalon. All images were obtained in an anatomical plane parallel to a line joining the midpoint of the lower border of the splenium and the genu of the corpus callosum.

Object recognition task:

Each BOLD image was acquired in 3.15 s; a contiguous sequence of 16 BOLD images was acquired during each experimental sub-block (duration = 50.4 s); eight contiguous sub-blocks of data were acquired in this way to form a single major block (128 BOLD images with duration = 403.2 s). Four major blocks of BOLD data were acquired in this way (512 BOLD images with total duration = 1612.8 s [26 min 52.8 s]). Data from major blocks 1 and 2 was acquired as part of the same scanning sequence; data from major blocks 3 and 4 was acquired as a separate sequence immediately afterwards, without scanner recalibration. Mental rotation task: BOLD images were acquired every 3.15 s; a single contiguous sequence of 128 images was acquired during one block (duration = 403.2 s [6 min 43.2 s]).

Data processing

Following problems during the downloading and reconstruction of image data from the scanner, BOLD signal data from three participants was found to be incomplete and therefore excluded from further analysis. Image processing and analysis on the remaining nine participants' data was performed using TINA image analysis software (Pollard et al., 1989) for coregistration. Data were resliced using SINC interpolation (Thacker et al., 1998) to minimise motion artefact (Friston, Williams et al., 1996). Correction was made for time varying gain artefacts (Vokurka et al., 1999) and residual motion artefacts (Thacker et al., 1999). Data from each participant were then aligned into a common (Talairach) space and resliced. Correlation analysis between BOLD signal and behavioural task conditions was then performed on data from each participant for the following comparisons:

Object recognition task

Misoriented (r) - canonically-oriented (c) orientation-dependent (A) stimuli (**Ar – Ac**)

Misoriented (r) - canonically-oriented (c) orientation-invariant (B) stimuli (**Br – Bc**)

Misoriented (r) orientation-dependent (A) stimuli - misoriented (r) orientation-invariant (B) stimuli (**Ar – Br**)

Mental rotation task

Angularly disparate - aligned prime and target stimuli (**MR**).

Correlational BOLD data were then tested for residual motion artifact (Thacker et al., 1999), and Monte Carlo analysis was used to correct z-scores for the effects of the variable phase offset employed in the correlation analysis. Data were tested for spatial correlation, evidence of which was not found. Data for each participant in each correlational comparison were added and averaged to give a mean volumetric z-score distribution for each of the above contrasts comprising 26 axial slices of 64 x 64 volume elements (voxels). Finally, z-scores in the averaged data were corrected to ensure normal data distribution with unit width.

An a priori significance level corresponding to $z = 3.7$ standard deviations from the mean ($p < 10^{-4}$) was adopted as the criterion for assessing significant activation in each averaged data set. Talairach coordinates of all voxels exceeding the significance threshold were logged and their cortical region determined using the Talairach Daemon (Lancaster et al., 1997; Lancaster et al., 2000). All such voxels centred on Talairach coordinates within cerebral cortex and the immediately underlying white matter were recorded.

4.4 Results

4.4.1 Psychometric data

All data-points greater than 3.0 standard deviations from the mean, and data from all trials where incorrect answers was given, were excluded from analysis (data omitted in this way accounted for 2% of the total data in the object recognition task and 15% of the data in the matching task, in which much higher error rates were recorded). Mean response-time data for each condition and each task are listed in Table 4, and illustrated in Figures 14 - 17.

Table 4: Mean (N=12) RTs, in ms, over successive blocks in each condition (OD: orientation-dependent; OI: orientation-invariant) for stimuli at each orientation (object recognition task) or angular disparity (mental rotation task), and their corresponding regression slopes (ms per degree).

	Stimulus orientation			*Row*	***Regression***
Object recognition Task	***0°***	***60°***	***120°***	*means*	***slope (ms/deg)***
OD, block1	839	1010	1116	*988*	***2.31***
OD, block2	731	936	995	*887*	***2.20***
OD, block 3	757	879	901	*846*	***1.20***
OD, block 4	727	920	916	*854*	***1.58***
OD column means	*764*	*936*	*982*	*894*	**1.82**
OI, block1	824	926	927	*892*	***0.86***
OI, block 2	728	828	810	*789*	***0.68***
OI, block 3	708	799	875	*794*	***1.39***
OI, block 4	768	783	809	*787*	***0.34***
OI column means	*757*	*834*	*855*	*816*	**0.82**
Total column means	*761*	*885*	*919*	*855*	**1.32**

	Angular disparity			*Row*	***Regression***
	0°	***60°***	***120°***	*means*	***slope (ms/deg)***
Mental rotation task	1170	1343	1473	*1329*	**2.52**

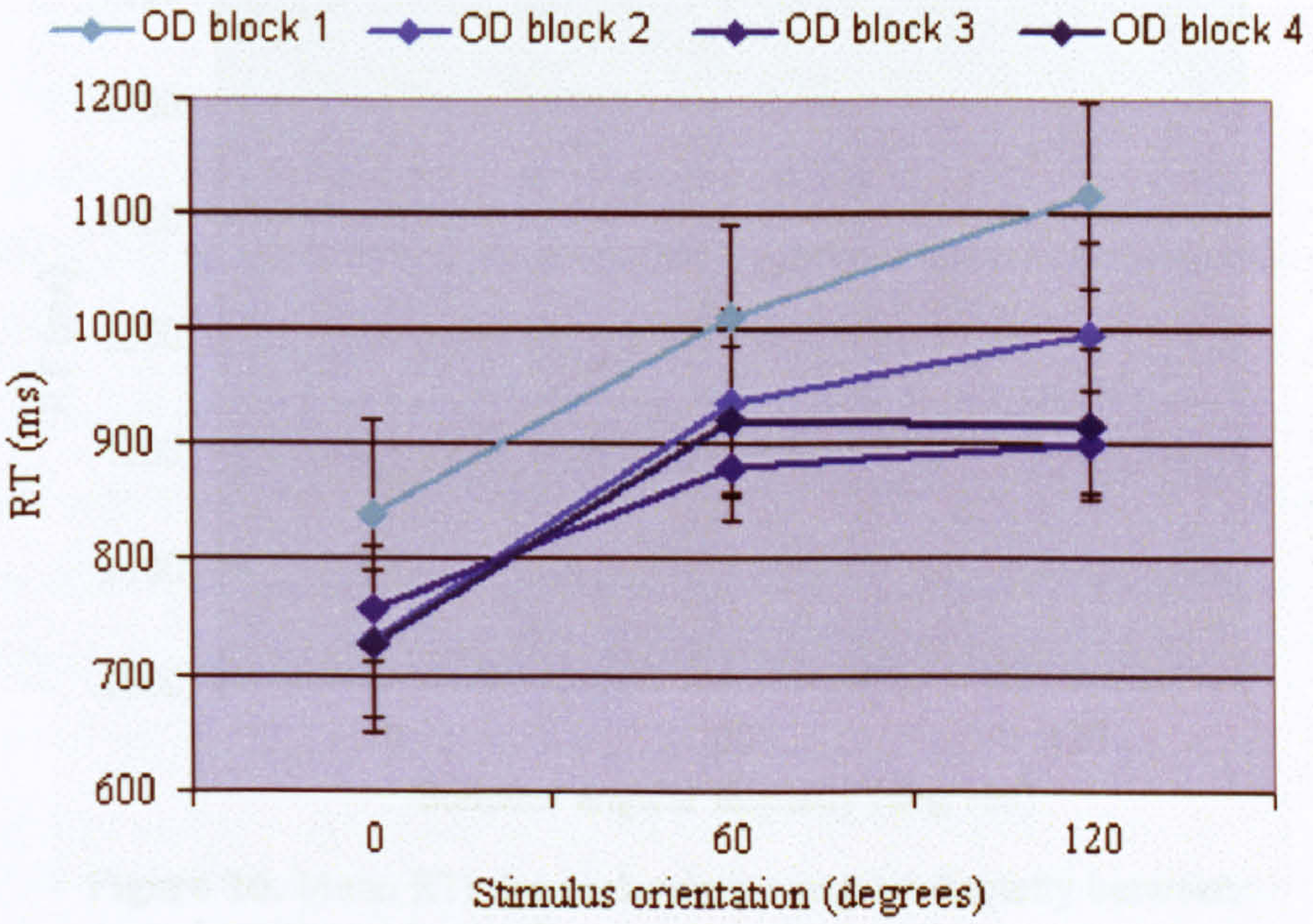

Figure 14. Mean RTs evoked by recognition of orientation-dependent (OD) stimuli at each orientation in each block of trials.

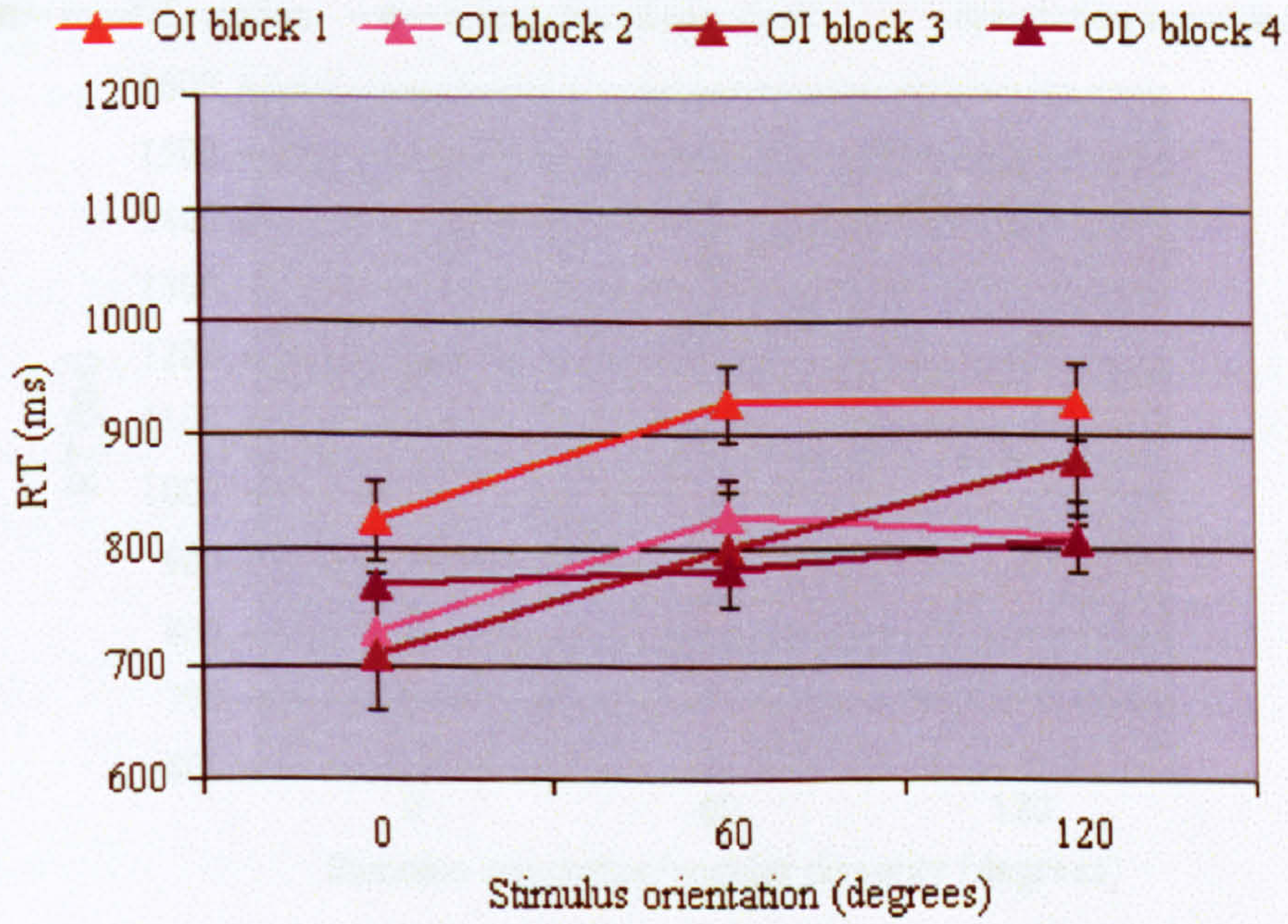

Figure 15. Mean RTs evoked by recognition of orientation-invariant (OI) stimuli at each orientation in each block of trials.

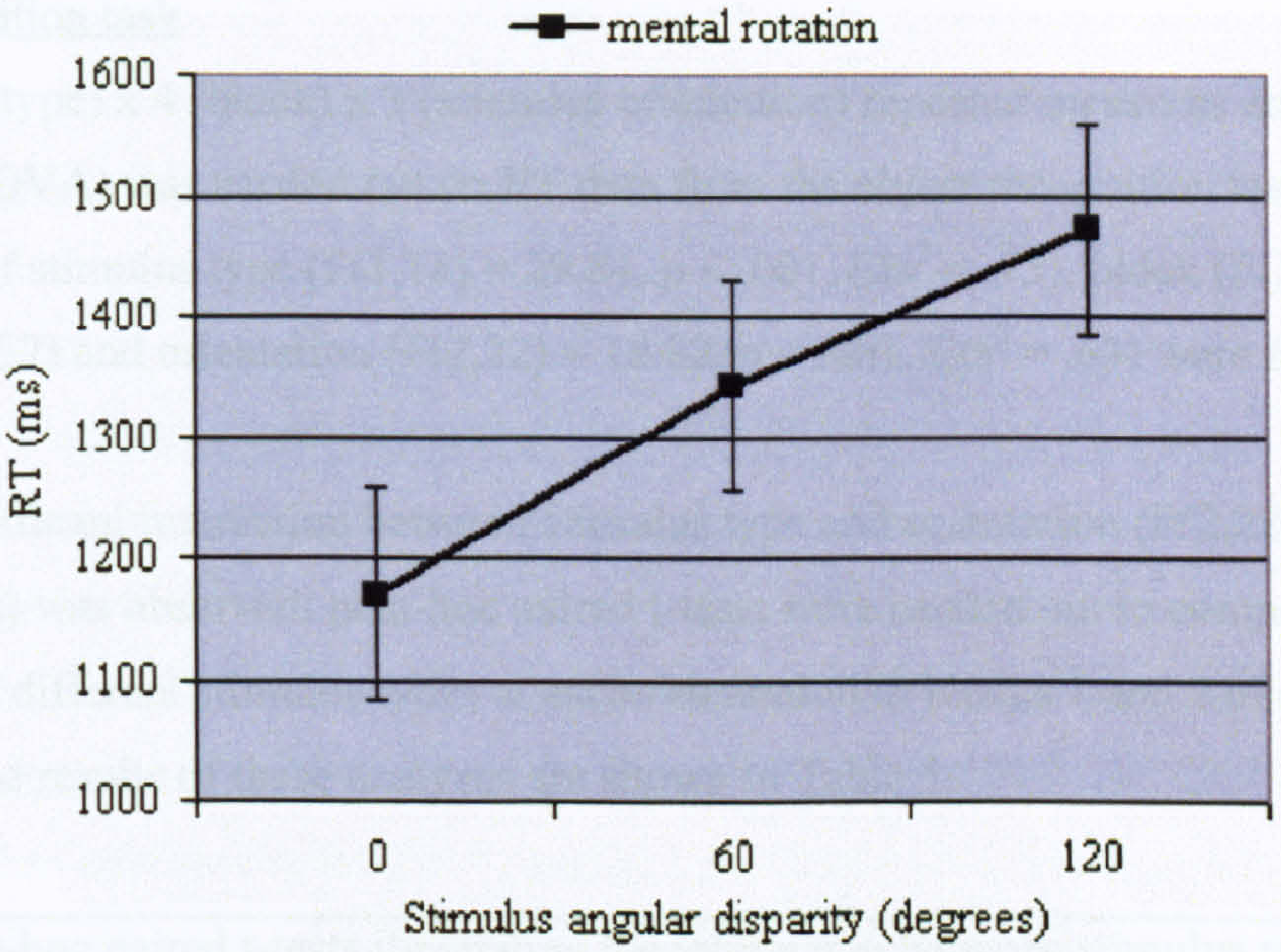

Figure 16. Mean RTs for each relative angular disparity between mental rotation task stimuli.

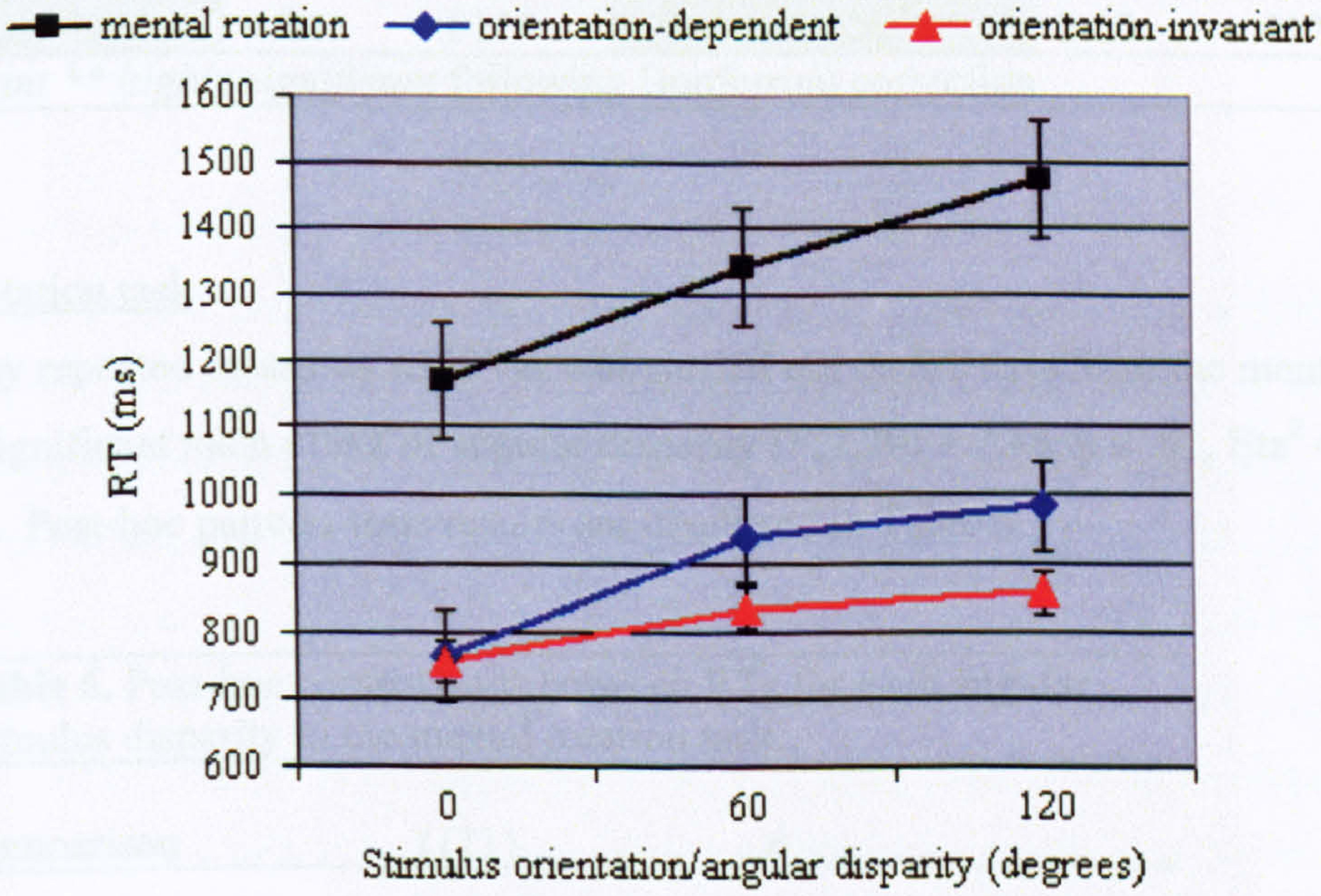

Figure 17. Mean RTs for each task at each stimulus orientation, with object recognition RTs (orientation-dependent and –invariant) collapsed across block.

Object recognition task

A 2 (stimulus type) x 4 (block) x 3 (stimulus orientation) repeated measures analysis of variance (ANOVA) was carried out on RT data from the object recognition task. Significant main effects of stimulus type (F(1,11) = 29.84, p < .001, Eta^2 = .73), block (F(3,33) = 6.41, p < .01, Eta^2 = .37) and orientation (F(2,22) = 18.82, p < .001, Eta^2 = .63) were found.

A significant interaction between stimulus type and orientation (F(2,22) = 8.04, p < .01, Eta^2 = .42) was observed; post-hoc paired t-tests were carried out to compare RTs evoked by the different stimulus types at each orientation in blocks 1 and 2 of each condition. The results of these analyses are shown in Table 5.

Table 5. Post-hoc paired t-tests illustrating the interaction between stimulus type and orientation (OD = orientation-dependent; OI = orientation-invariant) for Blocks 1 and 2.

Block 1			Block 2		
Comparison	*t*(11)	*p*	Comparison	*t*(11)	*p*
OD1 vs. OI1 0º	.621	.55	OD2 vs. OI2 0º	-.32	.76
OD1 vs. OI1 60º	1.79	.10	OD2 vs. OI2 60º	2.37	.05*
OD1 vs. OI1 120º	4.04	.01**	OD2 vs. OI2 120º	3.60	.01*

* *significant* ** *highly significant* following Bonferroni correction

Mental rotation task

A one-way repeated measures ANOVA was carried out on RT data from the mental rotation task. A significant main effect of angular disparity (F(2,20) = 7.35, p < .01, Eta^2 = .43) was observed. Post-hoc paired t-tests results are displayed in Table 6.

Table 6. Post-hoc comparisons between RTs for each angular stimulus disparity in the mental rotation task.

Comparison	*t* (11)	*p*
0º vs. 60º	-2.04	.68, n.s.
0º vs. 120º	-3.10	.01*
60º vs. 120º	-2.83	.02†

† *marginally significant* * *significant* following Bonferroni correction

4.4.2 FMRI data

Object recognition task

Orientation-dependent recognition of misoriented stimuli (Ar-Ac)

A complete list of cortical and subcortical regions identified in the subtraction between BOLD data in the 'rotated' and 'canonical' conditions of the orientation-dependent condition (Ar-Ac) is listed in Table B1 (see Appendix B). Areas of cortex found to be preferentially recruited during viewpoint-dependent recognition (as measured by the differential BOLD signal evoked by recognition of misoriented, compared to canonical, orientation-dependent stimuli) included inferior frontal (BA11 and 47), prefrontal (BA10), cingulate (BA24 and 25) and anterior premotor regions (BA6 and 8). BOLD signal in the ventral and anterior regions listed was evident bilaterally, but the suprathreshold BOLD signal found in BA6 and BA8 was observed solely in the left hemisphere. Subcortical activity also recorded in these regions exhibited hemispheric distribution very similar to the cortical activity reported, though significant subcortical BOLD signal was detected in one small region of right superior frontal cortex. BOLD signal detected subcortically was most evident in the left superior and middle frontal gyri in the region of BA6/8.

Orientation-invariant recognition of misoriented stimuli (Br-Bc)

Cortical and subcortical regions identified by the 'rotated - canonical' subtraction of BOLD data in the orientation-invariant stimulus condition (Br-Bc) are listed in full in Table B2 (see Appendix B). Cortical regions found to be preferentially involved in recognising misoriented orientation-invariant stimuli were cingulate cortex, bilaterally (BA25 and 32), and left anterior premotor cortex (BA6 and 8). Suprathreshold BOLD signal was also recorded in the underlying white matter in these regions. Sub-cortical activation peaks were also evident in left inferior frontal cortex in the region of BA47, and in the right parahippocampal gyrus. The overall volume of BOLD signal activation exceeding the significance threshold in this condition was considerably smaller than that observed in the Ar-Ac condition.

Viewpoint-dependent versus viewpoint-invariant recognition of misoriented stimuli (Ar-Br)

Cortical and sub-cortical areas identified by the subtraction between misoriented orientation-dependent and orientation-invariant stimuli (Ar-Br) are listed in full in Table B3 (see Appendix B). Areas found to be preferentially recruited during recognition of misoriented orientation-dependent stimuli, relative to misoriented orientation-invariant stimuli, were right inferior frontal cortex (BA45 and 47), cingulate cortex (BA25) and anterior prefrontal cortex (BA10). Significant loci of activation were also identified in subcortical white matter in the same regions, and additionally in the right parahippocampal gyrus and the left superior frontal gyrus. A relatively small number of voxels was found to exceed the BOLD significance threshold in the Ar-Br subtractive comparison, presumably reflecting a broadly similar pattern of cortical recruitment during viewpoint-dependent and viewpoint-invariant misoriented object recognition.

Mental rotation task (MR)

Regions found by to be preferentially recruited during matching of angularly disparate, but not aligned, stimuli, are listed in full in Table B4 (see Appendix B). Cortical regions selectively recruited when matching task stimuli were angularly disparate were left DLPFC (BA9) and left premotor cortex (BA6). Significant subcortical foci of the BOLD signal were also identified, both in these regions and in left inferior prefrontal, medial frontal, and superior frontal gyri, and in the left precuneus. A summary of the cortical regions found to be preferentially recruited during each task and condition is shown in Table 7.

Table 7. Cortical regions of interest where significant BOLD signal differed between groups and conditions. Brodmann areas (BA) and the relevant anatomical landmarks where significant BOLD signal was recorded are listed.

AC = anterior cingulate; GC = cingulate gyrus; GFd = medial frontal gyrus; GFi = inferior frontal gyrus; GFm = middle frontal gyrus; GFs = superior frontal gyrus; GR = rectal gyrus; GSC = subcallosal gyrus

Condition	***Ar-Ac***		***Br-Bc***		***Ar-Br***		***MR***	
Hemisphere	R	L	R	L	R	L	R	L
Region								
BA6		GFs, GFd, GFm		GFm				GFs
BA8		GFm		GFm				
BA9								GFm
BA10	GFd				GFd			
BA11	GR							
BA24	GC							
BA25	GSC	AC	GSC	AC		AC		
BA32			GC					
BA45					GFi			
BA47	GSC	GSC			GSC			

Selected axial slices showing regions of suprathreshold BOLD signal are shown in Figure 18.

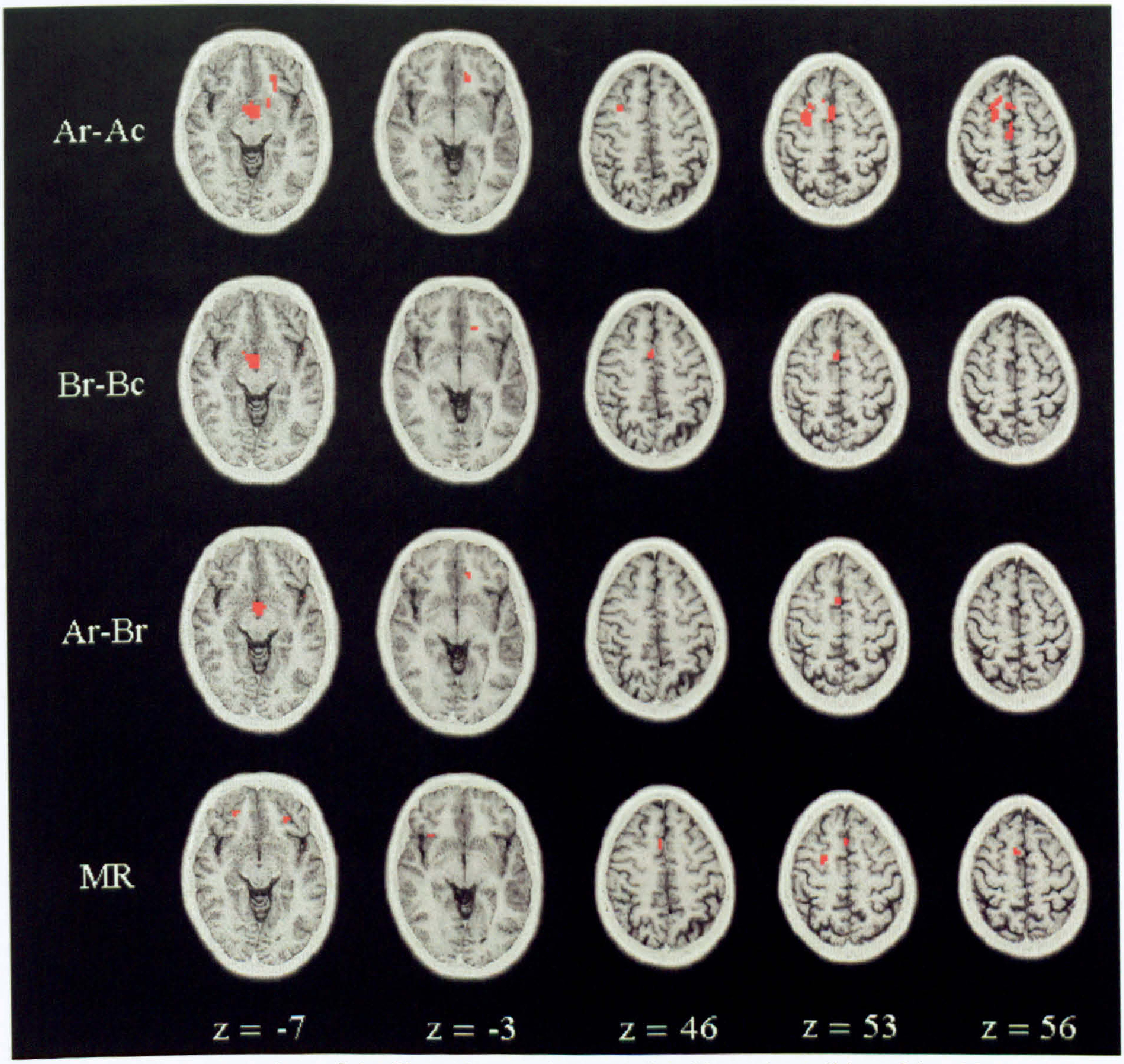

Figure 18. Regions of significant ($z < 3.70$) BOLD signal in each condition of the object recognition task (Ar-Ac, Br-Bc and Ar-Br) and the mental rotation task (MR), superimposed on selected axial anatomical slices. z indicates slice depth, in mm, above or below a line passing between the anterior and posterior commissures. Left and right are as shown. Not all cortical regions identified in the analysis are visible in the slice shown.

4.5 Discussion

The sections below review the psychometric and functional imaging data from the present study. These results are then discussed in the context of the results of the fMRI study presented in Chapter 3 and related literature, and the findings from the two studies are integrated to develop a theory of how the brain computes viewpoint-dependent and viewpoint-invariant recognition, and the extent to which each of these processes may recruit the visuospatial transformation mechanism believed to underpin simple mental rotation.

4.5.1 Summary of psychometric data

Object recognition task

The orientation-dependent and -invariant RTs reported by Tarr & Pinker (1990) were successfully replicated. Stimuli in the orientation-dependent condition invoked a mean regression slope of 1.82 ms/deg, slightly faster than those reported by Tarr & Pinker (1989; 1990) and Leek et al. (submitted), who found rates of around 2.40 ms/deg. Stimuli in the orientation-invariant condition elicited a mean rate of rotation of 0.82 ms/deg, a finding consistent with the previous observation by several authors that rates of less than 1 ms/deg are unlikely to reflect viewpoint-dependent processes (Cohen & Kubovy, 1993; Corballis et al., 1978; Tarr & Pinker, 1989). Generally, rates of rotation, particularly those recorded in response to orientation-dependent stimuli, were found to decrease with practice, corroborating similar reports in previous studies of misoriented object recognition (Leek et al., submitted; Murray, 1995, 1999; Murray et al., 1993; Tarr & Pinker, 1989) and possibly reflecting the acquisition of orientation-invariant information with increasing exposure (Eley, 1982; Jolicoeur, 1985, 1990).

Mental rotation task

Matching task data show larger RTs corresponding to greater angular disparity between prime and target stimuli. This constitutes reasonable evidence that some kind of visuospatial transformation process was successfully induced by matching the angularly-disparate Tarr and Pinker orientation-dependent stimuli used in this task. The mean regression slope in the mental rotation task was 2.52 ms/deg, a rate of transformation rather slower than that observed in the object recognition task. The mental rotation task required participants to respond ‘no’ when the two stimulus objects were identical: the slightly counterintuitive nature of this design, in retrospect, may account at least in part for the larger RTs observed in this task relative to the object recognition task (this hypothesis is supported by the finding that the mental rotation task used in Chapter 5, which required a more intuitive response, produced RT data that were not statistically different from those obtained during the orientation-dependent condition of the recognition task). It is, however, worth noting that rates of rotation in mental rotation tasks have generally been found to be slower than those reported in tasks of misoriented object recognition (Cohen & Kubovy, 1993; Shepard & Metzler, 1971; Takano, 1989).

Behavioural results from both mental rotation and object recognition tasks suggest that the anticipated cognitive processes (viewpoint-dependent and viewpoint-invariant recognition, and visuospatial transformation) were indeed invoked by the present experiment, and that therefore the functional imaging data may reasonably be inferred to reflect these processes.

4.5.2 Summary of fMRI data

A narrower range of cortical and subcortical areas was found to be preferentially recruited in the present experiment than in the study reported in Chapter 3. This is to be expected, since the experimental design of the present study represents considerable refinement of the design employed in the previous chapter: the experimental contrast between conditions here involved two tasks identical but for stimulus orientation, and thus a number of regions recruited by the general process of visual perception are likely to cancel out across the two conditions. Regions of significant BOLD signal in the present study were observed in several regions of medial prefrontal, anterior and subcallosal cortex, in ventrolateral prefrontal cortex (VLPFC), and in several areas within anterior premotor cortex. Several regions of significant BOLD signal were also observed in the white matter immediately beneath cerebral cortex; for the most part, these adhered to the topography of the BOLD signal observed cortically. Detection of BOLD signal in white matter is likely to reflect venous drainage immediately adjacent to the cortical regions recruited by the experimental task (Hall et al., 2002), but this discussion will focus specifically on the BOLD signal detected within cerebral cortex.

Viewpoint-dependent recognition (Ar-Ac)

Recognition of misoriented, relative to canonical, orientation-dependent stimuli was found to correlate with increases in BOLD signal in left superior and medial premotor cortex (BA6 and 8), right medial prefrontal cortex (BA10), bilateral ventromedial prefrontal cortex (BA47), right orbitofrontal cortex (BA11), and bilateral anterior cingulate and right subcallosal cortex (BA24 and 25).

Viewpoint-invariant recognition (Br-Bc)

Recognition of misoriented, relative to canonical, orientation-invariant stimuli was found to correlate with increased BOLD signal in left dorsal prefrontal cortex (BA6 and 8), bilateral cingulate cortex (BA25 and 32), and right subcallosal cortex (BA25 and 32).

Viewpoint-dependent vs. viewpoint-invariant recognition (Ar-Br)

Cortical areas recruited preferentially during viewpoint-dependent, relative to viewpoint-invariant, misoriented stimulus recognition were right medial prefrontal cortex (BA10), left anterior cingulate cortex (BA25), right subcallosal cortex (BA47) and right VLPFC (BA 45).

Mental rotation (MR)

Matching of angularly-disparate, relative to aligned, stimuli in the mental rotation task was found to correlate with increased BOLD signal in left superior premotor cortex (BA6) and left DLPFC (BA9).

Thus, a differential pattern of functional recruitment was observed in each condition, suggesting that different cognitive processes were indeed taking place in each. The hypothesised preferential involvement of the dorsal and ventral pathways in viewpoint-dependent and viewpoint-invariant recognition, respectively, did not materialise; likewise, there was no clear evidence of preferential dorsal pathway recruitment during the mental rotation task. The following sections address these issues and discuss the implications of the cortical profiles of each cognitive process.

4.5.3 Cortical correlates of visuospatial transformation (MR)

4.3.5.1 Superior premotor cortex mediates visuospatial transformation

The mental rotation task provided a functional activation profile of the visuospatial transformation of angularly-disparate, relative to aligned, stimuli: it was found that this transformation correlated with increased BOLD signal in left superior premotor cortex (BA6). Superior frontal gyrus in the region of BA6 has previously been implicated to form part of a network, with superior parietal cortex, specialised for spatial working memory function (Carlesimo, Perri, Turriziani, Tomaiuolo, & Caltagirone, 2001), consistent with the hypothesised global stimulus percept transformation believed to underpin performance of mental rotation and viewpoint-dependent recognition. Recordings from populations of neurons in the primate brain implicate dorsal premotor cortex in the computation of population vector transforms for the integration of visuomotor information (Grezes et al., 2003; Rizzolatti et al., 1996). Visuospatial transformation therefore seems likely to proceed via a global transformation of one stimulus percept into alignment with the other. It has been hypothesised that premotor cortex is part of a network specialised for object manipulation (e.g., Binkofski et al., 1999); this would be consistent with the commonly-reported subjective experience that performance of mental rotation tasks involves imagined manipulation of stimuli, and the finding that similar regions of motor and premotor cortex are recruited during real and imagined motor function (Leonardo et al., 1995). The involvement of premotor cortex in mental rotation may indicate that visuospatial transformation is a mental analogue of physical object manipulation, a hypothesis supported by the finding that congenitally blind participants' performance on tactile mental rotation tasks elicits the same linear increase in response-times as that seen in sighted participants during conventional, visually-presented mental rotation paradigms (Carpenter & Eisenberg, 1978; Marmor & Zaback, 1976).

4.3.5.2 DLPFC involvement in mental rotation may reflect increased demands on working memory during stimulus percept transformation

The apparent involvement of DLPFC in visuospatial transformation is consistent with previous studies utilising mental rotation tasks (Cohen et al., 1996; Vanrie et al., 2002) and investigating the mental manipulation of stimuli (Frith & Dolan, 1996; Just et al., 2001). DLPFC is known to share a large number of reciprocal connections with parietal cortex – itself regularly implicated in studies of object constancy – in the primate brain (Cavada &

Goldman-Rakic, 1989; Ungerleider & Mishkin, 1982; Webster et al., 1994). Parietal cortex is believed to form the site of integration for information from discrete sensory reference frames (e.g., Andersen et al., 1995); thus, areas highly connected to it, such as DLPFC, may also be closely involved in such processes. Recruitment of DLPFC during visuospatial transformation may reflect increased reliance on spatial working memory (Goldman-Rakic, 1996; Jonides et al., 1993) during maintenance and transformation of stimulus percepts. Concurrent recruitment of BA6 in the superior frontal gyrus, observed in the present study, provides additional support for increased demands on spatial working memory during mental rotation performance – superior frontal gyrus has been implicated, with superior parietal cortex, as part of a network for visuospatial working memory function (Carlesimo et al., 2001). DLPFC is also hypothesised (MacDonald, Cohen, Stenger, & Carter, 2000) to underpin conscious maintenance of, and adherence to, task demands (here, the need to generate a 'mirror/non-mirror' decision) – demands which, in the present study, as already noted, were quite challenging and which led to longer response-times than anticipated in the mental rotation task. However, since these task demands were constant across the angularly-disparate and aligned conditions, this is not a wholly convincing explanation of the DLPFC recruitment observed. More generally, the involvement of DLPFC may reflect increased cognitive effort during visuospatial transformation (Duncan & Owen, 2000).

Left superior premotor cortex and left dorsolateral prefrontal cortex are therefore implicated, by the present study, in mediation of the visuospatial transformation mechanism presumed to underpin the performance of the mental rotation task. Recruitment of these areas in the other experimental conditions may therefore be interpreted as indicating the recruitment of this object constancy mechanism in those conditions.

4.5.4 Cortical correlates of viewpoint-dependent misoriented object recognition (Ar-Ac)

In Chapter 3, viewpoint-dependent recognition (relative to a passive viewing baseline condition) was found to correlate with recruitment of DLPFC, anterior prefrontal, superior parietal, and premotor cortex. In the present study, viewpoint-dependent recognition of misoriented, relative to canonical, shape was found to correlate with significant BOLD signal in left premotor (BA6/8), right anterior prefrontal (BA10), right cingulate (BA24) and bilateral anterior cingulate (BA25), and medial orbitofrontal (BA11, BA25 and BA47) cortex.

4.5.4.1 Superior premotor cortex may mediate visuospatial transformation

The region of superior frontal gyrus (BA6) recruited during viewpoint-dependent recognition closely matched a similar area recruited during the mental rotation task. A similar region was also found by Sugio et al. (1999) to correlate with misoriented object recognition. In Chapter 3, dorsal premotor cortical recruitment was observed to correlate with viewpoint-dependent recognition. Thus, it would appear that this region of superior frontal gyrus is a strong candidate area for mediating the visuospatial transformation mechanism hypothesised to underpin performance of mental rotation and viewpoint-dependent recognition.

4.5.4.2 DLPFC may not be required for viewpoint-dependent recognition

There was no evidence of significant BOLD signal in DLPFC during viewpoint-dependent recognition in the present study, as might be expected if viewpoint-dependent recognition and mental rotation rely on the same visuospatial transformation mechanism. There are several possible interpretations of this finding. Firstly, and most simply, if DLPFC is a genuine marker of visuospatial transformation, this mechanism may not in fact be recruited during viewpoint-dependent recognition, indicating that viewpoint-dependent and mental rotation tasks are solved by similar, but not identical, mechanisms. However, the Talairach coordinates of the BOLD signal recorded in DLPFC during mental rotation are very similar to those reported by Sugio et al. (1999) in their study of misoriented object recognition (discussed in Chapter 3). Some functional correspondence between these two findings thus seems likely. Second, DLPFC recruitment may represent a cognitive process that is recruited to a greater (suprathreshold) extent by the mental rotation task than by viewpoint-dependent recognition; DLPFC recruitment has been shown to be sensitive to varying working memory demands in a mental rotation task (Just et al., 2001). Mental rotation tasks require maintenance and alignment of two stimulus percepts, with no recourse to stored stimulus representations. By contrast, viewpoint-dependent recognition involves maintenance of a single object percept only, and may benefit from a certain degree of top-down information based on stored object representations. Thus, mental rotation may exert greater demands on working memory – and so evoke a larger BOLD signal in DLPFC – than viewpoint-dependent recognition. Since DLPFC was identified as a marker of viewpoint-dependent recognition in Chapter 3, in which there was a much more generous contrast between experimental and baseline conditions, and in which BOLD signal consequently differed between the two conditions in many more cortical areas, this second interpretation appears to be quite plausible – that is, the subtractive BOLD comparison between misoriented and upright stimuli may be too subtle to detect DLPFC recruitment in the present design.

A third possibility is that DLPFC recruitment during the mental task represents indirect evidence of dorsal pathway involvement in that task. DLPFC has been found to have strong reciprocal anatomical and functional connections with superior parietal cortex and the intraparietal sulcus (Binkofski, Buccino, Posse et al., 1999; Binkofski, Buccino, Stephan et al., 1999; Goldman-Rakic, 1996). Preferential recruitment of the dorsal pathway, and superior parietal cortex in particular, was proposed by Gauthier et al. (2002) to be necessary for the performance of mirror-image/non-mirror-image decision tasks (i.e., mental rotation), in contrast with viewpoint-dependent recognition, which, the authors argue, may be mediated by the ventral pathway. Selective recruitment of DLPFC during mental rotation, but not viewpoint-dependent recognition, provides inferential support for these proposals.

4.5.4.3 Pre-SMA may mediate stimulus percept maintenance in viewpoint-dependent recognition

In the present study, viewpoint-dependent recognition was found to recruit an area of medial premotor cortex known as the pre-supplementary motor area (pre-SMA), a region that was not recruited during mental rotation task performance. An area previously implicated in mental rotation by several studies (Cohen et al., 1996; Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Richter et al., 2000; Richter et al., 1997), pre-SMA has been proposed as a locus of visuomotor coordination that is involved in the maintenance of sensory information (Picard & Strick, 2001). The finding that pre-SMA was selectively recruited during viewpoint-dependent recognition in the present study may indicate that this region is involved in the maintenance of the stimulus percept during its global transformation to match it against a stored canonical representation. In Chapter 3, viewpoint-dependent recognition was also associated with preferential recruitment of areas in pre-SMA in participant group 1, though not group 2 (possibly as a result of generally reduced BOLD signal in the second group). As discussed in the previous section, Chapter 3 also reported the involvement of DLPFC in viewpoint-dependent recognition. It thus seems plausible that both regions are involved in stimulus percept maintenance, though there may be some functional dissociation of the regions preferentially recruited during viewpoint-dependent recognition and mental rotation.

4.5.4.4 BA10 and anterior cingulate cortex may indicate greater demands of viewpoint-dependent misoriented, relative to canonical, recognition

Regions identified as being selectively recruited during viewpoint-dependent recognition of misoriented stimuli and which are not implicated in visuospatial transformation seem likely to be involved in comparing the stimulus percept against stored representations (since this process comprises the principal distinction between mental rotation and misoriented object recognition tasks). There is evidence to suggest that the pattern of functional recruitment observed during viewpoint-dependent recognition of misoriented, relative to canonical, stimuli may reflect the greater cognitive demands of the former process. This idea that viewpoint-dependent recognition is more cognitively expensive than viewpoint-invariant recognition has intuitive appeal: transformation of a global stimulus percept is likely to be a more computationally expensive process than the detection of invariant features or spatial normalisation of local feature information (Thacker et al., 1995). Recruitment of BA10, which correlated with viewpoint-dependent recognition in the present chapter and in the study reported in Chapter 3, has previously been found to correspond to increased difficulty in decision-making (Rogers et al., 1999). Recruitment of anterior cingulate cortex, another area implicated in viewpoint-dependent recognition, has also been found to increase when task performance becomes more difficult (Mulert, Gallinat, Dorn, Herrmann, & Winterer, 2003). BA10 may be important in controlling maintenance of stimulus percept representations in working memory (Fletcher & Henson, 2001).

Recruitment of right-hemispheric BA10 during viewpoint-dependent recognition may also indicate more a more effortful comparison between the stimulus percept and stored representations, as this area is implicated in studies of retrieval, as well as working memory (MacLeod, Buckner, Miezin, Petersen, & Raichle, 1998). Orbitofrontal cortex (BA11 and 47) and the anterior cingulate/subcallosal area (BA25), all apparently implicated in viewpoint-dependent recognition by the present study, are thought, based on studies of the rhesus monkey brain, to mediate formation and retrieval of memory for objects (Bachevalier, Meunier, Lu, & Ungerleider, 1997; Meunier, Bachevalier, & Mishkin, 1997). This association of anterior cingulate cortex with object-based memory may account for the apparent non-involvement of this region in the mental rotation task, in which encoding and retrieval of long-term stimulus representations are not required. Area 10 has also been implicated in motor intention (Terry & Rosenberg, 1995), a finding that may provide some support for visuospatial transformation as a mental analogue of physical object manipulation.

4.5.4.5 Orbitofrontal cortex may mediate judgements of stimulus misorientation

Medial prefrontal, including orbitofrontal, cortex was also found in the present chapter to be recruited preferentially during viewpoint-dependent recognition of misoriented shape. Orbitofrontal cortex is also thought to be involved in visual detection of stimulus variation (Petrides, Alivisatos, & Frey, 2002), which in the context of this study might be interpreted as detection of unusually-oriented stimuli. Selective recruitment of orbitofrontal cortex during viewpoint-dependent recognition may reflect judgement of the stimulus percept as 'misoriented' (i.e., unrecognisable, and lacking sufficient orientation-invariant features for recognition), and in need of transformation to a canonical, recognisable orientation. This interpretation would be consistent with the finding that orbitofrontal cortex was recruited during viewpoint-dependent recognition, in which stimuli are presumed to be compared an orientation-dependent representation, but not during viewpoint-invariant recognition, in which the stored stimulus representation is presumed to be orientation-free (and the concept of 'unusual orientation' is thus meaningless).

4.5.5 Cortical correlates of viewpoint-invariant misoriented object recognition (Br-Bc)

Viewpoint-invariant recognition of misoriented, relative to upright, stimuli was found to preferentially recruit a small region of left premotor cortex (BA6/8), and bilateral anterior cingulate/posterior orbitofrontal cortex (BA25). Significant BOLD signal was not identified in superior premotor cortex or in DLPFC, providing no evidence that visuospatial transformation mechanisms were active during viewpoint-invariant recognition. The possible contribution of anterior cingulate and orbitofrontal cortex was addressed in previous sections.

As with the study reported in Chapter 3 (and those reported by Vanrie et al., 2002), the results relating to viewpoint-invariant recognition indicate that the cortical areas recruited preferentially during this process apparently represent a subset of those involved in viewpoint-dependent object recognition, recruiting fewer cortical regions and comprising a smaller overall volume of voxels with significant BOLD signal. While premotor and cingulate cortex were inferred, from the results of the present study, to be involved in viewpoint-invariant misoriented object recognition, these regions were also implicated in viewpoint-dependent recognition, and thus seem unlikely to represent a network specialised for viewpoint-invariant recognition. Apparent premotor involvement in viewpoint-invariant recognition may indicate either that population vector transforms are required for the computation of viewpoint-invariant recognition (for example, in resolving the stimulus percept with a global object-based stored representation), or that some other process requiring the computation of vector transforms, such as viewpoint-dependent recognition, is engaged concurrently, suggesting parallel recruitment of both viewpoint-dependent and -invariant mechanisms. Simultaneous recruitment of viewpoint-dependent and viewpoint-invariant recognition mechanisms has previously been proposed to account for the non-linearity of RT data at larger orientations (Corballis et al., 1978; Jolicoeur, 1990). This possibility is explored further in Chapter 5.

A further possible explanation for the presence of significant premotor BOLD signal during the orientation-invariant condition is that participants actually relied on viewpoint-dependent mechanisms to perform at least some of the trials; this is supported by the finding that mean response-times in this condition were not wholly invariant to stimulus orientation, but increased slightly with increasing stimulus misorientation. This was particularly true of trials in block 3 of the orientation-invariant condition (for which the mean regression slope was greater than the nominal viewpoint-dependent threshold of 1 ms/deg), though the reason for this atypical pattern of responses is unknown.

4.5.6 Viewpoint-dependent versus viewpoint-invariant recognition (Ar-Br)

Cortical areas found to be preferentially recruited during viewpoint-dependent, relative to viewpoint-invariant, misoriented object recognition were right anterior prefrontal cortex (BA10), right VLPFC (BA45), bilateral anterior cingulate/subcallosal cortex (BA25), and medial orbitofrontal cortex (BA47). As related earlier, selective involvement of BA10 and anterior cingulate in viewpoint-dependent recognition may relate to increased perceptual difficulty (Mulert et al., 2003; Rogers et al., 1999) and perhaps increasingly effortful retrieval of stored stimulus representations (MacLeod et al., 1998; Meunier et al., 1997), while recruitment of medial orbitofrontal cortex may reflect a process of assessing stimulus orientation (Petrides et al., 2002). That these areas are also recruited preferentially by viewpoint-dependent recognition when compared directly with viewpoint-invariant recognition suggests that the former process makes greater cognitive demands than the latter – in other words, that viewpoint-dependent recognition is more computationally expensive.

4.5.6.1 VLPFC may mediate object-based working memory or 'active retrieval' in viewpoint-dependent recognition

The experimental contrast between viewpoint-dependent and viewpoint-invariant misoriented object recognition identified preferential recruitment of left VLPFC during the former process. It has been demonstrated that VLPFC shares extensive reciprocal connections with inferotemporal cortex (Cavada & Goldman-Rakic, 1989; Ungerleider & Mishkin, 1982); the results of the present study may therefore provide indirect support of Gauthier et al. (2002), who hypothesised that viewpoint-dependent recognition may be mediated by the ventral pathway. Based on the extent of these prefrontal-inferotemporal connections, it is hypothesised that VLPFC may be involved in object-based working memory (Goldman-Rakic, 1996). Selective recruitment of left VLPFC, reported in the present study, has previously been found to correlate with working memory for two-dimensional novel abstract shapes (Manoach et al., 2004). This suggests that preferential VLPFC recruitment during viewpoint-dependent recognition in the present study may reflect increased demands on object-based working memory – perhaps reflecting maintenance of the stimulus percept while stored stimulus representations are accessed. It is difficult to resolve such findings with the studies, already reported, that implicate DLPFC in the maintenance of stimulus percepts during mental rotation – however, there is some evidence from studies of the primate brain to suggest that VLPFC may also share some connectivity with parietal cortex (Cavada & Goldman-Rakic, 1989), and thus the two areas of LPFC, and the cognitive functions they mediate, may have more in common than might initially be supposed. Recently, intracranial EEG recordings have implicated VLPFC in planning for reaching (Rizzuto, Mamelak, Sutherling, Fineman, & Andersen, 2005), which in the context of the present study supports the idea that viewpoint-dependent recognition may function as a mental analogue of physical object transformation, and introduces the possibility that VLPFC mediates spatial, as well as object-based, perceptual processes. Recruitment of VLPFC has also been associated with 'active retrieval' of stored stimulus representations that are not readily resolvable with the stimulus percept due to some visual ambiguity, such as misorientation (Petrides, 2002). Involvement of VLPFC during viewpoint-dependent, relative to viewpoint-invariant, recognition might therefore indicate greater reliance on active retrieval in the former process than in the latter, in which stimulus (mis)orientation is presumed not to be encoded, and therefore does not constitute a visual ambiguity.

4.5.7 Perception of misoriented shape

A few cortical regions were found to be preferentially recruited during viewpoint-dependent and viewpoint-invariant misoriented, relative to canonical, object recognition. It is possible that this finding may indicate cognitive processes involved in the perception of misoriented shape in general. The sections below discuss some possible explanations of these findings.

4.5.7.1 BA8 recruitment may mediate visual reference-frame updating in misoriented object recognition

In the present study, viewpoint-dependent and viewpoint-invariant recognition of misoriented, relative to upright, stimuli were both associated with BOLD signal in ventral frontal cortex in BA6 and BA8. Classically, areas of cortex in BA8 have been known as the frontal eye fields (FEF), activity in which can be shown to correlate with saccadic activity (Fox, Fox, Raichle, & Burde, 1985). However, the areas of significant BOLD signal observed in BA8 in the present study were not located within the region outlined by Paus in a review of the FEF literature (Paus, 1996). This is consistent with the proposal that FEFs are actually not actually located in BA8 in humans at all, but in BA6 (Petit, Clark, Ingeholm, & Haxby, 1997). Such results could also be explained with reference to the proposal that BA8 is involved in the control of balance when no visual information is present, suggesting a possible role for this area in the updating of visual reference frame information (Ouchi, Okada, Yoshikawa, Nobezawa, & Futatsubashi, 1999).

5.4.7.2 Ventral BA6 may underpin saccadic activity during misoriented object recognition

Signficant regions of BOLD activation within the rostral FEF region described by Paus were identified in the experimental contrasts Ar-Ac and Br-Bc in the object recognition task and during the mental rotation task; these were located within BA6 and the underlying white matter. It is possible that the recruitment of FEFs during misoriented object recognition and angularly disparate stimulus presentation relates to the manner in which the stimulus percept is compared (either against a stored representation, as in object recognition, or with the previous stimulus held in working memory, as in the mental rotation task). It has been proposed, for example, based on observation of visual saccades, that performance on mental rotation tasks may proceed by the act of segmenting invididual object features and subjecting them to visuospatial transformation one at a time (Just & Carpenter, 1985). The finding in the present study that more regions of FEF cortex were recruited during viewpoint-dependent than during viewpoint-invariant misoriented recognition may corroborate this theory. However, since viewpoint-invariant misoriented object recognition also elicited recruitment of the FEF area, and this process is hypothesised to rely on identification and matching of individual stimulus features, it may be meaningless to speculate about the respective natures of these two object constancy processes on the basis of FEF recruitment alone.

5.4.7.3 Anterior cingulate cortex may mediate attentional shifts between reference-frames

In the present study, regions of anterior cingulate and subcallosal cortex (BA25) were implicated in viewpoint-dependent and viewpoint-invariant recognition of misoriented objects. Although these areas have been implicated in studies of object-based memory (see section 4.5.4.4), they may also relate to the orienting of visual attention, a process with which premotor and posterior parietal cortex are also associated (Nobre et al., 1997). As discussed in Chapter 2, recruitment of posterior parietal cortex is associated with cognitive processes requiring the integration of information from different perceptual reference-frames (e.g., Andersen et al., 1995), while premotor cortical recruitment may indicate the computation of vector-transformations (e.g. Rizzolatti et al., 1996) for the integration of visual and motor functions.

The implication from these findings – namely, that anterior cingulate cortex is in some involved in implementing reference-frame transformations – is supported by additional recent evidence implicating this region as part of a cortical network specialised for shifts of attention between discrete coordinate reference-frames (Wilson, Waldorff, & Mangun, 2005). The results of the present study thus suggest that the recognition of misoriented, relative to upright, stimuli places increased reliance on reference-frame integration – and that this is particularly true of viewpoint-dependent, relative to viewpoint-invariant, misoriented object recognition. Significant BOLD signal in anterior cingulate cortex may thus indicate more cognitively expensive tasks (misoriented, relative to upright, or viewpoint-dependent, relative to viewpoint-invariant, recognition) – however, no such conclusion may strictly be drawn from this data since BOLD is a probabilistic technique which is not, in the present design, employed parametrically. In other words, increased BOLD signal does not correspond to greater cortical recruitment, but simply to increased certainty of a significant difference between two experimental conditions. However, recruitment of anterior cingulate cortex has been demonstrated elsewhere, in a parametric fMRI study, to correspond to increasing cognitive demands during memory retrieval (Gould, Brown, Owen, ffytche, & Howard, 2003), providing some support for this hypothesis. No significant BOLD signal in anterior cingulate cortex was identified during the mental rotation task, possibly indicating that attention-shifting between reference-frames of the kind proposed by Wilson and colleagues is not required during visuospatial transformation, but only during the resolution of non-canonical stimulus percepts with stored canonical representations in memory.

4.5.8 The role of superior parietal cortex in object constancy

Previous studies of mental rotation have strongly implicated superior parietal cortex in mental rotation tasks (Alivisatos & Petrides, 1997; Carpenter et al., 1999; Cohen et al., 1996; Harris et al., 2000). However, this region was not identified when contrasting misaligned with aligned stimuli during performance of the mental rotation reported here, although significant BOLD signal was detected in one subcortical region, the precuneus (underlying BA19). Failure to find evidence of parietal cortical involvement is not necessarily due to the relatively subtle experimental contrast in the present study, since similar contrasts have been employed in previous studies identifying parietal recruitment during mental rotation (e.g., Cohen et al., 1996). It has been proposed (Gauthier et al. – see Chapter 2) that mental rotation must involve the dorsal pathway, but that viewpoint-dependent recognition need not. If this is the case, then it would be expected that both the angularly-disparate and aligned conditions of the present mental rotation task, both requiring a mirror-image/non-mirror-image decision, would recruit the dorsal pathway (specifically, superior parietal cortex), and that BOLD signal in both might therefore cancel out across the experimental contrast. This explanation would account for failure to identify significant BOLD signal in superior parietal cortex in the present mental rotation task, though is inconsistent with findings reported by Cohen et al., who utilised a similar experimental paradigm. The only indication in the present study that the dorsal pathway may be selectively recruited during visuospatial transformation is highly inferential, deriving from the observation, in the mental rotation task, of significant BOLD signal in DLPFC, an area that, as described earlier, is believed to share substantial neuroanatomical and functional connectivity with parietal cortex.

Additionally, there was no preferential recruitment of superior parietal cortex during viewpoint-dependent recognition, a finding previously reported in several previous studies of misoriented stimulus recognition (Harris et al., 2000; Kosslyn et al., 1994; Sugio et al., 1999) as well as in Chapter 3. As noted above, this region was not recruited during visuospatial transformation in the mental rotation task, though as discussed, evidence of superior parietal recruitment may have been 'subtracted out' in that experimental contrast. The failure to identify significant BOLD signal in superior parietal cortex during viewpoint-dependent recognition suggests either that parietal cortex-mediated visuospatial transformation of the kind proposed by Gauthier et al. is not required for viewpoint-dependent identification of misoriented shape, or that such a mechanism is recruited but is also lost in the experimental contrast between misoriented and upright stimulus presentation. Given the weight of literature implicating superior parietal cortex in the performance of both mental rotation and viewpoint-dependent recognition, the latter explanation appears to be the most parsimonious.

4.5.9 Relative hemispheric recruitment during object constancy processes

The study reported in Chapter 3 found that bilateral premotor cortical recruitment was apparently required during viewpoint-dependent recognition, but that viewpoint-invariant recognition required only right-hemispheric premotor cortical involvement: thus, the viewpoint-dependent recognition process could be said to require the additional recruitment of left hemispheric premotor cortex. The present study found that perception of misoriented, relative to upright, stimuli in both object recognition conditions was correlated with significant BOLD signal in left premotor cortex, though more regions of premotor cortex were identified during viewpoint-dependent recognition. It is therefore quite possible (and would be consistent with the study reported in Chapter 3) that right premotor cortex was recruited during all conditions of the present experiment, and that significant BOLD signal in that region therefore cancelled out across the experimental contrasts employed. A related interpretation of the finding that stimulus misorientation or angular disparity in the present study evoked predominantly left hemispheric increases in cortical BOLD signal concerns the extent of cognitive effort required in those conditions. As discussed in Chapter 3, in previous studies investigating the cortical correlates of misoriented object recognition or mental rotation, parietal cortex involvement has often been found to extend from right-hemispheric to bilateral as task complexity increases (Kosslyn et al., 1994; Milivojevic et al., 2003; Sugio et al., 1999). Several of the studies cited above emphasise the greater cognitive demands of viewpoint-dependent, relative to viewpoint-invariant, and misoriented, relative to upright, recognition – it is therefore possible that the increases in left-hemispheric recruitment observed under such conditions in the present study can be interpreted as reflecting increased cognitive demand, for example in terms of coordinate transforms or stimulus percept maintenance.

An alternative interpretation of the results reported here and in the previous chapter, which indicate preferential recruitment of mainly left-hemispheric areas during misoriented object recognition and mental rotation is that, despite much evidence to suggest that visuospatial functions are usually right-hemisphere dominant, the demands of object constancy processes are mediated principally by the left hemisphere – support for which can be derived from some of the functional imaging and clinical neuropsychological studies reviewed in Chapter 2 (Alivisatos & Petrides, 1997; Mehta & Newcombe, 1991; Mehta et al., 1987). The apparent preferential recruitment of left premotor cortex during recognition and matching of misoriented stimuli may relate to judgements of stimulus orientation as part of preparation for grasping ('perception for action' – Goodale and Milner, 1992), since stimulus orientation would necessarily affect intended prehension. Preferential recruitment of left premotor cortex has previously been found to correlate with stimulus manipulability (Chao & Martin, 2000; Gerlach, Law, & Paulson, 2002; Mecklinger, Gruenewald, Besson, Magnie, & Von Cramon, 2002). If left premotor cortical recruitment is indicative of preparation for grasping, this would be consistent with the hypothesised involvement of medial orbitofrontal cortex, concurrently implicated in viewpoint-dependent recognition, in judging stimulus orientation. The finding that a region of left premotor cortex is similarly involved in matching angularly disparate stimuli in the mental rotation task (which controlled for absolute stimulus orientation) suggests that orientation-judgements (and their corresponding reference-frame transformations in preparation for object grasping) may be made at relative, as well as absolute, stimulus orientations. Such a finding is consistent with psychometric studies demonstrating that visual frames of reference may be re-set according to recent visual stimulus alignment (Koriat & Norman, 1988, 1989; Koriat et al., 1991). However, no preferential recruitment of orbitofrontal cortex was observed in the mental rotation task, and the involvement of this region in judging stimulus orientation may thus be somewhat speculative.

4.6 Summary

Previous studies have failed to establish a clear relationship between misoriented object recognition and visuospatial transformation. This chapter sought to compare directly the cortical correlates of viewpoint-dependent and viewpoint-invariant misoriented object recognition with those recruited during a mental rotation task. Evidence for the hypothesised differential recruitment of dorsal and ventral pathways in viewpoint-dependent and viewpoint-invariant recognition was not found. Visuospatial transformation of misaligned stimuli during the mental rotation task was found to preferentially recruit left superior premotor cortex and DLPFC. Involvement of these areas in visuospatial transformation suggests that this process recruits a mental process analogous to motor prehension to resolve the two stimulus percepts into alignment. Stimulus percept maintenance during this resolution of angularly disparate objects is theorised to place increased demands on working memory. Viewpoint-dependent recognition of misoriented shape was found to preferentially recruit the same region of superior premotor cortex as the mental rotation task, suggesting that this object constancy process is reliant on the same visuospatial transformation mechanism. The involvement of more regions of premotor cortex in recognising misoriented orientation-dependent than misoriented orientation-invariant stimuli supports increased reliance of transformational object constancy processes on vector transforms. However, DLPFC was not implicated in viewpoint-dependent recognition, which may reflect reduced dependence on visual working memory when only one stimulus percept must be maintained and transformed. Stimulus percept maintenance during viewpoint-dependent recognition may also be mediated by pre-supplementary motor cortex.

Other areas (orbitofrontal and anterior cingulate cortex) found to be preferentially recruited during viewpoint-dependent recognition were interpreted to be involved in comparing the misoriented stimulus percept against stored stimulus representations. Involvement of right medial prefrontal cortex may indicate that viewpoint-dependent recognition of misoriented stimuli is more difficult, and that retrieval of the stored canonical representation for comparison with the stimulus percept may be more effortful. Greater difficulty in determining stimulus orientation, a process that may be mediated by orbitofrontal cortex, might be responsible for the eventual selection of a viewpoint-dependent mechanism. Direct comparison between the cortical areas recruited during viewpoint-dependent, relative to viewpoint-invariant, misoriented recognition also revealed that ventrolateral prefrontal cortex (VLPFC) was recruited by the former process. This area may mediate 'active retrieval' of canonical shape representations during viewpoint-dependent recognition, and has also been implicated in object-based working memory.

Viewpoint-invariant recognition of misoriented, relative to upright, stimuli was not associated with preferential recruitment of any area not already recruited during viewpoint-dependent recognition. One criticism of this study is that, unlike the work reported in the previous chapter, mean response-times in the orientation-dependent recognition condition were longer than those in the orientation-invariant condition, meaning that BOLD signal in the former condition had a greater chance of saturating within a given trial (and so across a block of trials). The apparent involvement, in viewpoint-invariant recognition, of premotor cortex may indicate parallel recruitment of viewpoint-dependent and invariant mechanisms, or that viewpoint-invariant recognition is reliant on reference-frame transformations, albeit to a lesser extent than viewpoint-dependent recognition.

Anterior cingulate cortex, preferentially recruited during viewpoint-invariant recognition of misoriented, relative to upright, stimuli, may be indicative of greater task difficulty generally when recognising misoriented objects. This area is also implicated in the orienting of visual attention, which is consistent with the idea that misoriented object recognition is more reliant on reference-frame transformations. Anterior cingulate and premotor cortical recruitment during viewpoint-invariant recognition suggests that even viewpoint-invariant processes may require the resolution of information from different reference-frames. Perception of misoriented stimuli in general was also associated with increased recruitment of prefrontal areas thought to correspond to the frontal eye-fields, increased BOLD signal in which may reflect the updating of visual reference-frames or feature identification.

The mainly left-hemispheric cortical recruitment observed during misoriented object recognition and mental rotation is consistent with the results of Chapter 3 and previous studies, indicating that performance of these tasks generally involves right-hemispheric areas (consistent recruitment of which would not be detected by BOLD fMRI), but must additionally recruit left-hemispheric regions when cognitive demands (such as stimulus misorientation or angular disparity) increase.

The following chapter will pursue a slightly different approach to assessing the relationship between these different object constancy processes. Chapters 3 and 4 have provided some evidence to support the recruitment, during viewpoint-dependent recognition, of visuospatial transformation mechanisms, and suggest that such a mechanism is probably not engaged during viewpoint-invariant recognition. However, the results of these studies were somewhat equivocal, both in determining exactly which cortical areas mediate visuospatial transformation, and in clarifying the extent to which parallel object constancy processes may operate during misoriented object recognition. Chapter 5 utilises EEG to obtain a different kind of marker for visuospatial transformation, evidence of which is then sought during viewpoint-dependent and viewpoint-invariant recognition.

Chapter Five

5. Electrophysiological Correlates Of Object Constancy

5.1 Introduction

The two previous chapters used fMRI to attempt to elucidate the neurobiological basis of mental rotation, viewpoint-dependent and viewpoint-independent object recognition. On the basis of these findings, there is some evidence that viewpoint-dependent recognition and mental rotation recruit the same visuospatial transformation mechanism. However, these tasks were also found to recruit additional, task-specific areas of cortex, and the relative involvement of these regions in visuospatial transformation is not wholly clear. Chapters 3 and 4 also found that, while premotor cortex seems likely to mediate imagined global stimulus manipulation of the type thought to underpin viewpoint-dependent recognition and mental rotation, recruitment of some regions of premotor cortex was also identified during viewpoint-invariant recognition. Superior parietal cortex, heavily implicated by previous similar studies in viewpoint-dependent recognition and mental rotation, was preferentially recruited during viewpoint-dependent recognition in the study reported in Chapter 3, but not implicated in either task in Chapter 4. The extent to which misoriented object recognition may recruit parallel object constancy processes is thus somewhat unclear. The present chapter attempts to address these issues by identifying a different, and possibly less ambiguous, marker of visuospatial transformation, and assessing the extent to which this is present in viewpoint-dependent and viewpoint-invariant recognition.

The previous chapters also demonstrated the limited extent to which fMRI can be used to infer the presence or absence of object constancy mechanisms during viewpoint-invariant object recognition. One such limitation is that the temporal resolution of functional processes by fMRI is constrained by the brain's haemodynamic response (see Chapter 3). Although some authors, such as Richter and colleagues, have attempted to overcome this state of affairs by using event-related fMRI (Richter et al., 2000; Richter et al., 1997), many studies utilising fMRI continue to employ block paradigms. It may therefore be difficult to infer, using fMRI, the presence of cognitive processes that may be fleeting, and which are therefore lost amid the longer haemodynamic response or across a block of several experimental trials. It is also difficult to infer selective recruitment of networks that coexist within a relatively small area of the brain (and which are therefore supplied with blood by the same cerebral arteries and local vasculature), such as the recruitment of dorsal and ventral pathways within the occipitoparietal region. This is particularly problematic in fMRI studies acquiring images with relatively low spatial resolution, such as those described in the previous chapters. Lastly, and perhaps the problem most pertinent to the previous two experimental chapters, BOLD fMRI does not identify regions that are consistently recruited across experimental and control conditions. Electrophysiological studies can address these issues, and complement the findings of fMRI studies, by providing measures of cognitive processes that are temporally sensitive, and which are not necessarily localised to the underlying cortical topography. The field of electroencephalography (EEG) offers several putative correlates of object constancy processes, which are discussed below.

5.1.1 Introduction to EEG

The spontaneous generation by the brain of regular electrical fluctuations was first demonstrated in humans by Berger, whose pioneering work paved the way for the wider study of functional brain activity in later decades (Berger, 1929). EEG is conducted by monitoring changes over time in the potential difference (voltage) between a given point on the scalp and a separate reference point. Electrical activity at the level of individual neuronal transactions is not measurable due to both the tiny amount of electrical charge involved and the 'cancelling out' effect of adjacent, randomly-oriented neurones. However, when large groups of neurones aligned in parallel are simultaneously active, the summation of their action potentials relative to those produced by other, differently active groups of neurones, has the effect of creating electrical 'dipoles', voltage gradients along which a measurable current flows. Since it is mainly in the cortex that such parallel arrays of neurones are seen, the majority of electrophysiological activity detectable at the scalp is considered to derive from cortical activity. Measurement of such electrical activity can be made to very high temporal resolution: cortical events lasting just a few milliseconds are detectable, and a range of characteristic brainwave frequencies relating to different states of consciousness may be observed.

As well as temporally sensitive measures, EEG may in theory provide some limited information about the cortical distribution of electrical activity, for example providing an indication of hemispheric asymmetry. However, spatial resolution of EEG topography is dependent on the number of electrodes used and is not likely to be accurate to much more than a centimetre. Furthermore, variations in scalp potential even in high-resolution EEG systems are only detected over a range of several electrode sites, and do not have high spatial frequency components. An additional problem is that the observed topography of an electroencephalogram may be the net result of many unknown subcortical 'generators' of electrical activity whose location and activation latency are not known. Identifying the neuroanatomical point of origin of an electrophysiological event is made more difficult by the three-dimensional nature of cerebral cortex, the convoluted state of which makes summated action potentials, detectable on the scalp's surface, complex and ambiguous. This ambiguity is known as 'the inverse problem', and may be most easily solved by the simultaneous use of another functional imaging technique such as magnetoencephalography (MEG), which may improve estimates of dipole source localisation (Baillet, Garnero, Marin, & Hugonin, 1999; Cohen & Cuffin, 1987), or event-related fMRI (Menon, Ford, Lim, Glover, & Pfefferbaum, 1997), which may identify concurrently active candidate dipole source locations. Many mathematical models of source localisation have also been proposed (Musha & Okamoto, 1999). However, given the complex nature of the inverse problem, interpretation of EEG signal topography with regard to the function of the underlying areas of cerebral cortex should certainly be done with caution.

5.1.2 Event-related potentials

When the technique of EEG is applied specifically to measure the effect of an extrinsic stimulus such as a sound or visually presented object on the brain's intrinsic processes, the resulting pattern of voltage fluctuation is referred to as an "event-related potential" (ERP). Rather than being a single point of flux in an encephalogram, the ERP may be composed of one or more commonly observed, temporally-distinct components, several of which have been implicated in visual perception and object recognition – some examples of such components are outlined briefly below. ERP component nomenclature tends to reflect component negativity (N) or positivity (P), and either ordinality (for example, the first large positive-going element in an ERP epoch is usually referred to as the P1) or timing following stimulus onset (e.g. the N400, a negative-going component associated with contextually inappropriate verbal information that is typically observed at around 400 ms post-stimulus (Kutas & Hillyard, 1980)). The amplitude and latency of ERP components is understood to be modulated by variations in the perceptions or cognitive processes that they reflect.

5.1.3 Examples of commonly-occuring 'visual' ERP components

The components outlined in this section have been widely reported in ERP studies at large, but the examples given here are included because they have also been found to reflect processes germane to visual object constancy (note that the list is not intended to be exhaustive). Greater ERP component latency is associated with increasing levels of cognitive involvement: while early components in the region of 100ms following stimulus onset, such as the P1 and N1, reflect the demands of visual attention and the processing of exogenous, stimulus-related information, later components, such as the N400, are thought to be underpinned by endogenous cognitive processes (Coles & Rugg, 1995).

N1 and P1 – Markers of visual attention and perception

The P1 is a positive component that usually occurs at a little under 100 ms following stimulus onset; the N1 a negative component that can occur anywhere from around 100 ms to 200 ms. Occipitally-measured amplitudes of the N1 and P1 components have been found to be greater when attended than when unattended (Eason, Harter, & White, 1969; Mangun & Hillyard, 1990), or to reflect the ease with which stimuli are detectable (Luck et al., 1994). The P1 has been associated with the perceptual closure of objects, following the observation that this component is reduced dorsally in patients with schizophrenia who have trouble with perceptual closure in object recognition (Doniger, Foxe, Murray, Higgins, & Javitt, 2002). N1 has been shown to be sensitive to object category in a forced choice task (Curran, Tanaka, & Weiskopf, 2002).

The N1 was originally described as slightly more parietal in origin (Mangun, Hillyard, & Luck, 1993), whereas P1 was found to be largest over the occipital lobe and was believed to originate in the extrastriate cortex of the ventral pathway (Mangun & Hillyard, 1990). This observation led to the proposition by Mangun and Hillyard (1990) that the N1 and P1 were indicative of dorsal and ventral stream processes, respectively. Subsequent dipole modelling approaches indicate that an N1/P1 dorsal/ventral segregation may be oversimplified, with subcomponents of the N1 and P1 waveforms associated with areas in both pathways (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Doniger et al., 2002).

N200 (N2) – Selection/mismatch negativity

The N2 is a negative component, or set of components, usually occurring at around 200 ms following stimulus onset. Amplitude of the N2, like earlier components, may be modulated by attention (Woldorff, Hackley, & Hillyard, 1991). 'Mismatch negativity' occurs when the N2 component follows a rare or inconsistent stimulus or event. The 'N2b' is an altogether separate component elicited by the presence of task-relevant (e.g., target as opposed to distracter) stimuli, so-called 'selection negativity' when it is considered to act as a precursor to the P300 (P3b) component (Proverbio, Esposito, & Zani, 2002). Thus, the N2b component, at least, may be considered to reflect at least rudimentary processing of stimulus information (Coles & Rugg, 1995).

P300 (P3b) – Oddball component (Sutton, Braren, Zubin, & John, 1965)

The P300, as its name suggest, classically has an onset around 300 ms, but can occur hundreds of milliseconds later. It is usually observed over the parietal lobe. P3b amplitude reflects the probability of an unlikely stimulus or event; P3b latency reflects the ease of stimulus categorisation (Kutas, McCarthy, & Donchin, 1977).

N400 – Contextual deviancy (Kutas & Hillyard, 1980)

This component typically has a latency of around 400 ms. N400 amplitude is a classically considered to be a function of the semantic unrelatedness of a word to its context, usually in a sentence, but there is also some evidence that the N400 may relate to the context of non-lexical stimuli. Barrett and Rugg reported an 'N450' component which occurred in response to the second of a pair of pictorial stimuli when the second picture was unrelated to the first, but not when it was related (Barrett & Rugg, 1990).

5.1.4 Location of electrode sites

Scalp electrode positioning follows the international 10-20 system (Jasper, 1958) with electrodes placed at 10% and 20% intervals along two reference lines – the anterior-posterior axis running from nasion to inion (shown in Figure 19) and the coronal axis running from the left to the right post-auricular point (represented in Figure 19 by the sequence of electrodes T7, C5, C3, C1, Cz, C2, C4, C6, T8). The two axes bisect at Cz and other electrodes are positioned relative to these. Figure 19 illustrates the distribution of electrodes in the 64-channel array used in the present study.

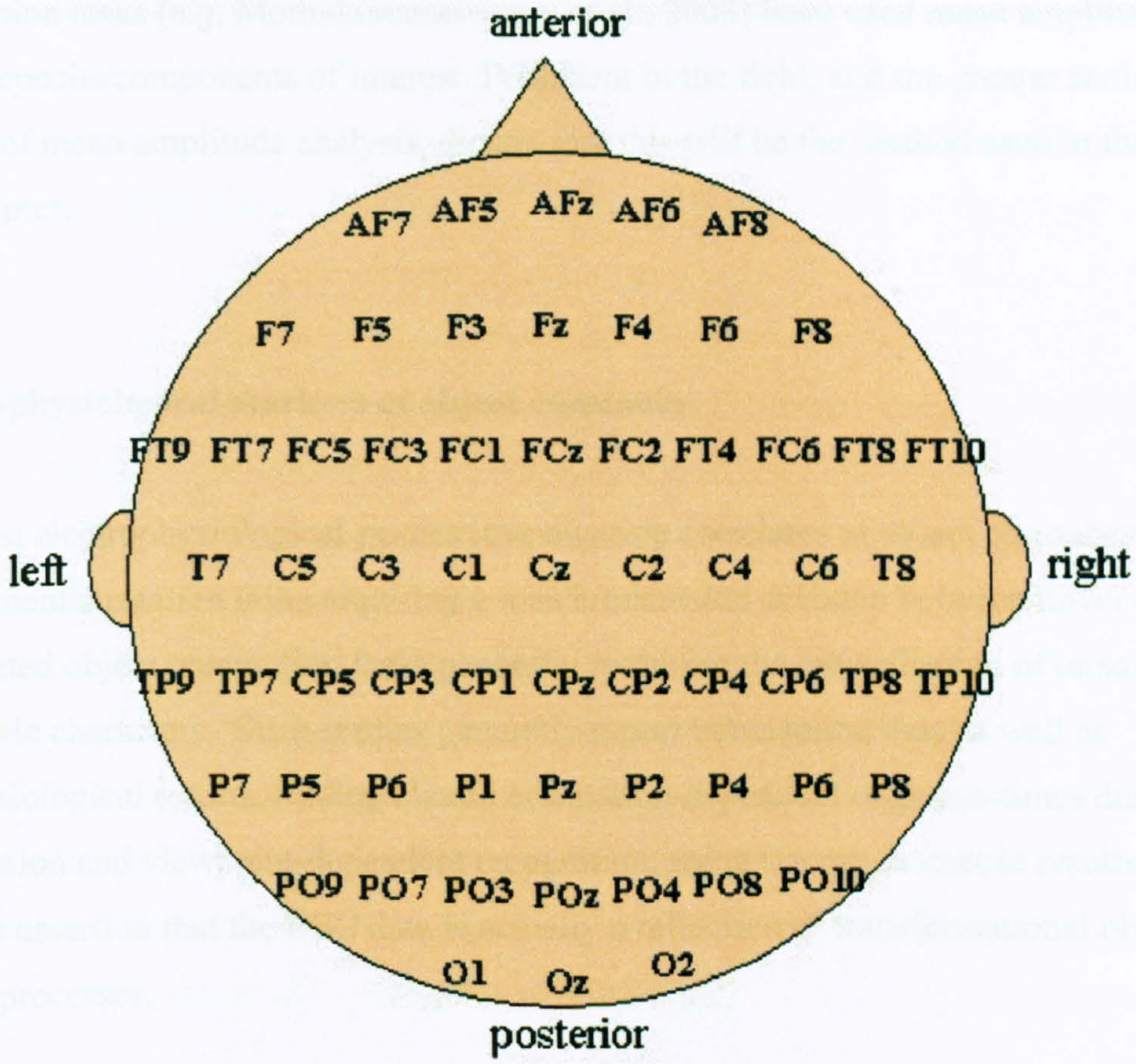

Figure 19. Positioning of a 64-electrode array on the scalp according to the international 10-20 system. Odd numbers denote the left hemisphere, even numbers the right hemisphere, with the midline denoted by *z*. AF = anterior frontal; F = frontal; FC = frontocentral; FT = frontotemporal; C = central; T = temporal, CP = centroparietal; TP = temporoparietal; P = parietal; PO = parieto-occipital; O = occipital.

5.1.5 Measurement methods

Several different aspects of EEG data may be used to compare waveforms: peak amplitudes, peak latencies and mean amplitudes. Peak amplitudes and peak latencies must be calculated with reference to a single electrode for an individual participant (since variability in timing across an array of electrodes necessarily relates to their relative spatial distribution, and this may differ substantially between individuals) (Picton et al., 2000). No such constraints apply to mean amplitude data, since the epoch of interest is the same for all participants - consequently, the use of mean amplitudes generally results in the least variance in the data. Previous studies investigating possible ERP markers of visuospatial transformation during mental rotation tasks (e.g. Muthukumaraswamy et al., 2003) have used mean amplitude data to identify epochs/components of interest. Precedent in the field, and the greater statistical robustness of mean amplitude analysis, dictate that this will be the method used in the present chapter.

5.2 Electrophysiological markers of object constancy

Most electrophysiological studies investigating correlates of object constancy have employed mental rotation tasks requiring a match/mismatch decision between novel objects, or misoriented object recognition tasks generally requiring the identification of misoriented alphanumeric characters. Such studies generally report behavioural data as well as electrophysiological results, finding classic orientation-dependent response-times during mental rotation and viewpoint-dependent recognition, using the psychometric results to support the assertion that the EEG data is actually a reflection of transformational object constancy processes.

Most studies examining visual object constancy processes have focused on later (>400 ms) ERP components, since later components are understood to reflect the more complex cognitive processes, such as those that might underpin object constancy, whereas earlier components are believed to relate to stimulus characteristics (Coles & Rugg, 1995). However, some earlier components (~200ms) have also been associated with object constancy processes. The literature on early and late components evoked during visual object constancy processes, and their relative temporal and topological characteristics, is reviewed below.

5.2.1 Early ERP markers of object constancy

A few studies investigating electrophysiological markers of object constancy have reported an early, apparently orientation-dependent, negative component occurring over occipital or inferior parietal cortex at around 200 ms following stimulus onset (Milivojevic et al., 2003; Muthukumaraswamy et al., 2003; Wijers et al., 1989). It has been concluded from such studies, which involve simple visual tasks recruiting object constancy processes, that these early components are likely to reflect preattentive processes that serve to determine stimulus orientation, and therefore may not themselves be indicative of any kind of transformational process (e.g. Wijers et al., 1989). The topological location of such components, over occipitoparietal cortex, may be indicative of the recruitment of visual association cortex in the initial assessment of stimulus orientation (Muthukumaraswamy et al., 2003).

There is evidence that the amplitude of this early component can be affected by the orientation of stimulus line fragments (Wicker & Long, 1978), with early negative component amplitudes found to be greater with increasing line orientation away from the vertical (Proverbio et al., 2002). These results are indicative of the 'oblique effect', the apparently greater perceptual saliency of vertically- (and horizontally-) oriented stimuli observed in behavioural and functional imaging studies (Cooper & Shepard, 1973; Furmanski & Engel, 2000; Jolicoeur, 1985; Proverbio et al., 2002). Such studies provide additional support for the idea that early (around 200 ms) negative occipitoparietal components associated with object constancy may correspond to the initial assessment of stimulus (or stimulus fragment) orientation, prior to mental rotation or other object constancy processes.

5.2.2 Late ERP markers for object constancy

Several studies report a negative parietal component occurring at around 400ms following stimulus onset, thought to correspond to object constancy mechanisms (Kawamichi et al., 1998; Milivojevic et al., 2003; Muthukumaraswamy et al., 2003; Peronnet & Farah, 1989; Pierret et al., 1994; Wijers et al., 1989; Yoshino et al., 2000). Such studies fall into one of two experimental paradigms, each of which is discussed in the following sections.

Mental rotation

A few studies have used mental rotation tasks to establish the electrophysiological correlates of visuospatial transformation. A study by Yoshino et al. (2000) required participants to mentally align two abstract 2-D line-drawn shapes presented sequentially, and determine whether they were identical or mirror-reflections of each other. The authors observed a negative component (maximal over the parietal area) peaking at around 438 ms after presentation of the second stimulus. The component was larger over the right hemisphere when the stimuli appeared at greater (120°) than at lesser (60°) angular disparity (Yoshino et al., 2000). This 'N400' component was interpreted by Yoshino et al. as a marker of visuospatial transformation, and the focus of its peak as evidence of right parietal involvement in such processes. A similar experiment by Inoue et al. (1998) required participants to discriminate between identical and mirror-image stimuli, and sought to differentiate between matching and angularly disparate stimulus conditions (thus utilising a subtractive paradigm designed to highlight the effects of stimulus rotation) (Inoue et al., 1998). The authors discovered a negative component, maximal at around 430ms, with the greatest differences in amplitude occurring over the right hemisphere; evidence of the component was also found in parietal, central and frontocentral regions. In a similar experiment to those carried out by Yoshino et al. and Inoue et al., Muthukumaraswamy et al. (2003) found that the angular disparity of novel polygonal stimuli in a mental rotation task was associated with negativity at right centroparietal electrodes between 424-492 ms, although they were not able to show that this was proportional to the angular disparity between stimuli (Muthukumaraswamy et al., 2003).

All three studies provide evidence for a clear marker of visuospatial transformation, the 'N400', which should be detectable as a negative component over the centroparietal region at around 450ms following stimulus onset. It should be noted that although these studies described the ERP components elicited by mental rotation as negative (the *N*400), the waveforms reported were typically part of a positive peak following an unambiguously negative peak, and thus the nomenclature 'negative' in such studies refers to the negative attenuation of the positive waveform in response to increasing angular disparity between stimuli.

Viewpoint-dependent recognition

Several studies searching for evidence of an ERP marker for object constancy have done so using viewpoint-dependent misoriented object or character recognition. Peronnet and Farah (1989) obtained electrophysiological measures during replication of an early behavioural experiment (Cooper & Shepard, 1973) that tested recognition of alphanumeric characters presented at varying orientations. The authors reported a negative parietal component (400-800 ms) corresponding to increasing stimulus misorientation (Peronnet & Farah, 1989). Wijers et al. (1989) required participants to identify letters that had appeared in a previously-learned set from a selection presented at varying orientations. They found a negative parietal component between 350-700 ms that corresponded with increasing stimulus misorientation (Wijers et al., 1989). Several subsequent studies testing misoriented stimulus recognition have reported a similar negative parietal component (Heil & Hennighausen, 1999; Milivojevic et al., 2003; Pegna et al., 1997; Roberts & Bell, 2002). Thus, ERP studies of misoriented object recognition reveal a very similar marker to the N400 observed by Yoshino et al. during mental rotation, which may reflect the implementation of similar transformation processes in both tasks.

5.2.3 Summary and aims of this chapter

The area of viewpoint-invariant recognition, and its relationship with visuospatial transformation processes of the kind believed to be recruited during mental rotation and viewpoint-dependent recognition, has received little attention to date. Attempts to clarify this relationship using fMRI, described in the previous two chapters, have met with limited success. The ERP studies reviewed above clearly identify, in the N400 described by Yoshino et al. (and others), a late negative parietal component that appears to reflect an internalised visuospatial transformation process, providing a detectable marker for this object constancy mechanism. The present study attempts to replicate this N400 component during a mental rotation task, and then to assess whether this component is also present during viewpoint-invariant and viewpoint-dependent object recognition. It is hypothesised that:

- An N400-like component, sensitive to angular disparity between stimuli, and representing a marker of visuospatial transformation, will be identified during the mental rotation task.

- The same N400-like component will be identified during viewpoint-dependent recognition.

- The N400-like component will not be present during viewpoint-invariant recognition.

- An earlier (around 200 ms) negative component may also be found. Such a component seems likely to indicate a process of stimulus orientation judgement; based on the findings of Chapter 4, this process may be more evident in viewpoint-dependent than in viewpoint-invariant recognition.

5.3 Methods

5.3.1 Design

Mental rotation task

A one-way repeated measures design manipulated angular disparity between prime and target stimuli on three levels (0°, +/- 60° and +/- 120°) while participants judged whether prime and target stimuli were identical.

Object recognition task

A 2 (stimulus type: symmetrical or asymmetrical) x 2 (experimental block) x 3 (stimulus orientation: 0°, +/- 60° or +/- 120°) repeated measures design was employed. Participants judged whether each stimulus was familiar (learned) or novel.

Response-times and EEG data were acquired during the performance of both tasks. The order in which participants performed the two tasks (mental rotation and object recognition) was counterbalanced across participants. The order in which participants performed each condition in the object recognition task (viewpoint-dependent and viewpoint-invariant) was also counterbalanced across participants.

5.3.2 Participants

Twenty-five undergraduate participants (four male, twenty-one female, aged 19.2–57.8 years; mean age 26.5 years) were recruited from University College, Bangor. All participants were assessed to be right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were not paid, but received print and participation credits for taking part, after providing informed written consent. The study was approved by the University College Bangor department of Psychology ethics committee.

5.3.3 Apparatus and stimuli

Stimuli

14 two-dimensional line-drawn stimuli (Figure 20: A and B) were obtained from a study by Tarr & Pinker (1990). Set A consisted of seven asymmetrical stimuli which had been found to elicit orientation-dependent response-times. Set B consisted of seven symmetrical stimuli found to elicit orientation-invariant response-times. Set A and Set B stimuli were used in the orientation-dependent and orientation-invariant conditions of the object recognition task, respectively. The remaining seven partially asymmetrical stimuli (Figure 20: Set C) were adapted from Tarr and Pinker's original stimuli for use in the mental rotation task. Stimuli were presented using E-Prime experiment generator software ("E-Prime," 1995). Participants were seated 0.6m from the screen with stimuli appearing 0.08m high in the centre of the screen, thus subtending 8° of visual arc.

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Figure 20. Asymmetrical (A) and symmetrical (B) stimuli found by Tarr and Pinker (1990) to elicit orientation-dependent (A) and orientation-invariant (B) response times. Partially asymmetrical shapes (C) were extrapolated from the first two sets for use in the matching task.

EEG and behavioural data acquisition

EEG signals were measured at 64 electrode sites (Figure 1) and amplified using the SynAmps amplifier system (Neuroscan, 1992). Data processing and analysis was carried out using Scan EEG analysis software (Neuroscan, 2001) Sampling rate was fixed at 1kHz. Continuous EEG was band pass filtered online at 0.5Hz low pass and 40Hz high pass. Data was then refiltered offline (with zero phase shift) with a 40Hz band pass filter (slope 48dB/Oct). Artifacts from eye-blinks were removed manually using the software. Epochs spanning each experimental trial were selected from the continous EEG data; epochs were not included in the analysis if they displayed muscular or other artifacts, although only a very small proportion (around 3%) of the total number were discarded for this reason, such that 30-36 epochs per participant were used to create an averaged waveform for each participant in each condition at each electrode site. These were then averaged across all participants to produce a grand average waveform for each condition at each of the 64 electrode sites.

Participants' response-times (RTs) to determine stimulus familiarity (in the object-recognition task) and stimulus similarity (in the mental rotation task) were measured using EPrime. RTs were measured in ms from the time of presentation of the target stimulus to the time at which subjects indicated their response with a key-press made with the right hand.

5.3.4 Procedure

Mental rotation task

Participants were instructed to make a match/mismatch decision about each pair of prime and target stimuli as they appeared. Each matching task trial began with a 200 ms fixation point. This was replaced by the first (prime) stimulus, presented for 500 ms (inter stimulus interval 250 ms). The prime stimulus was followed by the target stimulus (inter stimulus interval 500 ms), which remained on the screen for up to 2500 ms, or as long as it took participants to respond. Participants indicated with a right-handed key press (match, mismatch) whether or not prime and target stimuli were the same. Performance feedback (correct, incorrect, no response detected) was displayed for a further 1000 ms. Temporal order of a single trial is illustrated in Figure 21.

Participants undertook 324 such trials in a single block (162 'match' and 162 'mismatch' trials), with equal numbers of trials showing prime and target stimuli at 0, +/- 60 and +/- 120 degrees of angular disparity. Absolute stimulus orientation was also controlled, with equal numbers of trials presenting prime and/or target stimuli oriented vertically, at +/- 60 and at +/- 120 degrees.

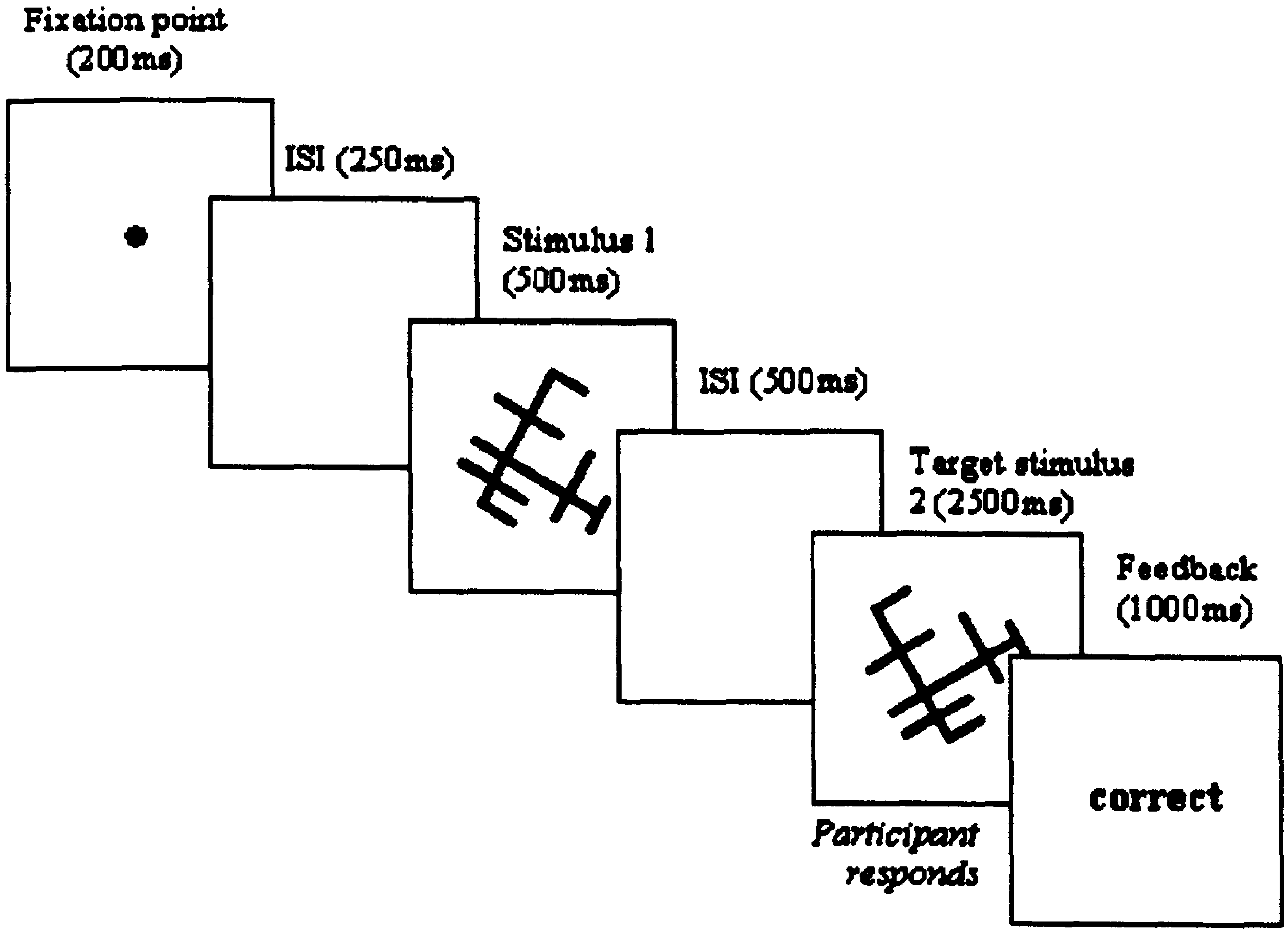


Figure 21. Progression of a single test trial in the mental rotation task.
Total trial time = 4950 ms.

<u>Object recognition task</u>

Learning phase: participants were shown one shape from each of sets A (asymmetrical) and B (symmetrical) of the Tarr and Pinker stimuli and asked to memorise them by copying the shapes with paper and pen. *Test phase:* recognition of each learned shape was then tested (one shape at a time) over two blocks consisting of 162 trials each, in which 108 presented target (learned), and 54 presented distracter, stimuli drawn from the same object set as the target stimulus. Target and distracter stimuli were viewed in equal numbers of trials at upright (0°), +/- 60° and +/- 120° orientations in each of the two blocks (total = 324 trials).

Each trial began with a 200 ms fixation-point in the centre of the screen, followed by a target or distracter stimulus shown at one of the test orientations (inter stimulus interval = 250 ms). Participants indicated by a right-handed key press (target, non-target) whether the stimulus was the previously memorised shape. Stimuli remained on the screen until participants had responded or for a maximum of 2500 ms. Feedback (correct, incorrect, no response detected) was then presented for a further 1000 ms. Temporal order of a single trial is illustrated in Figure 22.

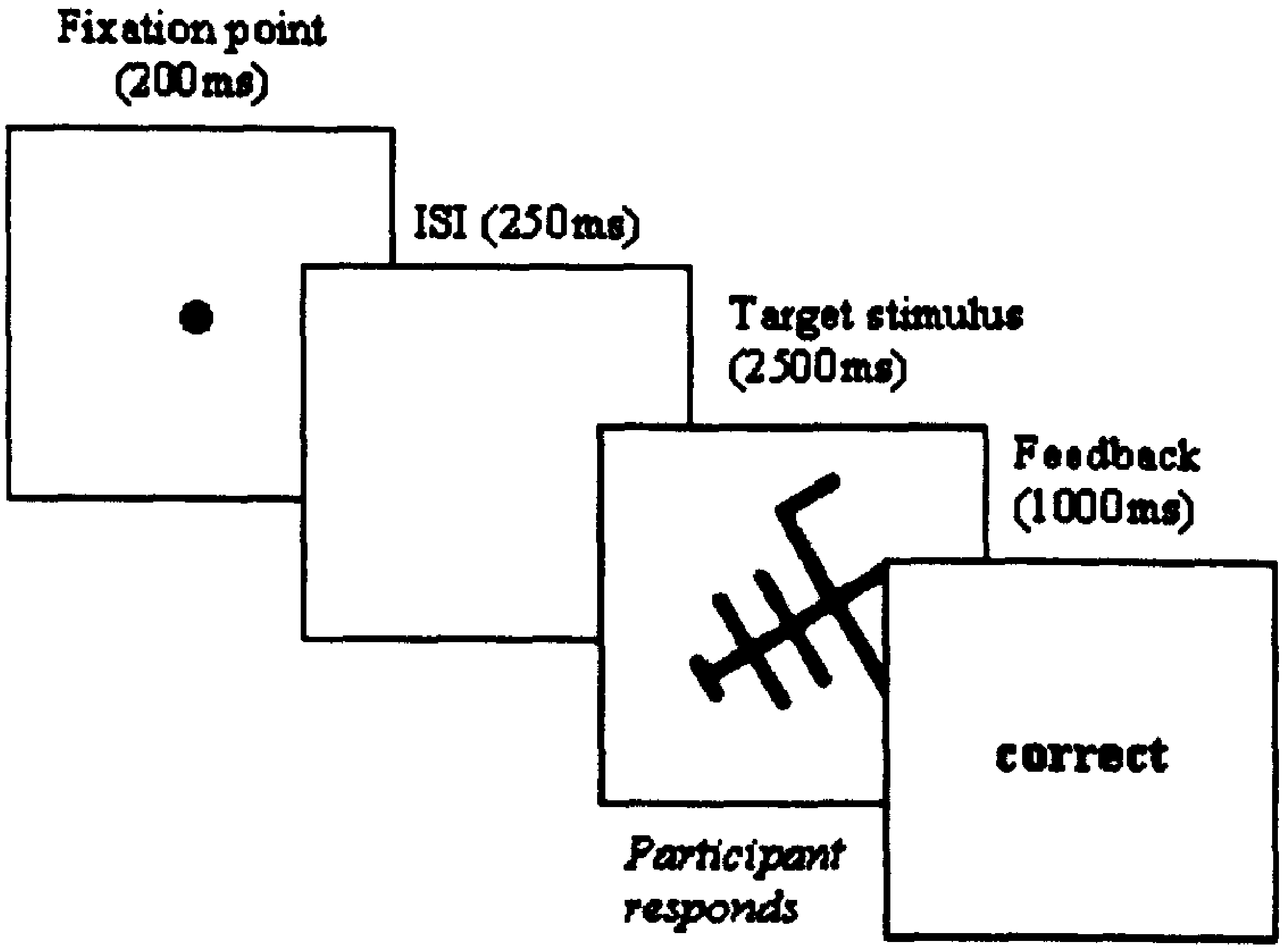


Figure 22. Progression of a single experimental trial in the object recognition task. Total trial time = 3950 ms.

In both object recognition and matching tasks, participants were required to complete 80% of 12 practice trials correctly before beginning the test trials where EEG measurements were obtained. All participants met this criterion.

5.4 Results

EEG and RT data from 'mismatch' trials in the mental rotation task and 'distracter' trials in the object recognition task were discarded. Also discarded were data from trials in which incorrect responses were given (resulting in the loss of around 3% of total data). Preliminary examination of each participant's averaged ERP data revealed that 5 participants' data was unsatisfactory, being of generally poor quality (due variously to unfilterable noise, 'sweat artifact' and high impedance). Thus, only 20 participants' data were retained for analysis of EEG and behavioural data. Statistical analysis of the RT data (see section 5.4.1) revealed that task order did not significantly affect performance; therefore, all participants' EEG data was collapsed across the various counterbalanced conditions. EEG and behavioural data were also collapsed across presentation blocks in the object-recognition task: although it would have been desirable to examine the effects of practice (from one block to the second) on ERP components and RTs, following the loss of five participants' data described above, there was insufficient ERP data to enable analysis on a per-block basis without sacrificing statistical validity. Thus, to enable direct comparison between ERP and behavioural measures, data was collapsed across these two blocks.

5.4.1 Behavioural data

Mean RT data from each task (collapsed across task order) are shown in Table 8.

Table 8: Mean RTs (N=20) from each task for stimuli at each orientation (object recognition task) or angular disparity (mental rotation task), and their corresponding regression slopes (in milliseconds per degree).

	Orientation/angular disparity			**Regression**
Condition	*0º*	*60º*	*120º*	**slope (ms/deg)**
Mental rotation task	611	798	823	***1.77***
Orientation-dependent recognition	647	746	783	***1.14***
Orientation-invariant recognition	579	589	615	***0.30***
Column means	*612*	*693*	*724*	**1.07**

Mean regression slopes for the object recognition and mental rotation tasks are illustrated in Figure 23.

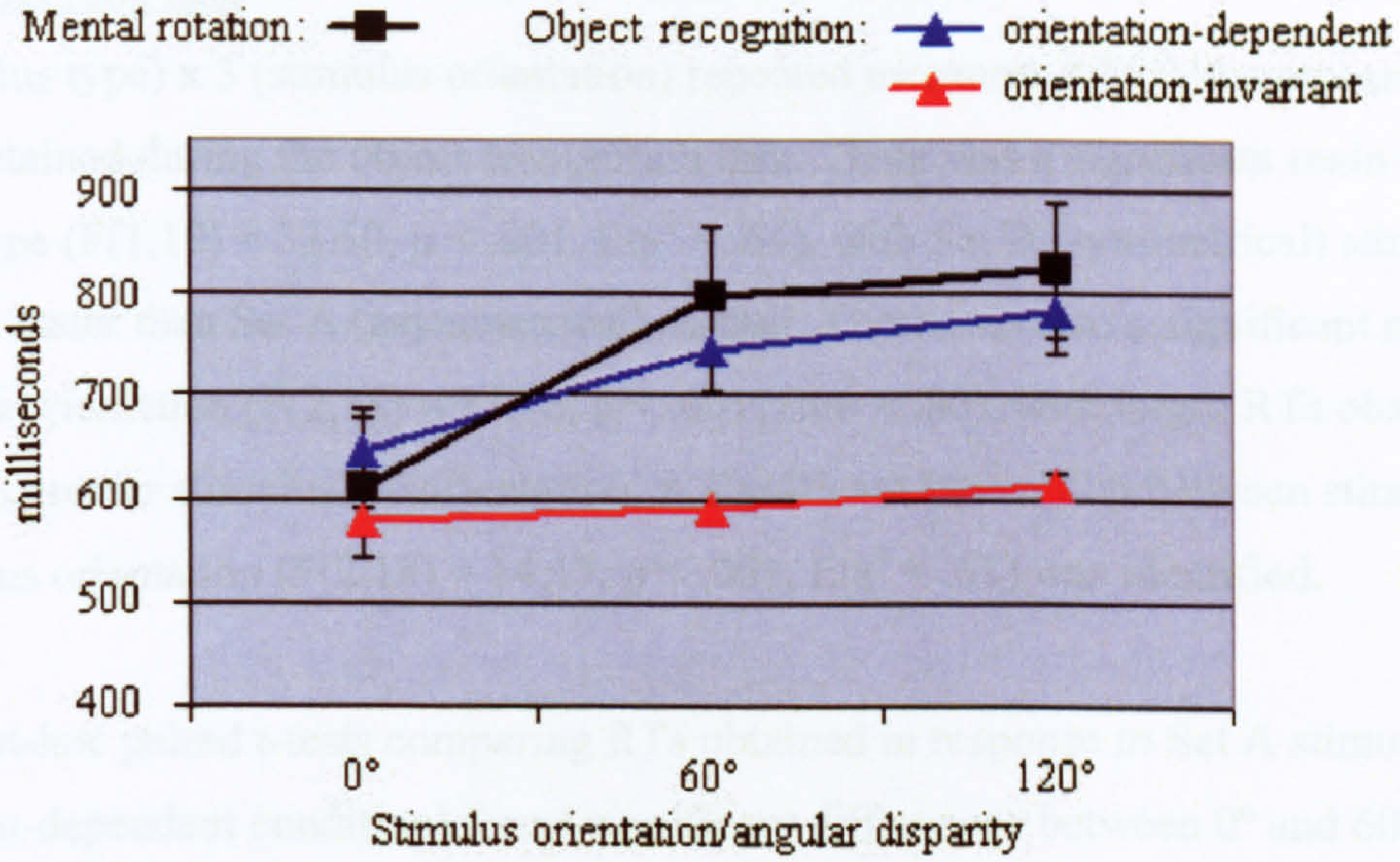


Figure 23: Mean response-times for each experimental task and condition

An exploratory 3 (experimental task: mental rotation task, orientation-dependent recognition and orientation-invariant recognition) x 2 (object recognition task order) x 2 (mental rotation task order) mixed design ANOVA was conducted on RT regression slope data to assess any effects of the counterbalanced design on task performance. As no significant effects of object recognition task order ($F(1,16) = .08$, $p = .78$, $Eta^2 = .01$) or matching task order ($F(1,16) = 1.15$, $p = .30$, $Eta^2 = .07$), and no significant interactions between these factors and task, or these factors and stimulus orientation, were found, it was deemed acceptable to collapse data from all 20 participants across all counterbalancing orders.

Mental rotation task

A one-way repeated measures ANOVA was carried out on RT data from the mental rotation task. This revealed a significant main effect of angular disparity ($F(2,38) = 66.62$, $p < .001$, $Eta^2 = .78$), with increasing angular disparity between stimuli yielding larger RTs. Post-hoc paired t-tests indicated significant differences between RTs at 0° and 60° angular disparity ($t(19) = -8.35$, $p < .001$), and between RTs at 0° and 120° angular disparity ($t(19) = -9.16$, $p < .001$). There was no significant difference between RTs at 60° and at 120° ($t(19) = -1.90$, $p = .07$).

Object recognition task

A 2 (stimulus type) x 3 (stimulus orientation) repeated measures ANOVA was carried out on RT data obtained during the object recognition task. There was a significant main effect of stimulus type ($F(1,19) = 33.50, p < .001, Eta^2 = .64$), with Set B (symmetrical) stimuli recognised faster than Set A (asymmetrical) stimuli. There was also a significant main effect of stimulus orientation ($F(2,18) = 35.36, p < .001, Eta^2 = .80$), with larger RTs observed in response to greater stimulus misorientation. A significant interaction between stimulus type and stimulus orientation ($F(2,18) = 14.17, p < .001, Eta^2 = .61$) was identified.

Post-hoc paired t-tests comparing RTs obtained in response to Set A stimuli (orientation-dependent condition) found significant differences between 0° and 60° ($t(19) = -5.43, p < .001$) and between 0° and 120° ($t(19) = -7.45, p <.001$). RTs obtained in response to Set A stimuli at 60° and 120° were not significantly different ($t(19) = -2.46, p = .024$, n.s. following Bonferroni correction).

Post-hoc paired t-tests comparing RTs obtained in response to Set B stimuli (orientation-invariant condition) found significant differences between 0° and 120° ($t(19) = -4.77, p < .001$) and between 60° and 120° ($t(19) = -3.60, p < .01$). RTs obtained in response to Set B stimuli at 0° and 60° were not significantly different ($t(19) = -1.57, p = .13$).

Since baseline (0°) RTs differed slightly across conditions in the object recognition task, regression slope (ms/degree) data, rather than absolute values, were used to compare RT effects between the two conditions of the object recognition task. A paired-samples t-test was carried out on regression slope data from the orientation-dependent and orientation-invariant recognition conditions. Regression slopes obtained in response to orientation-dependent stimuli were significantly steeper than those for orientation-invariant stimuli ($t(19) = 5.11, p < .001$).

5.4.2 EEG data

On the basis of previous studies (reviewed in sections 5.2.1 and 5.2.2), candidate markers of visuospatial transformation were sought at around 200 ms and 400 ms following stimulus onset. After inspection of data from the mean global field power (MGFP) channel, two such epochs of interest in the EEG data were identified, at 140-240 ms and 350-500 ms.

Based on previous findings that markers of visuospatial transformation are maximal over parietal cortex (Inoue et al., 1998; Muthukumaraswamy et al., 2003; Yoshino et al., 2000), a 10-electrode centroparietal region of interest (ROI; illustrated in Figure 24) was selected *a priori*. Selection of an ROI is in any case a sensible strategy for minimising the likelihood of a Type I error during ERP component analysis (Oken & Chiappa, 1986). For statistical analysis, electrodes in the ROI were grouped by anteriority (centroparietal or parietal).

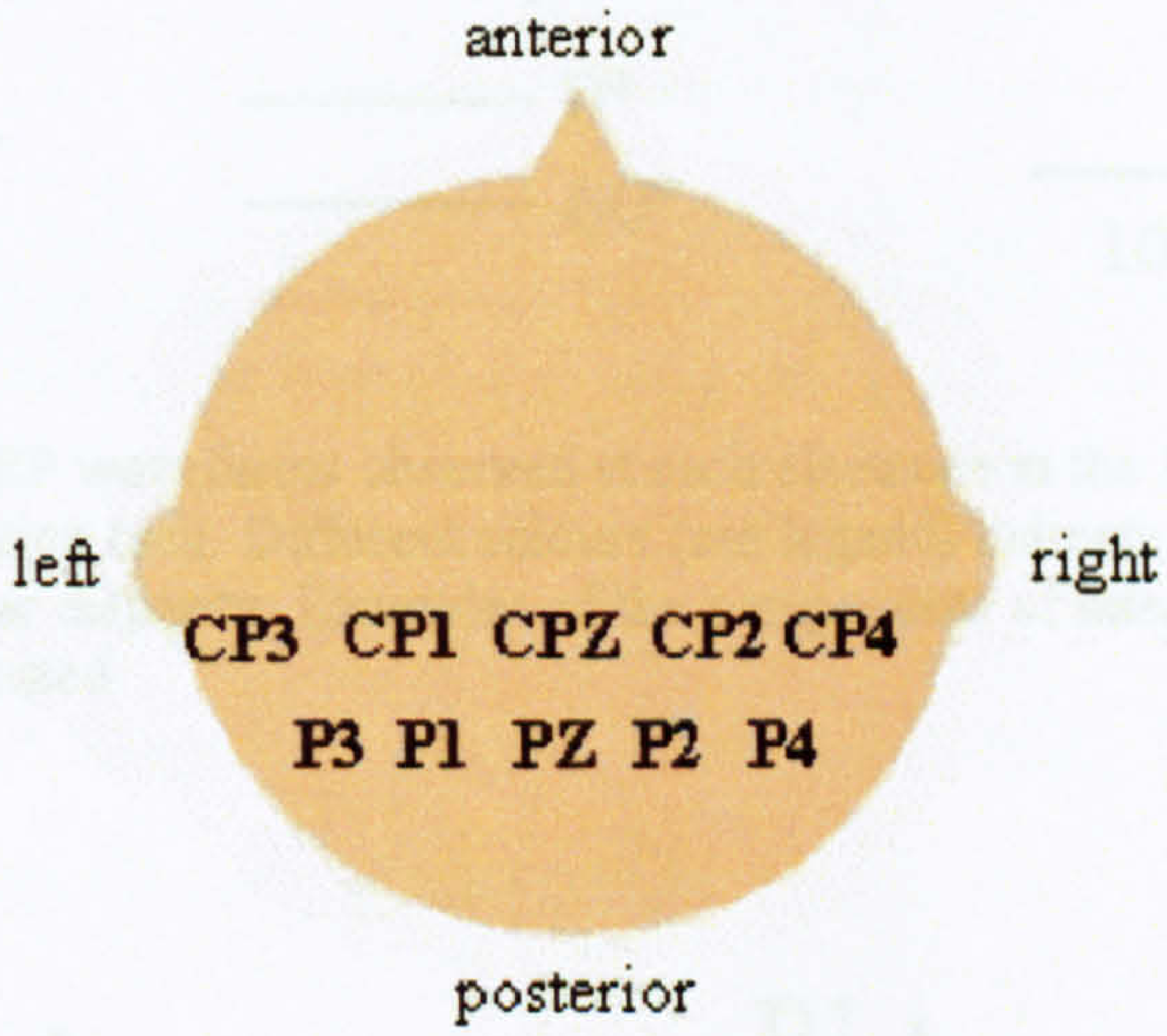


Figure 24. The 10-electrode array selected for ROI analysis. CP denotes centroparietal, and P, parietal electrodes. Even-numbered electrodes are right-hemispheric; odd-numbered electrodes are left-hemispheric. Larger numbers denote increasing laterality.

Mental rotation task

Mean waveforms recorded at each electrode in the ROI during the mental rotation task are shown in Figure 25a. Two main components were identified: an early negative component, the 'N170' (140-240 ms: Figure 25b) and a later, positive 'P400' component (350-499 ms: Figure 25c).

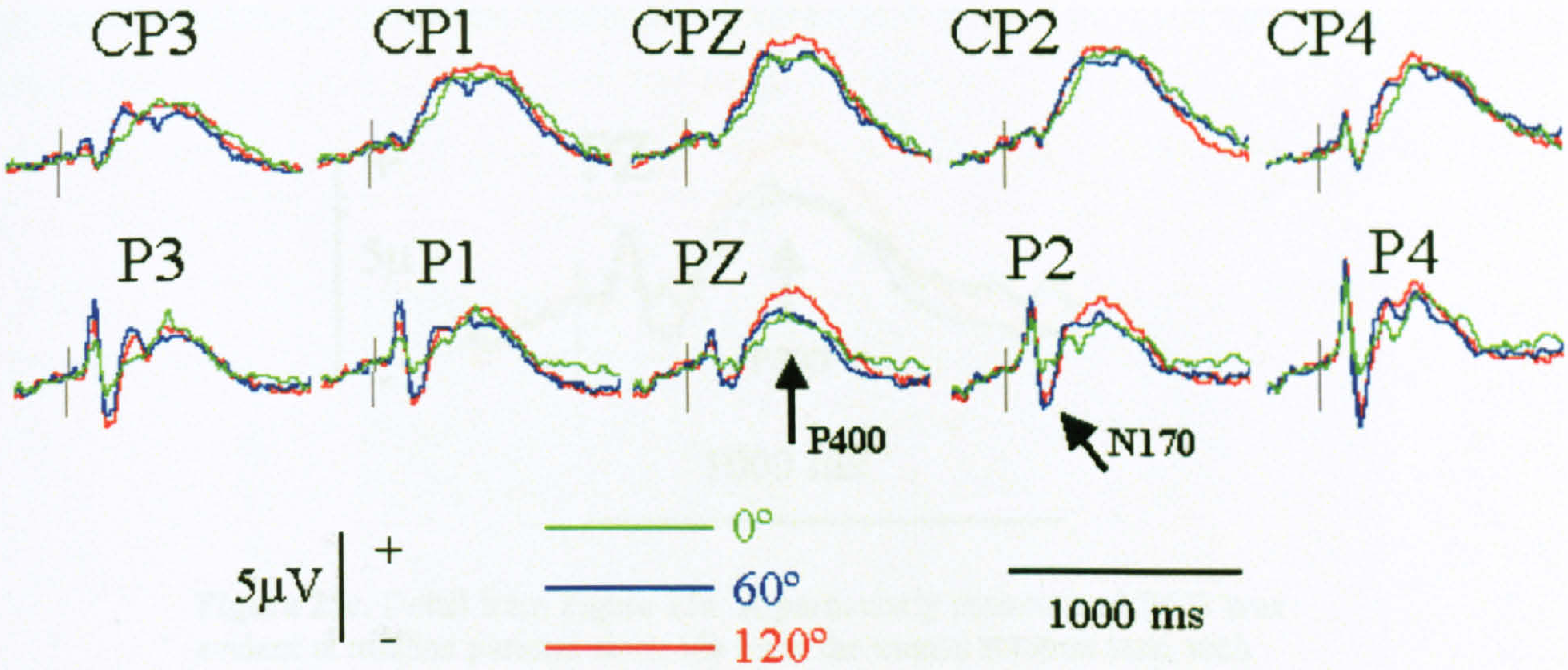


Figure 25a. ERP waveforms observed at each electrode in the ROI during the mental rotation task. Different colours (see legend) indicate different stimulus angular disparity. Examples of the components of interest (N170, P400) are indicated.

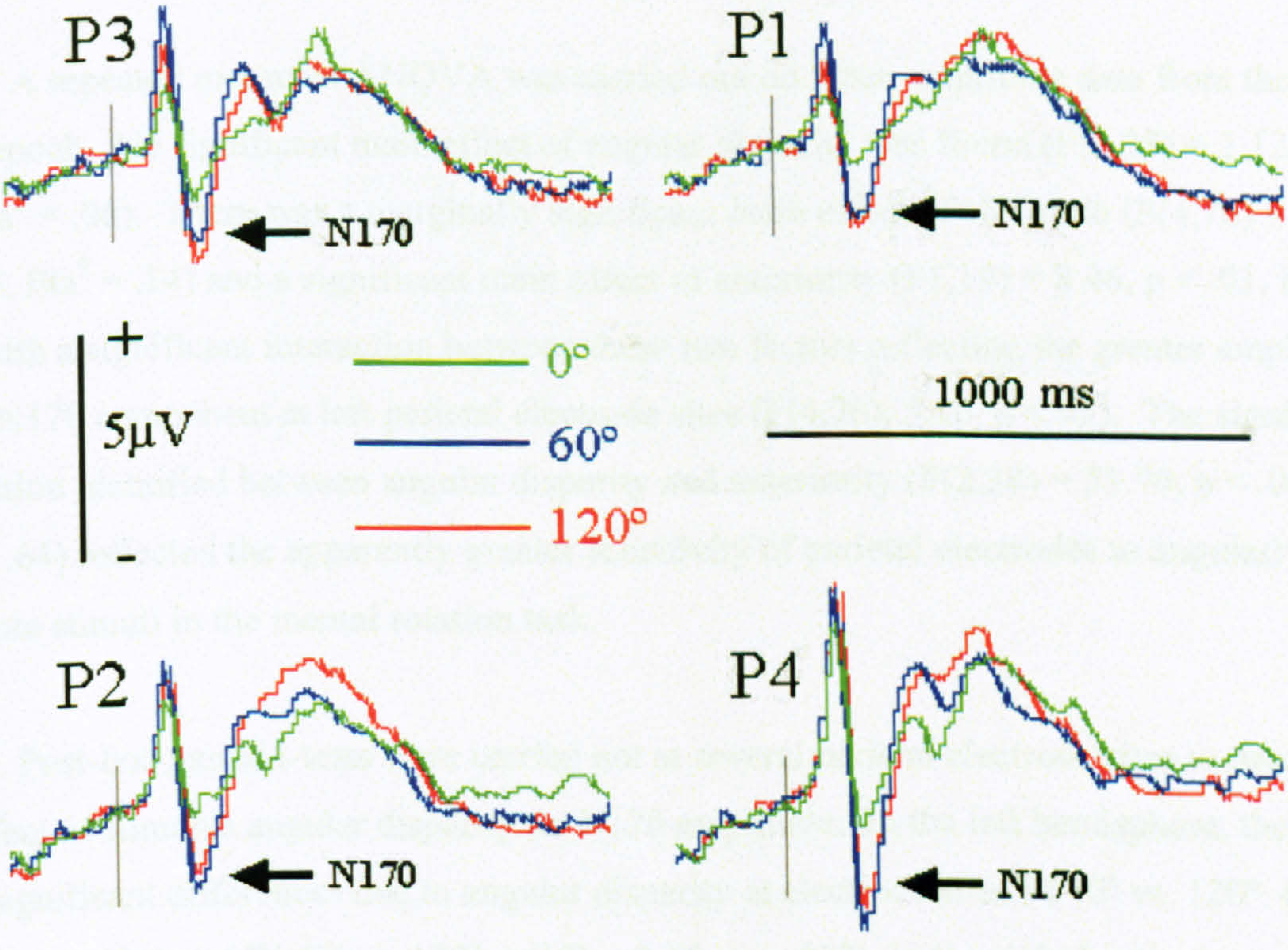


Figure 25b. An orientation-sensitive N170 component was evident at left parietal electrode sites P3 and P1, and right electrodes P2 and P4 in the mental rotation task. Increasing N170 amplitude relating to larger angular disparities between stimuli was particularly visible at electrodes site P3.

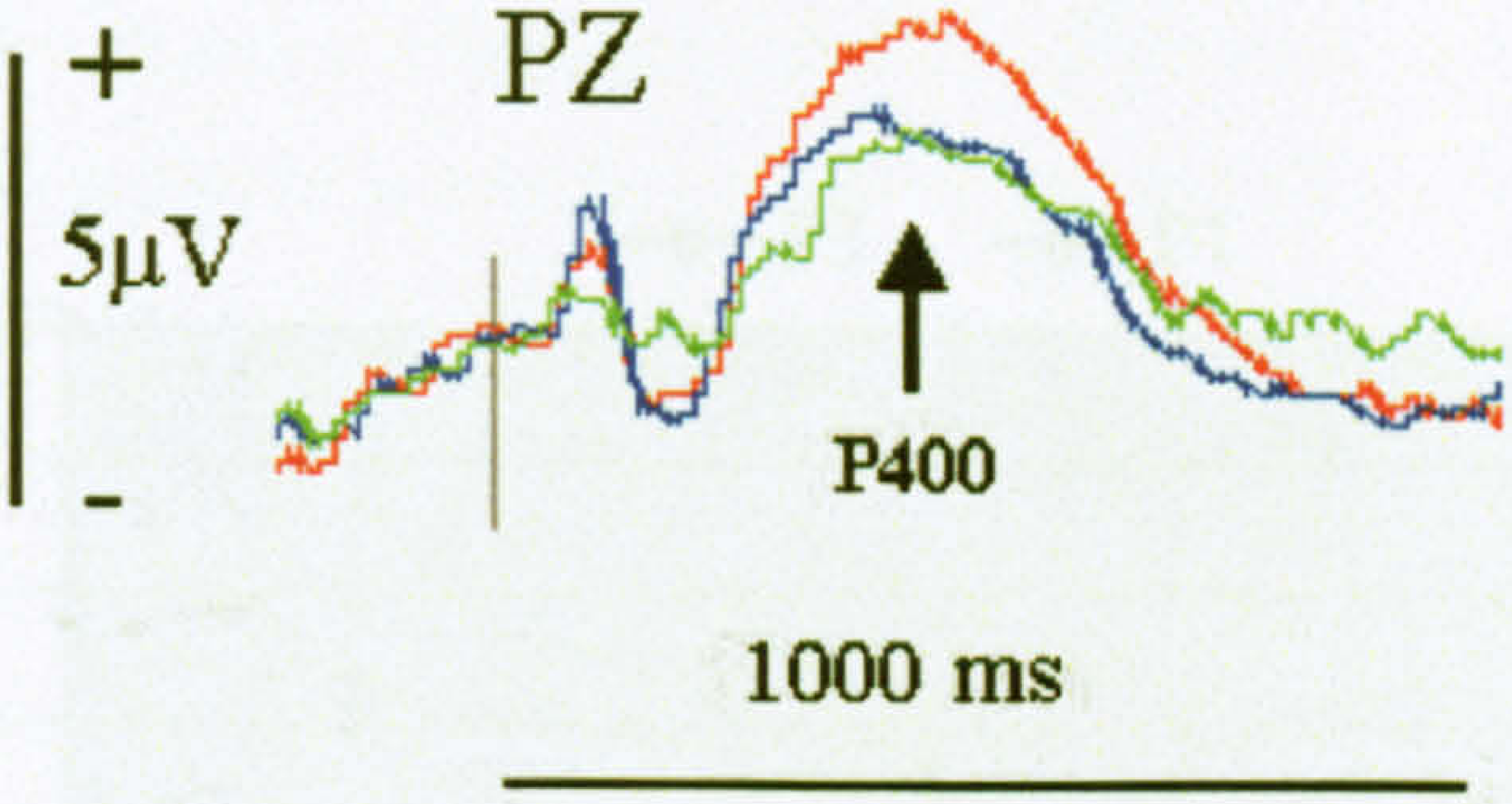


Figure 25c. Detail from Figure 25a. A particularly pronounced P400 was evident at midline parietal electrode Pz in the mental rotation task, with greatest stimulus angular disparity eliciting the largest P400 components.

The N170 (140-240 ms)

Mean amplitudes of the N170 component during the mental rotation task at each electrode in the ROI are shown in Table C1 (see Appendix C).

A repeated measures ANOVA was carried out on mean amplitude data from the N170 epoch. No significant main effect of angular disparity was found (F(2,38) = 1.12, p = .32, $Eta^2 = .06$). There was a marginally significant main effect of electrode (F(4,76) = 3.14, p = .07, $Eta^2 = .14$) and a significant main effect of anteriority (F1,19) = 8.46, p < .01, $Eta^2 = .31$), with a significant interaction between these two factors reflecting the greater amplitude of the N170 component at left parietal electrode sites (F(4,76), 5.10, p <.05). The significant interaction identified between angular disparity and anteriority (F(2,38) = 33.90, p < .001, $Eta^2 = .64$) reflected the apparently greater sensitivity of parietal electrodes to angularly disparate stimuli in the mental rotation task.

Post-hoc paired t-tests were carried out at several parietal electrode sites to determine the effect of stimulus angular disparity on N170 amplitude. In the left hemisphere, there were significant differences due to angular disparity at electrode sites P3 (0° vs. 120°: t (19) = 4.19, p < .001) and P1 (0° vs. 120°: t (19) = 3.68, p = .002). In the right hemisphere, there were significant differences due to angular disparity at electrode sites P2 (0° vs. 60°: t (19) = 3.22, p = .004) and P4 (0° vs. 60°: t (19) = 4.00, p = .001; 0° vs. 120°: t (19) = 3.93, p = .001) (all results significant following Bonferroni correction). These effects are illustrated in Figure 26.

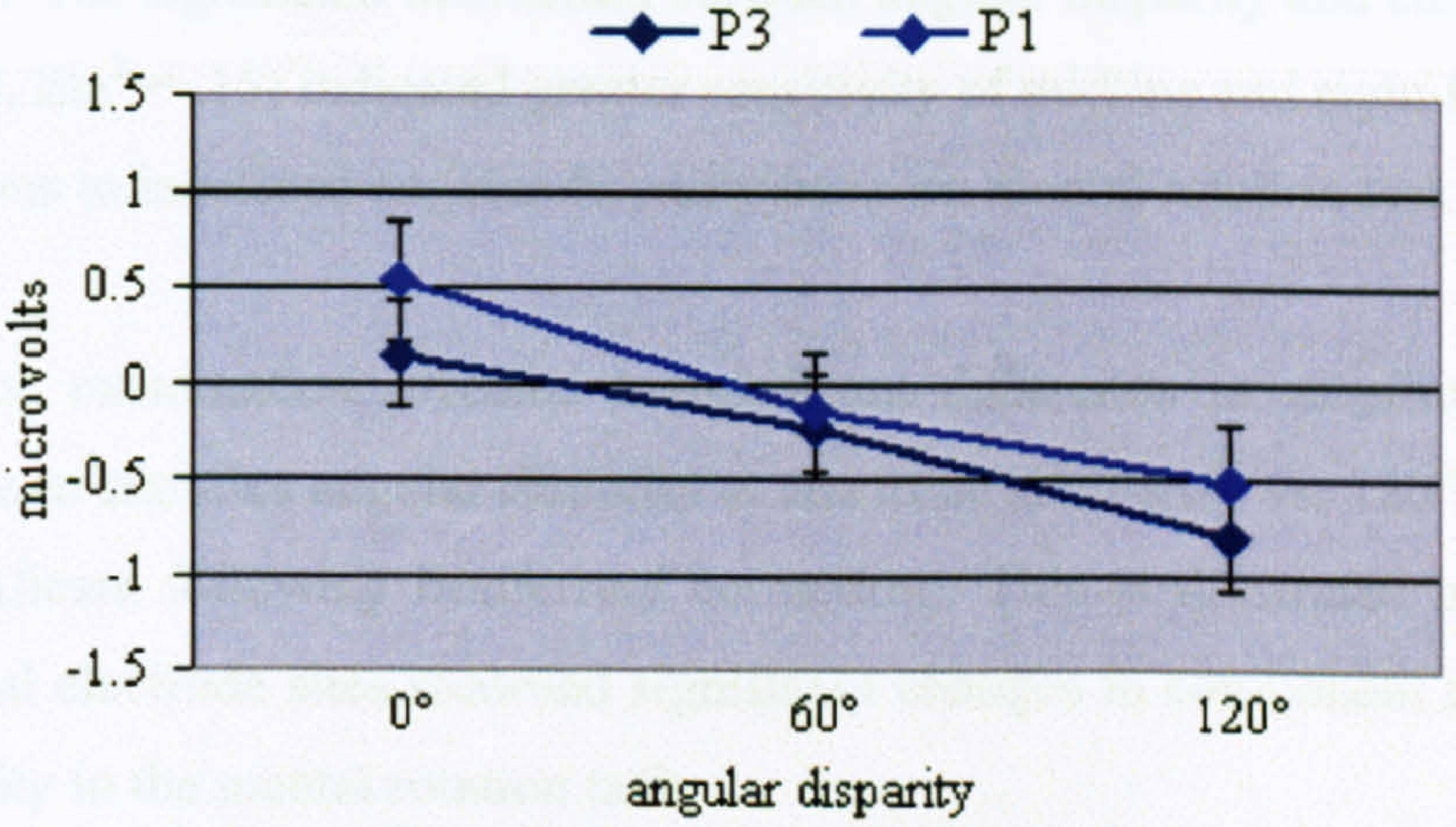
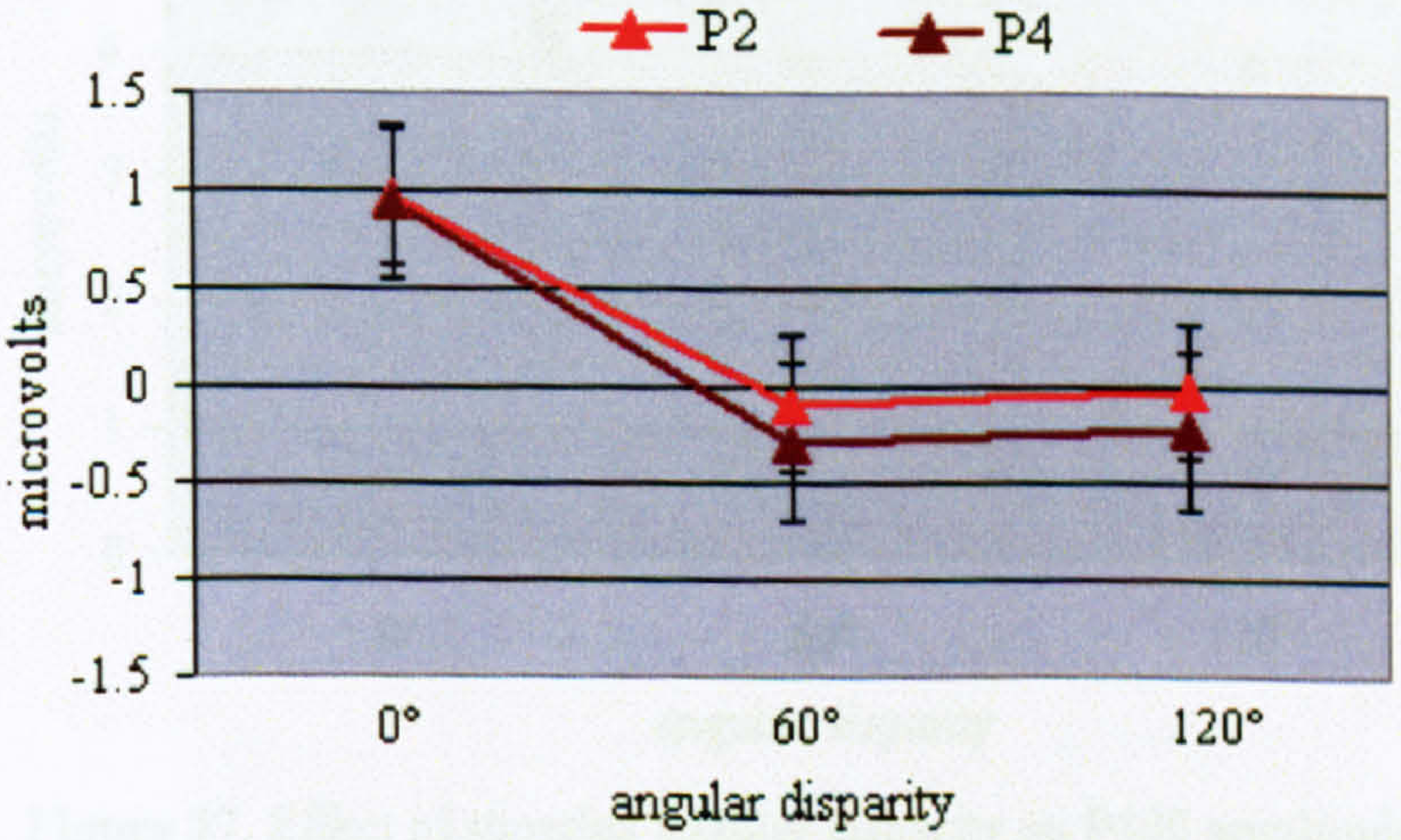


Figure 26. Interaction between electrode laterality and angular disparity, showing mean amplitudes at left parietal electrodes (above) and right parietal electrodes (below)



The P400 (350-499 ms)

Grand mean amplitudes of the P400 component during the mental rotation task at each electrode in the ROI are listed in Table C2 (see Appendix C).

A repeated measures ANOVA was carried out on mean amplitude data from the P400 epoch. No significant main effect of angular disparity (F(2,38) = 1.31, p = .28, $Eta^2 = .07$) was found. A significant main effect of anteriority (F(1,19) = 6.70, p < .05, $Eta^2 = .26$) and significant main effect of electrode (F(4,76) = 9.37, $p < .001$, $Eta^2 = .33$) were observed, with a significant interaction between these two factors (F(4,76) = 10.29, $p < .001$, $Eta^2 = .35$) reflecting the larger P400 amplitudes recorded at centroparietal and right-hemispheric electrode sites. The significant interaction between angular disparity and electrode (F(8,152) = 3.22, $p < .05$, $Eta^2 = .15$) indicated greater sensitivity of midline and right-hemispheric electrode regions to increased angular disparity between mental rotation task stimuli.

Post-hoc examination revealed a significant difference in amplitude of the P400 component due to stimulus angular disparity at electrode site Pz (0° vs. 120°: t(19) = -2.10, p = .024 – significant following Bonferroni correction). This is illustrated in Figure 27. No other individual electrode sites recorded significant changes in component amplitude due to angular disparity in the mental rotation task.

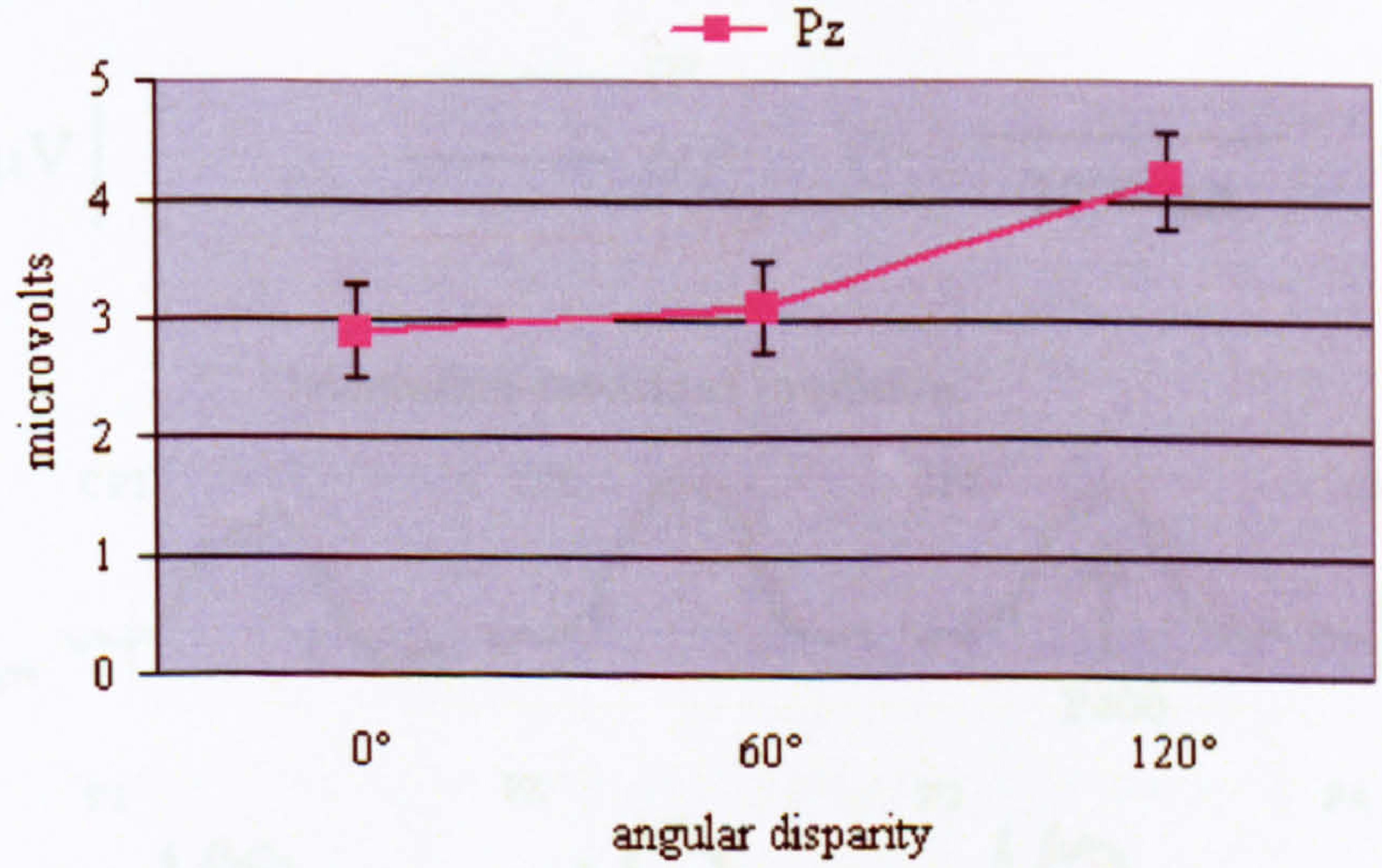
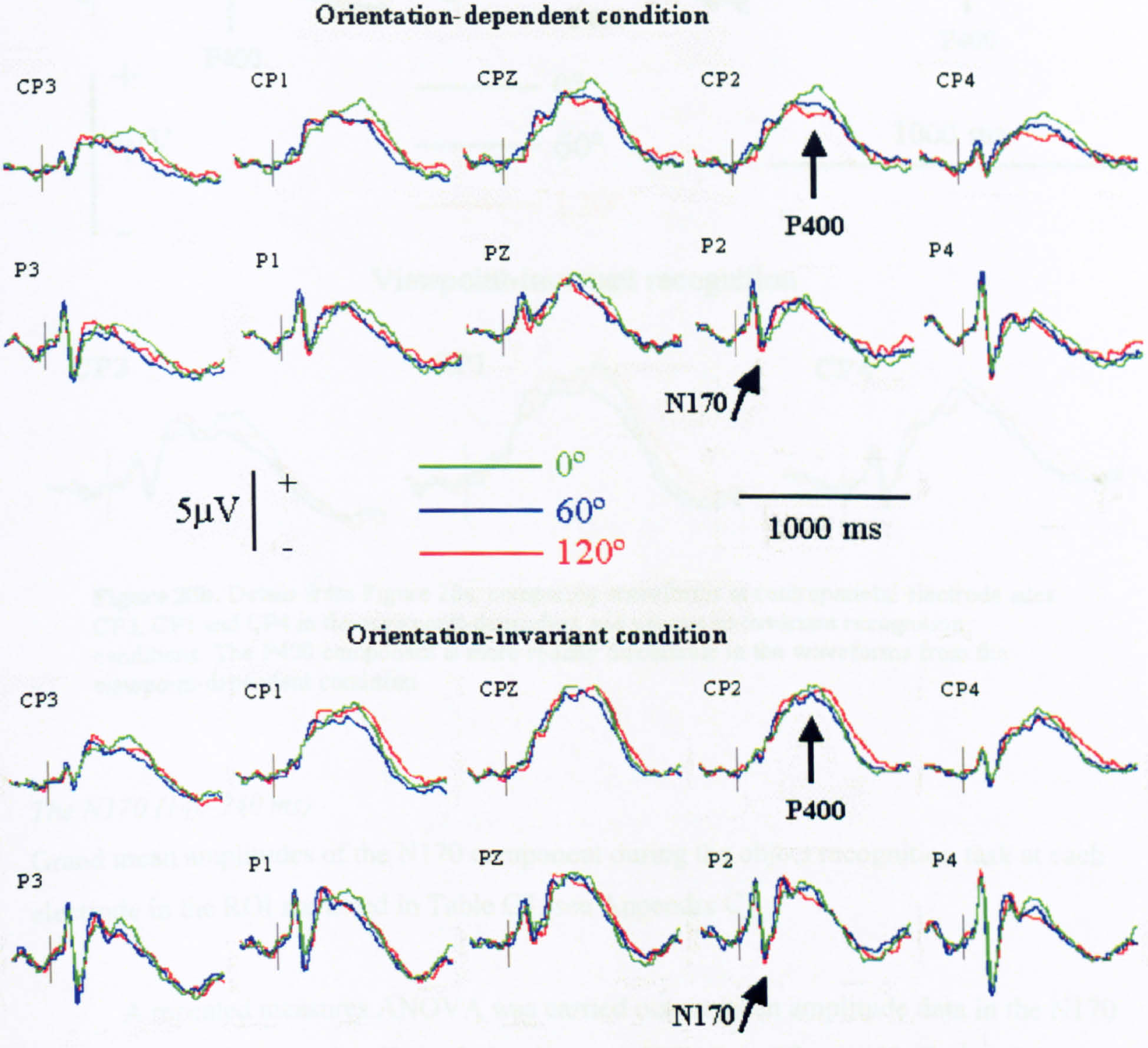


Figure 27. Effect of stimulus angular disparity on P400 amplitude at parietal electrode Pz in the mental rotation task.

Object recognition task

Having identified two putative markers of visuospatial transformation (N170 and P400) in the mental rotation task, evidence of these two markers was sought during each of the object recognition task conditions: orientation-dependent and orientation-invariant recognition.

Averaged ERP waveforms acquired at each electrode in the ROI during the object recognition task are illustrated in Figure 28a. As in the mental rotation task, two main components were identified: a negative 'N170' component (140-240 ms following stimulus presentation) and a positive 'P400' component (350-499 ms: see Figure 28b). Grand mean amplitude data at each electrode for each condition and block are listed in Table C3 (see Appendix C).



Orientation-dependent condition

Orientation-invariant condition

Figure 28a. ERP waveforms recorded at each electrode in the ROI during the orientation-dependent and orientation-invariant stimulus conditions. Different colours (see legend) indicate different stimulus orientation. Examples of each component of interest (N170, P400) are shown. The P400 component is more readily discernible in the waveform from the viewpoint-dependent condition.

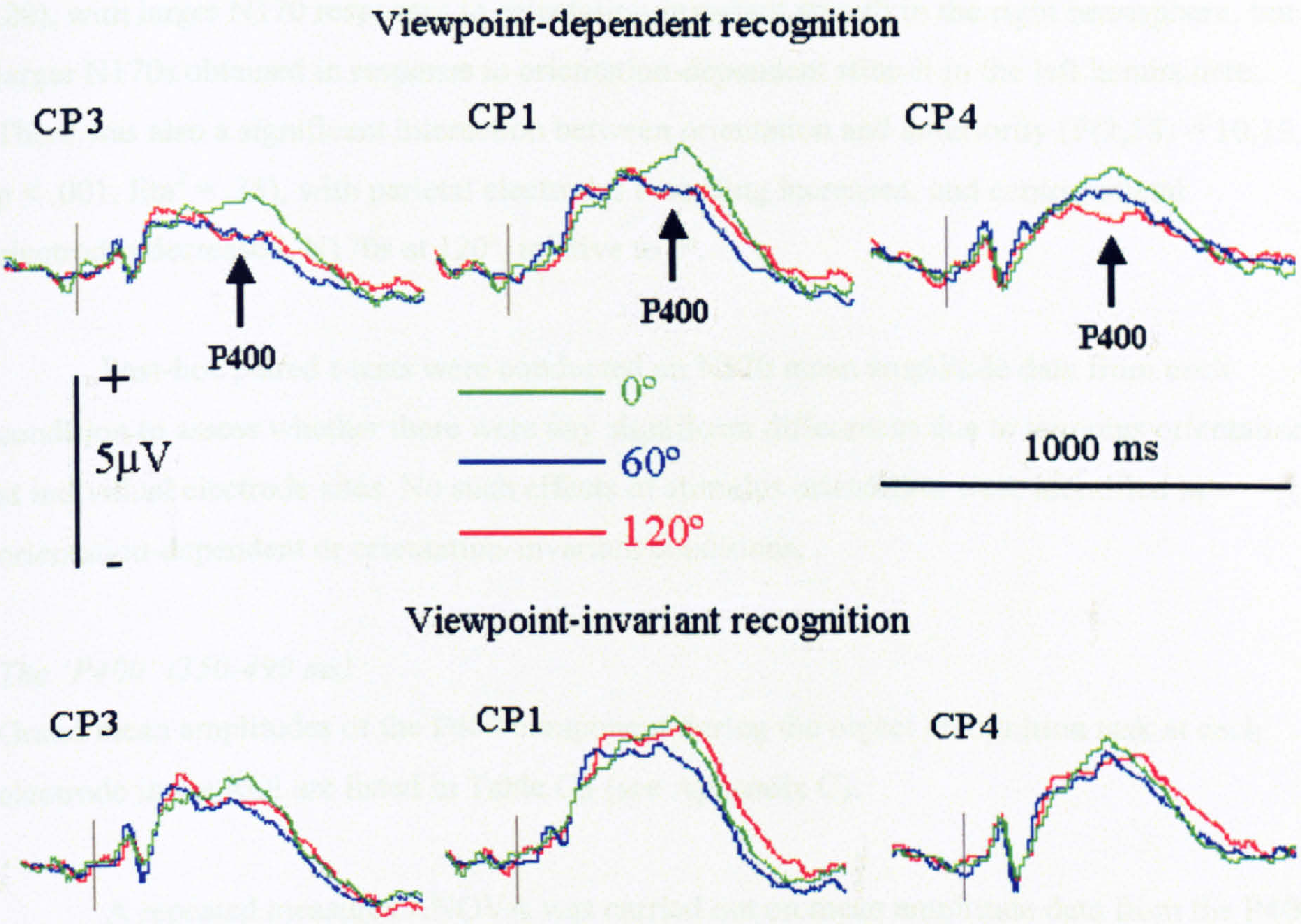


Figure 28b. Details from Figure 28a, comparing waveforms at centroparietal electrode sites CP3, CP1 and CP4 in the viewpoint-dependent and viewpoint-invariant recognition conditions. The P400 component is more readily discernible in the waveforms from the viewpoint-dependent condition.

The N170 (140-240 ms)

Grand mean amplitudes of the N170 component during the object recognition task at each electrode in the ROI are listed in Table C3 (see Appendix C).

A repeated measures ANOVA was carried out on mean amplitude data in the N170 epoch. No significant main effect of stimulus type ($F(1,19) = .17$, $p = .68$, $Eta^2 = .01$) was found. A significant main effect of orientation ($F(2,38) = 5.20$, $p < .05$, $Eta^2 = .22$) was identified, with the N170 component largest at 120° and smallest at 60°. There was also a significant main effect of electrode ($F(4,76) = 19.12$, $p < .001$, $Eta^2 = .50$), with lateral electrodes recording a larger N170 component than medial electrodes. A significant main effect of anteriority ($F(1,19) = 25.12$, $p < .001$, $Eta^2 = .57$) was also observed, with parietal electrodes recording much larger N170s than centroparietal electrodes. There was a significant interaction between stimulus type and electrode ($F(4,76) = 4.65$, $p < .05$, $Eta^2 =$

.20), with larger N170 responses to orientation-invariant stimuli in the right hemisphere, but larger N170s obtained in response to orientation-dependent stimuli in the left hemisphere. There was also a significant interaction between orientation and anteriority (F(2,38) = 10.19, $p < .001$, $Eta^2 = .35$), with parietal electrodes recording increased, and centroparietal electrodes decreased, N170s at 120°, relative to 0°.

Post-hoc paired t-tests were conducted on N170 mean amplitude data from each condition to assess whether there were any significant differences due to stimulus orientation at individual electrode sites. No such effects of stimulus orientation were identified in orientation-dependent or orientation-invariant conditions.

The 'P400' (350-499 ms)

Grand mean amplitudes of the P400 component during the object recognition task at each electrode in the ROI are listed in Table C3 (see Appendix C).

A repeated measures ANOVA was carried out on mean amplitude data from the P400 epoch. No significant main effect of stimulus type (F(1,19) = .02, p = .884, $Eta^2 = .00$) was found. A significant main effect of orientation (F(2,38) = 10.82, $p < .001$, $Eta^2 = .36$) was observed, with smaller P400 components elicited by stimuli at greater misorientations. There was also a significant main effect of electrode (F(4,76) = 34.96, $p < .001$, $Eta^2 = .65$), with medial electrodes recording larger P400 components. A significant main effect of anteriority was also observed (F(1,19) = 18.44, $p < .001$, $Eta^2 = .49$), with a larger P400 recorded at centroparietal electrode sites than at parietal sites. A significant interaction between stimulus type, orientation and anteriority was also found (F(2,38) = 4.61, $p < .05$, $Eta^2 = .20$), with more orientation-sensitivity of the P400 to Set A (orientation-dependent) stimuli at centroparietal electrodes and more orientation-sensitivity to Set B (orientation-invariant) stimuli at parietal electrode sites.

Post-hoc paired t-test comparisons were carried out on P400 mean amplitude data to assess the effect of stimulus orientation in each condition. In the orientation-dependent condition, significant decreases in P400 amplitude corresponding to increased stimulus misorientation were observed at CP1 (0° vs. 60°: t(19) = 4.97, $p < .001$), CP3 (0° vs. 60°: t(19) 4.11, p =.001) and CP4 (0° vs. 120°: t(19) = 4.48, $p < .001$) (all results significant following Bonferroni correction). No significant differences in amplitude due to stimulus orientation were observed at electrode sites in the ROI during the orientation-invariant condition. These effects are illustrated in Figure 29.

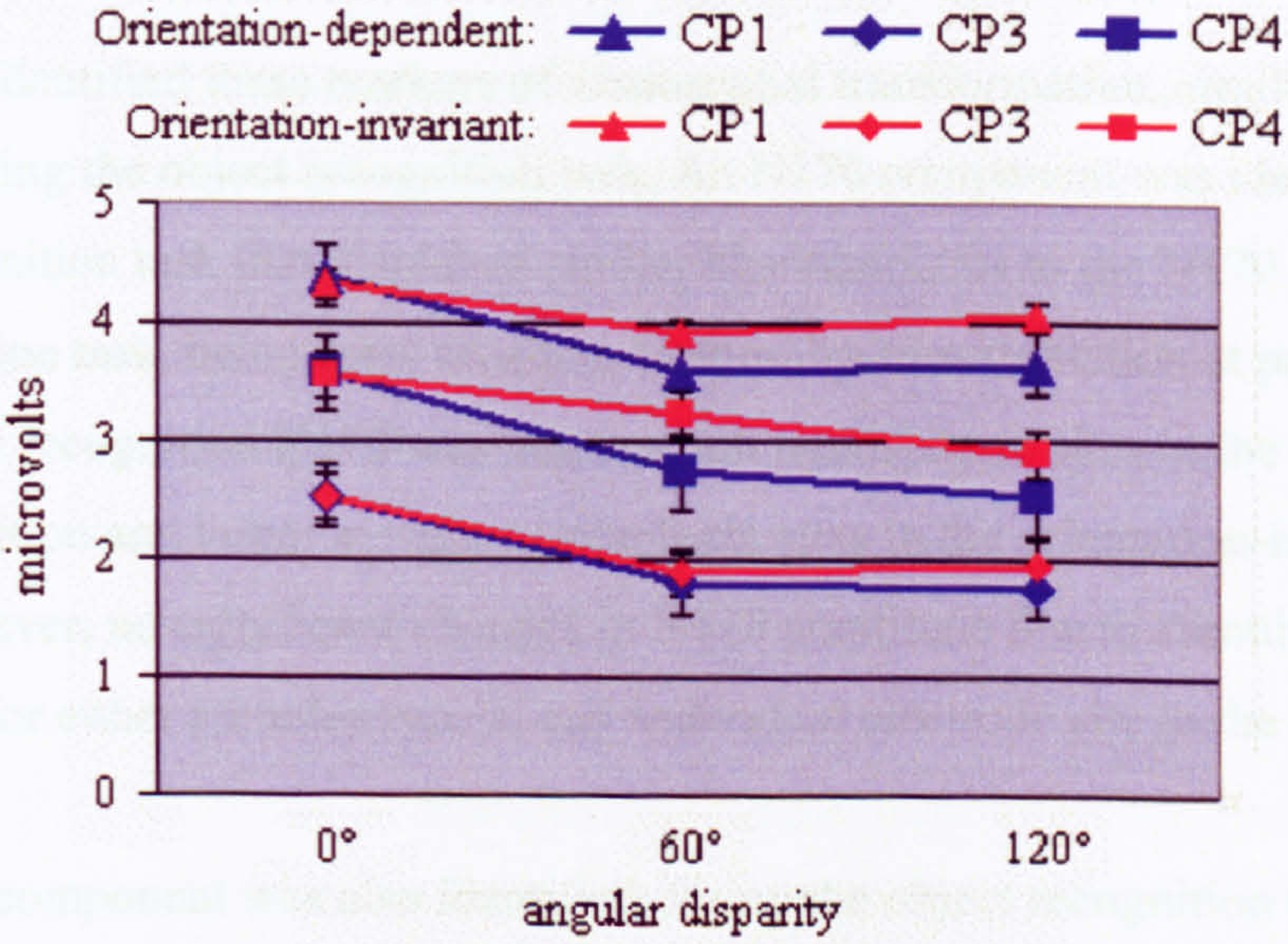


Figure 29. The effect of stimulus orientation on mean amplitude of the P400 at centroparietal electrode sites CP1, CP3 and CP4 during orientation-dependent and orientation-invariant recognition.

5.5 Discussion

5.5.1 Summary of main findings

Two putative ERP markers of visuospatial transformation, the N170 and P400 components, were recorded during the mental rotation task. Greater angular disparity between stimuli was associated with a more negative N170, and with a more positive P400. The N170 appeared to be most sensitive to angular disparity at lateral parietal electrode sites, maximal over left parietal cortex. The P400 displayed maximal sensitivity to stimulus angular disparity at the midline parietal electrode site. Behavioural data acquired concurrently with EEG recordings indicated that response-times increased with greater angular disparity between stimuli, suggesting that participants were indeed recruiting some kind of spatial transformation process during mental rotation. Thus, the N170 and P400 components, sensitive to angular disparities between stimuli in the mental rotation task, can be considered to reflect some aspect(s) of this visuospatial transformation process, and thus to constitute putative markers of object constancy processes related to those previously described by authors such as Muthukumaraswamy et al. (2003) and Yoshino et al. (2000), respectively.

Having identified these markers of visuospatial transformation, similar components were sought during the object recognition task. An N170 component was identified during the object recognition task that displayed similar characteristics to the N170 recorded during the mental rotation task, being most sensitive to stimulus misorientation at parietal electrode sites. The object recognition N170 was larger at left hemispheric sites in the orientation-dependent condition and larger at right-hemispheric sites in the orientation-invariant condition. However, no significant changes in N170 amplitude due to stimulus orientation were observed for either stimulus type at any individual electrode site in the ROI.

A P400 component was also identified during the object recognition task. This component exhibited orientation-sensitivity at lateral electrodes sites (predominantly over left parietal cortex) during recognition of misoriented orientation-dependent stimuli, but not during recognition of misoriented orientation-invariant stimuli. Thus, although the focus of the P400 was slightly different in the mental rotation task than in viewpoint-dependent recognition, these findings appear to provide evidence for the recruitment of visuospatial transformation processes during viewpoint-dependent, but not during viewpoint-invariant, object recognition. Behavioural data supported this distinction, with response-latencies in each condition of the object-recognition task consistent with prior literature: mean regression slopes of less than 1 ms/deg were recorded in response to orientation-invariant stimuli, and mean slopes of greater than 1 ms/deg recorded for orientation-dependent stimuli. It would therefore appear that participants were indeed recruiting distinct object recognition mechanisms in each condition, an inference supported by their differing electrophysiological and behavioural profiles.

The following sections discuss the ERP markers of visuospatial transformation recorded during mental rotation, explore the extent to which these markers may be present during viewpoint-dependent and viewpoint-invariant object recognition, and the discuss implications of these findings for our understanding of object constancy. The finding that the direction of the viewpoint-dependent P400 was reversed from that seen in the mental rotation task is also discussed.

5.5.2 The N170 – orientational cue, or index of visual expertise?

5.5.2.1 Mental rotation N170 may reflect relative stimulus orientation

The N170 component measured at lateral parietal electrode sites during the mental rotation task appears to be indicative of the angular disparity between prime and target stimuli. Negative parietal ERP components of similar latency have been interpreted in previous studies as indicators of absolute stimulus orientation (e.g. Wijers et al., 1989 – see following section). However, since matching task trials in this study were averaged across absolute orientation, it would appear that *relative* angular disparity (between prime and target stimuli) elicited an analogous ERP component. Negative components of similar latency occurring over posterior parietal cortex have previously been reported in a mental rotation task (Muthukumaraswamy et al., 2003). Such an explanation would also be consistent with previous psychometric evidence demonstrating that response latencies to novel stimuli presented successively at different orientations are orientation-dependent relative to the previous stimulus orientation (Koriat & Norman, 1988, 1989) (the use of frames of reference for the assessment of stimulus orientation was discussed in Chapter 1).

The N170 component recorded during the mental rotation task thus appears to emerge as an early index of the angular disparity between prime and target stimuli. As such, the parietal N170 may constitute an electrophysiological marker for the detection of relative (contextual) stimulus orientation, providing support for the recruitment of dynamic, context-dependent reference-frames in object perception.

5.5.2.2 Object recognition N170 may reflect absolute stimulus orientation

The N170-like component observed in the object recognition task appears to be orientation-sensitive, irrespective of stimulus type, and largest at parietal electrode sites. As noted above, early occipitoparietal negativity has previously been associated with the process of determining absolute stimulus orientation: Wijers et al. (1989) reported a negative occipital component between 200-300 ms specifically associated with orientation-dependent RTs, which the authors ascribed to a preattentive process involving classification of stimulus orientation and/or identity (target vs. distracter). Negative components of similar latency have also previously been recorded over occipitoparietal cortex during misoriented letter recognition (Milivojevic et al., 2003). Variation in N170 latency has also been associated with changes in stimulus orientation (Rossion, Joyce, Cottrell, & Tarr, 2003), supporting the idea that this component may be sensitive to such manipulations.

Since the effect of stimulus orientation on N170 amplitude was independent of stimulus type in the object recognition task, and it has been established that participants' behavioural responses were not, it seems likely that the N170 in this task does not reflect the visuospatial transformation process itself. As such, the N170 does not permit us to distinguish between viewpoint-dependent and viewpoint-invariant recognition mechanisms, but rather, may be indicative of an early attempt to establish stimulus orientation, consistent with the findings cited above. However, it should be noted that the amplitude of the N170 during object recognition did not appear to be proportional to the degree of stimulus misorientation, at least for electrode sites within the ROI. Therefore, the object recognition N170 may not be wholly reflective of orientation-detection processes, but may also be affected by other factors, such as those described in the following sections.

5.5.2.3 N170 may reflect implicit motion during internalised spatial transformation

An alternative explanation of the N170 observed in the present study comes from various observations that a similar negative components, occurring between 160-200 ms in the vicinity of the occipitotemporoparietal junction, may reflect implicit motion perception (Hollants-Gilhuijs, De Munck, Kubova, van Royen, & Spekreijse, 2000; Kuba & Kubova, 1992; Kubova, Kuba, Hubacek, & Vit, 1990; Muthukumaraswamy et al., 2003). The perception of motion during tasks that require some element of internalised transformation is consistent with subjective accounts that commonly report imagined rotation or manipulation of the stimulus object. Muthukumaraswamy et al. (2003) reported a slightly later, bilateral negative parietal component between 200-300ms in a mental rotation task, speculating that this component may reflect apparent stimulus motion during internalised visuospatial transformation. Such accounts are supported by the finding that area MT/V5, which is sensitive to implicit motion (Anderson et al., 1996; Zeki et al., 1993), is often recruited during tasks recruiting object constancy mechanisms (Alivisatos & Petrides, 1997; Cohen et al., 1996; Pegna et al., 1997; Vanrie et al., 2002). It might be argued that the N170 observed in the present study is therefore indicative of implicit stimulus motion during task performance. The more distinct effect of angle on N170 amplitude during mental rotation may reflect greater implied motion in this task resulting from the resolution of prime and target stimulus percepts – both held in working memory – into alignment.

However, it is not clear from accounts such as those described above (which infer a transformational solution to misoriented object recognition/mental rotation) whether participants' subjective experience of performing such tasks extends to cases in which viewpoint-invariant recognition takes place (the subjective experiences of participants in the present study were not recorded). Orientation sensitivity of the N170 measured at electrodes in the ROI during viewpoint-dependent recognition did not appear to differ from that observed during viewpoint-invariant recognition, despite some minor topographic variation between the two conditions. This suggests that, if the N170 is indeed indicative of implicit motion perception, then this phenomenon is not specific to viewpoint-dependent recognition.

5.5.2.4 Object recognition N170 as an index of visual 'expertness'

It has been proposed that that ERP components in the range 156-200 ms are sensitive to 'categorisation' – that is, deciding to which of two or more categories a novel shape belongs (Curran et al., 2002). The N170 is a component associated with ventral pathway activity, thought to reflect 'expertness' in recognising exemplars from specific object categories, particularly faces; N170 amplitude has been shown to be sensitive to non-face stimuli, but only when the viewer has acquired some expertise (Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Tanaka & Curran, 2001). In the present study, an N170 component was evoked by the Tarr and Pinker recognition task, in which participants determined whether or not each stimulus was one with which they were familiar. N170 may therefore reflect the task demand that participants distinguish between superficially similar objects sharing very similar features – in other words, that they become expert.

If the object recognition N170 reflects visual expertise, it is difficult to account for the finding that this component was also evoked by the mental rotation task, where no items had been memorised, and participants were therefore not making 'expert' decisions, since they were no more practiced at recognising one stimulus than another. Given that the N170 has been associated with a variety of visual processes (e.g., Rossion et al., 2002), it may be unwise to conflate superficially similar findings from the mental rotation and object recognition tasks when these may in fact reflect quite different early perceptual processes. It may be that changes in amplitude of the N170 during mental rotation reflect stimulus orientation judgements (since there is some evidence to suggest that successive presentation of differently oriented stimuli may affect visuospatial reference-frame selection [e.g., Koriat

& Norman, 1989]), whereas those changes observed in N170 amplitude during object recognition are representative of some other process more pertinent to familiar, learned objects, such as stimulus categorisation.

5.5.3 The P400 as a marker for visuospatial transformation.

The P400 component observed during the mental rotation task appeared to be sensitive to angular disparity between mental rotation task stimuli at medial parietal electrode sites, with largest P400s associated with greatest angular disparities. Previous electrophysiological studies of mental rotation have identified an orientation-sensitive negative component of similar latency over parietal or centroparietal cortex (Inoue et al., 1998; Muthukumaraswamy et al., 2003; Yoshino et al., 2000). However, one difference between the P400 observed in the present study and similar markers of visuospatial transformation identified in previous studies was that greater angular disparity here was associated with an *increase* in mean amplitude of the P400 component, a finding which is difficult to explain. Latency, location and the orientation-sensitivity of the P400 nonetheless suggest that the present study has successfully replicated a marker of visuospatial transformation. Behavioural data also indicated that solution of the mental rotation task was indeed a time-dependent function, and so the P400 component appears to constitute a plausible marker for visuospatial transformation. That such a marker was recorded in the parietal area is also consistent with the proposal, reviewed in Chapter 2, that the coordinate frame transformations necessary for object constancy are probably carried out in parietal cortex (Alivisatos & Petrides, 1997; Andersen, 1995; Andersen et al., 2000), though as noted earlier, the extent to which the topography of ERP components may be used to infer cerebral localisation is still uncertain.

5.5.4 Evidence for visuospatial transformation processes during viewpoint-dependent object recognition

The P400 marker for visuospatial transformation was found to be sensitive to angular disparity between prime and target stimuli in the mental rotation task. Evidence for a component similar in latency and location, and which was sensitive to stimulus orientation, was sought in the ERP data from the orientation-dependent recognition condition. A P400 component, amplitude of which was found to be sensitive to stimulus orientation at bilateral centroparietal electrode sites, was subsequently identified in the orientation-dependent recognition condition. In contrast to the mental rotation task P400, the effect of stimulus orientation on P400 amplitude during viewpoint-dependent recognition adhered to the pattern described in previous studies, showing a decrease in amplitude (increased negativity) with greater stimulus misorientation. Topography of this component was also slightly different from the P400 observed in the mental rotation task: sensitivity of the P400 to angular disparity during mental rotation was most evident at parietal electrode site Pz, but orientation-sensitivity of the viewpoint-dependent P400 component was greatest at centroparietal electrode sites CP3, CP1 and CP4. However, on the basis of latency, global topography and orientation-sensitivity, the similarities between the P400 observed during the mental rotation task and the component reported during viewpoint-dependent object recognition seem likely to indicate a shared visuospatial transformation mechanism. This assertion is further supported by the behavioural data, which recorded regression slopes of greater than 1ms/degree in both tasks which, as discussed in Chapter 1, suggests recruitment of a transformational mechanism in both processes.

Similarity between ERPs evoked by viewpoint-dependent recognition and mental rotation may be inferred from prior literature (Heil & Hennighausen, 1999; Inoue et al., 1998; Milivojevic et al., 2003; Muthukumaraswamy et al., 2003; Pegna et al., 1997; Peronnet & Farah, 1989; Roberts & Bell, 2002; Wijers et al., 1989; Yoshino et al., 2000), but had not previously been compared directly. It would appear on the basis of the comparison in the present study that viewpoint-dependent object recognition may recruit the same internalised visuospatial transformation mechanism as mental rotation. The following sections attempt to elucidate possible reasons for the observed differences in P400 amplitude direction between the two tasks.

5.5.4.1 Viewpoint-dependent P400 amplitudes may reflect access to stored canonical shape representations

In the present study, it was found that viewpoint-dependent recognition and mental rotation exerted opposing effects on an otherwise similar component: P400 amplitude was enhanced by greater angular disparity in the mental rotation task, but attenuated by increasing stimulus misorientation during viewpoint-dependent recognition. One possible explanation for this difference involves the differing demands of each task. In object recognition, the stimulus percept must be compared against a long-term stored representation, whereas in mental rotation, the first stimulus is maintained in the visual buffer (a component of working memory) until it can be compared against the second stimulus. Viewpoint-dependent recognition may therefore be considered to consist of two component processes: access to stored object representations *and* a visuospatial transformation process.

This difference in reliance – or non-reliance – on a long-term stored representation may underpin the opposing direction of the P400 effects elicited by viewpoint-dependent recognition and mental rotation: 'old' items, when recalled, have been found to evoke more positive ERPs than new ones (Friedman, 1990: cited in Rugg & Coles, 1995). Old/new decisions about novel object stimuli have also been found to affect parietal ERP waveforms in the range 400-800 ms, with familiar stimuli eliciting more positive components than unfamiliar (Curran et al., 2002). Such findings are consistent with the observation in the present chapter that orientation-dependent stimuli presented at familiar (canonical) orientations elicited larger (i.e., more positive) N400 components than unfamiliar (non-canonically oriented) stimuli. By contrast, in the mental rotation task, the prime and target stimuli are both unfamiliar, suggesting that the mental rotation P400 may represent a 'purer' measure of stimulus percept transformation, since the process is not reliant on access to long-term stored representations. Observed directional differences in the P400 between viewpoint-dependent recognition and mental rotation tasks may thus reflect the reliance of the former process on reference to stored stimulus representations during object recognition. Failure to detect an orientation-sensitive P400 during viewpoint-invariant recognition (see section 5.5.5) suggests that, rather than reflecting the overall process of comparison between stimulus percept and stored representation, the P400 evoked by viewpoint-dependent recognition reflects comparison of the stimulus percept against an orientationally-specific (i.e., canonical) stored shape representation.

5.5.4.2 'Orientational unexpectedness' may underpin viewpoint-dependent P400 amplitudes

The viewpoint-dependent P400 component observed in the present study may reflect participant expectancy of canonical stimulus orientation. Although the classic 'N400' component (Kutas & Hillyard, 1980) has been established as a marker of contextual deviancy for unexpected words in a sentence, more recent interpretations of the N400 admit the possibility that it reflects non-lexical incongruity: lack of relatedness between two pictures in a matching task has been shown to elicit an 'N450' (Barrett & Rugg, 1990). Repeated exposure to incongruent stimuli in a sentence-reading context has been found to attenuate the N400 (Besson, Kutas, & Van Peten, 1992), a process which may be analogous to the acquisition of object invariances with repeated stimulus exposure (e.g., Eley, 1982). However, attempts to propose the N400 as a non-modality-specific 'context integrator' have been criticised (e.g. Rugg, 1995). It has also been demonstrated that the N400 is unlikely to reflect a late 'mismatch negativity' (Holcomb & Neville, 1990).

In the present study, P400 amplitude was found to attenuate (become more negative) during viewpoint-dependent recognition of misoriented stimuli – this could be interpreted as a traditional N400 in the sense that non-canonical (unfamiliar) stimulus orientations may have been 'unexpected', relative to canonical presentations. Indirect support for this interpretation comes from the results of the fMRI study reported in Chapter 4, in which viewpoint-dependent recognition was found to correspond to increased BOLD signal in inferior prefrontal region BA47. Recruitment of BA47 has previously been associated with 'active retrieval', a process required when stimulus percepts and stored representations are not readily resolvable due to some ambiguity, such as differing orientation (Petrides, 2002). It is therefore possible that the negative attenuation of the P400 component observed during viewpoint-dependent recognition, and recruitment of a region dedicated to the integration of stored and sensory information as described in the previous chapter, result from initial failure to identify the stimulus object on the basis of orientation-invariant features, leading to active retrieval of the canonical object representation from memory. This explanation would be consistent with the observation in Chapter 4 that BA47 was not recruited during mental rotation, a task in which retrieval of long-term stored information is not required. The N400 has in fact been proposed as an index of retrieval that does not directly encode stimulus familiarity, supported by the observation that patients who have experienced left temporal lobectomy (and who suffer associated memory deficits) do not display N400 components when tested on verbal memory (Smith & Halgren, 1989).

5.5.5 Evidence for visuospatial transformation processes during viewpoint-invariant object recognition

An orientation-sensitive ERP marker of visuospatial transformation, of the sort identified during mental rotation and viewpoint-dependent recognition, was not found during viewpoint-invariant recognition. Behavioural data also indicate that recognition most likely proceeded in a viewpoint-invariant manner. Failure to find evidence of visuospatial transformation processes during viewpoint-invariant recognition supports the existence of (at least) two separate object constancy mechanisms underpinning misoriented object recognition, consistent with the many behavioural studies that have inferred such a distinction (Biederman, 1987; Biederman & Gerhardstein, 1993; Cave & Kosslyn, 1989; Corballis et al., 1978; Tarr & Pinker, 1989, 1990).

5.5.6 Object constancy mechanism selection has occurred by 400 ms

It should be possible to infer from the results discussed above something about the extent to which object constancy mechanisms function in parallel until a decision is reached about an object's identity (e.g., Jolicoeur, 1990). Naturally, the correct mechanism cannot be selected *a priori*, since the stimulus has not yet been identified. The presence or absence of early and late ERP markers of visuospatial transformation-related processes during viewpoint-dependent and viewpoint-invariant object recognition may provide some indication as to the time-course of such putatively competitive processes.

Presence of an N170 component during viewpoint-invariant recognition, and its apparent similarity to the N170 recorded during viewpoint-dependent recognition, indicates that whatever early visual process this represents (the assessment of stimulus orientation or some early aspect of stimulus categorisation being two such candidate processes), the process is common to these two types of misoriented object recognition. It is possible that the N170's presence in both conditions indicates the recruitment of parallel viewpoint-dependent and viewpoint-invariant mechanisms – N170, associated with object recognition expertise, may constitute a marker for viewpoint-invariant processes. However, since the component is rather early in ERP terms, at less than 200 ms following stimulus onset, it seems more likely that at this stage, information about the stimulus is still being processed prior to preferential engagement of one or more object constancy mechanisms.

The P400, our putative marker of visuospatial transformation, was not evident during viewpoint-invariant recognition. This suggests that by around 400 ms following stimulus onset in the viewpoint-invariant condition, the transformational mechanism has been discontinued. It follows that preferential selection of one or other object constancy mechanism – and extinction of the unselected process – is likely to take place at some point between 170-400 ms following stimulus onset. However, without a specific ERP marker of viewpoint-invariant recognition, it remains difficult to prove that the viewpoint-invariant mechanism is similarly extinguished in the equivalent period during viewpoint-dependent recognition.

5.6 Summary

This chapter used electrophysiological measures to establish a marker of visuospatial transformation and assess the extent to which this measure was present during viewpoint-dependent and viewpoint-invariant recognition. A review of the event-related potential (ERP) literature indicated two candidate markers of object constancy processes: an early negative component at around 200 ms, theorised to relate to stimulus orientation judgements, and a later, negative, orientation-dependent component at around 400 ms, thought to indicate the recruitment of a transformational object constancy mechanism. The mental rotation task elicited an early negative 'N170' component that was highly sensitive to relative angular disparity between stimuli. A later, positive, 'P400' component sensitive to angular disparity between mental rotation task stimuli was also recorded. ERP data obtained during viewpoint-dependent and viewpoint-invariant misoriented object recognition was examined for evidence of these two components. Both processes elicited a somewhat orientation-sensitive N170, suggesting that this component did not represent transformational object constancy mechanisms, but may represent attempts to ascertain stimulus orientation. An alternative explanation is that the N170, previously found to reflect expertise in object recognition, may reflect early feature-sensitive viewpoint-invariant processes and have a quite separate aetiology from the mental rotation N170.

A P400 component was identified in the object recognition task – this component was sensitive to changes in orientation during viewpoint-dependent, but not during viewpoint-invariant, recognition, and was therefore inferred to indicate recruitment of a transformational mechanism in the former process only (an inference supported by concurrently-measured response-time data). Differing directional effects of orientation on viewpoint-dependent and mental rotation P400s may reflect the different task demands of these two processes. Increasing negative amplitude of the P400 with greater angular disparity between mental rotation task stimuli is probably a marker of straightforward visuospatial transformation. The more positive P400 components elicited by canonical stimulus presentation during viewpoint-dependent recognition may indicate that canonically-oriented stimuli are judged to be familiar, whereas misoriented shapes, at least initially, are not. Greater P400 negativity was observed in response to orientation-dependent stimuli at unfamiliar orientations, indicating that the P400 may reflect orientational unexpectedness, and/or that greater effort is required to resolve the misoriented stimulus percept with stored representations. Finally, the findings of this chapter suggest that there is no real difference in the object constancy mechanisms recruited at 170 ms following stimulus onset, but that by around 400 ms, preferential selection of a transformational or non-transformational solution appears to have been made.

Chapter Six

6. General Discussion And Conclusions

6.1 Introduction

'Object constancy' is the term used to describe the stable and consistent nature of our internal representation of objects despite potentially confounding factors such as occlusion, and changes in location, orientation and illumination. The process by which the brain achieves object constancy across changes in orientation is not well understood. The aim of this thesis was to identify the areas involved and extrapolate from these the nature of its constituent processes. The following sections summarise the contribution of each chapter in turn. The conclusions that may be drawn from the findings are then presented. The thesis concludes with a final statement on the research.

6.2 Summary

Chapter 1 reviewed the psychometric literature investigating object constancy processes. The existence of viewpoint-dependent and viewpoint-invariant mechanisms for recognising misoriented shape is inferred from response-time studies. It is theorised that viewpoint-dependent recognition proceeds by global transformation of the stimulus percept to match a canonical stored representation, and viewpoint-invariant recognition via the comparison of local feature invariances against an orientation-free object description. Studies of mental rotation, requiring resolution of angularly disparate shapes, demonstrate response-times dependent on the angle between stimuli, from which the recruitment of a visuospatial transformation for global stimulus percept realignment is inferred. Viewpoint-dependent recognition may recruit the same transformational mechanism, whereas it would appear that viewpoint-invariant recognition does not. However, the most apposite recognition strategy cannot be recruited *a priori*, and it therefore seems likely that these two mechanisms operate in parallel until one is deemed to be preferable or a solution is reached. Chapter 1 thus posed questions about the extent to which viewpoint-dependent and viewpoint-invariant recognition mechanisms operate in parallel, the global or local nature of stored object representations, and the extent to which viewpoint-dependent recognition and mental rotation might recruit the same visuospatial transformation mechanism.

Chapter 2 reviewed the cortical correlates of object constancy processes. The brain's dorsal and ventral visual pathways have been proposed as mediating viewpoint-dependent and viewpoint-invariant recognition, respectively. There is functional imaging evidence for involvement of the dorsal stream in viewpoint-dependent recognition, but no studies have conclusively demonstrated whether viewpoint-invariant recognition preferentially recruits the ventral stream, or directly compared these two mechanisms. The dorsal pathway also appears to mediate visuospatial transformation during mental rotation tasks. Functional anatomy thus provides some evidence that visuospatial transformation also underpins viewpoint-dependent recognition, though no studies have directly compared these processes. The network of cortical regions apparently involved in transformational object constancy processes suggests that they may represent a visual analogue of physical object manipulation. Use of familiar objects as stimuli has not permitted previous studies to control for the effects of prior learning on the encoding of specific object views. Chapter 2 posed questions about the cortical correlates of viewpoint-dependent and viewpoint-invariant recognition of novel object recognition, and the extent to which each process overlaps with the cortical correlates of mental rotation. This chapter also discussed the nature of object constancy processes, such as whether they are implemented on the basis of global or local feature information, based on current knowledge of the cortical regions involved.

No previous studies have compared the cortical correlates of viewpoint-dependent and viewpoint-invariant misoriented object recognition. **Chapter 3** identified the cortical correlates of each of these object constancy processes. Viewpoint-dependent and viewpoint-invariant recognition were both found to recruit regions in dorsal and ventral pathways. The regions involved in viewpoint-dependent recognition were consistent with previous studies using familiar objects, and suggest that viewpoint-dependent recognition recruits a network of areas that includes parietal, premotor and dorsolateral prefrontal cortex, and which is specialised for object manipulation. Chapter 3 provides evidence that the manipulation of stimulus percepts may be closely related to the manipulation of actual objects. The additional recruitment of a region associated with retrieval of information from memory indicates that viewpoint-dependent recognition may be more cognitively demanding than viewpoint-invariant recognition, a hypothesis supported by the finding that the former process apparently requires bilateral recruitment of several of the cortical regions implicated in object constancy. No regions of cortex were specifically associated with viewpoint-invariant recognition. Rather, the areas apparently involved in this process represented a subset of those recruited by viewpoint-dependent recognition. The finding that premotor cortex, heavily implicated in viewpoint-dependent recognition, was also recruited, though to a lesser extent, in viewpoint-invariant recognition, was interpreted as support for parallel recruitment of these two object constancy processes, though may also reflect a degree of reliance, in viewpoint-invariant recognition, on reference-frame transformation.

Previous studies have failed to establish the relationship between misoriented object recognition and visuospatial transformation. **Chapter 4** sought to compare directly the cortical correlates of viewpoint-dependent and viewpoint-invariant misoriented object recognition with those recruited during a mental rotation task. This chapter also sought to refine the BOLD fMRI study design from that used in Chapter 3. No preferential recruitment of dorsal or ventral regions was found in any of the three object constancy mechanisms examined. Mental rotation and viewpoint-dependent recognition were found to recruit the same area of superior premotor cortex, and this region was theorised to underpin visuospatial transformation. Stimulus percept maintenance during these transformations seems likely to be mediated either by dorsolateral prefrontal cortex or the pre-supplementary motor area. Viewpoint-dependent recognition was also found to recruit the same anterior prefrontal area identified in Chapter 3, as well as other prefrontal regions indicating that this object constancy process is more cognitively expensive than viewpoint-invariant recognition. A region of ventrolateral prefrontal cortex was found to be preferentially recruited in viewpoint-dependent, relative to viewpoint-invariant recognition, suggesting that the former process may rely on so-called 'active retrieval' when stimulus orientation cannot be ascertained.

Superior premotor cortex was not recruited during viewpoint-invariant recognition, confirming that this object constancy process is not likely to involve the visuospatial mechanism thought to underpin viewpoint-dependent recognition and mental rotation. However, other regions of premotor cortex, a region which is known to be involved in the integration of visuomotor information for object prehension, were identified as being recruited during viewpoint-invariant recognition, suggesting either that this process nonetheless depends on some element of visuomotor integration, or that such recruitment constitutes residual evidence of parallel viewpoint-dependent and viewpoint-invariant processes. Misoriented object recognition was found to correlate with greater recruitment of areas thought to be involved in saccadic eye-movement and the visual updating of reference-frames, suggesting that non-canonically oriented shapes are subject to intense visual search, possibly in an attempt to identify stimulus orientation or orientation-invariant features.

The exact areas underpinning visuospatial transformation were not completely clear from the results obtained in Chapters 3 and 4, and these chapters did not adequately resolve the extent to which viewpoint-dependent and viewpoint-invariant recognition mechanisms operate in parallel. The study presented in **Chapter 5** sought to identify an alternative, electrophysiological, marker of visuospatial transformation, such as those reported in previous studies. Evidence of such a marker, the 'P400', an orientation-sensitive EEG component, was obtained during a mental rotation task. An earlier component, the 'N170', also appeared to be highly sensitive to the relative angular disparity between mental rotation task stimuli, and was hypothesised to reflect reference-frame updating between stimuli. Evidence of both components was sought from EEG data obtained during viewpoint-dependent and viewpoint-invariant recognition. An N170 component of lesser orientation-sensitivity was observed in both, and was theorised to represent feature-sensitive viewpoint-invariant processes. A P400-like component was identified during viewpoint-dependent, but not viewpoint-invariant, recognition, supporting previous indications that the former process is depends on the same visuospatial transformation mechanism as mental rotation. Differences in the direction of the P400 component are hypothesised to reflect the reliance of viewpoint-dependent recognition on stored object representations. Failure to identify a marker of visuospatial transformation during viewpoint-invariant recognition suggests that parallel object constancy mechanisms do not operate beyond about 400 ms following stimulus onset.

6.3 Conclusions

6.3.1 The relationship between viewpoint-dependent recognition and mental rotation

On the basis of the work presented in this thesis, mental rotation and viewpoint-dependent recognition seem to rely on a common mechanism. This visuospatial transformation mechanism is hypothesised to involve global manipulation of the stimulus percept into alignment with either stored representations or another stimulus percept.

Visuospatial transformation appears to be mediated principally by an extended dorsal network involving premotor cortex and superior parietal cortex, areas that are important for object manipulation and prehension. Visuospatial transformation thus appears to be analogous to the physical manipulation of objects, based not just on the areas apparently involved, but also on response-time studies that suggest the time taken to manipulate stimulus percepts is a close analogue of the time taken to right misoriented real objects. The brain may thus achieve global stimulus manipulation in a manner that is largely modality-free, a conclusion supported by studies of blind participants also demonstrate a linear relationship between angle and response time in tactile mental rotation tasks (Carpenter & Eisenberg, 1978; Marmor & Zaback, 1976). Evidence from the mental rotation tasks described in Chapters 4 and 5 suggests that information about absolute and relative stimulus orientation may invoke visuomotor processes in preparation for stimulus prehension. Changes in stimulus orientation may lead to reference-frame updating –adaptation of grasping has been shown to be highly sensitive to sudden changes in environmental orientation (Ghafouri, McIlroy, & Maki, 2004). Studies of clinical neuropsychology indicate a functional dissociation of the ability to perform either viewpoint-dependent recognition or mental rotation (e.g., Farah and Hammond (1988); Turnbull & McCarthy, 1996). Patients in such case studies have generally sustained damage to parietal or occipital cortex. It is possible that specific areas of cortex within those regions are essential to performance of either viewpoint-dependent recognition or mental rotation – but that the process is still mediated principally by premotor cortex, a region generally unaffected in such clinical cases.

6.3.2 Visuospatial transformation is cognitively expensive

Evidence from Chapters 3 and 4 suggests that both viewpoint-dependent recognition and mental rotation require more effort than viewpoint-invariant recognition. This could previously be inferred from the finding that misoriented objects with a well-defined canonical orientation take longer to recognise than their upright counterparts. Transformation of a global stimulus percept is theorised to be a much more resource-intensive method of recognising shape than detection of individual features (Ashbrook, 1996; Thacker et al., 1995). Stimulus maintenance and transformation appears to place high demand on working memory, indicated by recruitment of dorsolateral and ventrolateral prefrontal cortex, though the pre-supplementary motor area and VLPFC are also implicated.

The finding in Chapter 3 that viewpoint-dependent recognition requires bilateral recruitment of premotor, parietal and dorsolateral prefrontal cortex also provides evidence that this process is more resource-hungry than viewpoint-invariant recognition. Additional supporting evidence that viewpoint-dependent recognition is cognitively expensive comes from the preferential recruitment of BA10, BA47 and anterior cingulate cortex during this process, suggesting that it may be harder to retrieve and resolve stored canonical stimulus representations using this mechanism than by viewpoint-invariant means. Orbitofrontal cortex, implicated in viewpoint-dependent recognition, may be the site at which stimulus orientation judgements are mediated; failure to identify an object's identity or orientation based on initial assessment of the available orientation-invariant features (a process which may underpin the N170 component observed during misoriented object recognition in Chapter 5) may then lead to active retrieval of stored object representations and recruitment of a viewpoint-dependent mechanism (underpinned by the P400 component in Chapter 5). An alternative possibility is that initial assessment of orientation-invariant features is sufficient to confirm the object's identity, but that because the stimulus percept is not aligned with the stored canonical orientation, stimulus identity is considered to be ambiguous, and transformation of the stimulus percept must be carried out before a decision is made. This 'double-checking' approach (Corballis, 1988) has been used to account for the non-linearity of response-times to extremely misoriented objects (Jolicoeur, 1990; Lawson & Jolicoeur, 1999).

6.3.3 Viewpoint-invariant recognition

While viewpoint-invariant recognition is undoubtedly dependent on perceptual processes mediated by the ventral pathway (implicated, in Chapter 3, in both viewpoint-dependent and viewpoint-invariant recognition, and by authors such as Logothetis (1995) and James et al. (2002)), no cortical areas were identified that were preferentially recruited during this object constancy process. In fact, this may simply reflect the nature of viewpoint-invariant recognition, which, if it depends on the identification of orientation-invariant object features, will be no more cognitively expensive when an object is misoriented than when it is upright. Viewpoint-dependent recognition of misoriented objects, by contrast, would be expected to be more cognitively expensive than recognition of upright shapes, because it relies on global stimulus transformation, which, as discussed above, is more resource-intensive. Therefore, subtractive comparison between misoriented and upright stimulus presentation will tend to produce a differential BOLD signal for viewpoint-dependent recognition, but is unlikely to do so for viewpoint-invariant recognition.

This thesis indicates that viewpoint-invariant recognition recruits similar cortical regions to those implicated in viewpoint-dependent recognition, suggesting that the dorsal pathway is involved to some extent in mediating both processes. However, the results presented in Chapter 5 suggest that viewpoint-invariant recognition does not involve visuospatial transformation. Involvement of premotor cortex thus suggests that even viewpoint-invariant recognition may rely on the computation of vector transforms for visuomotor integration, possibly in resolving the viewpoint-centred stimulus percept with a stored object-centred representation. As such, this finding may provide evidence for global, object based viewpoint-invariant stored representations (e.g., Humphreys and Riddoch, 1984), rather than a feature-based description (e.g., Marr & Nishihara, 1978). Involvement of anterior cingulate cortex and BA8 in viewpoint-invariant recognition of misoriented, relative to upright, shapes suggests that this process may also depend on the acquisition and integration of information from different visual reference-frames, and that it may require more effort than when shapes are upright (possibly because in such cases, resolution of the global stimulus percept with stored canonical object representations is a relatively straightforward and computationally inexpensive process. Consequently, there is little ambiguity in the results obtained by both object constancy mechanisms). However, the most plausible interpretation of these results may be that they indicate parallel recruitment of object constancy mechanisms (see following section).

6.3.4 Parallel recruitment of viewpoint-dependent and -invariant object constancy mechanisms

The finding that areas associated with transformational object constancy mechanisms were also implicated, albeit to a lesser extent, in viewpoint-invariant recognition may be interpreted as indication of parallel routes to object constancy. It is, of course, impossible to engage a single mechanism preferentially *a priori*, and so the initial recruitment of parallel mechanisms must be assumed. As noted above, parallel object constancy processes with some degree of interdependence have been used to explain the sometimes non-linear relationship between stimulus orientation and response-time. The results from Chapter 5 indicate that, at least in viewpoint-invariant recognition, viewpoint-dependent processes appear to be extinct by around 400 ms following stimulus onset (in the absence of a definitive marker of viewpoint-invariant recognition, it is hard to say definitively whether viewpoint-invariant processes are similarly extinguished by the same point during viewpoint-dependent recognition). This finding, in the context of the other results reported in this thesis, suggests that if recognition can proceed by computationally-inexpensive viewpoint-invariant means, it will – but if viewpoint-invariant recognition is not successful, the more computationally-expensive viewpoint-dependent mechanism is recruited. However, fleeting recruitment of viewpoint-dependent processes that are ultimately terminated in favour of a viewpoint-invariant solution may still account for the BOLD signal observed in premotor and parietal cortex during the latter process.

6.4 Final statement

Our understanding of how we recognise and encode object shape is incomplete – and, until recently, derived mainly from studies of response-times to recognise or compare misoriented objects. This thesis presents the first studies to examine the cortical correlates of viewpoint-dependent and viewpoint-invariant object recognition using novel objects to eliminate the confounding effects of prior experience. It also presents the first studies to compare directly the cortical correlates of mental rotation, viewpoint-dependent and viewpoint-invariant recognition. The thesis further uses electrophysiological markers of visuospatial transformation to clarify the relationship between these object constancy processes. Viewpoint-dependent recognition and mental rotation were shown to recruit a common transformational mechanism for the manipulation of global stimulus percepts. This mechanism is not dissimilar to that involved in physical object manipulation, and its implementation is associated with increases in response-time and greater demand on cognitive resources. It was demonstrated that viewpoint-invariant recognition does not require such a transformational mechanism. Involvement of some of the same cortical areas in viewpoint-invariant as in viewpoint-dependent recognition demonstrates initial parallel recruitment of these two mechanisms. Object recognition using a viewpoint-invariant mechanism, which is computationally inexpensive, is preferable. However, if this process is unsuccessful, or the results are ambiguous, a more computationally expensive viewpoint-dependent mechanism is engaged.

Appendices

Appendix A:

Anatomical locations and Talairach coordinates of peak BOLD signal recorded in Chapter 3.

Table A1 in this section relates to the findings of the fMRI study described in Chapter 3. A legend is provided below for interpretation of the table (which appears on the following two pages).

Table A1. Regions of significant cortical recruitment in each condition for each participant group. Talairach coordinates (*x*, *y*, *z*) and z-scores are shown for the most significantly active voxel in each Brodmann area (BA); the total number of suprathreshold voxels and the cortical features where significant activation was observed in each BA are also shown (where activation in a given BA was observed in more than one feature, these are listed in descending order of z-score). 1 voxel = 49 mm^3. Coordinates are listed in descending order of *y*-coordinate, from anterior to posterior. Negative values for the x-coordinate indicate left-hemispheric regions of significant BOLD signal, positive values right-hemispheric regions.

Cu = cuneus; GAng = angular gyrus; GC = cingulate gyrus; GF = fusiform gyrus; GFd = medial frontal gyrus; GFi = inferior frontal gyrus; GFm = middle frontal gyrus; GFs = superior frontal gyrus GL = lingual gyrus; GOi = inferior occipital gyrus; GOm = middle occipital gyrus; GOs = superior occipital gyrus; GPrC = precentral gyrus; GSM = supramarginal gyrus; GTi = inferior temporal gyrus; GTm = middle temporal gyrus; GTs = superior temporal gyrus; Ins = insula; LPi = inferior parietal lobule; LPs = superior parietal lobule; PreCu = precuneus

Group 1

Condition A (orientation-dependent)					*Condition B (orientation-invariant)*				
x,y,z	*area*	*z*	*Feature(s)*	*voxels*	*x,y,z*	*area*	*z*	*Feature(s)*	*voxels*
Frontal					**Frontal**				
45,50,13	BA10	3.39	GFm	*10*	42,50,26	BA10	3.52	GFs, GFm	*6*
49,40,26	BA46	3.08	GFm	*1*	45,43,25	BA46	3.24	GFm	*2*
49,19,3	BA45	3.80	GFi	*2*	49,19,3	BA45	3.34	GFi	*2*
5,19,46	BA8	3.01	GFd	*1*	-50,12,6	BA44	3.10	GPrC	*1*
-53,8,36	BA9	3.34	GFm, GFi	*4*	49,5,26	BA9	5.62	GFi, GFm, GPrC, GFs	*29*
-53,8,39	BA8	3.07	GFm	*1*	-53,5,33	BA9	3.12	GFi	*5*
49,5,26	BA9	4.23	GFi, GFm, GPrC	*19*	45,1,26	BA6	4.72	GPrC, GFd, GFs, GFm	*15*
45,1,33	BA6	4.01	GFi, GFm, GPrC, GFd, GFs	*30*	-2,1,49	BA6	4.03	GFd, GPrC, GFs, GFm	*14*
-50,-2,39	BA6	4.19	GPrC, GFm, GFd, GFs	*19*					
-46,-13,49	BA4	3.18	GPrC	*1*					
Limbic					**Limbic**				
5,8,46	BA32	3.43	GFd	*1*	5,8,46	BA32	3.03	GFd	*1*
-2,5,46	BA32	3.58	GFd	*2*	5,1,46	BA24	3.23	GC	*2*
-2,1,46	BA24	3.78	GFd	*2*	-2,5,46	BA32	3.12	GFd	*1*
					-2,1,46	BA24	3.74	GC	*2*
Parietal					**Parietal**				
-40,-41,36	BA40	4.81	GSup, LPi	*16*	-40,-44,39	BA40	4.23	LPi, GSM	*16*
42,-48,49	BA40	3.94	LPi	*17*	39,-55,42	BA40	4.90	LPi	*25*
					35,-62,39	BA39	5.47	LPi	*4*
35,-62,42	BA39	4.39	LPi	*3*	-33,-62,36	BA39	4.79	PreCu, LPi, Gang	*5*
-33,-62,36	BA39	4.24	PreCu, LPi	*3*	25,-69,46	BA7	8.31	LPs, PreCu, LPi, Cu	*71*
25,-69,46	BA7	6.31	LPs, PreCu	*47*					
-26,-72,43	BA7	5.13	PreCu,,LPs, Cu, LPi		-23,-72,39	BA7	5.84	PreCu, Cu, LPs	*22*
Temporal					**Temporal**				
-40,-62,-14	BA37	3.93	GF, Gti, GOm	*7*	62,-34,19	BA42	3.57	GTs	*2*
					62,-37,19	BA22	3.89	GTs	*1*
					59,-41,19	BA13	3.74	GTs, Ins	*3*
					52,-62,-7	BA37	5.24	GOm, GF, GTi, GTm	*17*
					-50,-65,-10	BA37	4.89	GOm, GF, GTi	*7*
Occipital					**Occipital**				
-43,-69,-14	BA19	4.93	GF, PreCu, GOm, GOi	*30*	25,-72,19	BA31	4.01	PreCu	*2*
-16,-76,36	BA7	3.87	PreCu, Cu, LPi, LPs	*9*	-43,-72,-4	BA19	6.71	GOi, PreCu, GOm, GF, Cu	*67*
35,-79,-4	BA19	6.66	GOi, GOm, PreCu, GF, Cu	*49*	-19,-76,29	BA31	3.48	PreCu	*5*
22,-79,-10	BA18	6.77	GL, GOi. GOm, Cu, GF	*83*	35,-79,-4	BA19	7.97	Goi, GOm, Cu, PreCu, GOs, GF	*100*
-36,-83,7	BA18	5.84	GOm, GOi, GF, GL	*72*	35,-83,-4	BA18	8.23	GOi, GOm, GL, Cu, GF	*112*
18,-93,3	BA17	5.83	Cu, GL	*19*	-33,-86,3	BA18	6.85	GOm, GOi, GL, Cu, GF	*118*
-19,-93,-10	BA17	4.42	GOi, GL, Cu	*15*	18,-93,3	BA17	6.95	Cu, GL	*19*
					-12,-93,-7	BA17	4.18	GL, Cu, GOi	*24*

Group 2

Condition A (orientation-dependent)

x,y,z	*area*	*z*	*Feature(s)*	*voxels*
Frontal				
42,54,16	BA10	3.08	GFs, GFm	*5*
45,40,19	BA46	3.30	GFm	*1*
56,12,19	BA45	3.16	GFi	*1*
49,5,29	BA9	3.51	GFi, GFm	*10*
-50,5,36	BA9	3.23	GFm	*1*
45,1,29	BA6	3.76	GPrC	*4*
-50,1,36	BA6	3.59	GPrC	*1*
Limbic				
-				
Parietal				
42,-48,46	BA40	4.74	LPi	*14*
-36,-55,46	BA40	4.28	LPi	*19*
35,-62,39	BA39	3.53	LPi	*2*
-2,-76,39	BA7	4.91	PreCu, LPi, LPs	*21*
18,-79,36	BA7	6.41	PreCu, LPs, Cu, LPi	*59*
Temporal				
52,-62,-7	BA37	4.40	GOm, GTi, GTm	*5*
-50,-72,0	BA37	3.96	GTi, GOm, GTm, GF	*10*
Occipital				
25, -72, 19	BA31	3.60	PreCu	*1*
-19,-76, 29	BA31	3.97	PreCu,	*4*
-43,-76, -4	BA19	5.47	GOi, GOm, Cu, GF	*48*
15,-79,36	BA19	6.94	Cu, PreCu, GOi, GOm, GFs, GF	*81*
28,-86,-7	BA18	6.13	GOi, GOm, GL, Cu	*10* *7*
-29,-86,3	BA18	6.23	GOm, GL, Cu, GOi	*77*
18,-93,3	BA17	6.33	Cu, GL, GOi	*31*
-9,-97,0	BA17	5.81	Cu, GL, GOi	*24*

Condition B (orientation-invariant)

x,y,z	*area*	*z*	*Feature(s)*	*voxels*
Frontal				
49,26,19	BA45	3.05	GFi	*1*
39,-2,49	BA6	3.08	GFm	*1*
Limbic				
-				
Parietal				
-40,-44,49	BA40	3.12	LPi	*2*
42,-48,46	BA40	3.21	LPi	*4*
35,-62,42	BA39	3.04	LPi	*1*
-2,-65,46	BA7	3.48	PreCu, LPi	*8*
25,-76,39	BA7	5.17	PreCu, LPs, Cu, LPi	*41*
Temporal				
52,-62,-7	BA37	3.45	GOm, GF	*3*
-46,-62,0	BA37	3.98	GTm, GF, GTi, GOm	*8*
Occipital				
-23,-65,-10	BA19	5.34	GF, GOm, GOi, Cu	*35*
25,-72,19	BA31	3.44	PreCu	*1*
-23,-72,19	BA31	3.64	PreCu	*2*
-19,-72,-10	BA18	5.90	GL, GOm, Cu, GOi	*56*
32,-83,6	BA19	5.95	GOm, Cu, PreCu, GF, GOi, GOs	*93*
28,-86,3	BA18	5.91	GOm, Cu, GOi, GL	*90*
18,-93,0	BA17	6.39	Cu, GL, GOi	*29*
-16,-93,3	BA17	5.92	Cu, GL, GOi	*19*

Appendix B:

Anatomical locations and Talairach coordinates of peak BOLD signal recorded in Chapter 4.

The tables in this section relate to the results of the fMRI experiment described in Chapter 4.

Table B1 lists cortical and sub-cortical peaks in BOLD signal during condition Ar-Ac of the object recognition task.

Table B1. Ar-Ac: Talairach coordinates and associated cortical/sub-cortical regions of significant BOLD signal during misoriented, relative to canonical, presentation of orientation-dependent stimuli. Coordinates are listed in ascending order of z-score (ventral to dorsal axial slices). The number of suprathreshold voxels in each region ($z > 3.70$; 1 voxel = 48mm^3) is also indicated.

AC = anterior cingulate; GC = cingulate gyrus; GFd = medial frontal gyrus; GFm = middle frontal gyrus; GR = rectal gyrus GSC = subcallosal gyrus

Talairach coordinates (*x*, *y*, *z*)	Brodmann area	Anatomical region	Hemisphere	Peak z-score	Number of suprathreshold voxels
8, 19, -23	11	GR	R	3.89	2
-15, 15, -13	47	GSC	L	4.88	13
15, 15, -13	47	GSC	R	5.07	16
5, 4 -13	25	GSC	R	4.71	10
-2, 7, -7	25	AC	L	5.72	18
15, 48, -3	10	GFd	R	4.18	5
21, 60, 3	-	GFs	R	3.80	1
-31, 52, 3	-	GFm	L	3.95	5
-5, 22, 33	-	GC	L	3.83	1
-11, -7, 33	-	GC	L	4.07	5
5, -3, 33	24	GC	R	4.25	8
-28, 22, 46	8	GFm	L	4.35	4
-11, 26, 53	6	GFs	L	3.79	1
-25, 22, 53	6	GFm	L	3.89	3
-28, 4, 53	-	GFm	L	5.10	12
-5, 15, 53	-	GFs	L	5.43	8
-15, 30, 56	-	GFs	L	5.64	6
-18, 11, 56	-	GFs	L	4.74	8
-2, 22, 56	6	GFs	L	4.67	5
-2, 4, 56	-	GFs	L	4.49	3
-2, -7, 56	6	GFd	L	4.39	4
-5, 11, 60	-	GFs	L	6.04	10

Table B2 lists cortical and sub-cortical peaks in BOLD signal during condition Br-Bc of the object recognition task.

Table B2. Br-Bc: Talairach coordinates and associated cortical/sub-cortical regions of significant BOLD signal during misoriented, relative to canonical, presentation of orientation-invariant stimuli. Coordinates are listed in ascending order of z-score (ventral to dorsal axial slices). The number of suprathreshold voxels in each region ($z > 3.70$; 1 voxel = 48mm^3) is also indicated.

AC = anterior cingulate; GC = cingulate gyrus; GFd = medial frontal gyrus; GFm = middle frontal gyrus; GFs = superior frontal gyrus; GPHc = parahippocampal gyrus; GSC = subcallosal gyrus; sub = sub-gyral

Talairach coordinates (*x, y, z*)	Brodmann area	Anatomical region	Hemisphere	Peak z-score	Number of suprathreshold voxels.
5, 7, -17	-	GFd	R	4.48	8
11, 11, -17	-	GFd	R	4.21	13
-15, 19, -13	-	GSC	L	4.56	7
-11, 11, -13	-	GSC	L	4.51	9
5, 4, -13	25	GSC	R	4.56	13
15, 11, -13	-	GSC	R	4.76	14
38, -24, -13	-	GPHc	R	3.72	1
-2, 7, -7	25	AC	L	5.59	15
11, 45, -3	32	AC	R	3.72	2
2, -7, 33	-	GC	R	3.95	2
-25, 26, 46	8	GFm	L	5.38	12
-35, 7, 46	6	GFm	L	4.54	7
-28, 4, 46	6	GFm	L	4.49	4
-5, 15, 53	-	GFs	L	4.22	5

Table B3 lists cortical and sub-cortical peaks in BOLD signal during condition Ar-Br of the object recognition task.

Table B3. Ar-Br: Talairach coordinates and associated cortical/sub-cortical regions found to be preferentially recruited during presentation of misoriented orientation-dependent, relative to misoriented orientation-invariant, stimuli. Coordinates are listed in ascending order of z-score (ventral to dorsal axial slices). The number of suprathreshold voxels in each region ($z > 3.70$; 1 voxel = $48mm^3$) is also indicated.

AC = anterior cingulate; GC = cingulate gyrus; GFd = medial frontal gyrus; GFi = inferior frontal gyrus; GFs = superior frontal gyrus; GPHc = parahippocampal gyrus; GSC = subcallosal gyrus; sub = sub-gyral

Talairach coordinates (*x*, *y*, *z*)	Brodmann area	Anatomical region	Hemisphere	Peak z-score	Number of suprathreshold voxels
-15, 19, -13	-	GSC	L	4.81	13
15, 15, -13	47	GSC	R	5.10	16
2, 4, -13	-	GSC	R	4.62	9
38, -24, -13	-	GPHc	R	3.97	2
-2, 7, -7	25	AC	L	5.30	12
15, 48, -3	10	GFd	R	3.89	3
61, 11, 20	45	GFi	R	3.92	2
-8, -7, 26	-	GC	L	3.71	1
-31, 11, 50	-	GFs	L	3.78	1
-5, 11, 53	-	GFs	L	4.23	4
-5, 11, 60	-	GFs	L	4.38	4

Table B4 lists cortical and sub-cortical peaks in BOLD signal during misoriented stimulus recognition in the mental rotation task.

Table B4. Regions recruited preferentially in the mental rotation task during matching of angularly disparate, relative to aligned, stimuli. Coordinates are listed in ascending order of z-score (ventral to dorsal axial slices). The number of suprathreshold voxels in each region ($z > 3.70$; 1 voxel = 48mm^3) is also indicated.

GFd = medial frontal gyrus; GFi = inferior frontal gyrus; GFm = middle frontal gyrus; GFs = superior frontal gyrus; PreCu = precuneus; sub = sub-gyral

Talairach (*x, y, z*)	Brodmann area	Anatomical region	Hemisphere	Peak z-score	Number of suprathreshold voxels
-31, 30, -3	-	GFi	L	4.32	2
-5, 33, 33	-	GFd	L	4.44	4
-41, 15, 33	9	GFm	L	4.06	5
-5, -65, 43	-	PreCu	L	3.86	2
-5, 22, 46	-	GFd	L	4.11	3
-2, 26, 53	6	GFs	L	4.00	2
-25, 4, 53	6	(sub)	L	4.45	5
-8, 15, 56	-	GFs	L	4.59	3

Appendix C:

Mean ERP waveform amplitudes at electrode sites in the region of interest recorded in Chapter 5.

The tables in this section relate to the ERP study described in Chapter 5.

Table C1 lists mean amplitude data recorded during the N170 epoch (140-240 ms) in the mental rotation task:

Table C1. Mean and grand mean amplitudes measured at each electrode in the centroparietal ROI during the epoch 140-240 ms (N170), for each relative angular disparity between prime and target stimuli (0°, 60°, 120°). All values are given in microvolts (μV).

	Centroparietal electrodes						***Parietal electrodes***						***grand***
	CP3	***CP1***	***CPZ***	***CP2***	***C P4***	*mean*	***P3***	***P1***	***PZ***	***P2***	***P4***	*mean*	***mean***
0	.32	1.10	1.39	1.46	.55	*.96*	.15	.54	.75	.97	.94	*.67*	*.82*
60	.70	1.52	1.76	1.58	.62	*1.24*	-.23	-.15	.13	.09	-.29	*-.13*	*.56*
120	.53	1.48	1.91	1.58	.57	*1.21*	-.80	-.52	.18	-.03	-.23	*-.28*	*.47*
mean	*.52*	*1.36*	*1.69*	*1.54*	*.58*	*1.14*	*-.29*	*-.04*	*.35*	*.29*	*.14*	*.09*	***.61***

Table C2 lists mean amplitude data recorded during the P400 epoch (350-500 ms) in the mental rotation task:

Table C2. Mean and grand mean amplitudes measured at each electrode in the centroparietal ROI during the epoch 350-500 ms (P400), for each relative angular disparity between prime and target stimuli (0°, 60°, 120°). All values are given in microvolts (μV).

	Centroparietal electrodes						***Parietal electrodes***						***grand***
	CP3	***CP1***	***CPZ***	***CP2***	***C P4***	*mean*	***P3***	***P1***	***PZ***	***P2***	***P4***	*mean*	***mean***
0	2.73	3.85	4.54	4.93	4.37	*4.09*	2.66	2.72	2.90	2.77	3.56	*2.92*	*3.50*
60	2.12	3.52	4.51	4.62	4.10	*3.77*	2.10	2.41	3.12	2.96	3.33	*2.78*	*3.28*
120	2.61	4.23	5.38	5.18	4.61	*4.40*	2.31	2.93	4.19	3.78	3.95	*3.43*	*3.92*
mean	*2.49*	*3.87*	*4.81*	*4.91*	*4.36*	*4.09*	*2.36*	*2.68*	*3.40*	*3.17*	*3.61*	*3.05*	***3.57***

Table C3 lists mean amplitude data obtained during the N170 epoch (140-240 ms) in the object recognition task:

Table C3. Mean and grand mean amplitudes measured at each electrode in the centroparietal ROI during the epoch 140-240 ms (N170). OD = orientation-dependent condition; OI = orientation-invariant condition. 1 = block 1; 2 = block 2. All values are given in microvolts (μV).

	Centroparietal electrodes						***Parietal electrodes***						***grand***
OD1	***CP3***	***CP1***	***CPZ***	***CP2***	***C P4***	*mean*	***P3***	***P1***	***PZ***	***P2***	***P4***	*mean*	***mean***
0	0.74	1.86	2.37	1.71	0.09	*1.35*	-0.75	0.42	1.24	0.23	-1.10	*0.08*	*0.68*
60	0.99	2.16	2.80	2.05	0.27	*1.65*	-0.72	0.42	1.37	0.45	-1.03	*0.10*	*0.88*
120	0.87	1.88	2.33	1.77	0.13	*1.39*	-0.59	0.02	0.79	-0.20	-1.29	*-0.23*	*0.58*
mean	*0.87*	*1.97*	*2.50*	*1.84*	*0.16*	*1.47*	*-0.68*	*0.28*	*1.13*	*0.19*	*-1.14*	*-0.04*	*0.71*
OD2													
0	0.66	1.81	2.40	1.85	0.33	*1.40*	-0.89	0.15	0.93	0.04	-1.35	*-0.22*	*0.59*
60	1.12	2.31	3.00	2.20	0.42	*1.79*	-0.48	0.68	1.74	0.71	-1.20	*0.32*	*1.06*
120	0.94	1.99	2.62	1.83	0.05	*1.49*	-0.93	0.17	0.92	-0.20	-1.53	*-0.31*	*0.59*
mean	*0.91*	*2.04*	*2.67*	*1.93*	*0.27*	*1.56*	*-0.77*	*0.33*	*1.20*	*0.18*	*-1.30*	*-0.07*	*0.75*
Mean	*0.89*	*2.01*	*2.59*	*1.89*	*0.22*	*1.52*	*-0.73*	*0.31*	*1.17*	*0.19*	*-1.22*	*-0.06*	*0.73*
OI1													
0	0.91	1.97	2.45	1.93	-0.05	*1.45*	-0.47	0.46	1.24	0.04	-1.46	*-0.03*	*0.71*
60	0.86	2.37	2.90	2.42	0.58	*1.83*	-0.56	0.60	1.49	0.50	-1.09	*0.20*	*1.01*
120	1.17	2.27	2.49	1.87	0.08	*1.56*	-0.45	0.44	0.89	0.09	-1.61	*-0.15*	*0.71*
mean	*0.98*	*2.20*	*2.61*	*2.07*	*0.22*	*1.62*	*-0.49*	*0.50*	*1.21*	*0.15*	*-1.39*	*-0.04*	*0.81*
OI2													
0	1.02	2.02	2.32	1.63	-0.24	*1.35*	-0.25	0.80	1.34	0.25	-1.52	*0.13*	*0.74*
60	1.44	2.65	3.10	2.33	-1.20	*1.94*	-0.20	2.65	3.10	2.33	-1.20	*0.41*	*1.18*
120	1.17	2.22	2.45	1.64	-0.81	*1.46*	-0.59	0.26	0.84	-0.34	-2.14	*-0.39*	*0.53*
mean	*1.21*	*2.29*	*2.62*	*1.87*	*-0.07*	*1.58*	*-0.34*	*0.67*	*1.35*	*0.18*	*-1.62*	*0.05*	*0.82*
mean	*1.10*	*2.25*	*2.62*	*1.97*	*0.07*	*1.60*	*-0.40*	*0.59*	*1.28*	*0.17*	*-1.51*	*0.01*	*0.81*

Table C4 lists mean amplitude data obtained during the P400 epoch (350-500 ms) in the object recognition task:

Table C4. Mean and grand mean amplitudes measured at each electrode in the centroparietal ROI during the epoch 350-500 ms (P400). OD = orientation-dependent condition; OI = orientation-invariant condition. 1 = block 1; 2 = block 2. All values are given in microvolts (μV).

	Centroparietal electrodes						***Parietal electrodes***						***grand***
OD1	***CP3***	***CP1***	***CPZ***	***CP2***	***C P4***	*mean*	***P3***	***P1***	***PZ***	***P2***	***P4***	*mean*	***mean***
0	2.47	4.27	5.63	5.03	3.42	*4.17*	1.65	2.98	4.30	2.84	1.65	*2.69*	*3.43*
60	1.84	3.46	5.02	4.20	2.55	*3.41*	0.86	2.26	3.76	2.34	0.94	*2.03*	*2.72*
120	1.62	3.46	4.83	4.14	2.35	*3.28*	1.09	2.12	3.58	2.17	0.92	*1.97*	*2.63*
mean	*1.98*	*3.73*	*5.16*	*4.45*	*2.78*	*3.62*	*1.20*	*2.45*	*3.88*	*2.45*	*1.17*	*2.23*	*2.93*
OD2													
0	2.61	4.52	6.09	5.37	3.71	*4.46*	1.81	2.92	4.15	3.02	1.73	*2.72*	***3.59***
60	1.75	3.73	5.43	4.66	2.93	*3.71*	1.13	2.60	4.28	2.93	1.32	*2.45*	*3.08*
120	1.98	3.83	5.50	4.56	2.68	*3.69*	1.20	2.70	4.23	2.56	1.23	*2.35*	*3.02*
mean	*2.08*	*4.03*	*5.71*	*4.83*	*3.11*	*3.95*	*1.31*	*2.74*	*4.22*	*2.84*	*1.43*	*2.51*	*3.23*
mean	*2.03*	*3.88*	*5.44*	*4.64*	*2.94*	*3.79*	*1.26*	*2.60*	*4.05*	*2.64*	*1.30*	*2.37*	*3.08*
OI1													
0	2.62	4.34	5.77	5.41	3.56	*4.34*	1.77	2.72	4.06	2.74	1.76	*2.61*	*3.48*
60	1.62	3.57	5.08	4.93	3.34	*3.71*	0.87	2.06	3.66	2.75	1.49	*2.17*	*2.94*
120	1.95	4.10	5.14	4.69	2.91	*3.76*	0.76	2.11	3.46	2.23	0.80	*1.87*	*2.82*
mean	*2.07*	*4.00*	*5.34*	*5.01*	*3.27*	*3.94*	*1.13*	*2.30*	*3.27*	*2.58*	*1.35*	*2.22*	*3.08*
OI2													
0	2.44	4.32	5.63	6.26	3.56	*4.24*	1.74	2.97	4.11	3.12	1.90	*2.77*	*3.50*
60	2.16	4.26	5.66	5.11	3.12	*4.06*	1.17	2.40	3.77	2.62	1.37	*2.27*	*3.16*
120	1.97	4.00	5.26	4.64	2.86	*3.75*	1.00	2.31	3.59	2.22	0.64	*1.95*	*2.85*
mean	*2.19*	*4.19*	*5.52*	*5.01*	*3.17*	*4.02*	*1.30*	*2.56*	*3.82*	*2.66*	*1.30*	*2.33*	*3.17*
mean	*2.13*	*4.10*	*5.43*	*5.01*	*3.22*	*3.98*	*1.22*	*2.43*	*3.78*	*2.62*	*1.33*	*2.27*	*3.12*

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