An ERP investigation of the consequences of motor preparation on visual processing.

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Declaration

I, Luke Mason, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Signed:

Date:

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Abstract

Action and perception have traditionally be studied in isolation, as separate and unitary cognitive processes. More recent evidence has demonstrated a lively interaction between the two. Preparing an action – either a saccade or a manual movement - causes enhanced processing of action-relevant stimuli in the environment, at the expense of the action-irrelevant. The aim of the research reported in this thesis are to provide further detail about this effect.

The experiments are reported in this thesis are concerned with how the spatial, temporal and functional properties of action affect perception. Chapter three reports an experiment in which the spatial properties of a grasped object, which make different demands of accuracy, were manipulated. The experiment in chapter four compared goal and effector locations, and measured visual processing across the time course of motor preparation. Chapter five reports an experiment that measured visual processing not just at goal and effector locations, but also at more distant locations not involved in movement, in order to estimate the spatial profile of the effect.

Results showed clear enhancement of goal and effector locations simultaneously during motor preparation, although the goal location was enhanced over a broader time period than the effector, suggesting the two components of movement are not equivalent in terms of the relative priorities assigned to them during motor preparation. The spatial profile of the effect fell-off with distance from the goal and effector, and is discussed in terms of theories concerning the spatial profile of visual attention.

Taken together, the results of all three experiments suggest that the processes initiated by motor preparation cause shifts in the patterns of perceptual facilitation and inhibition that ultimately achieve selectivity. The inclusion of the effector location in this process suggests that it is not limited to one representation at a time, but operates instead as a flexible and dynamic rebalancing of perception that adapts to any given cognitive task.

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CHAPTER 1: **GENERAL INTRODUCTION**

Overview

Action and perception have traditionally been studied in isolation, under the often implicit assumption that whilst the outputs of perceptual processes are used by the motor system to guide action, action has no reciprocal effect upon perception. More recent work has shown this assumption to be incorrect and demonstrated a lively interaction between motor and perceptual processes. Whilst it is obvious that ‘what you see affects what you do’, it is now clear that the converse is also true: ‘what you *do* affects what you *see’*. In the broadest sense, this relationship is mediated by a top down rebalancing of the priority with which perceptual information is processed, by biasing action-relevant stimuli in the environment at the expense of the action-irrelevant.

A familiar example of top-down adjustment of sensory processing is that of attentional selection. Stimuli that are more relevant to the goal of the current task bias sensory processing in their favour, whether these stimuli are defined by spatial location (e.g. Eriksen & Eriksen, 1974), by low-level visual features (e.g. motion, Chaudhuri, 1990); or even by higher level visual features (e.g. faces and houses, O’Craven, Downing, & Kanwisher, 1999). Irrelevant features suffer processing consequences in the other direction, partially or completely fading into the background of perception.

The subject of this thesis is how the top-down demands of manual movement affect sensory perception, in terms of how processing priorities are balanced between action relevant stimuli and the rest of the immediate physical environment. The precise detail of how this happens are yet to be fully worked out, but, as the rest of this chapter will show, a consensus has formed that enhanced perceptual processing can be observed at the goal location of an action. The simplest explanation for this effect of action is that of an attentional system that selects between action-relevant and irrelevant stimuli. This thesis will argue that this simplest form of selection-for-action is not able to account for the experimental data reported here and elsewhere. Perceptual processing under differing action conditions will instead be framed in terms of dynamic patterns of facilitation and inhibition, and it is this pattern that achieves selection.

The remainder of this chapter will first summarise relevant theoretical models before describing the research that informs the experiments reported in subsequent chapters.

Empirical work will be reviewed in an approximately chronological order, charting the progress of research that first examined the perceptual consequences of eye movements, then simple manual movements, then more demanding manual movements such as reaching out and grasping an object (this last class of action is investigated experimentally in chapter three). Subsequent sections of the review will cover evidence relating to how the effector used to carry out a movement may affect perceptual processing (the background to the investigations reported in chapters four and five), and to the shape of the patterns of inhibition and facilitation that achieve selection during movement planning, including theories relating to the shape of the locus of attention in non-motor tasks (investigated experimentally in chapter five). The specific research questions that are the subject of this thesis are described in more detail at the end of this chapter. Broadly put, together they seek to address the question of how the spatial characteristics of the goal, and of the effector used to move towards the goal, affect the pattern of perceptual processing in time and in space across the visual field. More broadly still, the experiments in this thesis are concerned with the finer detail of how what you do affects what you see.

Theoretical underpinnings: selection-for-perception, selection-for-action

Many of the cognitive processes that give rise to our conscious perception of the world have a limited capacity, and as such are not able to operate on more than a certain number of objects or features at one time (e.g. Rensink, 2000). Overcoming these capacity limitations requires the ability to select only a part of the entire range of incoming perceptual information. Selection via visual attention (selection-for-perception) has been studied extensively, and has been shown to be involved in a wide range of cognitive activities, such as the detection of stimuli (Posner, 1980), visual search for a target amongst distracters (Wolfe, 1994), object recognition (LaBerge & Brown, 1989) and short term memory (Bundesen, 1990), to name but a few.

During the planning stage of action some form of selection may also be occurring (selection-for-action, Allport, 1987; Neumann, 1987). If one is standing in front of an apple tree and wishes to reach out and pluck an apple from a branch, it is necessary to select one ‘target’ apple amongst many ‘distracter’ apples toward which to plan a movement. Selection of one item from an array of many is not, however, solely sufficient to ensure an effective outcome of action. There may be other apples and branches in the way that must be avoided; the location and orientation of these, too, must be considered and a detour planned in order to reach the target apple. A final requirement for selectivity is to prevent cross-talk within processes upon which action planning depends. These processes may not simply require one object of many to be selected as their input, they may fail entirely if interference from irrelevant representations is not suppressed (Mozer & Sitton, 1998).

Integrated competition

Duncan, Humphreys, & Ward's (1997) integrated competition hypothesis (ICH) provides a working model of how, in neural terms, such selectivity may be achieved. Whilst bottom-up physical features, such as brightness and movement, cause activation of their parent object's neural representation (e.g. Jonides & Yantis, 1988), Duncan assumes that top-down processes are the most important in the selectivity that underlies processes such as object recognition and movement planning. The ICH posits that all neural representations compete for processing priority within a limited capacity system. Those representations that receive the most activation win out in this system, and all others are inhibited. The outcome of these twin processes of facilitation and inhibition is selectivity.

Importantly, the ICH does not assume the existence of a dedicated control network responsible for the activation of different representations. According to the model, selectivity is achieved by adjusting the firing rate of the very same neural populations that encode the representation of a particular object, or a particular area of space. This adjustment effectively primes one representation amongst many, causing a "cascading ascendancy" (p. 256) throughout higher levels of processing and ensuring that the primed representation is the eventual winner of any competitive processes. In more familiar cognitive language, attention has shifted to the object represented by the primed neural population.

An additional prediction of the theory is that, once an object has won this competition, the activation that caused the victory will spread to its other 'type-level' features. If, for example, one is to detect red 'X's' amongst an array of green 'O's', type-level representations that correspond to the letter 'X', the colour red, and the location of the red 'X' in space will all become dominant over competitor representations.

The Visual Attention Model (VAM)

If competitive processes allow selectivity to occur (and it is taken as read that selectivity is a necessary part of action planning), *and* if the outcome of victory within such competitive processes is a spreading of activation required to bind disparate features of an object, does this tell us anything about the coupling of action and perception? If by 'features' we mean only visual characteristics such as colour or shape, then perhaps not. If, however, we include in the category of ‘features’ such characteristics as location and orientation in space, then perhaps it does.

Visual processing within the cerebral cortex of primates is to some extent divided into two processing streams, comprising of a dorsal stream reaching posterior parietal cortex (PPC) and a ventral stream reaching inferotemporal cortex (IT) (Mishkin & Ungerleider, 1982; Mishkin, Ungerleider, & Macko, 1983). Goodale & Milner (1992) suggest that the dorsal stream transforms and computes spatial information used for action, such as an object’s location and orientation, whilst the ventral stream computes information necessary for perceptual tasks such as object recognition. This approach to visual processing is assumed, at least in part, to be an evolved strategy to achieve view invariance in object recognition.

The Visual Attention Model (Schneider, 1995) attempts to integrate selection-for-perception and selection-for-action in a unified theory of visual attention that is biologically relevant to what is known about these two processing streams. It assumes that:

1) Selection-for-perception occurs in the ventral stream, amongst somewhat high-level cognitive representations of objects. The consequences of selection within this stream are to enhance perceptual processing (detection, discrimination, etc.) in the ventral stream, and to prime simple, retinotopic, stimulus features (such as local line contrasts) belonging to separate objects in earlier visual areas.
2) Selection-for-action occurs within the dorsal stream. The consequence of this selection is the production of a motor programme, the execution of which may or may not be executed. The particular motor programme may refer to saccading, grasping, reaching, pointing etc.
3) A common attention mechanism exists that gives processing priority to representations belonging to selected objects at V1[1]. Once established, this priority cascades through both processing streams (cf integrated competition, Duncan, 1997),

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[1] VAM suggests that the ‘anatomical origin’ of selection is V1. At the time of writing, it has not been established whether or not visual attention affects activity as early in the processing chain as V1. ERP studies, with superior temporal resolution, have tended not to find effects at the range in time of V1 processing, and fMRI studies that have directly observed activation there may reflect the results of feedback processes from later visual areas *to* V1 (e.g. Martinez et al., 1999). Recent ERP research, involving an unusually large number of trials and participants, have reported modulation of the C1 component (Proverbio et al., 2010), suggesting attentional effects in V1, at least for some classes of stimuli. VAM clearly proposes that V1 is the anatomical origin of the attentional cascade through visual areas, but note that in chronological terms activation begins in higher visual areas and feeds *back* to V1.

causing enhanced perceptual processing in ventral areas, and setting up motor programmes - using the selected object as the movement goal - in dorsal areas.

VAM thus integrates the two visual processing streams with selectivity as the mediator. It follows that:

1) Shifting perceptual focus to an object will enhance action-related processing to it. In this direction, the coupling between action and perception achieves motor priming. Simply looking at an object, for example a door handle, will cause a motor programme to be set up towards it, even in the absence of an explicit intention to act upon it (e.g. Tucker & Ellis, 1998).
2) Intending to perform an action upon an object will enhance perceptual processing of the object. The intention to reach out and grasp the door handle will cause enhanced perception at the location of the handle, even in the absence of an explicit intention to ‘study’, or ‘pay attention to’ it.

The Premotor Theory of Attention

Another explanative framework for understanding the link between action and perception is the Premotor Theory of Attention (Rizzolatti, Riggio, & Sheliga, 1994; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). The theory makes two assumptions, firstly that the same brain structures that code representations of space are responsible for motor planning, and secondly that shifts of attention occur as a weaker activation of the same circuits that code for motor programmes. In this view a shift of visual attention is an eye movement, the execution of which has been inhibited.

According to the Premotor Theory, a relevant issue for understanding action is how the brain represents space. An intuitively appealing account is one in which space is represented somewhat akin to how retinotopically organised areas of the visual cortex represent the two dimensional surface of the retina. In this view, space is represented as a three dimensional box, with us in the centre and the rest of the environment spread out in Euclidean space around. This is how we consciously experience space, and so it is logical that the brain must code space on a neural level in much the same way. A common conclusion to this line of reasoning is that a single brain structure is responsible for representing space in this way.

The evidence, from human and animal studies, does not favour this view (see Rizzolatti et al., 1994, for a review). Instead it is more accurate to say that dedicated dorsal brain structures within the inferior parietal lobule compute *action* (cf. Goodale & Milner, 1992), and a representation of space is produced as a consequence of this computation. Further to this, different areas compute action for different effectors, such that reaching areas compute action in terms of peripersonal space, and occulomotor areas compute space in retinotopic coordinates. Rizzolatti et al refer to these circuits as "pragmatic spatial maps" (p. 232). Our conscious, unified experience of space as a large three dimensional box is, according to this view, the result of computation and transformation of information rather than selective activation of a brain structure able to intrinsically represent space in this way. In other words, our perception of space is derived from software, not from hardware.

The 'spotlight' metaphor of attention, in which attention is focused on an area of space like the beam of a torch, loses some of its intuitive simplicity when representations of space are produced online from multiple, anatomically separate, pragmatic representations of space. The metaphor may help in understanding how the focus of attention moves around the visual field, but it is less useful as a means of understanding what is going on within the brain when attention has been deployed. The Premotor Theory postulates that:

1) Spatial attention originates within the pragmatic maps that represent space as a by-product of computing action. There is no such thing as a selective attention circuit in the brain outside of these maps.
2) The intention to perform a goal directed action, which requires spatial coordinates to be computed, causes facilitation of premotor neurons within these spatial maps.
3) Neurons within different spatial maps will become active depending upon the effector to be used. Due to the development of foveal vision in primates, saccades play a central role in visual attention in the human brain[2]. A shift of visual attention in this view is an eye movement that has not been executed.

The Premotor Theory and the VAM share many similarities. Both predict a strict and obligatory[3] coupling of perception and action, specifically by visual attention, and both make reference to dorsal and ventral processing. However, some differences exist between them:

1) VAM is more specific about precisely *what* the level of selection is during motor planning and spatial attention. The Premotor Theory refers to neural populations

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[2] A fact that becomes clear when saccade and manual movement locations are forced to compete for perceptual resources, in which case the eye movements appear to dominate (Song & Mcpeek, 2011)

[3] See later section for a discussion on whether this coupling actually is always obligatory.

within spatial maps, without mentioning object-based selection. VAM explicitly predicts that selection will be object-based, since neural activation originates in ‘object-tokens’ used to bind together low-level visual features belonging to the same object.

2) As hinted at above, the two theories differ in terms of where the flow of activation that underlies selection begins. VAM states that attention originates in areas that represent either stimulus driven or task dependent attributes, then activates early retinotopic neurons in V1, from which activation spreads to higher level areas and affects motor planning and visual perception. Simply put, visual attention leads to motor planning.

   The Premotor Theory reverses this flow of activation, stating that motor programming, regardless of effector, is the origin of visual attention. Whilst Rizzolatti et al do not explicitly describe how activation spreads to V1 and to the ventral stream, it is assumed that this occurs. In summary, motor programming leads to visual attention.

Motor planning and motor plans

Whilst the experiments in this thesis concentrate exclusively on the effects of motor preparation on visual perception, and the phase after execution is not investigated, “motor preparation” and “motor planning” are referred to throughout in a general sense.

Motor preparation begins with an internal cognitive representation of the required behaviour, as well as the goal of the action itself (note that it is upon this representation that this thesis concentrates). A motor plan is then written according to the effector that is to be used, the distance that the action covers in space, and the velocity and trajectory of the desired movement, and involves a close coordination of the neuromuscular systems that govern control of movement. At this point the stage of execution of the movement is reached, after which online updates are made according to visual, tactile and proprioceptive feedback (Jeannerod, 2006).

Neural activity underlying spatial attention

Sensory gain control as a mechanism of attention

Both the Premotor Theory of Attention and the Visual Attention Model postulate close links between action and perception, in the form of enhanced processing of action-relevant stimuli. This enhanced processing is often interpreted as a shift of visual attention, and much of the evidence for links between action and perception revolves around the demonstration of striking similarities in terms of behavioural and neural responses during tasks that manipulate action states, or states of spatial attention. In order to justify the logic behind the methods and experiments described throughout this thesis, it is helpful to consider the neural basis of perceptual processing, and how spatial attention alters it.

There is much behavioural evidence showing that attending to a stimulus enhances responses to it (e.g. Posner, 1980), an effect that can be explained by more than one theory of underlying neural activity. Much effort was concentrated on the debate between early selection, in which perceptual information is enhanced by attention at some of the first stages of processing, and in which unattended stimuli are simply not available for higher stages of cognition (e.g. Hawkins et al., 1990), and late selection, in which perceptual information is processed up to a point, and response selection is enhanced or suppressed by attention (e.g. Shiu & Pashler, 1995; Sperling & Dosher, 1986).

The methods of cognitive neuroscience allow a finer-grained investigation of how attention operates at the neural level, and lend weight to accounts that emphasise relatively ‘early’ selection of incoming perceptual information. These accounts describe attention as arising from an amplification, or gain increase, of the neural populations that code for an attended stimulus.

Findings such as that attending to a particular stimulus feature, for example colour or motion, causes increased cortical blow in regions specialised for processing that particular attribute (Corbetta, Miezin, Dobmeyer, & Shulman, 1990) suggest that attention operates within the same regions as perception itself, rather than being supported by distinct brain areas. Furthermore, the amplitude of event related potentials (ERPs, averaged brain responses to particular cognitive events, such as the onset of visual stimuli) is modulated in a very similar way either by increasing the luminance of the evoking stimulus, or by directing attention to that stimulus (Wijers, Lange, & Mulder, 1997). This is strong evidence that attention can be accounted for by a modulation to existing processing, without the need to posit any further mechanisms.

The gain control account can explain attention to a variety of different features across sensory modalities. If auditory stimuli are attended, and visual stimuli unattended, then the gain of neural populations in the auditory cortex is increased at the expense of those populations in visual cortex. Likewise, if stimuli at a particular location in the visual field are attended, then the retinotopic neurons in early visual cortex that code for that part of the field have their gain increased[4]. A very wide variety of evidence now supports this account (see Hillyard, Vogel, & Luck, 1998, for a detailed review), which underlies the logic of the 'probe evoked potential' technique used in many of the experiments reviewed below, in the experimental chapters reported in this thesis, and described in detail in the experimental methods chapter. The effects measured by this technique occur at early, but not the very earliest, stages of visual processing. ERP components that reflect activity in V1 are generally not modulated by attention, whereas those in early retinotopic and later non-retinotopic regions of V2 do show modulation(Hillyard & Anllo-Vento, 1998).

A fronto-parietal control network for attention

ERP methods have been central in accounting for spatial attention in terms of sensory gain control, and as is described below, cued movement tasks show strikingly similar effects on perception as do cued attention tasks. Additionally, they have provided evidence for a putative fronto-parietal attentional control network (Corbetta & Shulman, 2002; Corbetta et al., 1998; Gitelman et al., 1999) that is thought to be responsible for the preparation of goal directed attentional shifts[5]. When participants' EEG is recorded following a cue that directs attention to a particular location in space, two components are elicited, the Anterior Directing Attention Negativity (ADAN) and the Late Directing Attention Positivity (LDAP), both reflecting a relative voltage difference between the hemisphere contralateral and ipsilateral to the attended hemifield (Eimer & Van Velzen, 2002; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000). These signals are thought to represent the neural control signal that directs attention in the first place, and they have been shown to be supramodal, both in terms of operating across sensory modalities, but also across both cued attention *and* cued motor tasks (e.g. Praamstra, Boutsen, & Humphreys, 2005)

Experimental evidence for a coupling between action and perception

Early investigations into the coupling of action and perception concentrated on saccades. The methods established in these studies were quickly adapted to goal directed manual movements, and very similar patterns of results were recorded across both classes of action.

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[4] Note that this early gain control is entirely compatible with the Integrated Competition Hypothesis (Duncan et al., 1997) described above, in which early biasing of the neural activity representing a particular object "cascades" through higher levels of cognitive processing, ensuring that an early attentional effect is still active at much later processes, including even response selection and execution.

[5] Note the similarities between this account of how attention is deployed, and the central tenets of the Premotor Theory, that spatial maps are responsible for the planning of goal direction actions.

Saccades

One of the earliest hints that the programming of eye movements was linked to attention was provided by Crovitz & Daves (1962), who presented discrimination targets for 100ms (less time than is required to make a saccade) at varying distances from fixation, and found that performance was correlated with the direction of the first saccade made *after* participants responded, suggesting that some aspect of the preparation of saccades enhanced perceptual processing on a spatially selective basis.

Similar effects are observed in cued covert spatial attention tasks, where participants are instructed in advance to attend to a particular location in space *without* moving their eyes (e.g. Posner, Snyder & Davidson, 1980). Participants then perform a detection or discrimination task on visual targets that are sometimes presented at the locations that attention was previously directed to, and sometimes at locations where it was not. Despite the target stimuli being physically identical, performance is better when they appear at attended as opposed to unattended locations.

The Premotor Theory arose out of an attempt to account for these kind of effects in studies of spatial attention. Various explanations existed to explain such phenomena, such as selectivity at the level of the visual hemifield, or of a moving ‘spotlight’ or attention, but these were not compatible with the finding that, whilst attentional ‘costs’ increased when the target fell at an unattended *location,* these costs increased further when the target fell in the opposite and unattended *hemifield* (the ‘meridian effect’, Rizzolatti et al., 1987).

Rizzolatti et al explained these effects in terms of saccades. The meridian effect can be understood if eye movements and shifts of visual attention share common brain mechanisms; in this case a shift of attention becomes an eye movement which has not been executed. The meridian effect arises from the fact that saccade programming is assumed to involve two input parameters, distance and direction. Reprogramming only for distance (e.g. to an unattended but *same*-hemifield location) requires only an adjustment of an existing plan, whilst reprogramming for direction (e.g. to an unattended location in the *opposite* hemifield) requires a more extensive rewriting of the programme, now in terms of both distance and direction, with greater associated attentional costs.

Later experiments adapted these spatial attention tasks to action, now cueing participants in advance to make a saccade to a particular location, and then presenting behavioural targets at either cued or un-cued locations *before* saccade onset. Enhanced processing at the location of the planned saccade was recorded both in terms of reaction times (Posner, 1980; Shepherd, Findlay, & Hockey, 1986) and in terms of target discrimination accuracy (e.g. Hoffman & Subramaniam, 1995), suggesting that the intention to make a saccade was associated with enhanced processing at the goal location, much the same as in the case of shifts of covert attention.

Results from electrophysiological studies are in agreement with those from behavioural investigations. Using a similar paradigm to that described above, Eimer, Van Velzen, Gherri, & Press (2006) showed that ERPs elicited by task-irrelevant visual probe stimuli presented at the location of cued saccades were larger than for those probes presented elsewhere. Such modulation of visual ERPs is evidence of top-down influence on relatively early (V2) stages of processing, and is highly reminiscent of the electrophysiological effects of shifting covert spatial attention around the visual field (e.g. Mangun & Buck, 1998).

Other measures concentrate on preparatory processes elicited by the symbolic cues used in studies that direct action or attention in space. Lateralised ERPs present in attentional tasks and thought to represent the activity of a putative attentional control network (ADAN and LDAP, Van Velzen, Forster, & Eimer, 2002) were also present when participants planned saccades (Eimer, Van Velzen, Gherri, & Press, 2007), suggesting similar preparatory processes, perhaps based upon shared brain regions, in both covert and overt shifts of attention.

Neuroimaging studies have reinforced this interpretation by demonstrating a large overlap in brain activation during saccade planning and shifts of visual attention, both in healthy individuals (Corbetta et al., 1998) and in patients with hemispatial neglect (Perry & Zeki, 2000). Neuropsychological evidence showing that patients with damage to occulomotor brain regions (Craighero, Carta, & Fadiga, 2001), and even to eye muscles (Smith, Rorden, & Jackson, 2004) exhibit deficits in covert shifts of attention provide further evidence for shared brain mechanisms.

The primate frontal eye fields (FEF) are organised according to saccadic coordinates, and are an example of the kind of ‘pragmatic spatial map’ in which the Premotor Theory predicts that action planning and spatial attention originate. Stimulation of the FEF in monkeys causes saccades to the location in the visual field that is represented by the stimulated neurons (Schiller & Tehovnik, 2001). Applying sub-threshold stimulation to the same areas does not elicit a saccade, but enhances target discrimination at the location in the visual field that, if stimulated with a stronger current, would be the goal location of an eye movement (Moore & Fallah, 2004), a piece of evidence that validates the Premotor Theory's assertion that shifts of attention are simply a weaker activation of the same circuits used to make saccades.

A similar role for the putative human homologue of the frontal eye fields has been suggested. Direct stimulation of the brain in humans is of course difficult, but trans-cranial magnetic stimulation (TMS) applied to the frontal eye fields of humans can selectively impair (Neggers et al., 2007) and enhance (Van Ettinger-Veenstra et al., 2009) target detection at saccade targets, and when combined with fMRI imaging, possible feedback projections from these areas to the visual cortex have been observed. This observation was strengthened by taking advantage of the high temporal resolution of EEG during a replication of Deubel & Schneider (1996), where frontal activity was observed and localised to the FEF during the interval between the cue and the execution of a saccade (Gutteling, Van Ettinger-Veenstra, Kenemans, & Neggers, 2010). This frontal activity preceded, and was correlated with, activity in the parietal areas, suggesting that the coupling between covert and overt attention originates in the FEF and projects to the visual cortex where its effects on perception occur.

Goal directed manual movements

It is, perhaps, not surprising to observe a close link between eye movements and shifts of visual attention, since in the real world the two almost always occur in unison. A much more radical prediction of both the Premotor Theory and VAM is that the same principles apply to all goal direction manual movements, such as reaching and grasping (Rizzolatti et al., 1994). The experimental evidence for this assertion, though, is strong:

Deubel, Schneider, & Paprotta (1998) adapted their cued saccade paradigm (cf. Schneider & Deubel, 1995) to pointing movements. Instead of saccading to pre-cued elements of an array in order carry out a discrimination task, participants pointed at each element; target stimuli were unmasked in the interval between cue and the execution of the movement. Discrimination performance was significantly better when the target appeared at the location to which a pointing movement had been planned, a pattern of results similar, if not identical, to that observed in both overt shifts of attention involving eye movements but also during covert shifts of attention made in their absence. Similar evidence is provided by ERP studies in which participants were cued to lift a finger on either their left or right hand. ERPs elicited by task-irrelevant visual probes (Eimer & Van Velzen, 2006) at each hand were larger at the cued versus the un-cued hand.

All of the experimental evidence summarised so far has involved a single action goal, either the end point of a saccade or of a manual movement. Baldauf, Wolf, & Deubel (2006) cued participants to perform a sequence of multiple manual movements and used behavioural and ERP (Baldauf & Deubel, 2008a) methods to show enhanced processing at *each* of the movement targets in parallel before the first movement had been executed. Across multiple movements, it seems, goals can be processed together.

During a grasping movement, however, it can be said that two goals present themselves, since two digits – the index finger and thumb – each make contact with two separate parts of the object. Schiegg, Deubel, & Schneider (2003) addressed this issue by presenting visual discrimination targets at two ends of a graspable object, observing improved performance to-be-grasped contact points but not elsewhere. In this case, multiple goals are processed within one single movement.

The experiment reported in chapter three extended this paradigm to investigate how the shape of these multiple goal locations may bias the degree of processing that each receives. By altering the two graspable points of an object so that one requires more accuracy to make contact with than the other, the effect of the spatial properties of the goal was investigated.

An obligatory coupling?

A question regarding these effects is whether the observed coupling between action and perception is obligatory. Just because attention shifts to the goal does not mean that it must do so in order to plan a movement, or that removing attention from that location would hinder action. Beyond such obvious concerns to do with causation, the functional architecture assumed by VAM suggests that no more than one object can be selected at a time, regardless of whether this selection stems from voluntary orienting of covert attention or as a consequence of motor planning (Schneider, 1995). Studies addressing this question informed participants of the location of the target stimulus in advance, and varied whether the cued saccade location was the same or different, using both peripheral (Schneider & Deubel, 1995) and central cues (Deubel & Schneider, 1996). Results showed that even when participants' best strategy for success at the experimental discrimination task was to shift their attention to the known target location, the very act of planning a movement to another location prevented them from doing so: the allocation of perceptual resources appears to prioritise movement above other top-down considerations.

Whilst this is strong evidence for an obligatory coupling between perception and action, contradictory evidence exists in the form of a modification of Deubel et al's paradigm that was used with a patient (CF) suffering from left visual field optic ataxia following stroke (Khan et al., 2009). He was able to make saccades to the contra-lesional visual field that were indistinguishable from both his own ipsi-lesional saccades and those of intact controls, but target performance at the saccade target was impaired in the contra- as compared with the ipsi-lesional visual field.

Hunt & Kingstone (2003) cued participants to perform either a saccade or a covert shift of attention most of the time in each block, but on a low proportion of trials the opposite task was invoked. When the effect of these occasional task reversals on the primary task of either performing a saccade or detecting a target was measured, a disassociation between visual attention and eye movements was observed (although there is some question as to whether the timing of the experiment invalidated these results, see Deubel, 2008).

Belopolsky & Theeuwes (2009) attempted to clarify this disagreement between experimental results by using a paradigm that was able to separate covert shifts of attention from the planning of eye movements. Participants were cued to make a shift of attention, the target of which then cued them to make a saccade. Whilst shifting attention to a new location was always associated with planning a saccade, *maintaining* attention at a location either enhanced or suppressed saccadic reaction times depending upon the probability of making a saccade to that location on the previous trial. In interpreting this complicated pattern of results, the authors concluded that whilst occulomotor programs are responsible for shifting covert attention, they are not involved in the maintenance of attention.

Whilst this evidence is a problem for the strongest interpretations of the Premotor Theory and VAM - that action and perception are obligatorily coupled under any and all situations - the findings summarised above require only a minor adjustment to both theories and are not in conflict with the evidence that supports their main contentions. In conclusion, whilst certain situations and brain injuries can elicit a disassociation between overt and covert attention, in the vast majority of cases the two are functionally coupled. The details of how accurate the Premotor Theory's prediction that shifts of attention always occur in precisely the same circuits that plan action are yet to be worked out, but the consensus is clear: in most cases, healthy human brains will couple perception and action almost all of the time. The existence of the exceptions serve to emphasise the existence of the rule.

Allocation of attention to the effector

During the planning stage of eye movements the goal location must be selected. In manual movements, such as reaching and grasping, however, another component of movement is involved beyond the goal: the effector that will be used to execute the movement.

The Premotor Theory of Attention is often interpreted as predicting that attention, in the form of enhanced perceptual processing, will shift to the goal location of the movement as a consequence of neural priming in the spatial maps that represent that location within the brain. It can be argued, however, that the goal is not special, but that it is simply one action-relevant location. As described above, empirical investigations that have looked for enhanced processing at the goal have found it, but these have largely neglected to examine the effector location. In fact when multiple goal locations are relevant to a movement they each receive enhanced processing in parallel (Baldauf & Deubel, 2008a, 2008b; Baldauf et al., 2006), suggesting that the effect of action on perception is not limited to one *goal* location at a time. A central question addressed by the experiments reported in this thesis is whether the effector also counts as an action-relevant location, worthy of the allocation of enhanced processing during the planning stage of movement? If so, is there a functional equality in terms of how the brain processes the components of movement, or do goal locations still occupy a privileged position in relation to effector locations? This question has not been addressed directly, but some studies have investigated the role of the effector during motor preparation, albeit without this particular question in mind. These are summarised below:

Early evidence for an effect of movement preparation at an effector is provided by Eimer et al. (2005), who cued participants to lift the index finger of either their left or right hand. Task irrelevant tactile probe stimuli were delivered to either the cued or the un-cued hand in the interval between the cue and the execution of movement. Results showed enhanced tactile processing at the cued as compared to the uncued hand, in the form of larger P90 and N140 somatosensory ERPs. This paradigm is in some ways the manual analogue of cued saccade tasks, in that the effector and the goal are one and the same (in fact both tasks – saccades and finger lifts - have been compared and highly similar brain responses observed in each, Eimer et al., 2006).

Forster & Eimer (2007) took the next logical step by disassociating the goal and the effector. Here, participants were cued to touch the tip of the index finger of one hand with the tip of the index finger of the other hand. Tactile probes were delivered either to the hand that was moving (the effector), or to the hand that was stationary (the goal), in the cue-execution interval. The somatosensory N140 component was larger for probes delivered to the effector than to the goal. The earlier somatosensory P90 told a slightly more complicated story, in that it was influenced by task instructions. Half of the participants were cued in terms of which hand was to be moved (effector cue), and the other half in terms of the hand that was to be touched (goal cue). The P90 was larger for probes delivered to the effector only when effector cueing was used, no difference was observed between conditions when goal cueing was used.

Similar results have been reported using visual, as opposed to tactile, probes (Van Velzen, Gherri, & Eimer, 2006). Cues provided information relating either to the direction that the movement would involve, to the effector that was to be used to carry out the movement (left or right hand), or to both. Providing partial information elicited enhanced processing at the effector locations but not the goal, full information elicited enhanced processing at the goal only when it fell in the same hemifield as the effector.

Gherri, Van Velzen, & Eimer (2009) systematically altered the task instructions, biasing them toward the effector or the goal. Cues instructed participants to make a manual movement in either an inward or outward direction, and visual probes measured processing at either the effector or the goal before movement began. Participants were instructed either to move in a particular *direction* (e.g. “move to the left”, direction cueing), or to move a particular *effector* (e.g. “move your left hand”, effector cueing). The movements themselves were identical across the two conditions. Analysis of the visual ERPs elicited by the probe stimuli showed that cueing the effector caused enhanced processing at effector locations, whereas cueing direction caused enhanced processing at the goal.

With regard to what exactly is selected by the brain during action planning, these studies provide a slightly confusing picture. Certain themes emerge:

1) Attention does not *have* to shift to the goal location; clear evidence has been found for enhanced processing at the effector, at least under certain conditions.
2) The general pattern of results is such that attention appears to shift to either the effector or to the goal, but is not evident at both. This is perhaps surprising, given that studies using multiple goal locations have shown that multiple locations receive enhanced processing in parallel (e.g. Baldauf & Deubel, 2008a).

3) Task instructions have a large top down effect on the balance of processing between effector and goal. This is also surprising, particularly if the coupling between perception and action is presumed to occur to enhance movement planning (or even to make it possible in the first place), in which case enhanced processing should be directed according to the movement itself, regardless of how the characteristics of this movement are framed to the participant.

However, in terms of answering the question at hand, namely how processing is balanced between effector and goal, these studies have various methodological or conceptual issues that prevent a clear answer from emerging:

1) When participants were cued to touch one index finger with the other (Forster & Eimer, 2007), the effector finger would ultimately end up at the location of the goal finger by the end of the movement. In other words, if somatotopic representations of space are translated to spatiotopic or retinotopic coordinates as a part of action planning, then the effector and goal locations will converge - they will only remain separate within somatotopic coordinates. It is uncertain whether, and if so how and when, such translations occur during the interval between a cue and a "go" stimulus; this uncertainty makes interpreting these findings, in terms of the question at hand, problematic.
2) The delayed response (S1/S2 or 'go/no-go') paradigm used in these studies, in which participants experience a delay between preparing a movement and executing it, is rather unnatural and may not represent how motor preparation occurs in a more ecologically valid setting. Particularly difficult to know is the time course of shifts of processing priority between locations. If both goal and effector are processed in series, in a manner akin to serial visual search, then it is possible that these paradigms only probe one of the two locations at the right time point to see evidence of enhanced processing, missing it at the other location.
3) This is particularly worrisome when task instructions are taken into account, since different instructions may only serve to bias the order or the timing at which such processes take place; again the probe may be measuring an unrepresentative snapshot of the state of perceptual processing. It is difficult to accept that the degree of specificity with which perception is coupled to action is the result of anything other than the result of evolutionary processes that selected the strategy that allowed for the quickest and most efficient actions. That such subtle nuances in task instructions

> really can turn these effects on their head seems improbable. What is more likely than *either* the goal *or* the effector being selected is that both are relevant to the movement, both are taken into account during action planning, and that task instructions are able to some extent to bias the balance between the two.

The experiments reported in chapters four and five aim to investigate the role of the effector without the problems listed above. The experiment reported in chapter four does not use an S1/S2 paradigm, instead participants treated the cue that informed them *where* to move as the go signal also. This allowed perception to be probed at differing time points in the chain of processing that occurs as a movement is being set up, sometimes probing at the effector and sometimes at the goal. Chapter five returned to the S1/S2 paradigm to investigate whether the effector is treated as just another movement-relevant location identical to the goal, or whether the activation it receives biases perception differently.

The spatial profile of action-induced perceptual processing

Behavioural and electrophysiological evidence agrees that changes to perceptual processing - be they as a consequence of cued spatial attention (e.g. Mangun & Buck, 1998; Posner, Snyder, & Davidson, 1980) or motor preparation (Eimer et al., 2005; Rizzolatti et al., 1987) - are spatially selective. Stimuli at relevant locations, however relevance is defined, are processed differently to stimuli at neutral or irrelevant locations. The spatially selective nature of these effects begs the question: what is the shape, or spatial profile, of the field of enhanced processing?

Very little evidence from the motor-perceptual literature speaks to this issue. Given the concordance between findings in motor paradigms and the spatial attention paradigms upon which they were based, *and* given the large extent of overlap in activated brain areas between the two paradigms (e.g. Craighero, Carta, & Fadiga, 2001), it is reasonable to take evidence relating to the shape of the focus of spatial attention as a starting point for an investigation into the shape of action-induced perceptual processing.

The earliest models of attention employed perhaps the most intuitively appealing description of its shape by using a ‘spotlight’ metaphor (Posner, 1980; Posner et al., 1980), in which attention is characterised as being like a beam of light from a torch which can be shone on an area of interest. The spotlight model has been adapted to a ‘zoom lense’ account (Eriksen & St. James, 1986), in which the size of the spotlight’s beam is variable, and the ability of the visual cortex to resolve detail trades off against the total area being attended. Here, the purely spatial description of attention that arises from spotlight models is integrated with the concept of limited capacity processing resources.

Another variation on the spotlight model is the gradient account (LaBerge & Brown, 1989) in which the edges of the focus of attention are not hard, but soft: here, attentional processing falls of gradually with distance from the centre of the focus.

A fourth variation on the spotlight metaphor is that of the Mexican hat (Müller & Kleinschmidt, 2004; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005). Here, like the spotlight, attention facilitates locations at the centre of focus. Like the gradient model, this facilitation falls off with distance, before coming to a ring of 'surround inhibition' which has the effect of suppressing locations or stimuli that fall at an intermediate distance from the centre; past this ring, the inhibition falls off. Items at the very centre of the focus of attention are thus processed at the highest priority, with items at an intermediate distance processed at the very lowest priority, and items further out from this ring of surround inhibition processed more highly (although still with a lower priority than those attended items at the very centre).

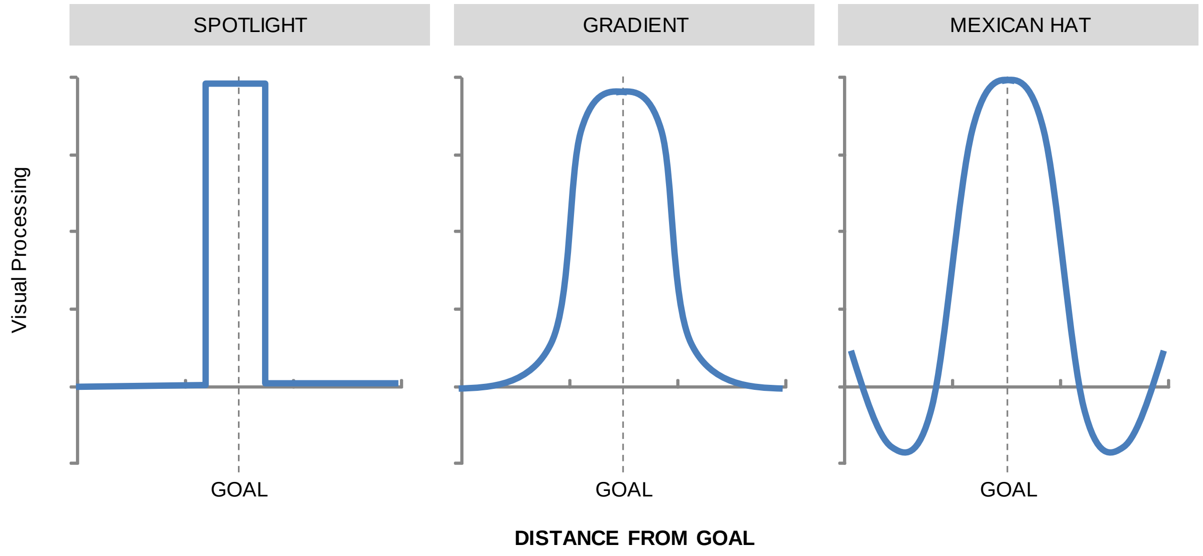

Figure 1. Three possibile spatial profiles of visual processing, as predicted by different models of spatial attention. Leftmost panel: a spotlight, in which processing is enhanced within the hard-edged spot, but not elsewhere. Middle panel: A gradient model, in which the edges of the focus of processing falls-off gradually. Right panel: a Mexican hat, in which processing falls off with distance, before coming to a ring of surround inhibition at intermediate distances, before recovering at locations further from the centre of focus.

How does this apply to the consequences of action? It firstly depends upon what is selected. As discussed above, there is good evidence that goal of an action receives enhanced processing. If this is conceived of as a shift of spatial attention (and most accounts do describe it this way), then one could imagine a moving spotlight falling upon the goal. When participants are cued to move to multiple goals there is evidence that each receives enhanced processing in parallel, but that locations on the trajectory between them do not (Baldauf & Deubel, 2008a). Two relevant points arise from this: firstly, whatever ‘shape’ enhanced processing takes, it can fall upon two discrete objects or locations at the same time; and secondly, this cannot be accounted for by one large spotlight centred over the two locations, because if this were the case then the trajectory of the movement from one goal to the other would also fall in the spotlight. At the very least, movements with more than one relevant functional location (in this case more than one goal, in the case of the experiments reported in this thesis, a goal and an effector) require more than one spotlight/zoom lense/centred gradient, or Mexican hat.

Most perceptual-movement paradigms, including those reported in chapters three and four of this thesis, probe visual processing at two functional locations: one that is involved in a current movement, and one that is not. Perceptual processing is then measured by calculating the difference between the two. Chapter five reports an experiment in which this technique is extended beyond the normal range of movement, by probing locations involved in movement, those nearby, and those further away. By plotting visual processing at locations which fall at an increasing distance from where movement is happening, the spatial profile of action-induced enhanced processing can be elucidated. A sharp fall-off would support a spotlight model with a hard edge, a gentle fall-off would be more compatible with a gradient model, and a gentle fall-off with a ring of surround inhibition would suggest that a Mexican hat model is the most appropriate way of describing this effect. In addition to the more general interest in discovering precisely how action-induced enhanced processing is mapped across space, these results will also allow comparisons between spatial attention, and processing changes caused by motor preparation.

CHAPTER 2: **EXPERIMENTAL METHODS**

Introduction

All of the experiments reported in this thesis have certain experimental methods in common. For ease of understanding and to reduce repetition in the experimental chapters, these methods are described here.

Mirror System

All experiments involved participants completing a movement task during which aspects of their visual processing were measured using task irrelevant probes. Two problems presented themselves with this approach:

1. The participant’s hand may cause an exogenous (attracting) shift of attention, to some degree biasing visual processing away from the state induced by the movement. Any inferences based upon measurements taken in this context may be invalid.

2. If both the goal of the movement (the target location) and the effector (the starting position of the hand) are to be considered, then the traditional method of delivering visual probes with LEDs at the goal and effector location becomes problematic: the hand can, at various stages during the execution of movement, obscure the probe. This also constrains the timings at which the probe can be presented, compressing them to earlier stages of movement during which it can be confidently predicted that the hand will not yet have started to move.

Both of these problems can be solved by separating the area of space in which the participant completes the movement task from the participant’s visual perception of that space. In other words, replacing what appears to be in front of and underneath the participant’s hands with an artificially ‘clean’ image. This was accomplished with a piece of apparatus that will be referred to as a ‘mirror system’ (Figure 2).

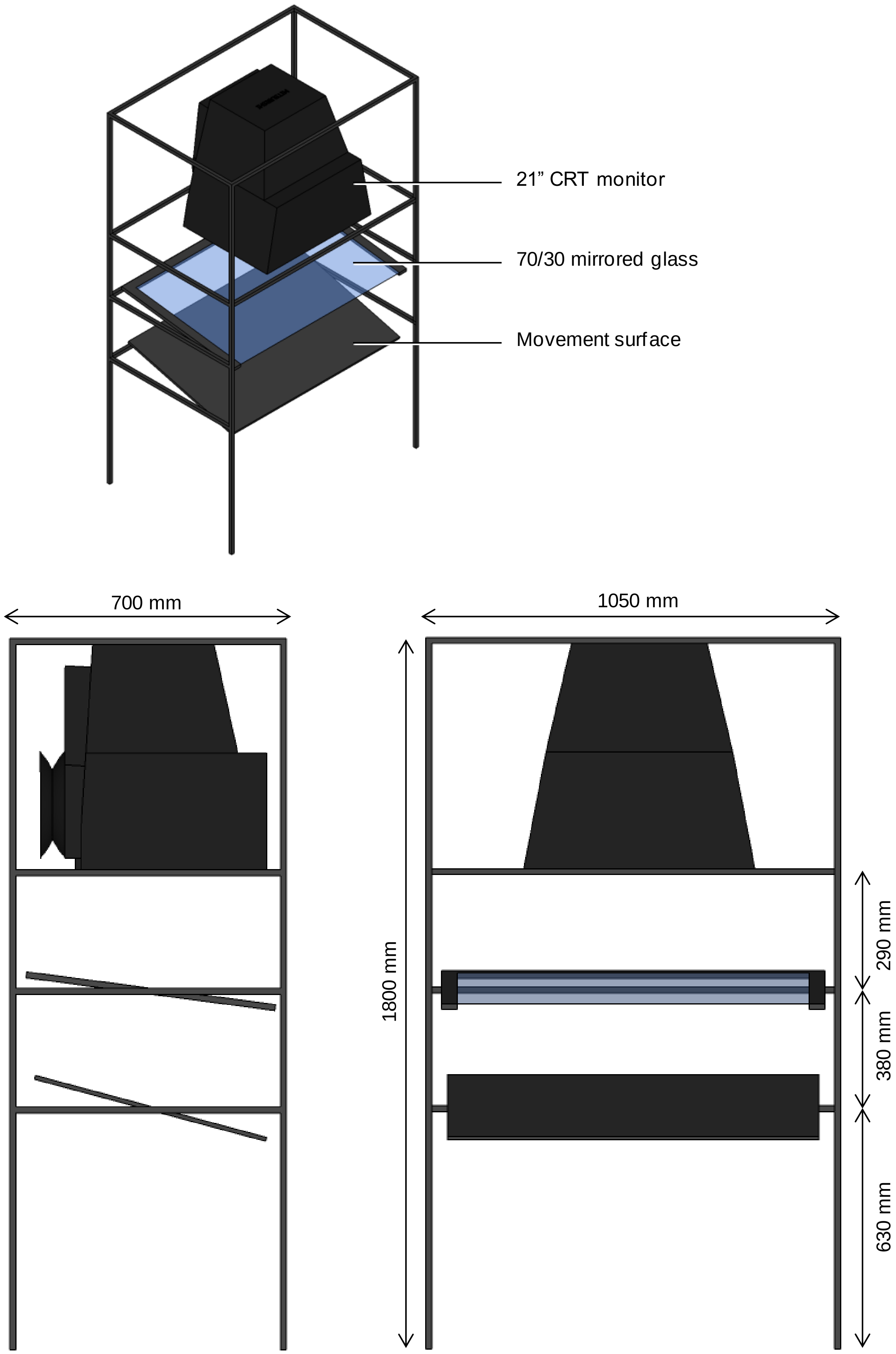

Figure 2. A scale drawing of the mirror system, including dimensions.

The apparatus consists of three main parts:

1. A 21” CRT monitor facing downwards, on which is displayed an exact replica of the stimulus used in the movement task. The light from this display projects onto the mirror below.

2. A large mirror made from autocue glass. This reflects 70% of light hitting the top side, whilst allowing 30% of light to pass through from below the underside. In conditions in which the brightness of light projected from the monitor onto the top surface of the mirror is equal to the ambient light illuminating the table underneath, the participant will perceive a brighter reflection from the monitor whilst seeing a darkened image of their hand and the surface of the table through the mirror. If the balance of lighting is shifted so that the ambient light in the room is reduced whilst the brightness of the monitor is kept constant there will come a point at which the participant can no longer see their hand through the mirror: they will then perceive the projected image as apparently originating from beneath the mirror.

3. A table sitting underneath the mirror. This contains any additional apparatus necessary for each individual experiment. The area between the table and the underside of the mirror is the movement space in which the participant carries out the experimental task.

By carefully aligning the position of the image projected from the monitor onto the glass, and by ensuring that the tilt angle of the mirror is exactly half that of the angle of the table, the image that hits the participant’s retina from the monitor will be spatially aligned and at the same apparent depth as the image from the surface of the table. The upshot of this arrangement is that the participant has no visual cues to suggest that what they are seeing is not a true image from the table in front of them. They will, of course, notice that they are unable to see their hand, but so long as the image from the monitor is in the correct spatial alignment, the illusion of seeing *through* the mirror is very convincing. Implicit in the fact that participants were all able to successfully carry out various movement tasks under the mirror – whilst the image that hit their retina was in fact originating from the monitor – shows that such an arrangement is no barrier to accurate movement.

Computerised control of experiments

All experiments utilised two Intel personal computers, one (the stimulus computer) to present stimuli, collect behavioural responses and to place event markers in the EEG; and another (the EEG computer) to acquire and save to disk the EEG and event markers. The stimulus and EEG computers were connected via a parallel port interface to allow event markers to be inserted into the EEG at the appropriate point in each experiment.

Stimulus computer

The stimulus computer ran the E-Prime suite of experimental software. This computer controlled the timing of the experiment, presenting stimuli via the mirror system monitor as required. It was connected to a speaker in the EEG cubicle through which auditory cues and feedback on behavioural performance were presented to the participant.

Behavioural responses such as reaction times were recorded within the E-Prime software and logged to a data file. Each trial was identified by participant number and a numerical code representing the exact combination of conditions presented in that trial. This code was sent to the EEG computer and integrated into the EEG as an event marker. This allowed both for the segmentation of the EEG into trial specific epochs, as well as providing a means to keep behavioural data recorded on the stimulus computer in synchronisation with the EEG.

EEG computer

The EEG computer ran the ActiView suite of EEG acquisition software from Brain Products GMBH, and was connected to the EEG amplifier via the USB port. Data was buffered and written to disk on this computer.

ERP Methodology

The origin of electrical activity in the brain

Electrical activity in the brain arises from two distinct neural processes, action potentials and post-synaptic potentials. Action potentials are the electrical charges that travel from cell bodies to axon terminals where neurotransmitters are released. Post-synaptic potentials arise from a later stage of this process, when neurotransmitters bind to a post-synaptic cell and cause ion channels to open or close. The difference in positive and negative charge between the post-synaptic cell body and dendrites is termed a *dipole* – a difference in electrical charge separated by a small distance.

Whilst single cell recordings can measure action potentials, it is not feasible to record such activity non-invasively from the scalp as neurons rarely fire in exact unison and both the physical orientation of axons and the inhibitory or excitatory nature of the neural connection cause the potentials from multiple neurons to tend to cancel out. Post-synaptic potentials, on the other hand, last considerably longer than action potentials and the activity from thousands or millions of cells firing in unison can, under certain circumstances, sum to a large enough voltage to be detectable at the scalp.

In order for this summation to take place, two conditions must be met in terms of the group of neurons that is firing: they must be spatially aligned, and they must receive the same type of input (either excitatory or inhibitory). Potentials from neurons that are aligned at random with each other will cancel out, as will potentials from two cells firing in unison where one is excitatory and the other inhibtory. Cortical pyramidal cells, which tend to lie perpendicular to the surface of the cortex, are the most suitable candidates for non-invasive electrophysiological recording techniques such as EEG (Coles & Rugg, 1995).

One final complication relating to summed potentials arises from the folding of the cortex. Populations of neurons that are perpendicular to each other in terms of their relative alignment may yet end up pointing in different directions if the part of the cortex that they inhabit is folded. Fortunately the dipoles within these folds sum to one large dipole that has an orientation equal to the average orientation of the individual dipoles[6] (De Munck, Van Dijk, & Spekreijse, 1988). So long as the orientation of the neural population due to cortical folding does not go too far beyond 90 degrees, then the potentials will sum in a suitable way for recording at the scalp (Luck, 2005).

Measuring electrical activity at the scalp

Hans Berger (1873-1941) was the first to attach a pair of electrodes to the human scalp, to amplify the differential signal between the two, and to plot the values to produce a waveform of electrical activity over time (Berger, 1929). This waveform is the *electronencephalogram*, or EEG. As discussed above, this does not represent the very fast and small scale activity resulting from action potentials, but rather paints a picture of a much larger scale, distributed and rhythmic pattern of brain activity that surpasses that of individual neurons firing alone and reflects something more of the organisation and functional architecture of the brain.

The voltages measured vary between ±100 µV and the frequencies extend up to at least 40Hz (Coles & Rugg, 1995). As noted above, EEG techniques involve recording the difference in potentials between two electrode sites. In modern EEG recording it is usual to record from 32, 64 or 128 electrodes sites across the scalp, to provide optimum spatial coverage. Each of

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[6] As a hypothetical example, if a fold of the cortex turned at a 90 degree right angle, such that half of the dipoles are aligned horizontally at zero degrees, and half vertically at 90 degrees, then the summed activity can be represented by one large dipole with an orientation of 45 degrees.

these electrode sites records the difference in electrical potential between its position on the scalp and the position of a ‘ground’ electrode.

The recordings reported in this thesis were all recorded relative to two reference electrodes placed on participants’ earlobes, although the tip of the nose, and the mastoids (behind the ears) are also common locations.

The important characteristic of a reference site is that it should be relatively unaffected by brain activity, but still be subject to external and internal sources of noise (such as electrical appliances and muscular activity, respectively). Scalp electrodes, on the other hand, record both brain activity *and* noise. The difference in voltages between scalp and reference electrodes should then reflect a relatively pure measure of brain activity, with as much common noise as can be recorded by the pair of electrodes subtracted from the signal.

Two points are important to note here. Firstly, as discussed above, the activity that is recordable at the scalp does not reflect the totality of brain activity due to how neural electrical activity summates; EEG recordings do not tell the whole story when it comes to brain activity. Secondly, whilst each electrode occupies a particular point on the scalp, it is a mistake to assume that the activity recorded at a particular electrode originated from an area of the cortex directly underneath it. The passage of electrical potentials from their neural generators to the scalp is not simple or straightforward, due to the biological material – the brain tissues, skull, dura and scalp – that these potentials must traverse on their way to the recording electrode. The way in which the signal travels from source to electrode is called *volume conduction*.

Volume conduction and source localisation

The pattern of voltage distribution recorded at the scalp is determined by two factors: the location of the neural generator of the signal within the brain, and the way the signal conducts through the brain, skull and scalp. The progress of electricity from dipole to conductor follows the path of least resistance. This causes the signal to ‘spread out’ through a conductive medium, rather than to follow a straight path from brain to outside world. The relatively resistant skull, in particular, causes such spreading to occur, and the signal will tend to spread laterally in an attempt to route around the obstruction.

This has the effect of ‘blurring’ the pattern of voltage recorded at the scalp, as compared to the pattern that leaves the brain. Additionally, as discussed above, folds in the cortex and the particular way in which individual dipoles sum can cause an effect to be projected at an angle – only measurable at an area of scalp some distance away from the source.

It is possible to predict, mathematically, the scalp voltage distribution that would occur if the location of the source generator is known (the ‘forward problem’). EEG data, of course, only provides the scalp distribution; if one wishes to know the source from this information alone (the ‘inverse problem’) then the prediction is much more difficult, not least because the number of possible source locations for a given scalp distribution is infinite (Luck, 2005).

Fortunately this figure can be reduced by applying certain constraints to the potential locations of the neural generator, the most obvious of which is only considering locations within the head. Others include the knowing (or assuming) the number of source generators, the time course of the effect, and sometimes the hemispheric symmetry of a particular effect. Simple models of source localisation use a sphere, or a set of three concentric spheres (modelling the brain, skull and scalp) to represent the conductive medium through which the signal passes. More advanced techniques use a standardised head model, or even unique models acquired from each experimental participant, obtained from structural MRI scans.

Once the pattern at the scalp is known, and constraints are applied to the possible locations of sources, the inverse problem can be approximated by model fitting techniques. By varying the location of potential neural sources within the model, it is possible to arrive at solutions that minimise the error between the observed scalp distribution and the distribution predicted by the model.

The accuracy of such methods has been tested experimentally by implanting artificial neural sources in the brains of human participants (usually epileptic patients) and then carrying out localisation of these known sources via their scalp voltage distribution. Whilst these studies necessarily involve small sample sizes, results nevertheless converge on an accuracy of approximately 10-12mm (e.g. Cuffin, Schomer, Ives, & Blume, 2001; Roth, Ko, von Albertini-Carletti, Scaffidi, & Sato, 1997). Whilst this is an impressive degree of accuracy given the model fitting approach used, a cubic centimetre of cortex is relatively large, and the results do not compare favourably with other functional imaging methods such as fMRI. The strength of EEG data is its superior temporal resolution (in the region of 2ms, depending on sampling rate) not its spatial resolution. Such source localisation as is possible can, however, provide confirmation that an effect that is measured at the scalp originates roughly in a location that is physiologically and functionally plausible.

Event related potentials

The EEG of a particular participant contains not only a recording of the brain activity related to a particular experimental task but also unrelated brain activity. An experiment will contrast conditions designed to elicit a particular brain response, but of course the brain is not only producing this specific response, it is also kept busy with general cognitive and neurological housekeeping. In other words, the EEG contains both task relevant *and* task irrelevant brain activity. Attempting to extract specific events from the raw EEG is extremely difficult – they are often not apparent, for example, under visual inspection of the waveform.

A simple solution to this problem is to employ event related potential (ERP) methods. This revolves around two basic principles: time locking and averaging. Consider a simple attentional paradigm, in which the participant's attention is either directed to, or away from, a particular stimulus. A researcher who is interested in measuring the brain's processing of this stimulus under the two different attentional conditions wants to measure the task-relevant brain activity with as little contamination as possible by activity that is task-irrelevant.

Placing a marker in the EEG at the precise time that the stimulus is presented during recording will allow the researcher to locate the particular part of the EEG that contains that brain response. Sections of the EEG are cut into sections (or 'epochs') of a second or two duration – each representing the neural consequences of a single trial – and lined up in relation to the marker.

These individual epochs will still contain both task-relevant and task-irrelevant brain activity, but importantly the relevant activity will be time locked to the beginning of each epoch, whilst the irrelevant activity will be randomly distributed in the time domain. If these epochs, each representing a separate trial, are then sorted into batches belonging to each experimental condition and their voltages averaged at each sampled time point then the random activity will tend towards zero and the relevant, time locked, activity will remain.

Post processing

Filtering

The EEG contains frequencies that are out of the range of interest to ERP researchers. A common source of noise in the EEG originated from alternating current mains appliances, the electromagnetic fields of which induce 50 Hz oscillations in the recording electrodes. Whilst in an ideal world all EEG recordings would take place within a Faraday cage that would eliminate this source of noise, sometimes electrical apparatus necessary for the experiment must be placed within the Faraday cage, and cables to stimulus computers and response boxes must pass through the cage. A ‘notch filter’ set between 49 and 51 Hz (in the UK) is often employed to remove this frequency.

Very fast electro-muscular-activity (EMG) above approximately 40 Hz is also filtered out by using a ‘low-pass’ filter, and sometimes slow activity below approximately 1 Hz, which can be caused by conductance changes due to sweating, is removed by use of a ‘high-pass’ filter.

An additional level of filtering is related to the process of digitising an analogue frequency and occurs in the EEG amplifier during recording. Simply put, any high frequencies that exceed half the sample rate will appear as artifactual low frequencies in the EEG, according to the Nyquist Theorem (Luck, 2005). For this reason, EEG amplifiers will filter out such frequencies at recording. All work reported in this thesis was sampled at 512 Hz, meaning that frequencies above 256 Hz were removed during acquisition.

Filtering unavoidably distorts the waveform, so a general rule is that less filtering is better. Removing very high (>80 Hz) and very low (<0.1 Hz) frequencies is unlikely to significantly distort ERPs, but as the boundaries of the filter approach the frequencies of interest, the risk of distorting the data increases. The desire to minimise distortion caused by filtering must be balanced against the need to remove as much noise as possible from the signal. The balance of these two competing concerns will often be shifted one way or the other depending upon the equipment used by an experiment, and the recording conditions (e.g. presence of absence of a Faraday cage).

Data in the present experiments was bandpass filtered between 1 Hz and 40 Hz.

Baseline correction

The amplitude of an ERP must be measured against something. Noise from any source can cause the voltage profile of an ERP to sum, meaning that the entire epoch has an artificially raised voltage. Any subsequent measurement of an ERP’s amplitude will then be raised by the same amount, without reflecting a true change in the size of that component. For this reason, an average voltage is computed for a pre-stimulus baseline period, during which it is assumed that any brain activity is unrelated to the yet-to-be-presented stimulus, and this average voltage is subtracted from the ERP waveform.

The duration of the baseline varies between researchers, but 200ms is generally accepted as being ideal, 100ms acceptable, and less than 100ms too short (Luck, 2005). The longer the baseline, the more representative an average voltage will be obtained, and the more reliable any amplitude measurements of ERPs will be. The baseline corrections for the analyses reported here were all of a 100 ms duration.

Artefact rejection

Whilst filtering will remove many unwanted artefacts from the data, there are two classes of noise that must be dealt with differently: eye movements, and blinks. The eyes function as a dipole with a negative pole at the back of the eye and positive at the front. Artefacts from a participant moving their eyes or blinking will be picked up by frontal electrodes and contaminate the signal of interest. Particularly problematic are the cases where a participant blinks or moves his or her eyes systematically on each trial, perhaps in response to a cue. This kind of activity will be somewhat time-locked to stimulus presentation and so can significantly distort the averaged ERPs. A variety of methods are employed to deal with this contamination by the electroocculogram (EOG).

Prevention is often better than the cure, and as such participants will usually be asked to keep their eyes focused on a central fixation point for the duration of the experimental trials. They may also be asked to avoid blinking during the period of each trial that is of interest (in other words, the portion that will be included in the averaged epochs). This can often mostly solve the problem, although some participants are better able to control their eye movements and blinks than others. Even the best behaved participant, however, will occasionally err, and some EOG artefacts inevitably end up in the EEG recording.

One post processing method for dealing with these blinks is to record the EOG by the use of external electrodes placed around the eyes. Depending on the nature of the task, and the directional nature of the eye movements that the task tends to elicit, these can be placed either side of the eyes to measure the horizontal EOG (HEOG), above and below the eyes (vertical EOG – VEOG), or both. By selecting epochs that contain a voltage change above a pre-specified value it is possible to isolate those trials that contain eye movements and then delete these epochs before averaging takes place.

Artefacts were rejected in the experiments reported here when voltage changes in the HEOG exceeded ±30 µV, and when changes at other electrodes exceeded ±80 µV.

Measurement of ERP components

The pattern of voltage resulting from the averaging and time-locking processes described above can be plotted as a *time* x *voltage* waveform, usually with negative voltages shown as upward going deflections on the *y* axis. The simplest way of quantifying a component is to measure the maximum (in the case of a positive going wave) or minimum voltage within a set time window. The visual N1 response – when measured at posterior electrodes, for example – peaks between 150 and 200 ms. Measuring the peak (in this case, minimum) voltage that is observed within this time window will produce a ‘peak amplitude’. There are, however, several reasons not to prefer this method of measurement:

1. Any overlapping components, for example the train of components that make up the brain response to a visual stimulus (C1, P1, N1 and so on – see later section for a full description), may cause the peak voltage to be artificially low or high. For the same reason, the peak of the component may not be the maximum or minimum voltage, if a wave of the opposite polarity follows soon after and overlaps to any extent.
2. Peak amplitude measures the voltage at a single time point, which may be distorted considerably by any noise in the data. Averages representing fewer trials are more likely to suffer, since the signal to noise ratio is lower. Thus it is inappropriate to compare conditions with different trial numbers, which is often necessary due to artefact rejection.

(Luck, 2005)

An alternative measurement that does not expose data to these problems is the ‘mean amplitude’: the average voltage at all of the time points within a time window. This has the advantage of allowing narrower time windows which can afford to miss the peak of the component due to individual differences in brain morphology and electrode placement between participants; the mean measure provides a safety barrier by not relying upon a single time point in order to quantify an effect that may last for 100 ms or more. Any noise present in the ERP is likely to have a negative followed by positive (or vice versa) deflection, which will cancel out under a mean measurement, allowing for trial numbers to be mismatched to some extent.

All of the experiments reported here used a mean amplitude measurement over a 40 ms time window centred on the peak of each component.

EEG data acquisition

EEG data were recorded continuously using a Biosemi system from 64 Ag/AgCl electrodes mounted on an elastic cap. The electrodes were positioned according to the international 10-20 system and were referenced to both earlobes (see Figure 3). Horizontal EOG was recorded from the outer canthi of both eyes. EEG was digitized at a sample rate of 512Hz and a depth of 32 bits per sample.

Further post processing was applied to the data offline. This process differed between experiments, and so is described in detail in the *method* section of each experimental chapter.

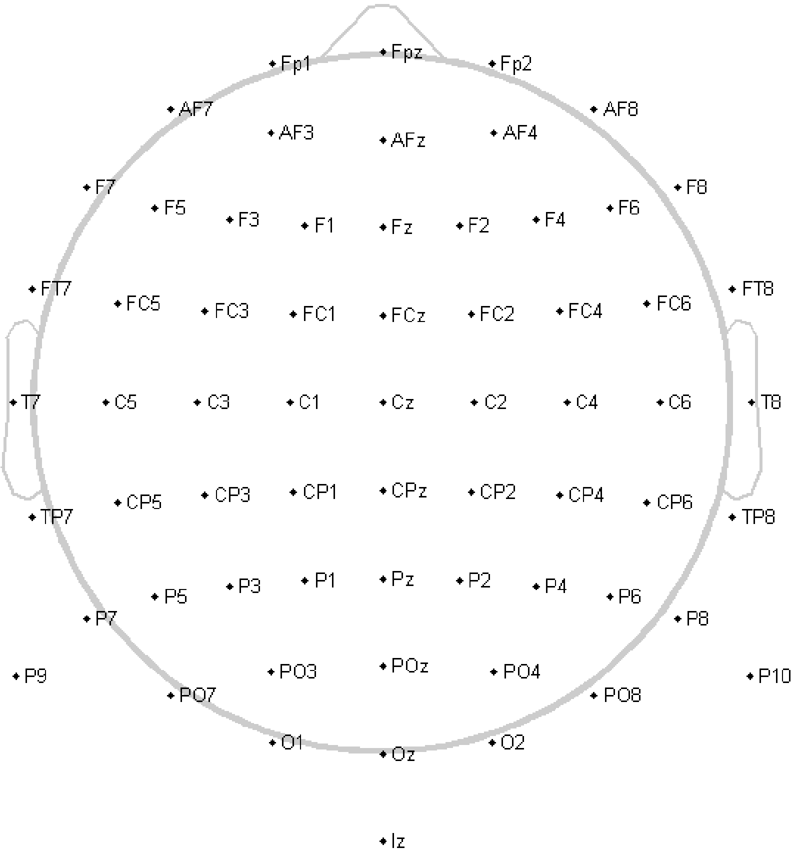


Figure 3. Recording electrodes were placed according to the international 10-20 standard for 64 channel EEG

Description of ERP components

The analyses reported in this thesis are focused on the visual evoked potential: the chain of ERP components elicited by sudden onset visual stimuli. These components represent the time course of visual processing, originating in very early visual areas where the receptive field of neurons is organised retinotopically, to higher level processing in the ventral stream, where neurons respond to pattern, shape and expectancy.

C1

The C1 is the first major component observed in the train of components representing the brain’s processing of a visual stimulus, onsets between 40-60 ms post stimulus, and is maximal at 80-100 ms. It is largest at posterior midline electrode sites.

Unlike other components it is not prefixed with a ‘N’ (for negative) or ‘P’ (for positive) because its polarity varies according to the position in the visual field of the stimulus that elicited it. The C1 originates in retinotopically mapped primary visual cortex (V1), specifically the calcarine fissure (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002), and due to brain morphology the potentials arising from this area exhibit a different polarity depending upon the vertical position of a stimulus in the visual field.

P1

The P1 component onsets between 60-90 ms post-stimulus, peaks at 100-130 ms and is largest at contralateral occipital electrode sites (Luck, 2005). There is some overlap with the C1 component, which makes precise measurement of the P1 latency difficult. The P1 appears to contain two sub-waves, with peaks measured at 75ms and 100ms (Clark, Fan, & Hillyard, 1995), and (in later work with a denser array of electrodes), between 80-110ms and 110-140ms, respectively (Di Russo et al., 2002). Mangun & Hillyard (1991) suggest that this latency difference between the early and late components is likely to reflect the time taken for information that is first received at the contralateral hemisphere to transverse the corpus callosum and present itself in ipsilateral cortex, rather than originating from a separate neural source.

Unlike the C1, the P1 appears not to be substantially affected by stimulus position; any variance according to position is likely to be caused by the slight overlap with the position-sensitive C1. The P1 has been localised to lateral extrastriate cortex, although over 30 distinct visual areas become active in the first 100 ms post-stimulus (Clark et al., 1995) so it seems likely that the P1 represents summed activity from many areas at the same time. Combined ERP dipole modelling and event related fMRI has localised the earlier P1 component to lateral mid-occipital cortex: area V3/V3a, and the region of the middle occipital gyrus immediately anterior to V3a. The later component appears to originate in ventral occipital cortex, in area V4v, and the region immediately anterior of the fusiform gyrus (Di Russo, Martínez, & Hillyard, 2003).

N1

The P1 wave is followed by the N1 which, once again, is comprised of several subcomponents. The earliest component peaks at 100-150 ms at anterior electrode sites, followed by a posterior component peaking at 150-200 ms (Clark et al., 1995).

The posterior component can be accounted for by the same neural sources at the P1 component, described above, whereas the anterior component was localised to a source in superior parietal cortex, near event related fMRI activations that were observed in the vicinity of the intraparietal sulcus (Di Russo et al., 2003). None of these areas of visual cortex appear to be retinotopically mapped, as the voltage distributions associated with them are not affected by stimulus location per se, although they are often more pronounced at electrode sites contralateral to the side of presentation.

P2

Following the N1 wave is the P2, about which comparatively little is known. The component peaks at about 200 ms, although the peak can vary between 150 and 275 ms and exhibits a fronto-central scalp distribution. The P2 is thought to reflect somewhat high level perceptual processing related to feature detection (being larger when elicited by the visual onset of target features during a detection task), similar to the P3 but elicited by simpler features (Luck & Hillyard, 1994). The P2 has also been shown to be involved in the processing of language, and has been speculated to be involved in comparing perceptual features with a trace in working memory (Evans & Federmeier, 2007). Whilst the featural and linguistic characteristics of the P2 are not relevant to the task-irrelevant probe stimuli presented in the experiments reported here, the P2 was modulated in at least some cases, and so is reported.

The P2 tends to overlap with a broad negative component beginning at 150-220 ms and extending for 200 ms or more, termed the ‘selection negativity’ and thought to represent the top down facilitation of brain regions responsible for processing particular features, such as color, motion, and so on (Anllo-Vento & Hillyard, 1996).

Top down modulation of ERPs

The C1 has traditionally has been thought not to show attentional modulation (e.g. Hillyard & Anllo-Vento, 1998) but recent research using large numbers of participants and trials has brought this assumption into question, at least for the simple classes of visual features that the C1 is sensitive to (Proverbio, Del Zotto & Zani, 2010). In general, the varying polarity and general absence of top down effects that are characteristic of this early component make its application less useful in the motor paradigms reported herein.

Hillyard, Luck, & Mangun (1994) reported a disassociation between the P1 and N1 components during a cued attention task. By using a paradigm with valid (attended), invalid (attention elsewhere) and neutral (no direction of attention) cues they were able to show that the P1 amplitude was the same for valid and neutral, but smaller for invalid, trials. The N1, in contrast, was larger for valid trials, as compared to neutral and invalid trials. Hillyard et al inferred from this data that the P1 represents the inhibitive processing of unattended stimuli that leads to the behavioural ‘costs’ of inattention – such as slower detection speed and poorer discrimination performance - whereas the N1 represents the facilitative processing of attended stimuli that leads to the ‘benefits’ of attention. This particular study did not differentiate between the anterior and the posterior N1 sub-components, unlike the study reported by (Di Russo et al., 2003), which describes the top down effects of attention separately for the two. Here it is the later parietal-occipital sub-component that appears to reflect the benefits of attention, whilst the effect on the anterior component sits somewhere between the P1 and posterior N1, being enlarged in amplitude for those stimuli that are attended, and reduced for those that are unattended.

Using ERPs to measure visual processing priority: the dot-probe paradigm

Given that visual ERPs reflect processing of a stimulus, and given that top down factors such as attention can modulate the amplitude of visual ERPs, it follows that these methods can be employed to measure visual processing at a particular area of space, or on a particular object.

By using a visual probe, sometimes in the form of the flash of light from an LED, and sometimes in the form of a bright dot presented on a computer display, it is possible – by reference to the amplitude of the ERP elicited by the probe – to quantify the processing priority assigned to the area of space by the brain.

Consider a simple reaching task, in which participants are cued to reach for one of two possible objects in peri-personal space. A probe is presented on ‘object one’ during the planning stage of action under two conditions, firstly when ‘object one’ is the current movement goal, and secondly when ‘object one’ is *not* the goal. Each object can then, on a trial-by-trial basis, be termed ‘moved-to’ when it is the goal object, and ‘not-moved-to’ otherwise.

If the visual environment is kept constant along with the luminosity of the probe, then the only difference between conditions is whether the probed object (or probed area of space) is involved in a movement or not. The amplitude of visual ERPs elicited by the probe can then serve as an index of processing priority at each of the two objects, when each is either a movement target or is not.

This principle can be applied to movement locations other than the goal. The experiments described in this thesis present visual probes at goal locations, at multiple other movement locations, and at the location of the effector (the hand or finger about to make a movement).

An important point to note here is that the probes themselves are task-irrelevant: the participant may be instructed to completely ignore these probes. What the participants' brains cannot ignore, however, is the presence of the probe – any visual stimulus within the visual field *will* be processed, the only question is what priority this processing occurs under. The answer to this question can be quantified reliably using a dot-probe paradigm, as described above. By knowing the relative processing priorities under different movement conditions it is then possible to speculate about the cognitive processes that give rise to these differing priorities.

Scalp distributions of components, and of effects

A rather subtle point when using a dot-probe paradigm is how to decide which electrode sites should be analysed. It is not always the case that the scalp distribution of an effect (e.g. the difference between a probe presented on a moved-to versus a not-moved-to goal location) matches the scalp distribution of the component that is elicited by the probe itself (e.g. the distribution of the visual N1 component).

The analyses reported in this thesis focus on the components, in terms of selecting which electrode sites to analyse. The alternative, to measure the distribution of the effect, and to analyse the electrodes where it is most apparent, can potentially lead to circular reasoning, and is in danger of taking advantage of random differences in amplitude at a particular region across two different conditions. In the interests of using well-established techniques, such as measuring the modulation of the visual N1 component, and avoiding exploratory analyses that are more difficult to interpret, the analyses reported here all focus on the distribution of components, not effects.

Notes on data analysis techniques

Lateralisation

Visual evoked brain responses are generally fairly strongly lateralised at the opposite hemisphere to the side of presentation: brain responses to probes presented in the left visual field are larger at scalp locations on the right hemisphere, and vice-versa. For the sake of brevity and simplicity, information regarding the absolute side of presentation and the hemisphere at which the associated brain response was recorded were collapsed to one variable, *hemisphere,* with two levels, *ipsilateral* (the brain response as measured on the same side as presentation) and *contralateral* (the brain response measured on the opposite side).

Where ERPs are plotted or described, electrodes are referred to as ‘P1/2 contralateral’, for stimuli presented in the left visual field and measured over the (right hemisphere electrode) P2, *and* for stimuli presented in the right visual field and measured over the (left hemisphere electrode) P1. When the reverse is true, electrodes are labelled ‘P1/2 ipsilateral’

Overlapping cue and probe brain responses

Two different types of movement paradigm are reported in this thesis. Chapter five uses a delayed response (‘S1/S2’ or ‘go/nogo’) paradigm. Here, the interval between the onset of the cue and the visual probe stimulus is quite large, at 800ms. Participants are instructed to prepare a movement, but to wait for a ‘go’ signal before executing it. Whilst they are waiting, their preparatory state is probed.

The experiments reported in chapters three and four operate differently, in that the auditory cue stimulus both instructs participants which movement to make, but also instructs them to execute the movement. In this case the interval between the cue and the probe is very short. Both the auditory cue and the visual probe stimulus elicit an ERP, and in these latter experiments, the two ERPs overlap. ERPs that overlap sum together, and this process can visually distort both the plots of the ERP and the maps of brain activation. This is illustrated in Figure 4.

Brain responses to the cue do not differ systematically on any variables that cause brain responses to the probe to differ; the two responses will be summed but the first response (to the cue) will remain constant across all trials and so any differences in the second response (to the probe) will still reflect the effect of the experimental manipulation just as if the components did not overlap at all.

Additionally the auditory evoked chain of brain responses to the cue has a different scalp distribution to that of the visual evoked chain of response to the probe. The auditory response is not lateralised, is present at anterior and central electrode sites and maximal at the Cz electrode (Naatanen & Picton, 1987). The visual response is often strongly lateralised and maximal posterior electrode sites (Luck, 2005). These differences allow the two responses to be differentiated with a high degree of confidence.

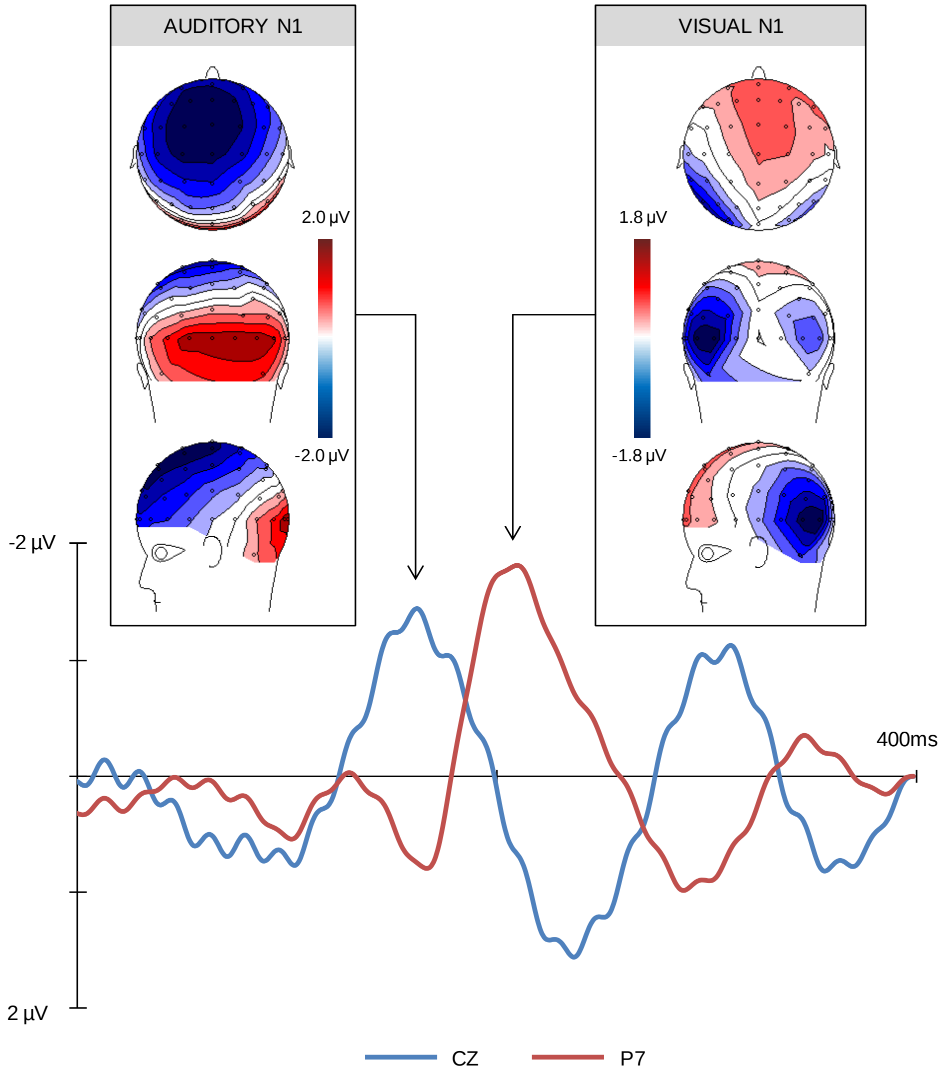


Figure 4. Overlapping ERPs elicited by the auditory cue, and the visual probe stimulus. Electrodes shown are CZ, in which the ERP in response to the cue is most apparent, and P7, in which the ERP in response to the probe is shown.

Presentation of graphs and ERP plots

All ERPs are presented, according to convention, with negative values going up on the y-axis. Bar and line graphs representing negative going ERPs (e.g. N1) use the same convention, those representing positive going ERPs (e.g. P1) are presented with positive values going up. In this way, ERPs can be read according to established convention, and other graphs show larger bars in an upward direction for larger components, regardless of the polarity of the component itself.

All graphs are presented with error bars representing +/-1 standard error. Where post-hoc tests are used to follow up a significant main comparison, brackets depicting the significance of the difference between conditions are shown.

Analysis of behavioural results

Behavioural data about movement time and accuracy was recorded for all experiments. The purpose of collecting this data was not to directly address the aims and hypotheses of each experiment, but a) to ensure that participants carried out the movement task correctly, and b) to determine to what extent the task-irrelevant probe stimuli exerted an effect on the characteristics of each movement.

It must be emphasised that even large effects of these stimuli on movement time and accuracy do not represent a challenge to the internal validity of the paradigms reported here. The electrophysiological measures – which *do* address the aims of each experiment – are collected by the probe stimuli themselves. Any effect of these stimuli on the subsequent execution of movement cannot impact upon these electrophysiological measures, as by that point in time the measurement has already been taken. The issue of interest to the experiments reported here is action *planning*, not execution; conclusions are drawn only from the state of visual processing in the brain at the time of probe presentation, not from behavioural measures of movement speed or accuracy after that point.

CHAPTER 3: **EFFECTS OF MOTOR PREPARATION ON VISUAL PROCESSING DURING GRASPING MOVEMENTS: ACCURACY AND TIME**

Abstract

The Premotor Theory of Attention (Rizzolatti et al., 1987) and the Visual Attention Model (Schneider, 1995) predict that planning a manual movement will cause enhanced perceptual processing at the movement goal. This experiment used ERP measures of visual processing to investigate this effect during a grasping movement.

Participants repeatedly grasped an irregularly shaped object comprised of two triangles arranged in a cross. Task irrelevant visual probes were presented at each of the four ends of the object when they were, and were not, about to be grasped, whilst participants' EEG was recorded. The effect of the spatial properties of the object, in terms of what degree of accuracy was required to successfully complete the movement, were investigated, as was the time course of any action-induced perceptual effect, by varying the time between cueing the movement and presenting the visual probe.

Results showed clear evidence of enhanced visual processing at action-relevant areas of the object 150ms after the onset of the cue. The spatial differences of the object, in terms of degree of accuracy, showed minor differences across the time-course of movement planning, with larger ERP amplitudes at easier to grasp ends of the object. This effect was reversed on the ungrasped object during later stages of movement planning.

Introduction

Perception and action have traditionally been studied in isolation, under the often implicit assumption that whilst perception is clearly necessary in order to plan efficient movements, there is no reciprocal effect of movement planning on perception. The current view, guided by such theoretical models as the Premotor Theory (Rizzolatti et al., 1994) and the Visual Attention Model (VAM, Schneider, 1995), is that the preparation of an action causes enhanced perceptual processing at the location of the goal. The objective of this experiment was to further investigate this effect in terms of its spatial and temporal characteristics.

Visual spatial attention can be decoupled from eye movements, such that a location in the visual field can be attended to whilst the eyes are fixated upon a different location. Attention in this sense is characterised by enhanced perceptual processing, measured as enhanced detection and discrimination performance (e.g. Posner, Snyder, & Davidson, 1980) and modulation of early sensory event related potentials (ERPs, e.g. Luck et al., 1994; Mangun & Buck, 1998). The Premotor Theory of Attention and the VAM both assume that shared brain mechanisms are involved in both shifting overt (involving eye movements) and covert attention (in the absence of eye movements). The predictions of the Premotor Theory are more detailed, in that overt shifts of attention are assumed to derive from a weaker activation of the same neural circuits that are used to plan saccades; in this case a shift of attention is a saccade that has not been executed.

Enhanced processing at the goal location of a saccade that has been planned, but not yet executed, has been reported in terms of effects of reaction times (Posner, 1980; Shepherd et al., 1986) target discrimination accuracy (Hoffman & Subramaniam, 1995), and modulation of visual ERPs (Eimer et al., 2006). Lateralised ERPs present in attentional tasks and thought to represent the activity of a putative attentional control network (ADAN and LDAP, Eimer & Van Velzen, 2002) are also present when participants plan saccades (Eimer et al., 2007), suggesting similar preparatory processes, possibly based upon shared brain regions, in both covert and overt shifts of attention. Neuroimaging studies (e.g. Corbetta et al., 1998; Perry & Zeki, 2000), animal studies that stimulate spatial maps in the frontal eye fields ('FEF', e.g. Moore & Fallah, 2004; Schiller & Tehovnik, 2001), trans-cranial stimulation of the FEF in humans (S F W Neggers et al., 2007; Van Ettinger-Veenstra et al., 2009) and neuropsychological evidence from patients (Craighero et al., 2001; Smith et al., 2004) further bolster this assumption.

The Premotor Theory and the VAM also predict that saccades are not special in terms of movement planning, and that the same enhanced processing should be observed at the goal location of any manual movement, regardless of the effector used to carry it out. Evidence from behavioural (Baldauf et al., 2006; Deubel et al., 1998), visual (Eimer & Van Velzen, 2006) and tactile (Eimer et al., 2005) ERPs, and direct recording in monkeys (Galletti et al., 2010), supports this hypothesis.

All of the actions considered so far have involved simple movements to single objects. In the case of a grasping movement the end goal of the movement is not the object itself, but the two contact points that the finger and thumb involved in the grasping movement will touch.

The present experiment is based upon Schiegg et al. (2003) which used a cross shaped object surrounded by discrimination targets (Figure 5) that participants responded to whilst grasping one ‘branch’ of the object between index finger and thumb. An auditory cue was used to instruct the participant to make the grasping movement with either their left or right hand, and the stimuli were unmasked before the hand began to move.

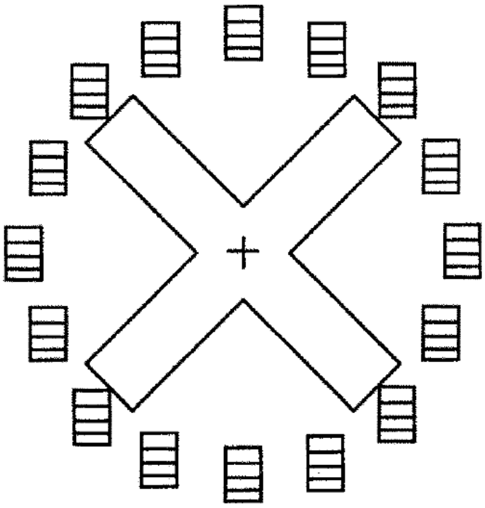


Figure 5 The object and stimuli used by Schiegg, Deubel and Schneider (2003)

This apparatus was used in two experiments, one in which the location of the discrimination target (DT) was varied randomly on a trial-by-trial basis, and a second in which the DT location remained constant across blocks. In both experiments, when the DT was at a to-be-grasped location, performance on the discrimination task was superior to when the DT was presented elsewhere. The second experiment confirmed that the coupling of action and attention appeared to be obligatory, otherwise participants would have directed attention to the location of the DT on each trial.

An additional difference in the second experiment was that attention was probed at differing stimulus onset asynchronies (SOAs), by varying the time at which the stimuli were unmasked. These SOAs were 100, 300 and 500 ms post cue onset. Results showed that the performance advantage had disappeared by the 500 ms SOA and was only evident at earlier timings.

The present experiment adapted the paradigm used by Schiegg et al by recording ERP - as opposed to behavioural - measures of visual processing. The aims of the present experiment were twofold:

1) To provide electrophysiological confirmation of the behavioural results reported by Schiegg et al, namely that the areas within an object that are most relevant to action receive enhance processing during the preparation phase of a movement.
2) To investigate whether the spatial properties of the action relevant parts affect how this enhanced processing is balanced. If one end of the object requires greater precision in order to successfully complete the movement, will this difference be reflected in the relative processing priority assigned to it during movement planning?

Method

Participants

A sample of 18 participants (eleven females) took part in the experiment after giving informed consent. Some were paid in cash, and some received course credit as payment for participation. Participants ranged in age from 19 to 29 (mean age was 23.4 years), all were right handed, had normal or corrected-to-normal vision and none had been diagnosed with any movement disorders. One participant was excluded from ERP analyses due to poor control over saccades and blinks, leaving a total of 17 participants.

Stimuli and Materials

Grasped object

Participants were presented with an object comprising two overlapping triangles, arranged at 180 degrees to each other. The object is shown in Figure 6, with contours added to highlight the two triangular sub-objects that comprised it. In reality the object had no visible contours and the join between the two triangular objects was completely flat. The object, as seen from above, measured 80mm wide by 80mm deep by 8mm tall, and was raised from the surface on which it sat by 10mm in order that it could be grasped without the participant’s hand making contact with the surface. Participants always used their right hands to grasp the object.

In the orientation shown on the right of Figure 6, when grasping object 1, the thumb will always make contact with the sharp end of the object, and with the blunt end when grasping object 2. Additionally, the two sharp ends of the object are always in the left visual field, and the blunt ends in the right visual field. In order to balance out these inconsistencies, two orientations of the object were used: one in which both blunt ends were on the left hand side (Figure 6 left panel), and a second that had been rotated 180 degrees such that the two blunt ends were now on the right hand side (Figure 6, right hand panel). Half of the participants used the first orientation, and the other half used the second.

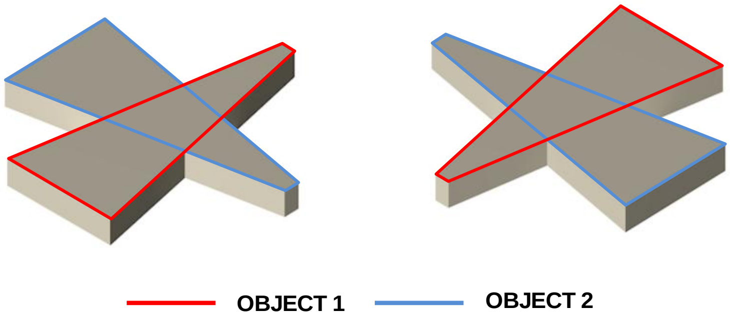


Figure 6 The graspable object. The left hand pane shows the orientation used by half of the participants, with sharp ends on the right hand side, and blunt ends on the left. The right hand pane shows the orientation used by the other half of the participants, with blunt ends on the right hand side, and sharp on the left. Each object was constructed from two triangular sub-objects, referred to as 'obejct 1' (shown with a red outline) and 'object 2' (shown with a blue outline).

Regardless of the orientation described above, each triangular sub-object required a grasp that differed in terms of the amount of rotation of the wrist that was required; these differences are illustrated in Figure 7.

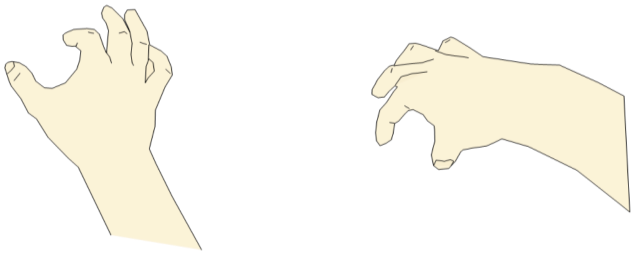


Figure 7 The two movements required in order to grasp object 1 (left hand side) and object 2 (right hand side). Note the rotation of the wrist for the grasp to object 2. The right hand was used for all grasping movements.

In order to detect when the participant had grasped the object and at which contact point, four Darlington transistor pairs were employed (see Hodges, 1999). These transistors function as touch sensitive switches that close when in contact with a finger or thumb (without any moving parts that may give tactile feedback of their operation to the participant). Each end (sharp/blunt) of each of the two triangular sub-objects contained such a device, allowing contact with each of the four ends to be recorded independently. Each time a digit made contact with a switch, a digital code representing which part of the object had been touched was sent to the stimulus computer.

Starting position

At the front of the surface, closest to the participant, was a raised ellipse, onto which the palm of the hand could be comfortably rested (see Figure 8). Inset in the centre of this ellipse was a cut out window, glazed with transparent plastic. Inside this window, underneath the plastic, was an infrared LED and infrared detector which together were capable of detecting when an object came within a few millimetres of it by measuring the amount of infrared light reflected back from it. As such, this served as the starting position for participants' hands, able to detect when the hand was resting on it and when the hand had left the starting position by only a very small amount. This allowed the onset of movement away from the starting position to be recorded precisely. Inputs from the infrared sensor were sent to the stimulus computer. The dimensions of the ellipse, as seen from above, were 70mm wide by 90mm deep, and raised 25mm from the surface at its highest point.

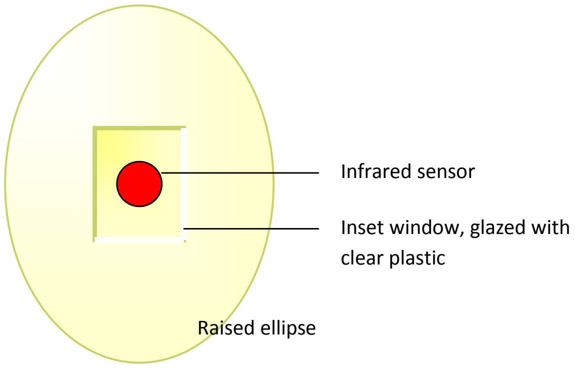


Figure 8. The starting position was a raised ellipse (seen here from above).

Cue

A symbolic auditory cue of 100 ms duration was employed, consisting of either a high (1000Hz) or a low (400Hz) tone. The meaning of the cue was counterbalanced across participants. Participants were instructed at the beginning of the experiment that a high tone represented an instruction to grasp one of the two sub-objects (see Figure 6), dependent upon counterbalancing. Auditory cues were presented from a speaker that was out of sight of the participant and centred so as not to bias attention to one side or another during the cueing period.

Probe

The dot-probe paradigm used in this experiment is described in detail in the chapter titled 'Experimental Methods'. The probe took the form of a white circle (0.37° x 0.37°) displayed upon one of the four graspable points of the object, one on each of the sharp ends, and one on each of the blunt ends. Figure 9 shows the object with a probe on one of these ends, in this case the blunt end of 'object 1'. This probe elicited the visual brain response, the measurement of which formed the dependent variable for this experiment, which is described below under the section 'EEG recording and data analysis'.

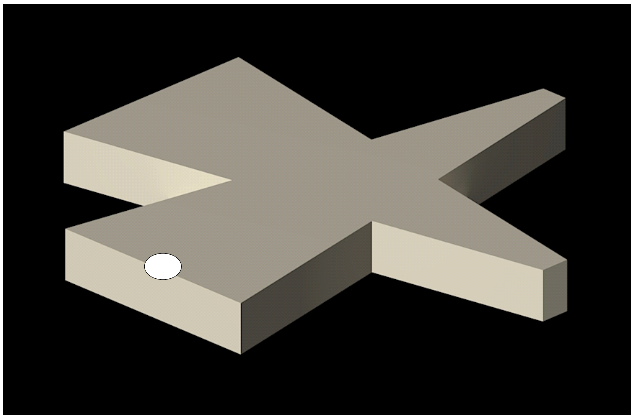


Figure 9. The graspable object shown with a probe displayed on one of the four possible locations. Here the probe is shown on the blunt end of object 1. Other possible locations for the probe were the sharp end of object 1, and the blunt and sharp ends of object 2.

Mirror system

For more detailed information on the mirror system, please see relevant section of the chapter of this thesis entitled *Experimental Methods*.

In order that the participant's hand did not cause an exogenous shift of attention when viewed in front of or alongside the object, and to prevent the hand concealing visual stimuli, a mirror system was used. This was comprised of three main sections: 1) the surface itself, a flat plane with the object attached to it, roughly at the height of the participant's stomach; 2) a one-way mirror into which the participant looked, which reflected any light from *above*, but was effectively opaque to any light coming from *below* (in dim ambient lighting conditions), at roughly the height of the participant's chest; and 3) a computer monitor facing downward toward the mirror, so that the display from the monitor was reflected back to the participant.

Participants sat at a distance of 620mm from the movement surface, upon which the reflected image from the monitor appeared to be projected. A fixation cross of dimensions 0.52° x 0.52° was presented at the centre of the surface. The projected outline of the graspable object was 6.13° x 6.86°.

Procedure

Participants sat in front of the mirror system with their left hand out of sight and their right hand near the starting position. On the surface of the mirror system was the graspable object, its orientation counterbalanced according to participant number. Instructions were presented on the mirror indicating the meaning of the auditory cue, with each high or low tone cueing the participant to grasp one of the two triangular sub-objects. Participants were told to move their hand as soon as they heard the cue, and to complete the grasp as quickly as possible.

In addition to an auditory cue, sound was used to give the participant feedback concerning the accuracy of his or her grasp. If the wrong object was grasped, if the object was not grasped within the correct time frame, or if only one end of the object (e.g. finger or thumb) was grasped, a buzzer would sound and a marker placed upon the EEG in order that the trial could be discarded prior to analysis.

500ms after each participant placed his or her hand onto the starting position the cue sound played for 100ms. After a variable SOA of 100, 150 or 200ms the probe was presented at one of the four corners of the object (see Figure 9), for a duration of 50ms. Participants were instructed to ignore the probes completely. The procedure then allowed a further 800ms in which the grasp must be completed. The sequence of events is illustrated in Figure 10.

Once the grasp had been successfully recorded on the stimulus computer, the participant returned his or hand to the starting position, at which point the next trial began. Participants sat a total of twelve blocks, each comprising 144 trials.

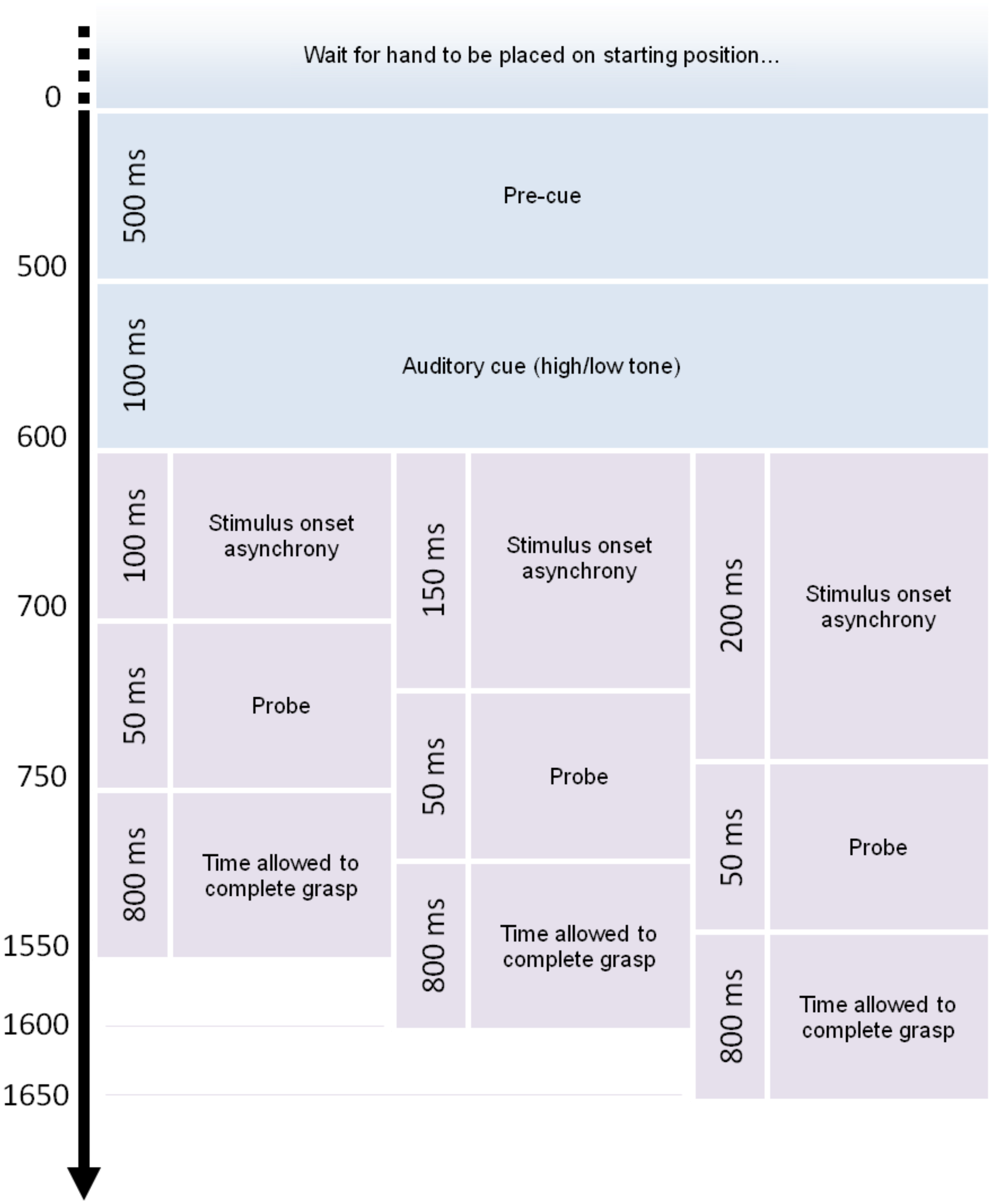


Figure 10. The sequence of events in each trial. Note three different columns representing the three different SOAs of 100, 150 and 200 ms.

Behavioural analysis

Behavioural performance was recorded in terms of speed and accuracy. The variables involved are listed in Table 1 below:

Table 1. A summary of the measures of behavioural performance

Movement Accuracy	Whether the participant grasped the cued (correct) or uncued triangular sub-object.
First contact RT (ms)	The time taken until the first digit made contact with the object, relative to the cue.
Second contact RT (ms)	The time taken until the second digit made contact with the object, relative to the cue.
Digit choice	Whether the first contact with the end of the sub-object was made with the finger or thumb

These dependent variables were entered into an ANOVA using *cued object* and *orientation* as independent variables. These are described in detail in Table 2. All results were corrected for violations of sphericity using the Greenhouse-Geisser method where appropriate.

EEG recording and data analysis

The EEG was filtered at a rate of 0.1 – 40 Hz using a band-pass filter, and segmented into 700ms epochs, running from 200ms before the auditory cue to 500ms after. Trials with eye blinks or movements (voltage in HEOG channels exceeding +/- 30 µV) or muscle artefacts (voltage at any other electrode site exceeding +/- 80 µV) were discarded. Epochs were averaged relative to a 100ms baseline before the onset of the auditory cue.

Where ERPs are presented visually they are plotted relative to the onset of the visual probe. Due to three different SOAs being used, the timing of the cue onset differs depending on probe timing. The 100ms baseline window moves with the cue. Where ERPs are presented collapsed over the variable SOA, the baselines plotted will represent an averaging of 100ms baseline calculations taken across the three time windows. Cue and probe onsets are marked on all ERP plots.

ERPs were analysed within 40ms latency windows centred on the peak of each component. These windows differed for each SOA, such that a window of 240-280ms was used for the 100ms SOA, 290-330ms for the 150ms SOA, and 340-380 for the 200ms SOA (all timings relative to cue onset). A mean ERP amplitude was calculated for each latency window and entered into a repeated measures ANOVA. All results were corrected for violations of sphericity using the Greenhouse-Geisser method where appropriate.

Separate averages were computed for each of the following variables: *movement preparation, probed object*, *probed end*, *SOA* and *hemisphere*. These variables are described in detail in Table 2.

Table 2 – Separate averages were computed for the following variables:

Movement preparation *(grasped/ungrasped)*	The object consisted of two triangular sub-objects superimposed upon each other (see Figure 6). Participants were cued to grasp one or other of the two sub-objects between thumb and index finger on each trial. *Movement preparation* refers to whether the probed sub-object was cued to be grasped on that trial, or whether the probe appeared on the uncued triangle.
Probed object *(object 1, object 2 – see Figure 6)*	Regardless of which of the two sub-objects the participant was cued to grasp, this variable coded for whether the probe appeared on one sub-object or the other. This variable was included in order to investigate whether the two sub-objects objects - in different orientations and therefore requiring quite different rotations of the wrist in order to grasp (see Figure 7) – were perceived differently.
Probed End *(sharp / blunt)*	Whether the probe was presented on the sharp or the blunt end of the object. A measure of the degree of accuracy required to successfully grasp each particular end of the sub-object.
SOA *(100/150/200 ms)*	Probes were presented at three different time points after the cue. *SOA* denotes which time point was probed on a particular trial. Three levels: 100, 150 or 200ms.

Hemisphere *(contralateral / ipsilateral)*	Recorded whether the measurement of the visual evoked brain response was taken at a scalp location contralateral or ipsilateral to the visual field of presentation. A measure of the degree of lateralisation of the visual response.
Orientation	Two orientations of the object were used as a counterbalancing factor between participants (see Figure 6).

Identification of ERP components

The visual probe stimuli elicited a posterior N1 component, maximal at electrode sites P1/2 contralateral, peaking at 170ms post onset. Scalp maps showing the distribution of this component are shown in **Error! Reference source not found.**. All statistical analyses were run on measurements at electrode sites P1 and P2.

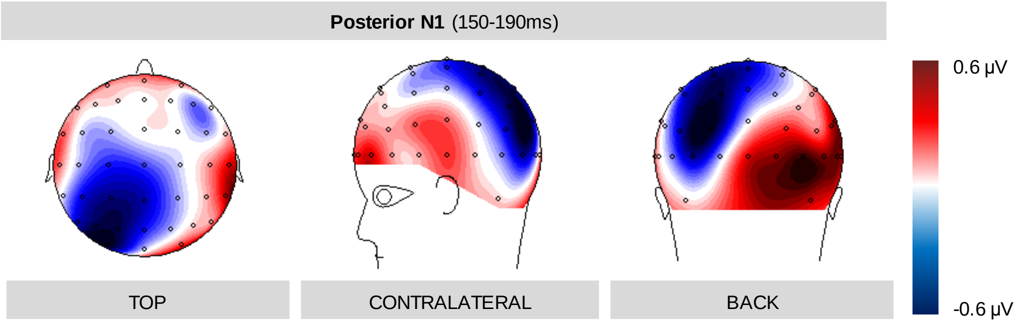


Figure 11. A map showing the location of electrode sites P1 and P2, with the activation associated with the visual evoked brain response to a right visual field probe.

Results

Behavioural Data

Summary of behavioural results

Behavioural data were analysed in order to ascertain whether any of the experimentally manipulated factors affected movement speed and accuracy.

Of the two different postures required to successfully grasp each of the independently cued sub-objects, no differences were found in movement accuracy. Significant differences in movement times were found, with the more difficult posture - involving a greater degree of rotation of the wrist - being slower.

Two different orientations of the whole graspable object were used for the purposes of counterbalancing the orientation between participants. Changes in orientation were associated with a small but significant drop in movement accuracy. Changing the orientation did not affect movement times.

Digit contacts

The number of trials on which the first digit of the participant's hand to make contact with the object was the finger, or the thumb, was recorded. This data was entered into an ANOVA with the factors *digit choice* (*finger/thumb*), *orientation* and *cued object*. The main effect of digit choice was marginally significant F(1,15)=4.254, p=.057, with more trials landing first with the finger than the thumb. The sub-object that the participant was cued to grasp did not affect digit choice as represented by the *cued object* x *digit choice* interaction, F(1,15)=.057, p=.815. The orientation of the object did affect the digit choice, *orientation* x *digit choice*, F(1,15)=20.529, p<.001, and interacted with the object being cued to grasp, *cued object* x *orientation* x *digit choice*, F(1,15)=19.147, p=.001. This interaction is illustrated in Figure 12.

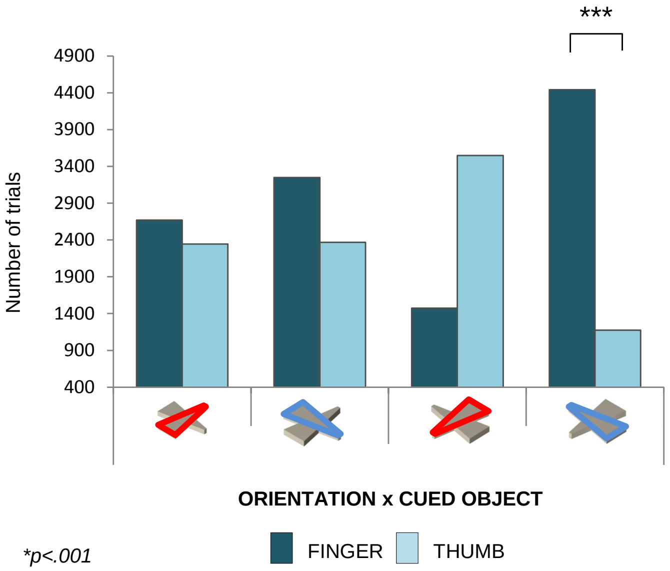


Figure 12. The number of trials on which participants first made contact with the sub-object using either their finger (dark bars) or their thumb (light bars), broken down by orientation (first two categories: orientation 1, second two categories: orientation 2) and cued object (pairs one and three: object 1, pairs two and four: object 2). Orientations and objects are shown graphically on the x axis. Results of paired-samples t-tests shown.

Post-hoc t-tests were performed on pairs of trial numbers on which the digit landed first on the finger or thumb, separately for each level of *cued object* and *orientation*. The difference was significant for orientation 2, when object 2 was cued, t(7)=9.354, p<.001, but not for any other combination of factors, all t's(7/8)<+/-2.181, all p's>.061.

Movement accuracy

Mean movement accuracy across all conditions and all participants was 92% (S.E. 9.38%). Accuracy was not affected by which object the participant was cued to grasp on a trial by trial basis, F(1,15)=.050, p=.825, but was affected by the overall orientation of the object, F(1,15)=17.637, p=.001. The second orientation (right hand data point of Figure 13) proved more difficult to grasp correctly than the first (left hand data point). The two factors did not interact, F(1,15)=.428, p=.523.

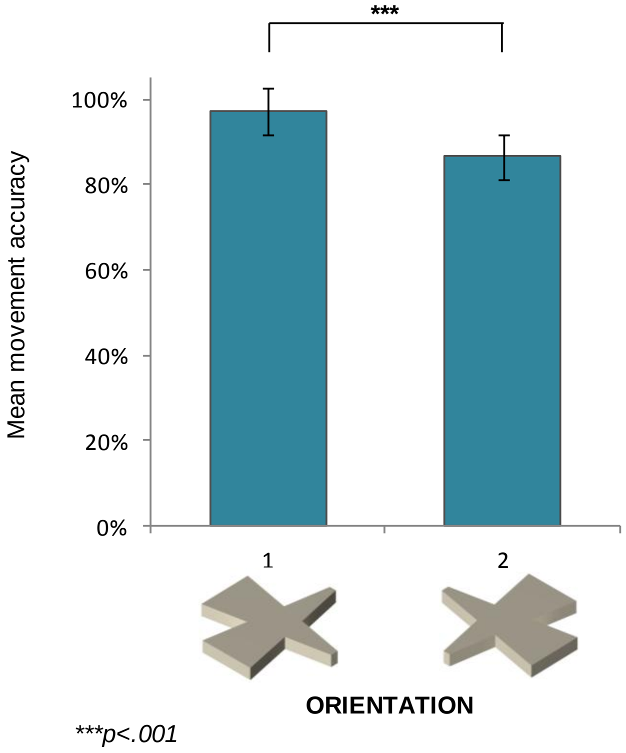


Figure 13. Mean movement accuracy for both orientations of the graspable object.

Movement times

Two movement times were recorded, the times for both the first and for the second digit (finger or thumb) to make contact with the object. Movement times were analysed with respect to which object was cued to be grasped, and to the overall orientation of the whole object. Figure 14 illustrates these results, participants grasped the object labelled ‘object 1’ (red outline) more quickly than ‘object 2’ (blue outline). This observation was confirmed by statistical analysis, both for the first digit to make contact, F(1,15)=75.268, p<.001; and for the second , F(1,15)=33.201. p<.001. No significant main effect was found for the orientation which the entire object was in for either digit, all F’s(1,15)<1.550, p=.232.

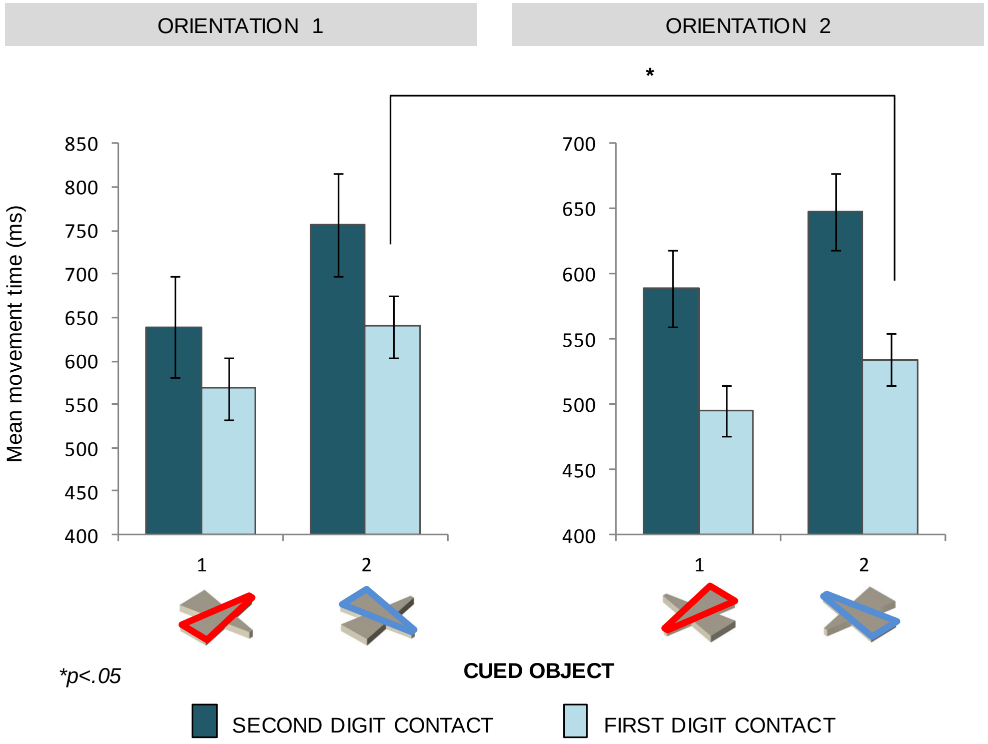


Figure 14. The effect of the overall orientation of the object, and the object that was cued to be grasped, on movement times. The left hand pane shows movement times for ‘orientation 1’ (blunt ends on the left hand side), the right hand pane for ‘orientation 2’ (sharp ends on left hand side). The cued object is highlighted in red and blue lines, with ‘object 1’ (the easier grasp) on the left hand side of each graph, and ‘object 2’ (the more difficult grasp) on the right hand side. The time for the first and second digits to make contact are shown by separate pairs of bars.

The interaction between the cued sub-object and the orientation of the whole object was significant, both for the first digit contact, F(1,15)=6.462, p=.023; and for the second, F(1,14)=6.551, p=.022. Post hoc independent samples t-tests for the first digit revealed no significant differences between the two orientations when the data was analysed separately for when object 1 and object 2 were cued, all t’s(15)<2.102, all p’s>.05. For the second digit to make contact, when object 2 was cued, times were significantly slower when the whole object was in orientation 1 compared to orientation 2, t(15)=2.156, p=.048, but this difference in movement times between orientations was not found when object 1 was cued, t(15)=.473, p=.643

ERP Data

Summary of ERP results

The amplitudes of visual N1 brain responses to probes presented on various parts of the graspable object, at various SOAs and under different movement conditions, are reported for electrodes P1 and P2, where the N1 effect was maximal.

Movement preparation modulated N1 amplitude, and this effect was found to be maximal 150ms post cue onset.

Probes presented on the blunt end of the object showed a trend toward being larger than those on sharp ends, but this was not significant. A four way interaction is described in which this trend towards larger N1 components for probes on blunt ends appears to be reversed for probes presented on the ungrasped object over the time course of movement planning.

Movement preparation

Figure 15 shows ERPs elicited by task irrelevant visual probes on the graspable object (comprised of two graspable triangular sub-objects - see Figure 6). ERPs are presented for conditions when cued (grasped, dark blue lines) and uncued (ungrasped, light blue lines) sub-object was probed. Probes on the grasped object elicited larger ERPs than probes on the ungrasped object.

This observation was confirmed by statistical analysis on electrodes P1 and P2: that movement preparation significantly increased N1 amplitude, F(1,15)=5.724, p=.03. This difference was not affected by the hemisphere (contra/ipsilateral) that the effect was measured at: the interaction of *movement preparation* x *hemisphere* was not significant, F(1,15)=1.303, p=.272.

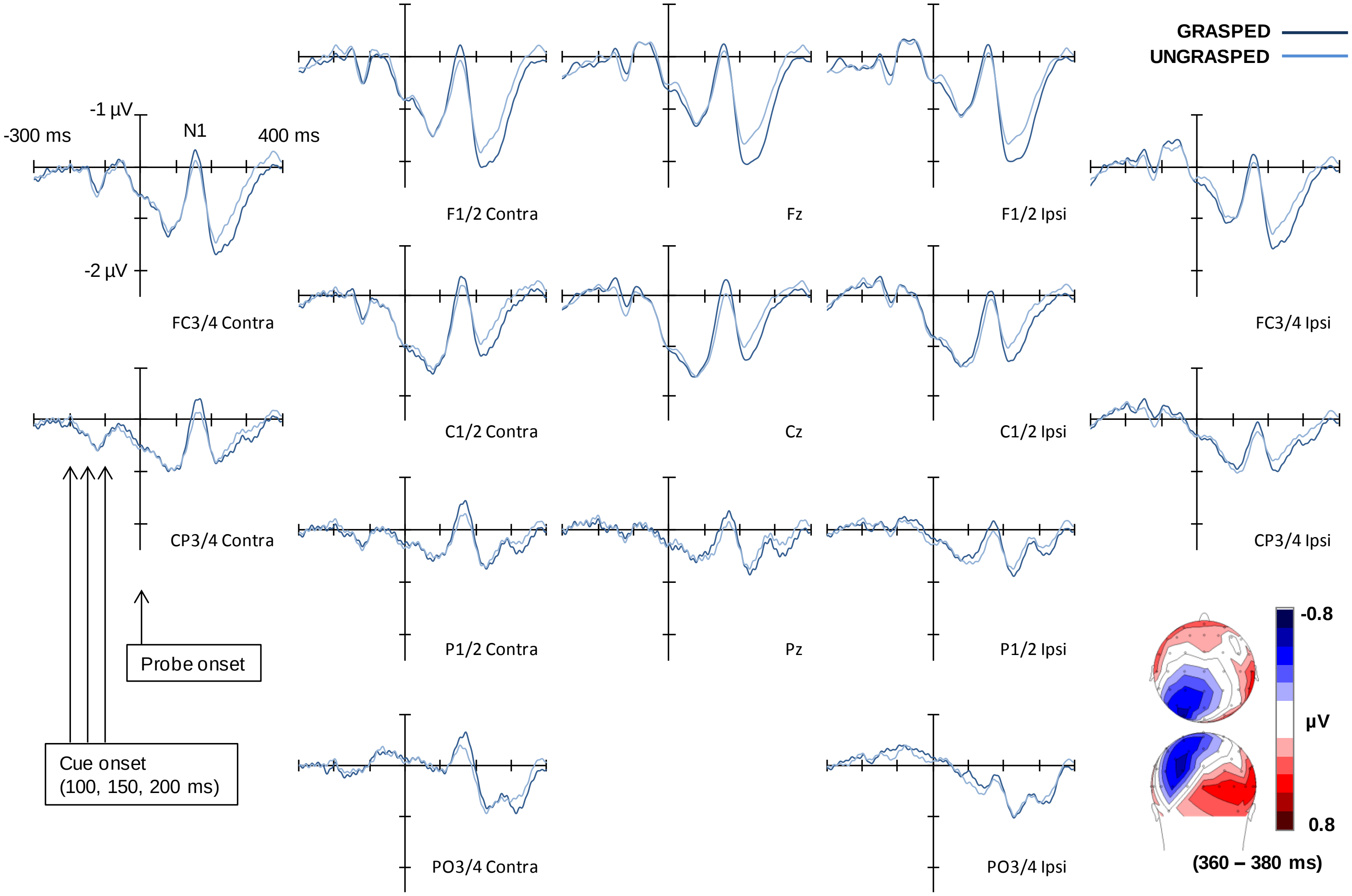


Figure 15. ERPs elicited by task irrelevant visual probes when the probed object was about to be grasped (dark blue lines), and when the probed object was not about to be grasped (light blue lines). ERPs are time locked to cue onset (0 ms), probe onsets for SOAs 100, 150 and 200ms are shown at -100, -150 and -200ms respectively. Data is collapsed across SOA.

The time course of movement preparation

The effect of movement preparation was analysed by reference to the interaction between *movement preparation* and *SOA*; this data is presented in Figure 16 and Figure 17. Statistical analysis revealed this effect to be significant, F(2,30)=4.086, p=.027. Post hoc analysis on *grasped* vs *ungrasped* conditions at each time point revealed a significant modulation of N1 amplitude as a result of movement preparation at 150 ms, t(16)=3.684, p=.002, but not at 100 and 200ms time points, both t(16)<1.661, p>.116. The interaction of *movement preparation* x *SOA* x *hemisphere* was not significant, F(2,30)=.358, p=.702: the modulation of N1 components, affected by movement preparation and timing, did not differ according to hemisphere.

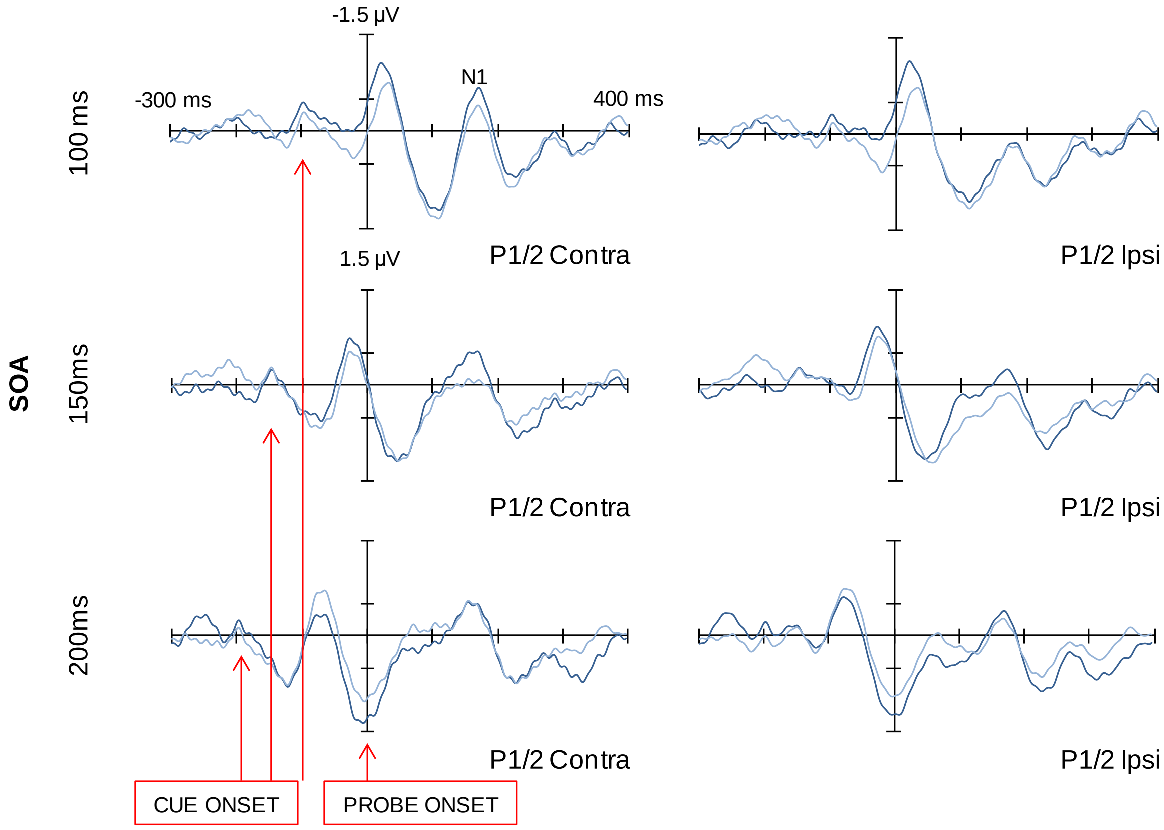


Figure 16. ERPs elicted by probes presented when the object was cued to be grasped (dark blue lines) and ungrasped (light blue lines), at three different SOAs. All ERPs are shown relative to cue onset (0 ms). Probe onset is shown by red arrows at -100, -150 and -200ms relative to the cue.

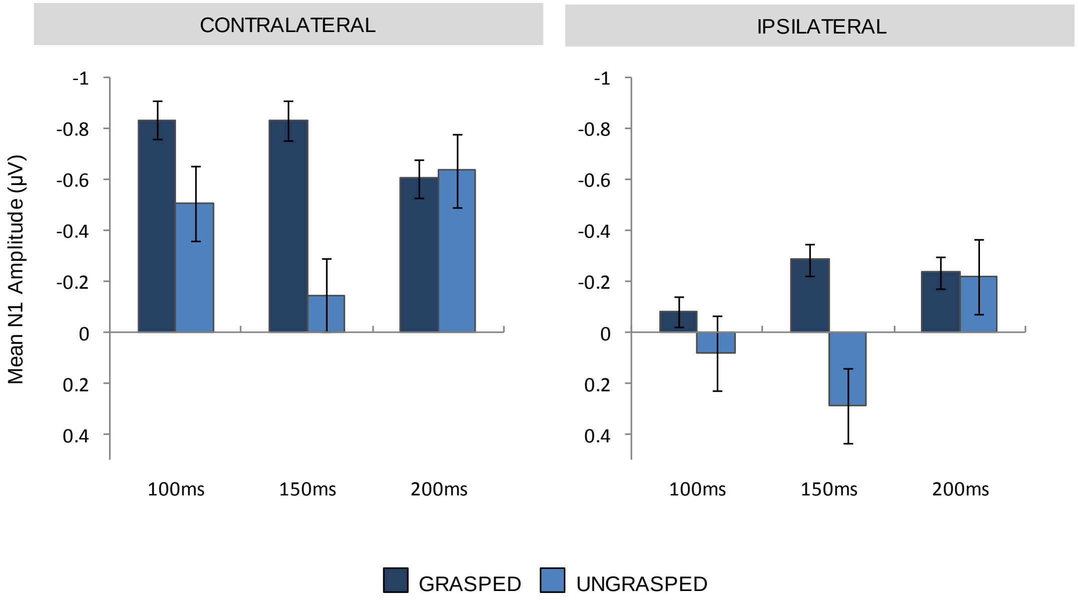


Figure 17. The effect of *movement preparation*, *hemisphere* and *SOA* (P1, P2).

The effect of the spatial properties of the grasped object

The main effect of *probed end* showed a trend towards larger N1 components to probes at the blunt compared to the sharp end, but this effect was only marginally significant, F(1,15)=3.142, p=.097. *Probed end* did not interact with *movement preparation*, *probed object*, *hemisphere*, all F(1,15)<.706, p>.347, nor *SOA*, F(2,30)=2.682, p=.085.

Figure 18 illustrates the four way interaction between *probed end*, *movement preparation*, *SOA* and *hemisphere*. This interaction was significant, F(2,30)=3.832, p=.033. Post-hoc tests were carried out for *blunt* vs *sharp* pairs at each combination of levels of the above factors. Two pairs were significant, in the grasped condition, on the ipsilateral hemisphere, at 150 ms, t(16)=2.851, p=.012; and in the ungrasped condition, on the contralateral hemisphere, at 100 ms, t(16)=3.065, p=.007.

Table 3. Post hoc tests on the interaction between *probed end*, *movement preparation*, *SOA* and *hemisphere.* Pairwise comparisons are listed for all *blunt* vs *sharp* differences at each combination of factors.

Hemisphere	**Movement Preparation**	**SOA**	**t**	**df**	**p**
Contralateral	Grasped	100 ms	-.701	16	.493
		150 ms	-1.059	16	.305
		200 ms	-.274	16	.787
	Ungrasped	100 ms	-3.065	16	**.007**
		150 ms	-.974	16	.345

		200 ms	1.913	16	.074
Ipsilateral	Grasped	100 ms	.485	16	.634
		150 ms	-2.851	16	**.012**
		200 ms	-.354	16	.728
	Ungrasped	100 ms	-1.599	16	.129
		150 ms	-.925	16	.368
		200 ms	.276	16	.786

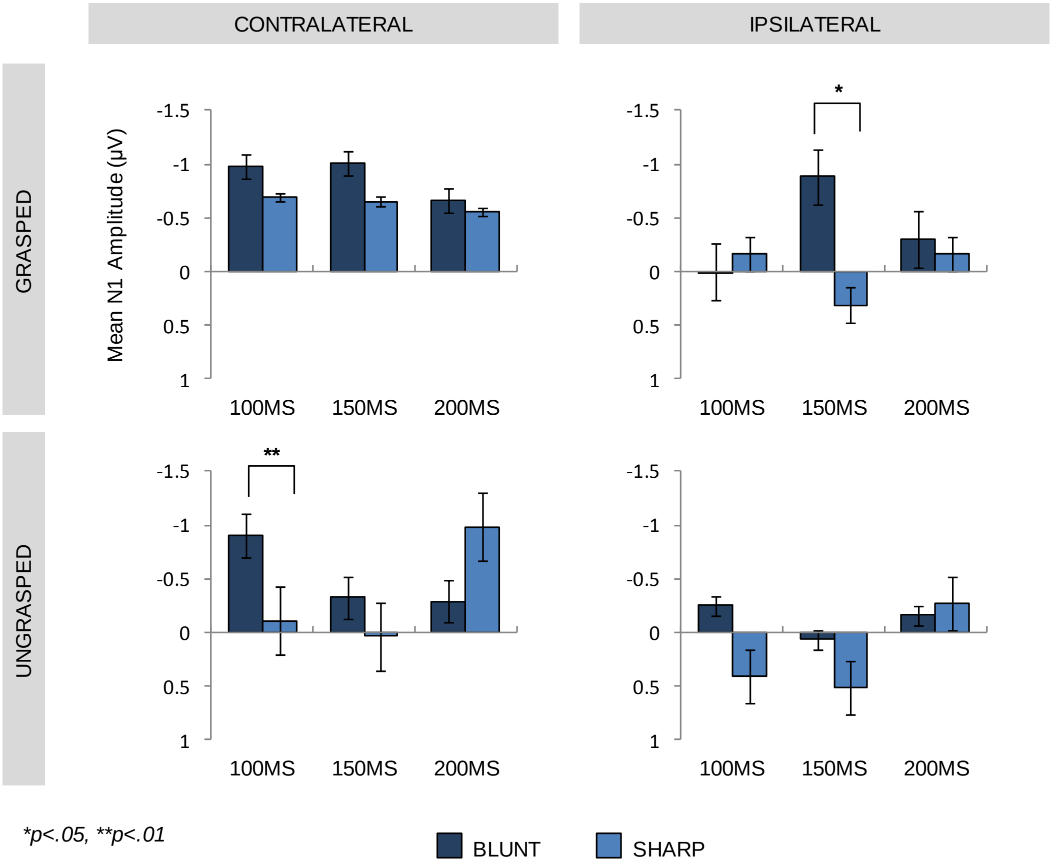


Figure 18. The four-way interaction between *probed end*, *movement preparation*, *SOA* and *hemisphere*, shown for electrodes P1 and P2.

These data are re-plotted in Figure 19 as mean N1 amplitude differences, arrived at by computing a *blunt – sharp* difference pair for each participant, at each combination of variables. The resulting graph is presented such that negative values represent larger N1 amplitudes at blunt ends of the object, with positive values representing larger N1s at the sharp end. A value of zero, marked with a dotted red line, represents no difference in N1 amplitudes between each end.

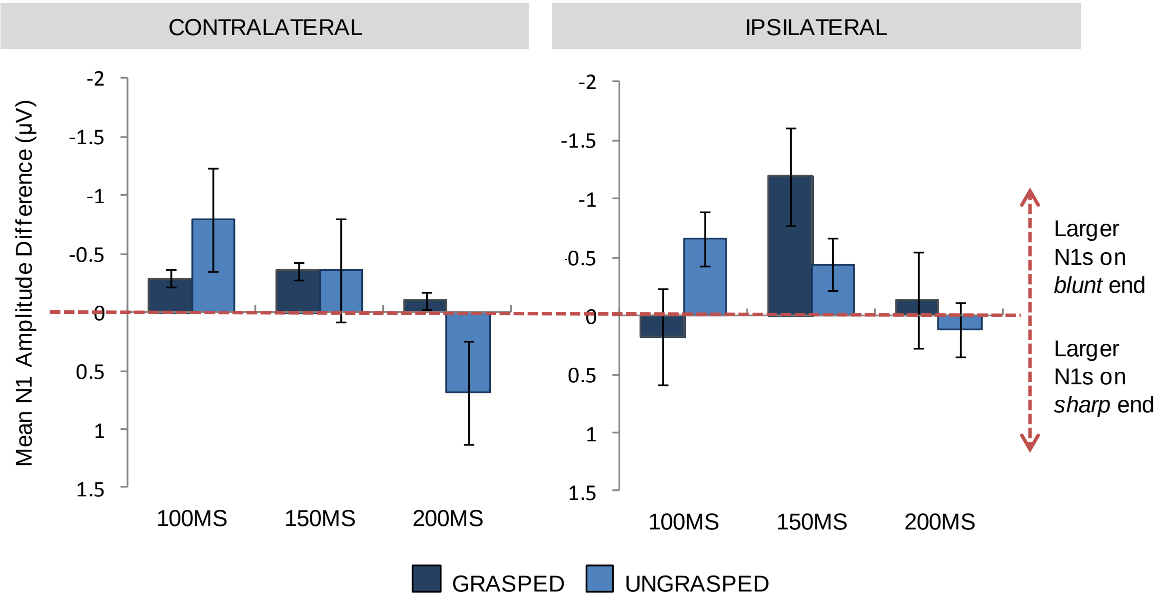


Figure 19. The differences in N1 amplitude, plotted by *SOA*, *hemisphere* and *movement preparation*, shown for electrodes P1 and P2. Negative values represent larger N1s at *blunt* ends of the object, positive values represent larger N1s at the *sharp* end.

When the probe was presented on the grasped object (dark blue lines), N1 amplitude was larger for probes on the blunt end of the object at all three time points, and this difference peaked at 150ms. The effect was more pronounced in the ipsilateral hemisphere.

A different pattern was observed when the probe was presented on the ungrasped object. At 100 and 150ms N1s elicited by probes presented on the blunt end of the object were larger, with this effect being greater at 100 than 150ms. By 200ms, however, probes presented on the sharp end of the object elicited larger N1s. This effect was more pronounced at the contralateral hemisphere.

Analysis of the two sub-objects

The variable *probed object* was entered into the analysis in order to determine whether some visual or kinematic difference between the two graspable triangular sub-objects was evident. The main effect of *probed object* was not significant, F(1,15)=2.078, p=.169, and it did not interact with any other variables. Despite the different orientations of the two objects presenting quite different visual features and requiring quite different hand postures to grasp, the N1 amplitudes recorded on both did not differ significantly.

Effect of counterbalanced object orientation on ERP components

Two different orientations (see Figure 6) were used to counterbalance the locations of sharp and blunt ends of the object in the left and right hemi-fields. Behavioural results showed that this orientation had a significant effect both on movement accuracy and on movement times.

This factor interacted significantly with *hemisphere* x *probed end*, F(1,15)=35.742, p<.001; and with *probed object* x *probed end*, F(1,15)=19.430, p=.001. The precise location and visual background of visual probes differed between orientations and between ends of the object, such that the projection of ERPs to electrode locations on the scalp also differed, a fact which is reflected in these significant interactions of orientation. The orientation factor, however, did not interact with any combination of variables related to *movement preparation*, and as such those interactions with *orientation* that were significant are not considered to be related to movement.

Lateralisation of ERP components

Although ERPs were clearly observed at both hemisphere, those measured at electrode sites contralateral to the side of probe presentation were bigger than those at ipsilateral sites, F(1,15)=23.358, p<.001. This result was expected and reflects a degree of lateralisation in the visual cortex. Note that, as stated above, movement preparation did not affect the degree of lateralisation; the modulation of the N1 as a function of movement preparation did not differ across hemispheres, F(1,16)=1.288, p=.273.

Discussion

Participants were cued to repeatedly grasp one of two irregularly shaped triangular objects, arranged perpendicularly in a cross shape, between index finger and thumb. After the cue, but before the onset of movement, visual probes in the form of small white discs were briefly presented at one of the four possible contact points, either the ‘sharp’ or the ‘blunt’ end of either the object that was being grasped, or the object that was not being grasped. Probes were presented at three different timings after cue onset, 100, 150 and 200ms. ERPs in response to these probes were calculated, and their amplitude compared according to whether they fell on a grasped or ungrasped object, the SOA of the probe, and whether they fell on the blunt (requiring less accuracy to make contact with) or the sharp (requiring greater accuracy) end of the object.

The effects on of movement preparation visual processing

One aim of this experiment was to provide electrophysiological confirmation of the findings of Schiegg et al., 2003. ERPs elicited by probes presented on parts of the object that were about to be grasped were significantly larger than those presented at ungrasped locations. This pattern of visual ERP effects is indistinguishable from that found in spatial attention tasks that do not involve movement (e.g. Eimer et al., 2006) and indicates modulation of information processing in relatively low level visual brain areas (cf. Mangun & Buck, 1998).

That this pattern of results was obtained when participants executed a manual grasping movement, as opposed to carrying out a voluntary shift of covert attention, is clear evidence that action-relevant locations in the environment are processed differently to locations that are irrelevant to action, and that, in the case of grasping movements, multiple contact points undergo enhanced processing in parallel.

The time course of perceptual effects of movement preparation

An intention to act caused a bias in perception at very early stages of processing. Behavioural measures, such as a button press in response to a detection or discrimination task, cannot definitively separate enhanced perceptual processing from speeded response selection. Differences in the chain of visual responses were found 150-200ms after the onset of the auditory cue that instructed participants which movement to make. It is noteworthy that this timeframe included interpretation of the cue, the true time to see an action related difference in processing may well be even shorter.

By varying the time between the cue that instructed the participant to move, and the probe that measured perceptual processing, it proved possible to estimate the time course of the perceptual effects caused by movement preparation. Schiegg et al. (2003) presented probes at 100, 300 and 500ms, and found effects of movement preparation at the two earlier SOAs. Pilot work, using the same physical object as in this current experiment, revealed no effect of movement preparation after 300ms, hence the choice of SOAs at 100, 150 and 200ms in this experiment. Despite the differences in choice of SOA between Schiegg et al and the present experiment, the pattern of results was similar; effects in early and late SOA conditions showed no difference between action relevant and irrelevant locations, but did in the 'middle' SOA condition (Figure 17, p. 72).

The difference in 'active' SOAs between this and Schiegg et al's experiment may be explained by a variety of factors. This experiment used a differently shaped graspable object, in a different environment, so certain non-specific effects may be at work on the time course of movement preparation. Additionally, the duration of the auditory cue in this experiment was 50ms, Schiegg et al used a 100ms cue. Depending upon how long it takes for participants to interpret the meaning of the cue and begin the process of movement preparation, it may be necessary to shift the timings used in this experiment by ~50ms for the purposes of comparison. Finally, the experiment by Schiegg et al used a behavioural discrimination task, whereas the probes presented in this experiment were task-irrelevant. Another advantage of ERP over behavioural measures are that they allow a view of what the brain is doing during a more ecologically valid movement condition. The fact that movement preparation appears at face value to be slower under these conditions is perhaps not surprising given the extra cognitive demands made of the participants in the behavioural version.

Differences between paradigms aside, the similarities are striking. The main effect of movement preparation shows how action can affect perception, but the analysis by SOA shows that this is a fleeting effect. It is not possible to say at what point movement preparation begins when using this paradigm, but by 100ms post cue-onset there is very little evidence of enhanced processing. After 150ms, the difference between ERPs elicited by probes at movement relevant and irrelevant locations is striking, and statistically significant. By 200ms, this difference has once again vanished.

The effect of the spatial properties of the grasped object

Each of the four contact points on the object presented a sharp and a blunt end to the participant. The amplitude of ERPs elicited by probes presented at each end were compared in order to investigate whether the degree of accuracy altered visual processing during movement planning.

The main effect of whether a probe landed on the blunt or sharp end of an object showed a trend toward larger elicited ERPs at the blunt end, however this was not significant. A four way interaction of *probed end* x *movement preparation* x *SOA* x *hemisphere* was significant. A 'blunt – sharp' difference was calculated for each data point; the resulting data is plotted in Figure 19 (p. 74).

It is noticeable that the majority of these data points fall above the red line, indicating that in general the blunt ends of the object received enhanced processing. When probes fell on a part of the object that was not about to be grasped, this effect declined across time. ERP responses to probes presented at early SOAs showed the largest bias towards blunt ends of the object, but at later SOAs this had reversed such that ERP responses to probes at sharp ends were now larger. If easier to grasp parts of the ungrasped object are considered during movement planning, then this reversal may reflect a mechanism by which component parts of the goal object are processed separately in series, and already-processed parts are 'selected out' in a manner similar to inhibition of return.

When the object was about to be grasped this reversal from larger-to-small probes at blunt-to-sharp ends was not evident. At the contralateral hemisphere, a relatively small bias toward the blunt end was observed, with a slight peak at 150ms, which from other results appears to be the time at which movement planning had the greatest effect on perceptual processing. On the ipsilateral side this slight peak toward a blunt end bias was more pronounced, but the data points at 100 and 200ms were very similar to the contralateral side.

The specifics of this effect are complex, however certain general points can be observed:

1. When the object is about to be grasped, 150ms appears to be the most active SOA in terms of movement planning. An increase in the size of ERP responses to probes was measured at both hemispheres for this time point. Even when considering a difference between two spatial properties of the object, in terms of the difference in visual processing between sharp and blunt ends, this time-course pattern still holds true.

2. Probes presented at blunt ends tend to elicit larger N1s than those at sharp ends. This may be because blunt ends of the object afford an easier grasp and so are more action relevant than sharp, but given the lack of a significant interaction between *probed end* and *movement preparation*, it is likely that this may reflect a simple visual bias toward blunt ends of the object. These two possibilities cannot be distinguished with the present experimental design.
3. Visual differences aside, the act of planning an action can affect the perception of locations not about to be grasped. The reversal of the size of ERP responses to probes, from blunt to sharp ends in the ungrasped condition, across time, shows that the spatial properties of an acted-upon object are processed in dynamically different ways across the time course of movement preparation. The present experiment may not have enough statistical power to describe this pattern in detail.

Movement accuracy

Movement accuracy was higher for participants who grasped 'orientation 1' of the two objects, rather than 'orientation 2' (Figure 6). Surprisingly, there was no effect on accuracy of which of the two sub-objects was grasped, despite each requiring a different grip. The only difference in terms of the mechanics of the grasp between the two orientations was which digit made contact with which end of the object. In the first orientation, participants cued to grasp 'object 1' would contact a blunt end with their thumb, and a sharp end with their finger. This was reversed for the second orientation.

Any inherent effect on accuracy of either the thumb or the finger making contact with either the blunt or sharp end can be discounted, as the interaction between *cued object* and *orientation* was not significant; the pattern of digit to sharp/blunt contact between objects and between orientations was determined by this interaction. Perhaps some aspect of the first orientation afforded greater accuracy in a way not defined by digits or sharp/blunt ends in different orientations, perhaps related to the – admittedly minimal – differences in visual or tactile perception offered by each orientation.

The two orientations were implemented by the use of two different physical objects, each with their own wiring supporting the ability to detect when the object was grasped. The accuracy difference recorded here may have been caused by a tendency of the object used for the second orientation to mark a certain number of correct grasps as errors. This possibility is strengthened by the fact that in the first orientation, participants managed a very high proportion of correct grasps (M=97.9%, S.E.=1.6%), suggesting that they did not in principle have difficulty in interpreting the cue and executing an efficient grasp the vast majority of the time. The figure for the second orientation (M=87.2, S.E.=1.8%) is considerably lower. To explain this difference without reference to which digit landed on each end of the object is difficult, therefore minor differences in the reliability between the two objects is the most plausible explanation for it.

Movement times

Movement times to ‘object 2’ were slower than ‘object 1’, which was expected since the two movements require different grasps. The main effect of *orientation* was not significant, but *orientation* and *cued object* did interact. The difference in movement times between the two grasps required for ‘object 1’ versus ‘object 2’ was smaller for the second orientation than the first. These differences of differences were small, 13ms for the first digit and 63ms for the second. In the context of standard errors for the estimates of mean movement times of between 19 and 27ms, whilst statistically significant, this interaction is not considered meaningful.

Relevance of behavioural measures to ERP results

The purpose of recording behavioural measures of movement was to ensure that any differences of movement and object did not invalidate the interpretation of ERP results. Whilst some statistically significant behavioural differences were found, it should be noted that 1) these were very small; and 2) neither of the factors that were significant in the behavioural results, namely *cued object* and *orientation,* had any effect on the ERP amplitudes discussed in the previous section. It is therefore concluded that any significant behavioural results stemmed from real differences that are nonetheless irrelevant to the aims of the experiment.

Conclusion

This experiment aimed to 1) provide electrophysiological confirmation of the results of Shiegg et al (2003); and 2) to investigate whether differing spatial properties of a movement target affected visual processing.

The first aim was met with complete success – visual processing was measured in a more direct way by comparing brain responses to visual probes, and a clear effect of movement preparation was found. The time-course effects were similar in pattern to Schiegg et al, but their latencies were shorter. Whilst it is possible that this was due to physical or perceptual differences between the apparatus used in each experiment, it is more likely that the extended latencies in the behavioural experiment represent the increased cognitive demands of the dual-task paradigm that was employed. If this is true, then the present experiment enhances our understanding of the time course of movement planning by using more direct measures of perceptual processing.

The second aim, to investigate how spatial differences in a movement target affect processing, was less clear-cut. Some differences were observed, and a statistically significant interaction was found. However, the underlying reason for the observation of this interaction is difficult to understand, and the simpler main effects and interactions that might have provided strong evidence for an effect on processing of the degree of accuracy required to grasp the object were not observed. There are at least two possible reasons for this: 1) the degree of accuracy does not affect visual processing, in which case the interaction observed was spurious and merely the result of statistical noise, or 2) the differences in degree of accuracy afforded by the relative sizes of the blunt and sharp ends of the object were not large enough in order for this design to detect them. Given that the results showed some hints towards differences in degree of accuracy, this second explanation cannot be discounted. A paradigm that is able to manipulate this degree of accuracy factor to a greater extent than in this experiment is needed in order to learn more.

CHAPTER 4: **SELECTION-FOR-ACTION OF GOAL AND EFFECTOR LOCATIONS, AND THE EFFECTS ON VISUAL PROCESSING OVER THE TIME COURSE OF MOTOR PREPARATION**

Abstract

The Premotor Theory of Attention (Rizzolatti et al., 1994, 1987) and the Visual Attention Model (Schneider, 1995) predict that planning a manual movement will cause enhanced perceptual processing at the movement goal, in order to select one goal amongst distractor stimuli. Much empirical evidence supports this prediction, but very few studies address the issue of *effector*-selection. This experiment aimed to measure visual processing at goal and effector locations, at multiple points in the time course of the preparation of a simple reaching movement.

Participants were cued to move either their left or right hand toward a target directly in front of them, whilst their EEG was recorded. Task irrelevant visual probes were presented at one of the two goal locations, or at one of the two effector locations, on a trial-by-trial basis. Probes were presented at 100, 200 or 300 ms after cue offset.

Results showed enhanced processing at goal locations across all three SOAs, and enhancement at the effector only at the middle (200ms) SOA. This was interpreted as evidence of simultaneous enhancement of goal and effector locations during motor preparation, suggesting that goal locations do not occupy a uniquely privileged position in terms of action planning. The disparity between the time course of goal and effector enhancement, however, shows that, in processing terms, the effector is not equivalent to the goal.

Introduction

The previous chapter described an experiment that investigated the time course of changes in perception, during motor preparation, at the location of an action goal. The objective of this experiment is to investigate whether this effect also applies to the effector used to execute the movement. Most previous studies that have used some form of perceptual probe stimuli (usually visual or tactile) have also employed a delayed response, or ‘go/no-go’ paradigm, in which the cue that instructs participants where to prepare to move is separated from a second cue, that instructs them to execute the movement. In this paradigm, perceptual processing is measured in the interval between the two cues. The present experiment uses the same ‘cued movement’ paradigm as that reported in the previous chapter, where a single cue instructs participants both where and when to move.

Early research on action and perception concentrated on links between saccades and shifts of visual attention, and showed enhanced visual processing at the saccade target (Eimer et al., 2006, 2007; Posner et al., 1980; Rizzolatti et al., 1987). Neuroimaging (Corbetta et al., 1998; Perry & Zeki, 2000) and neuropsychological work (Craighero et al., 2001; Smith et al., 2004), and work in non-human primates (Moore & Fallah, 2004), show that the neural structures underlying motor preparation and spatial attention show considerable overlap (described in detail in Chapter 1).

The Premotor Theory also predicts that enhanced perceptual processing is not just limited to saccades, but should be observed as a consequence of all goal-directed manual movements (Rizzolatti et al., 1994). Behavioural and electrophysiological investigations have provided support for this contention, in terms of pointing (Deubel et al., 1998), reaching (Baldauf & Deubel, 2008a, 2008c; Baldauf et al., 2006), and grasping (Schiegg et al., 2003). It is generally assumed that these perceptual consequences of action reflect a process of selection-for-action (Allport, 1987; Neumann, 1987) of goal locations, according to the functional dynamics described by Integrated Competition Hypothesis (Duncan et al., 1997), in which top-down considerations (such as relevance to an upcoming action) tip the balance of neural activation, thus adjusting the weights assigned to representations of objects or locations in the environment in favour of that which is action-relevant, at the expense of that which is action-irrelevant.

Effector selection

Possibly because of their origination in research involving saccades (in which the effector used to execute the movement does not have a location *per se*), those studies that investigate the dynamics of action induced changes in perception have been preoccupied with the goal of a movement. If, however, these perceptual changes occur as a means of ensuring accurate selection-for-action, there are surely other functional components of movement besides the goal that must be selected in order for movement to be, at least, efficient - or even possible. The effector used to carry out a manual movement - be it the hand, finger, foot, etc. – must also surely be selected for action, with concomitant effects on the perception of that effector.

Evidence for something like effector selection (or, at least, selection of the location in space that was occupied by the effector) has been shown in the tactile domain (Eimer et al., 2005) when participants prepared to lift one finger or the other. This is something of an unusual case of manual movements, however, since no goal is involved (or, the goal is the effector itself: similar to the case of saccades, in which distinctions between goal and effector break down). Effector selection has been shown in a goal directed manual movements (Forster & Eimer, 2007), although here the participant touched one finger with another, thus confounding goal and effector locations, at least in a retinotopic or spatiotopic frame of reference. Some work exists that uses ‘true’ goal-directed manual movements (Gherri et al., 2009; Van Velzen et al., 2006) but the results depended upon the task instructions given which, whilst an interesting and cautionary methodological finding, leaves open the question of whether effectors are processed similarly to goals, as essential components of action, or differently.

The present experiment measured visual processing systematically, at both the goal and the effector, during a simple reaching movement. Task-irrelevant visual ‘probe’ stimuli were presented either at the location of the goal or the effector that either was, or was not involved in an upcoming movement. ERPs elicited by probes presented at different locations under differing movement conditions were compared.

An additional aim of this experiment was to investigate how perceptual processing develops and changes over the time course of motor preparation. The simplest form of selection-for-action would be that goal and/or effector locations are selected, by means of spatial attention, in rapid serial sequence. If this were the case then it would be expected that goal selection occupies one particular time point during motor preparation, and effector selection another. If the effects of action on perception occur only in order to select individual functional components of the current action from other potential components (other goals, effectors, irrelevant distracters, obstacles etc.) then selection of a goal and effector at the same point in time would not be observed, since this would defeat the object of selection in the first place.

There are any number of more complicated possibilities than rapid serial selection of the components of movement. It may be that enhanced processing reflects the motor system requesting the most exquisite and detailed information available regarding the position and location of goals and effectors in order to plan the most efficient movement possible – a variation of selection for action that posits varying degrees of processing efficiency which is assumed to correlate with movement accuracy. In this view, the balance of perceptual processing reflects something like a limited processing bandwidth that can be tuned to representations of effectors and goals in order to make the most of the spatial information about them that has been gleaned from vision.

No specific predictions are made regarding the nature and purpose of goal and effector selection, since the possible permutations are endless. This experiment is able to rule out the simplest form of selection-for-action, by measuring perceptual processing separately at goal and effector locations, across three different points in time.

This was achieved by varying the temporal gap between the onset of the instructional cue, and the onset of the probe stimulus. Three different stimulus onset asynchronies (SOAs) were used: 100, 200 and 300ms. These were selected based upon both the results of the previous chapter, and the results of (Schiegg et al., 2003), which showed that the first 300ms before movement onset was the most active in terms of the perceptual effects of movement preparation.

Method

Participants

A sample of 14 participants (12 females) took part in the experiment after giving informed consent. Some were paid in cash, and some received course credit as payment for participation. Participants ranged in age from 19 to 29 (mean age was 23.4 years), all were right handed, had normal or corrected-to-normal vision and none had been diagnosed with any movement disorders. One participant was excluded from ERP analyses due to poor control over saccades and blinks, leaving a total of 13 participants.

Stimuli and apparatus

Participants carried out the movement task using a response console containing a starting position and a target for each hand. The console measured 600mm across by 400mm deep, and was shaped in a wedge such that the top face presented to the participant sloped upwards and away at an angle of 72° (see Figure 20). The experiment used the mirror system described fully in the chapter titled *Experimental Methods*.

Each starting position was comprised of a space between two rectangular blocks, wide enough for the participant to rest his or her hand flat on the console. In doing so, an infrared beam was broken between the blocks on either side of the starting position, and a signal recorded that the hand was in the ready position. This information was recorded independently for each hand.

The targets were two raised circular buttons with a radius of 20mm (3.60º x 3.79º) which could be physically depressed to trigger two micro-switches that recorded the end of each movement independently for the left and right button.

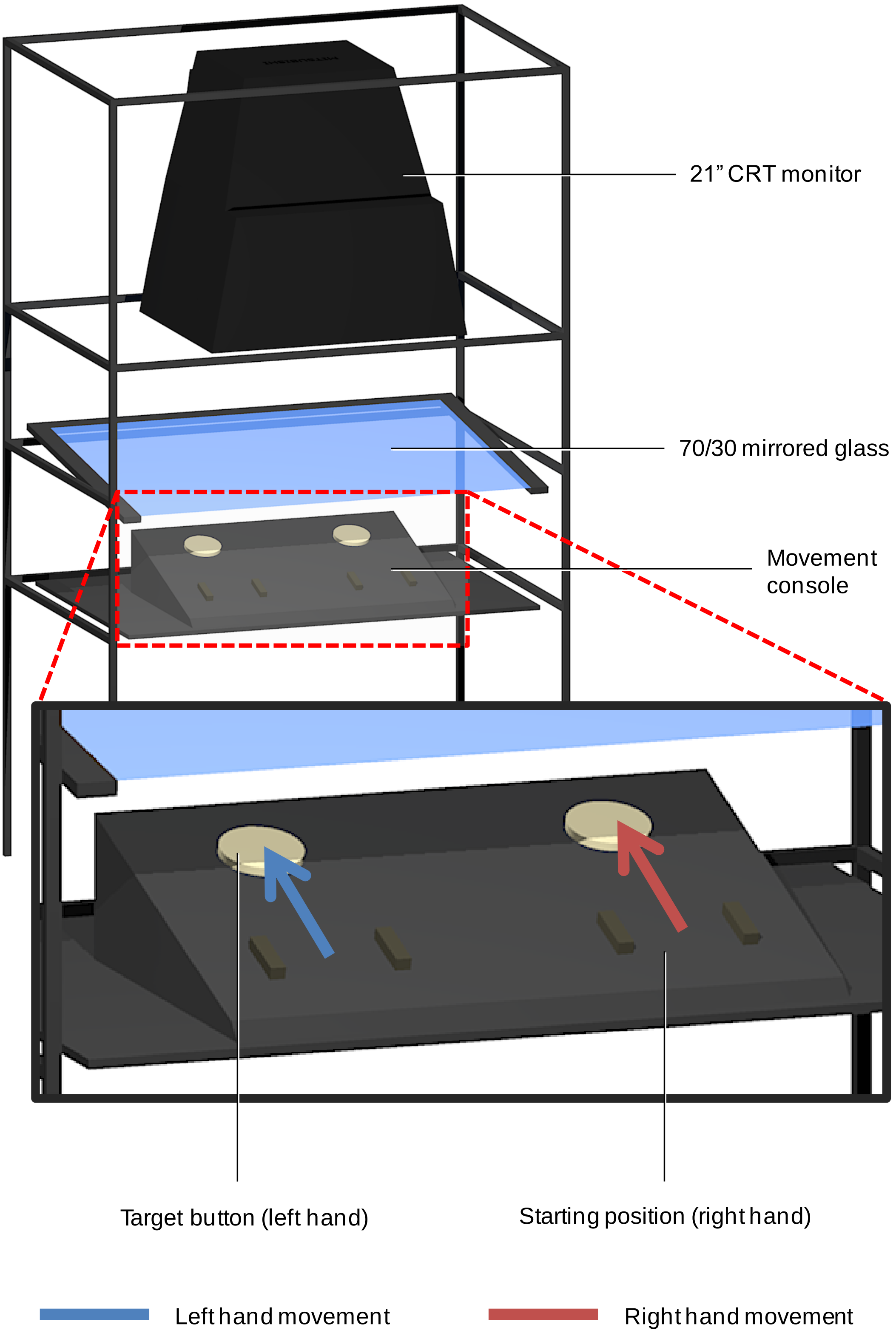


Figure 20. The movement console, shown as part of the mirror system. The participant interacted with the console, shown in detail on the bottom pane, whilst perceiving visual stimuli that were reflected on the 70/30 mirror arranged above the console. The console comprised of two starting positions, one on the left and one on the right side, upon which the participant places his or her left and right hands at the start of each trial, breaking an infrared beam which recorded the hands being in the ready position. The targets were two raised circular buttons, each arranged in a straight line away from the starting position. The movements that the participant was cued to make are shown on the figure in blue for the left hand, and in red for the right.

The mirror system served two purposes: 1) to prevent the participant from seeing his or her hand during the movement task; and 2) to allow visual stimuli to be overlaid on top of the console and the participant's hand. This was achieved by configuring the distances between the console, the mirror, and the monitor such that the participant perceived the image reflected in the mirror to be at the same apparent depth as the console. As such, any stimuli displayed on the monitor appeared to be projected directly on top of the console.

Three visual stimuli were presented in this fashion:

1) A fixation cross was displayed centrally, between the starting position and the target buttons.
2) Two white circular discs were displayed at the precise location of the target buttons. Since the experiment was carried out in the dark, this allowed the participant to see the buttons as if they were lit by normal illumination.
3) Dot probes were presented at various locations on the console (see following section for more details).

Cue

A symbolic auditory cue of 100 ms duration was employed, consisting of either a high (1000Hz) or a low (400Hz) tone. The meaning of the cue was counterbalanced across participants: for half, a high tone instructed them to move their left hand, and a low tone their right, and for the other half this mapping was reversed. Cues were presented from a speaker that was out of sight of the participant and centred so as not to bias attention to one side or another during the cueing period.

Probe

The dot-probe paradigm used in this experiment is described in detail in the chapter titled 'Experimental Methods'. The probe took the form of a white circle (0.35º x 0.36º) displayed upon either the left hand target, the right hand target, the left hand starting position or the right hand starting position. This probe elicited a visual brain response, the measurement of which formed the dependent variable for this experiment, which is described below under the section 'EEG recording and data analysis'.

Procedure

Participants sat in front of the mirror system and console in a darkened room. Instructions were presented on the surface of the mirror relating to the meaning of the auditory cue.

Participants were also instructed to keep their eyes on the fixation cross for the duration of the experiment, and to ignore the visual dot probe stimuli.

The sequence of events is summarised in Figure 21. To start the experiment, participants placed both hands on the starting positions of the console. After a random duration of between 500 and 1000ms the auditory cue sounded for a duration of 100ms. Participants moved either their left or right hand immediately after hearing the cue, and always to the target button that was directly in front of them (the hands never crossed). After an SOA of 100, 200 or 300ms post cue offset the probe was presented for 100ms at either the left hand target, the right hand target, the left hand starting position, or the right hand starting position.

In addition to an auditory cue, sound was used to give the participant feedback concerning the accuracy of his or her movement. If the wrong target button was depressed a buzzer sounded and a marker was placed upon the EEG.

At the end of each trial, the participant returned the cued hand to the starting position, alongside the uncued hand that was already there. After a random inter-trial interval of between 500 and 1000ms the next trial started. Participants sat ten blocks of 240 trials each.

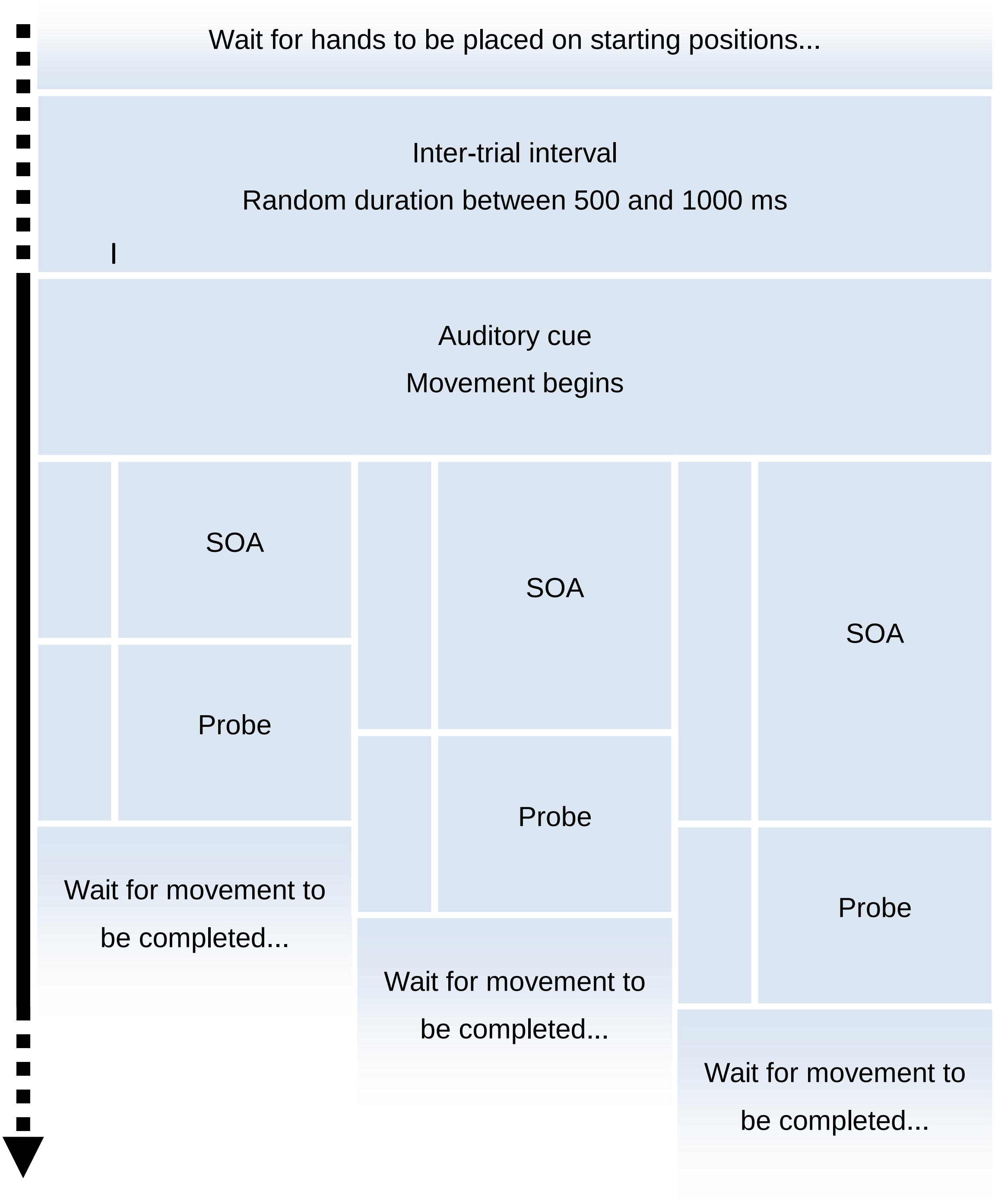


Figure 21. A graphic illustration of the sequence of events in each trial.

Data Analysis

Behavioural Analysis

Movement time and accuracy were recorded on a trial by trial basis, and separate averages were computed for each participant, and for each of the two variables *probe location* (*move-to, not-moved-to*), and *SOA* (*100, 200, 300ms*). These were analysed with repeated measures ANOVA.

EEG recording and data analysis

The EEG was filtered at a rate of 0.1 – 40 Hz using a band-pass filter, and segmented into 800ms epochs, running from 400ms before the presentation of the visual cue to 400ms after. Epochs were averaged relative to a baseline period 100ms before the onset of the auditory cue. Trials with eye blinks or movements (voltage in HEOG channels exceeding +/- 30 µV) or muscle artefacts (voltage at any other electrode site exceeding +/- 80 µV) were discarded.

Where ERPs are presented visually they are plotted relative to the onset of the visual probe. Due to three different SOAs being used, the timing of the cue onset differs depending on probe timing. The 100ms baseline window moves with the cue. Where ERPs are presented collapsed over the variable SOA, the baselines plotted will represent an averaging of 100ms baseline calculations taken across the three time windows.

ERPs were analysed within 40ms latency windows centred on the peak of each component. All results were corrected for violations of sphericity using the Greenhouse-Geisser method where appropriate.

On each trial, probes were presented either at one of the effector locations, or at one of the goal locations, and separate analyses were run for each. Within each analysis, the other variables remained the same. These were *movement preparation*, *SOA*, *hemisphere*. These variables are summarised in Table 4.

Table 4. Separate averages were computed for the following variables:

Movement preparation *(moved/not-moved)*	Participants used both hands in this experiment, and on each trial an auditory cue signalled which hand was to be moved. This variable codes whether the probe appeared on the side of space on which the participant was moving their hand (*moved*), or on the side that was not involved in a movement (*not-moved*).
SOA *(100/200/300 ms)*	Probes were presented at three different time points after the cue. *SOA* denotes which time point was probed on a particular trial. Three levels: 100, 150 or 200 ms.
Hemisphere *(contralateral / ipsilateral)*	Recorded whether the measurement of the visual evoked brain response was taken at a scalp location contralateral or ipsilateral to the visual field of presentation. A measure of the degree of lateralisation of the visual response.

Identification of ERPs

Separate averages were computed and measured for visual probe stimuli presented at the goal and effector locations. Three early visual ERPs were elicited in response to probe stimuli: a P1, N1 and P2 wave, the latencies of which differed depending upon whether they were elicited by probes at the location of the goal or the effector. The latencies of these components are listed in **Error! Reference source not found.**, the components themselves are illustrated in **Error! Reference source not found.**, scalp maps are shown in **Error! Reference source not found.**, and ERPs are shown, broken down by experimental condition, in Figure 26 and Figure 27.

Table 5. A summary of ERP latencies observed in response to visual probe stimuli, broken down by probe location, and ERP component.

	Observed peak latency (m.s.)		
Probe location	*P1(electrode P7)*	*N1(electrode P7)*	*P2 (electrode C1)*
Goal	158	208	205
Effector	130	195	235

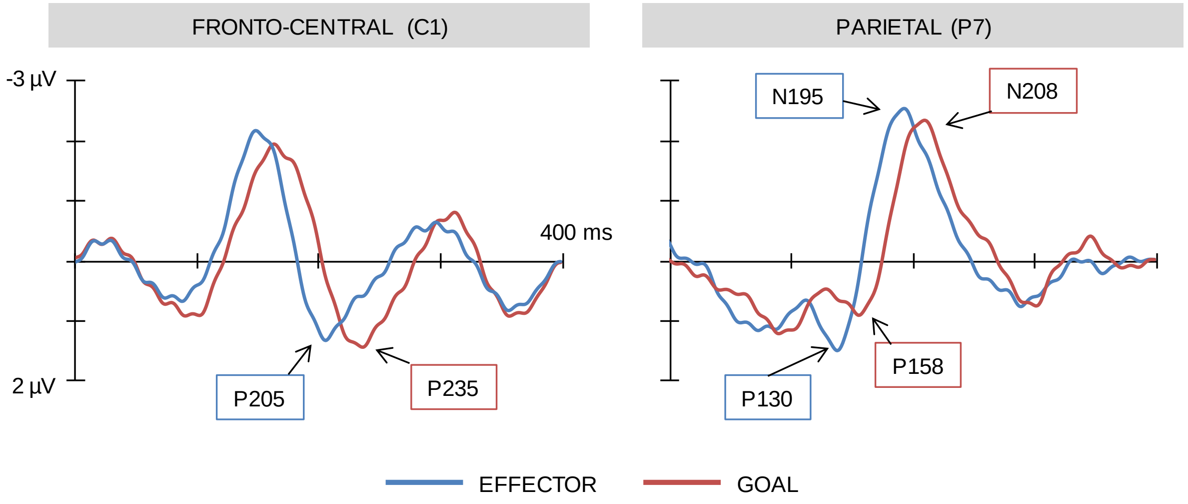


Figure 22. Two sample ERPs, elicited by visual probe stimuli presented at the effector (blue line) and the goal (red line). Note the different latencies for probes presented at the effector and goal. The left hand plot shows activity at C1, where the P2 components can be clearly observed. The right hand plot shows activity at P7, where the P1 and N1 components are observed. (The ERPs shown here represent summed activity from all SOAs and all experimental conditions).

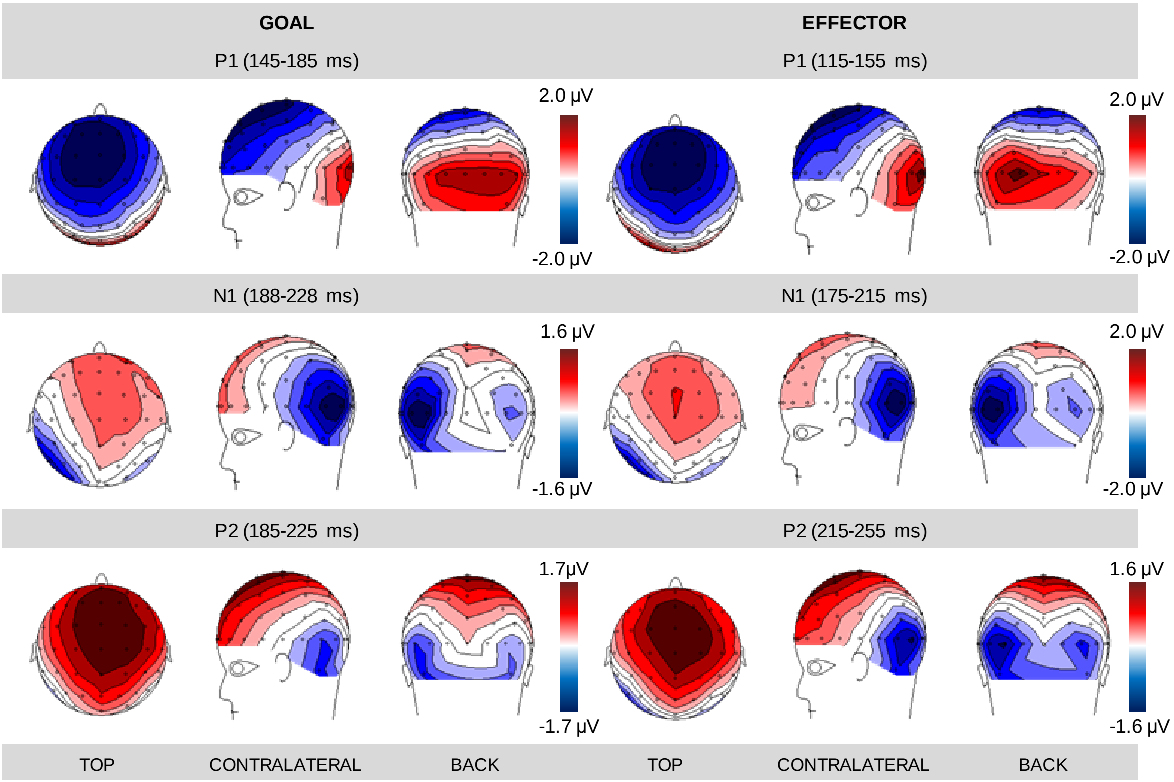


Figure 23. Scalp map showing the distribution of activity for the components reported in this section. Activity elicited by visual probe stimuli presented at goal locations are shown on the left hand column, activity from probes presented at effector locations are shown on the right hand column. The P1 components are shown on the top row, N1 components on the middle row, and P2 components on the bottom row. Scalp maps shown here represent the average activity across all three SOAs and across conditions in which a movement was and was not being prepared toward the visual probe.

Results

Behavioural results

Summary of behavioural results

Behavioural data was analysed in order to ascertain whether any of the experimentally manipulated factors affected movement speed and accuracy. These factors were *probe location* (whether the probe fell on the side of the currently cued movement, or not) and *SOA.* They were analysed separately for probe stimuli presented on goal and effector locations.

Movement time and accuracy was affected by *probe location* both when the probe was presented at the goal and at the effector, with movements on the probed side being faster and more accurate than those on the un-probed side.

Movement times also varied by SOA. For probes on the goal, movements were faster at each of the three SOAs, but more so at 100ms than at 200 or 300 ms. For probes on the effector, movements were only faster at the 100 ms SOA.

Behavioural measures of movement time (relative to the onset of the cue) and reaching accuracy were recorded. Trials with movement times longer than 1500ms or shorter than 400ms were discarded. The mean time to complete a movement from the starting position to the target was 823ms (SD=218ms), and the median time was 786ms. The distribution of movement times is presented in Figure 24.

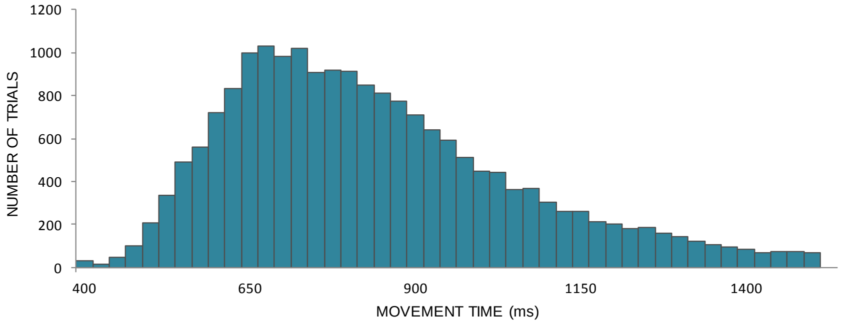


Figure 24. The distribution of movement times. Trials with movement times below 400ms or above 1500ms were discarded.

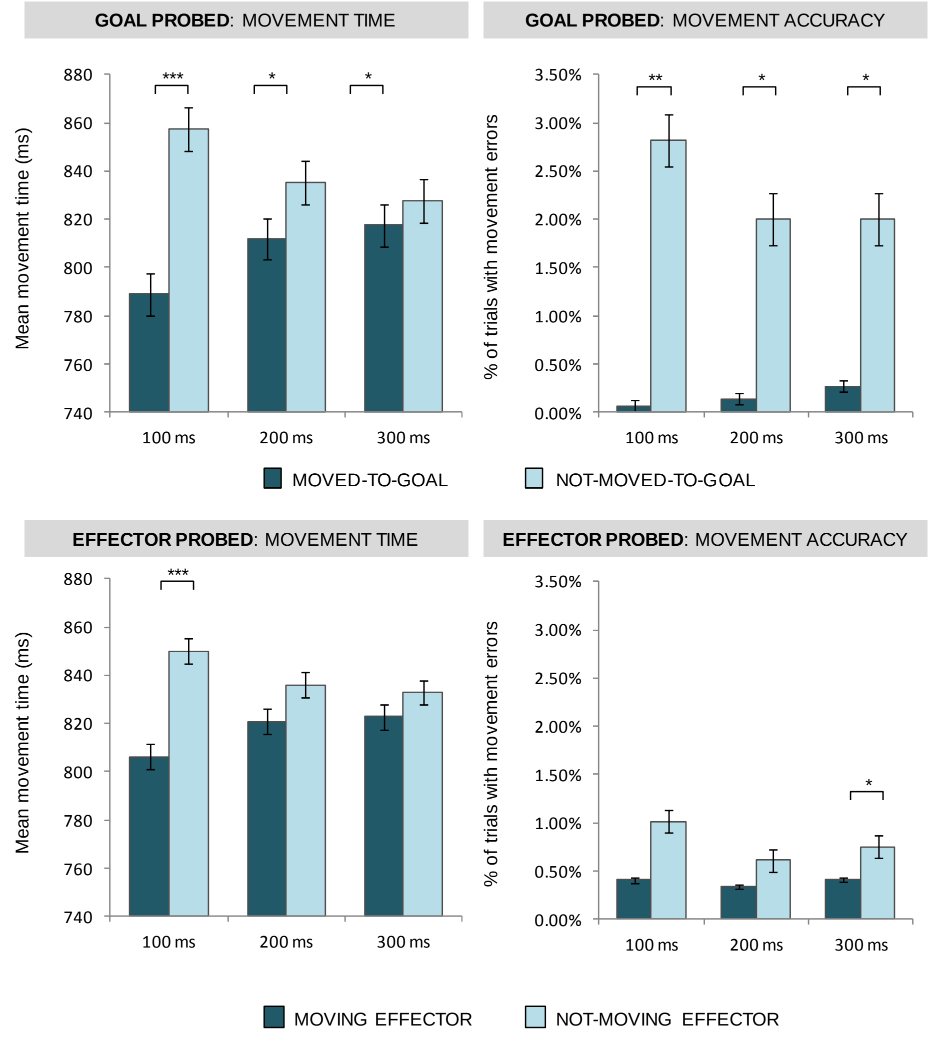
Each dependent variable was analysed with repeated measures ANOVA, separately for probes presented at the location of the effector and the goal, using the factors *probe location* (*moved-to*, *not-moved-to*), and *SOA* (*100, 200, 300ms*). The results are illustrated in Figure 25.

Effects on movement of probes presented at the goal:

Movements to the goal upon which the probe was presented were more accurate than those to the un-probed goal, F(1,12)=9.628, p=.009; they were also faster, F(34.164), p<.001. *Probe location* interacted with *SOA* for movement times, F(2,24)=31.509, p<.001, but not for accuracy, F(2,24)=1.916, p=.169. Post-hoc t-tests compared movement times for probed and un-probed goal trials, separately for each SOA. Movements were faster for the trials on which the goal was probed at 100 ms, t(12)=8.209, p<.001, 200 ms, t(12)=2.939, p=.012, and 300 ms, t(12)=2.615, p=.023.

Effects on movement of probes presented at the effector

Movements using the effector that was probed were more accurate than those using an un-probed effector, F(1,12)=8.540, p=.013; they were also faster, F(1,12)=23.825, p<.001. *Probe location* interacted with *SOA* for movement times, F(2,24)=7.398, p=.003, but not for accuracy, F(2,24)=.316, p=.732. Post-hoc t-tests compared movement times using the probed vs the un-probed effector separately for each SOA. Trials in which the probe was presented at 100 ms were faster when using the probed vs the un-probed effector, t(12)=5.885, p<.001, but not those in which the probe was presented at 200 or 300 ms, all t's(12)<2.005, all p's>.068.



**p<.05 ; **p<.01; ***p<.001*

Figure 25. The effects of *probe location* and *SOA* on movement times (left hand side) and accuracy (right hand side) for trials in which probes were presented on the goal (top) and effector (bottom). The results of separate post-hoc t-tests for each SOA on pairs of movement/no-movement conditions are shown.

ERPs elicited in response to visual probe stimuli

Summary of ERP results

A P1, N1 and P2 component was identified in response to the task-irrelevant visual probe stimuli:

N1: Probes on the goal showed enhanced processing at movement targets across all three SOAs. Probes on the effector only showed this enhanced processing effect at the middle (200ms) SOA.

P1: Larger components were observed for probes on the goal that was not a movement target. No such effect was seen for probes on the effector. Neither probe type showed any effect of SOA.

P2: A similar pattern was observed for the P2 component, with probes on the goal and effect not involved in movement being larger. This effect interacted with hemisphere and SOA.

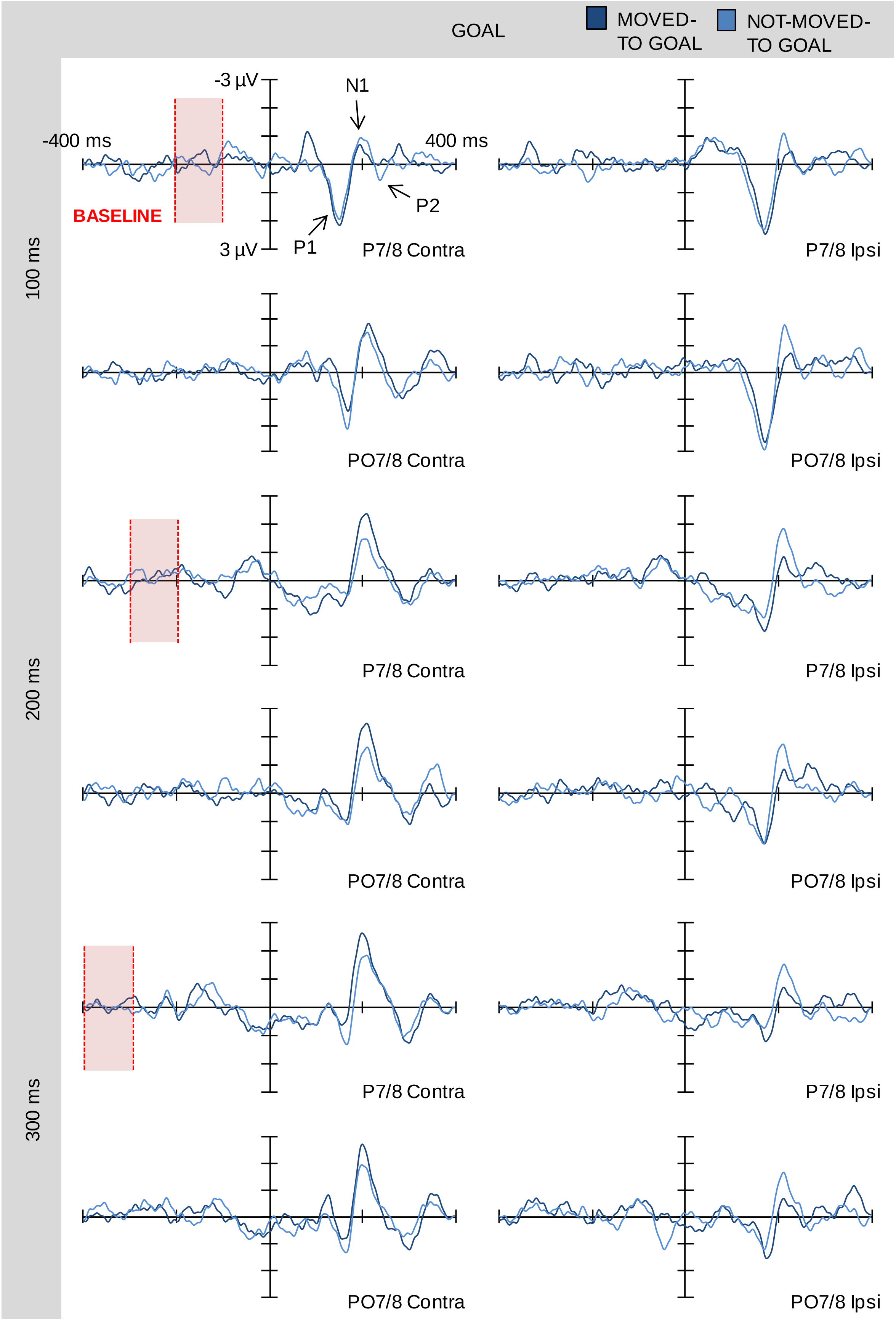


Figure 26. A selection of ERPs from the scalp region at which the N208 component was observed. Separate lines show ERPs elicited by visual probe stimuli presented at the location of the goal, at 100ms (upper panel), 200ms (mid panel) and 300ms (lower panel) after the onset of the auditory cue. Dark blue lines represent ERPs elicited by probes that were presented on the goal that was being moved to, light blue lines represent ERPs elicited by probes presented on the goal that was not being moved to. ERPs are plotted relative to a moving 100ms baseline window, starting before the onset of the auditory cue (marked in red).

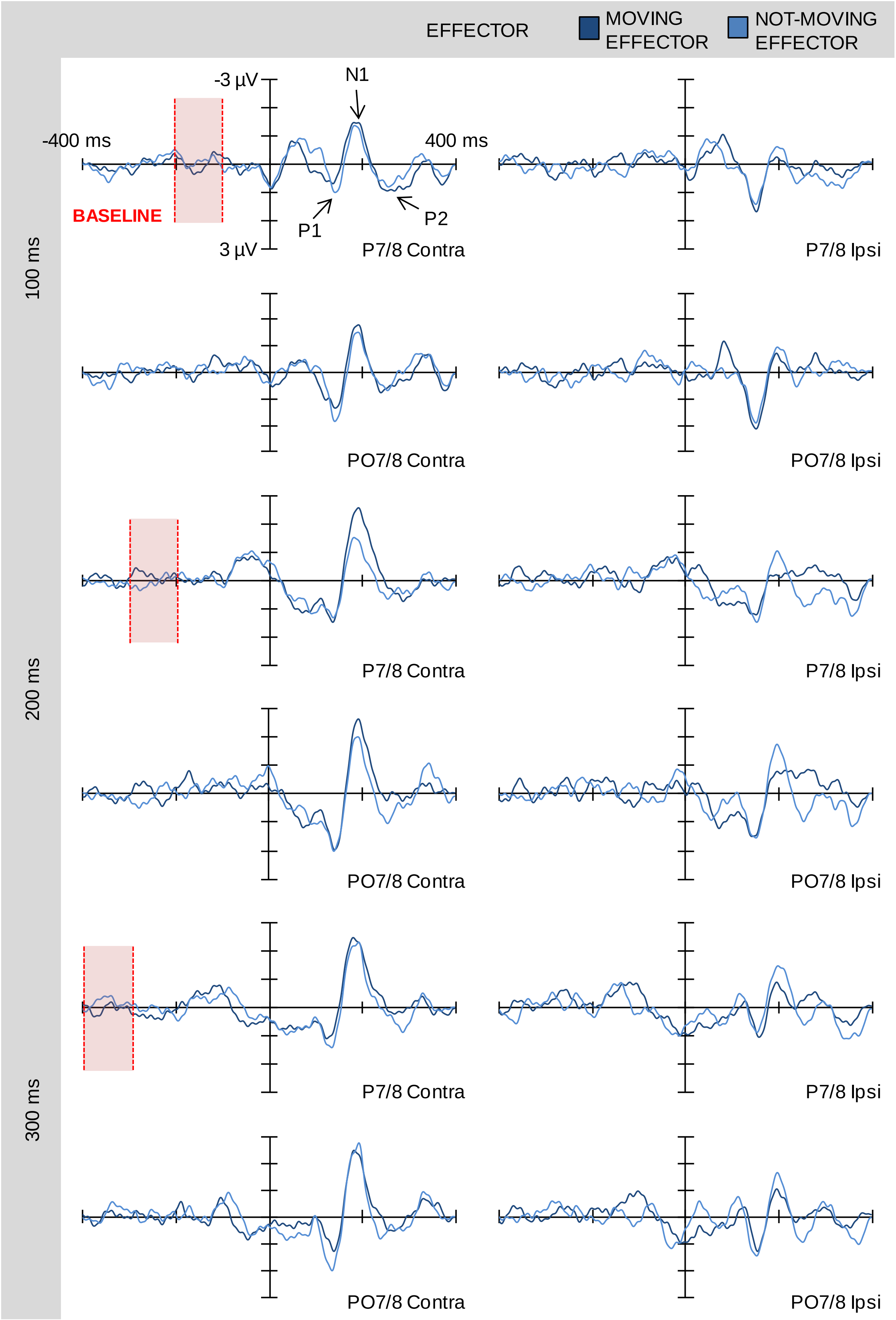


Figure 27. A selection of ERPs from the scalp region at which the N195 component was observed. Separate lines show ERPs elicited by visual probe stimuli presented at the location of the effector, at 100ms (upper panel), 200ms (mid panel) and 300ms (lower panel) after the onset of the auditory cue. Dark blue lines represent ERPs elicited by probes that were presented on the goal that was being moved to, light blue lines represent ERPs elicited by probes presented on the goal that was not being moved to. ERPs are plotted relative to a moving 100ms baseline window, starting before the onset of the auditory cue (marked in red).

The N1 components (N195, N208)

The N1 components elicited by probes presented at goals and effector locations showed a very similar scalp distribution, with a relatively focused area of lateralised negativity centred on parietal regions, maximal at P7/8 and PO7/8 contralateral.

N1 ERPs elicited by probes presented at the goal location:

Figure 28 shows the data from Figure 26 re-plotted in bar chart form. For contralateral electrode sites, a general pattern was observed of larger N1 amplitudes for probes presented at the goal of an upcoming movement, as compared to goals that were not a movement target. For ipsilateral electrode sites, this pattern appears to be reversed.

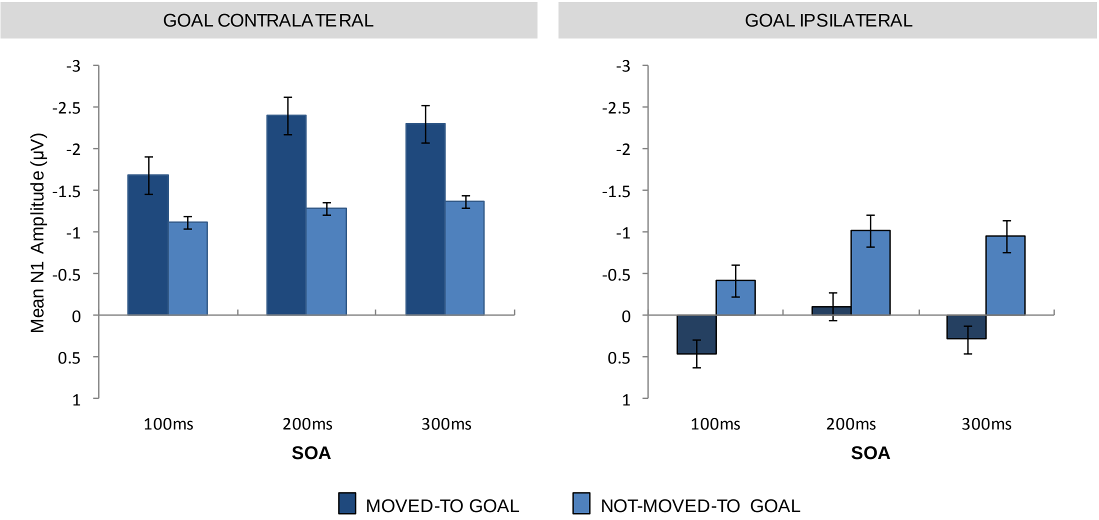


Figure 28. Mean amplitudes of the N1 component at electrodes P7/8 and PO7/8, elicited by visual probes presented at each of the two possible goal locations, shown separately for those goals that were the target of an upcoming movement (dark blue) and those goals that were not (light blue). A different pattern of results was recorded at electrode sites contralateral (left panel) as compared to ipsilateral (right panel) to the side of presentation. Mean N1 amplitudes are shown separately for each of the three SOAs between the onset of the auditory cue and the onset of the visual probe stimulus

These observations were followed up by repeated measures ANOVA, using the factors *hemisphere*, *SOA* and *probe location* (*moved-to, not-moved-to*). The main effect of *probe location* was not significant, F(1,12)=.204, p=.803, however *probe location* did interact with *hemisphere*, F(1,12)=11.339, p=.006. This interaction was followed up by post-hoc paired samples t-tests comparing the moved-to goal with the not-moved-to goal, separately for electrodes on the contralateral and ipsilateral hemisphere. Probes presented at a moved-to goal location elicited larger ERPs than at the goal that was not-moved-to, t(12)=4.345, p=.001, for contralateral electrodes. This pattern was reversed, and only marginally significant for electrodes on the ipsilateral hemisphere, t(12)=1.922, p=.079.

The significant main effect of *hemisphere*, F(1,12)=12.777, p=.004, confirmed the lateralised nature of the N1 component, with larger N1 amplitudes recorded at electrode sites contralateral to the side of probe presentation.

The main effect of *SOA* was not significant, F(2,24)=1.881, p=.174, and nor did it interact with any other variables, all F's(2,24)<.347, all p's > .690, indicating that the timing of the visual probe stimulus, relative to the onset of the cue, did not alter the amplitude of the elicited N1 components, and did not alter the pattern of N1 amplitude's caused by other variables.

N1 ERPs elicited by stimuli presented at the location of the effector:

Figure 29 shows the data from Figure 27 re-plotted in bar chart form. For contralateral electrode sites, a general pattern was observed of larger N1 amplitudes for probes presented at the location of an effector involved in an upcoming movement, as compared to effectors that were not involved in movement, however this effect appears to be contingent upon the SOA between the cue and the visual probe stimulus. For ipsilateral electrode sites, the pattern of movement induced modulation appears to be reversed, such that probes presented at the location of the unused effector elicit larger N1 amplitudes, and the SOA appears to have no effect.

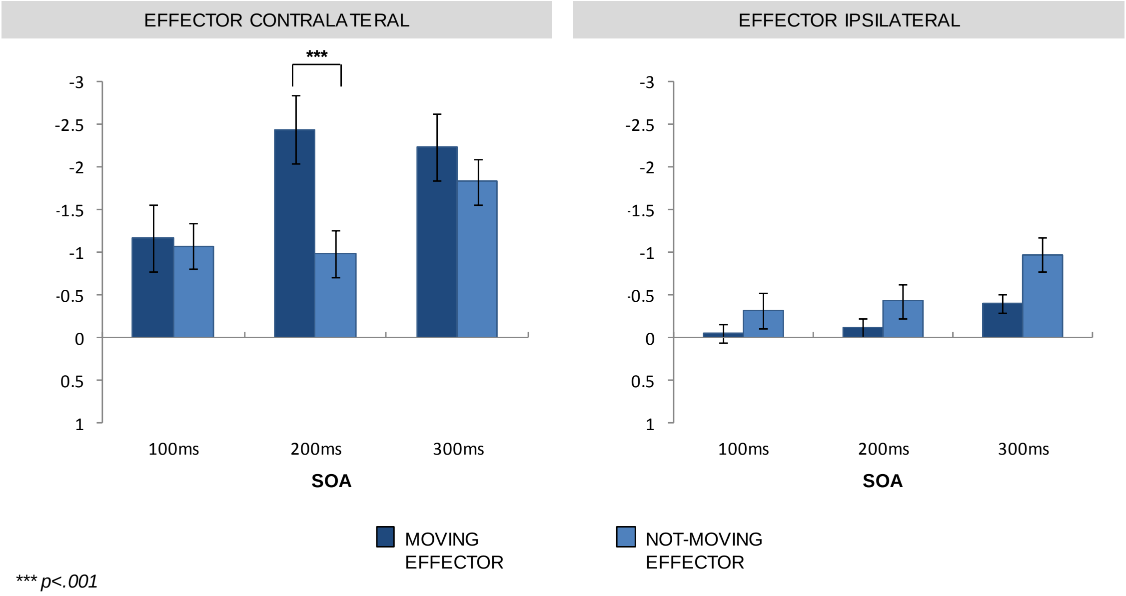


Figure 29. Mean amplitudes of the N1 component at electrodes P7/8 and PO7/8, elicited by visual probes presented at each of the two possible effector locations (pooled across left or right hand), shown separately for effectors that were about to be used in an upcoming movement (dark blue) and those effectors that were not (light blue). A different pattern of results was recorded at electrode sites contralateral (left panel) as compared to ipsilateral (right panel) to the side of presentation. Mean N1 amplitudes are shown separately for each of the three SOAs between the onset of the auditory cue and the onset of the visual probe stimulus. The results of separate post-hoc t-tests on moving/not moving pairs for each SOA are shown for the contralateral hemisphere only.

These observations were followed up by repeated measures ANOVA, using the factors *hemisphere*, *SOA* and *probe location* (*moving effector*, *not-moving effector*). The main effect of *probe location* was not significant, F(1,12)=.402, p=.538, but *probe location* did interact with *SOA*, F(2,24)=3.940, p=.047, and with *hemisphere*, F(1,12)=15.686, p=.002.

Post-hoc paired samples t-tests were performed on the *probe location* x *hemisphere* and *probe location* x *SOA* interactions, by comparing the amplitude of the N1 ERP for probes presented at the moving and the not-moving effector for each SOA, and for each hemisphere separately. The difference in amplitudes measured at electrodes ipsilateral to the side of presentation of visual probes was not significant, t(12)=1.387, p=.191, but was significant when measured at contralateral electrode sites, t(12)=3.353, p=.006.

When pooled across contralateral and ipsilateral electrodes the difference at the 200ms SOA was marginally significant, t(12)=2.016, p=.067, but was not significant at the 100ms and 300ms SOA, both t's(12)<.400, both p's > .696. Given the lateralised nature of the visual N1 ERP, these post-hoc tests were also performed on data recorded only at the contralateral electrodes. As before, the difference between the moving and not-moving effector was not significant at the 100ms and 300ms SOAs, both t's(12)>-1.195, both p's > .255, but at 200ms the difference was significant, t(12)=4.366, p=.001.

The P1 components (P135, P165)

The scalp distributions appeared to differ between P1 ERPs elicited by probes presented at the location of the goal and those presented at the effector (see **Error! Reference source not found.**, p. **Error! Bookmark not defined.**). Both probe locations elicited ERPs that were maximal at parietal-occipital locations, but ERPs elicited by probes at the effector showed a more contralateral distribution, maximal at electrodes O1/2, P7/8 and PO7/8 contralateral, than those elicited by probes at the goal, which were maximal at electrodes O1/2, PO3/4 and PO7/8.

The ERPs in Figure 26 (p. 98) and Figure 27 (p. 99) show a larger P1 component for ERPs elicited by probes presented at the goal location that is *not* the target of an upcoming movement, but no clear pattern for ERPs elicited by probes presented at the effector that either is, or is not, about to move. These data are illustrated in Figure 30, and were subjected to separate ANOVAs for ERPs elicited by probes presented at the goal and at the effector, with the factors *hemisphere, SOA* and *probe location* (*moved, not-moved goal/effector*).

The main effect of *probe location* was significant for probes presented on the moving vs the not moving goal, F(1,12)=4.724, p=.050, but not for probes presented at the effector, F(1,12)=1.595, p=.231. The main effect of *hemisphere* was also significant for probes presented at goal locations, F(1,12)=8.604, p=.013, but not at effector locations, F(1,12)=1.635, p=.225.

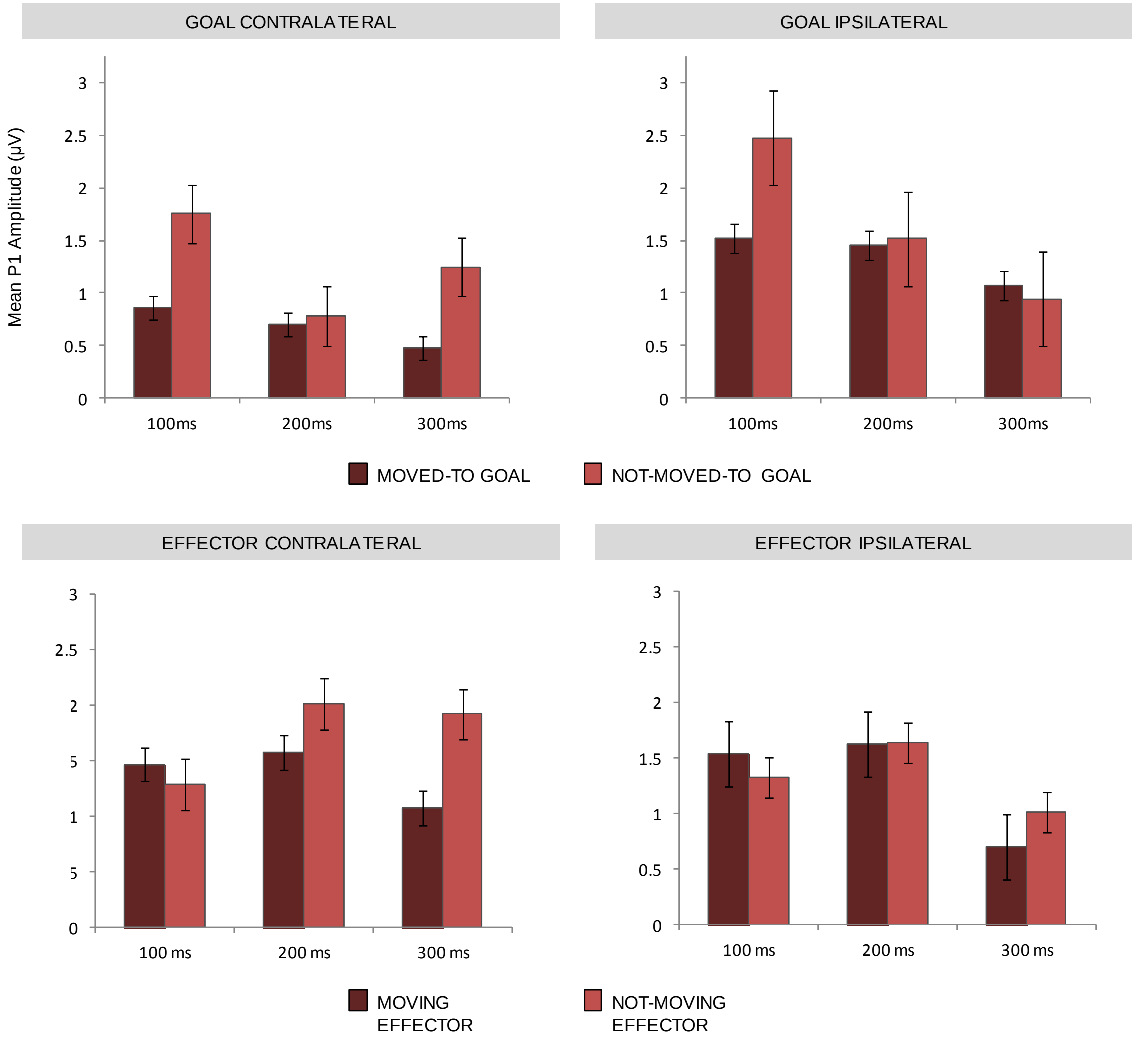


Figure 30. The effect of *probe location*, *SOA* and *hemisphere* on P1 amplitudes, shown separately for ERPs elicited by probes presented at the goal (O1/2, PO3/4, PO7/8; top row) and effector (O1/2, P7/8, PO7/8; bottom row).

The interaction between *SOA* and *hemisphere* was significant for ERPs elicited by probes presented at the goal, F(2,24)=4.135, p=.029, and marginally significant for ERPs elicited by probes presented at the effector, F(2,24)=3.355, p=.052. The use of differing SOAs resulted in differing degrees of overlap between the auditory N1 ERP elicited by the cue, and the visual evoked potentials elicited by the probe. Due to the summative nature of ERPs, this interaction is not unexpected but is not of any relevance to motor planning, and so will not be considered further.

The P2 components (P205, P235)

Figure 31 (below) presents a selection of ERPs showing the P2 components, which were broadly distributed over fronto-central electrodes. Only a very slight degree of lateralisation was observed. The components were maximal at FCz, and a separate ANOVA for ERPs elicited by probes presented at the goal and effector was performed on the mean P2 amplitudes measured at a sample of electrodes: F1, F2, FC1, FC2, C1, C2. The variables entered were *hemisphere, SOA* (*100, 200* and *300ms*), *probe location* (*movement, no movement).*

The P2 components overlapped to some extent with the N1 components. The N1 showed an earlier latency at front-central electrodes as compared to parietal, such that the P2 components peaked, at central electrodes, only 20ms later than the N1 peak measured at parietal and occipital electrodes. **Error! Reference source not found.** (p. **Error! Bookmark not defined.**) shows the distributions of the P2 components, and the later stages of the N1 can be seen on these maps at posterior electrode sites. However, the distribution of the P2 is relatively separate at fronto-central sites, and the peak can clearly be seen on the ERP plots.

The main effect of *probe location* was significant for ERPs elicited by probes presented both at the goal, F(1,12)=13.690, p=.003, and the effector, F(1,12)=5.544, p=.036, with larger P2 amplitudes at the goal that was not about to be moved to, and the effector that was not about to move.

This was followed up by post hoc paired-samples t-tests comparing *probe location* (*movement, no-movement*) separately for each SOA, and for ERPs elicited by probes presented at the goal and the effect. Larger P2 amplitudes were elicited by probes on the goal that was not about to be moved toward at the 200ms, t(12)=3.409, p=.005, and 300ms, t(12)=4.002, p=.002 SOA when measured over the contralateral hemisphere, and only at 100ms, t(12)=2.693, p=.020, over the ipsilateral hemisphere.

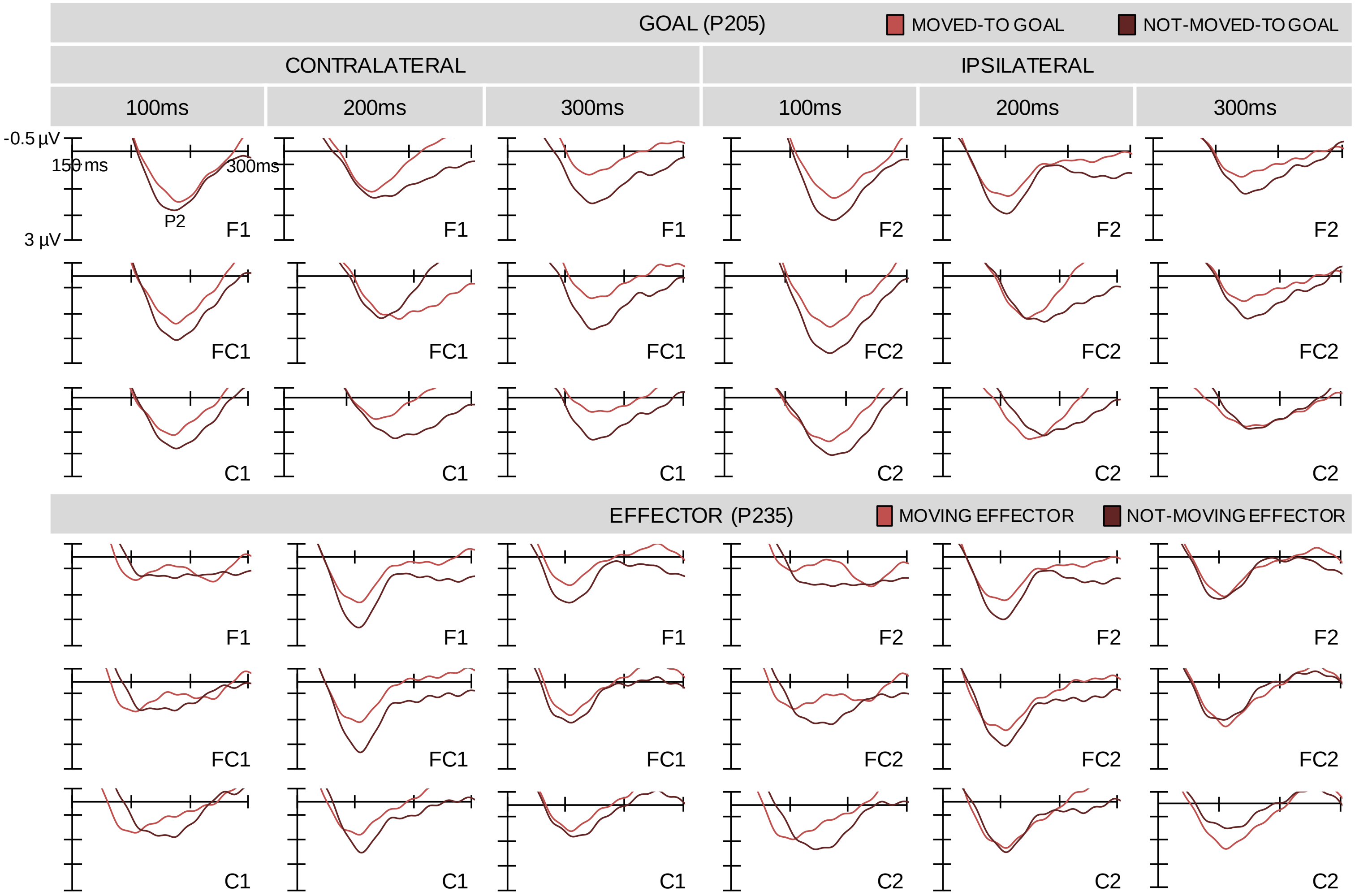
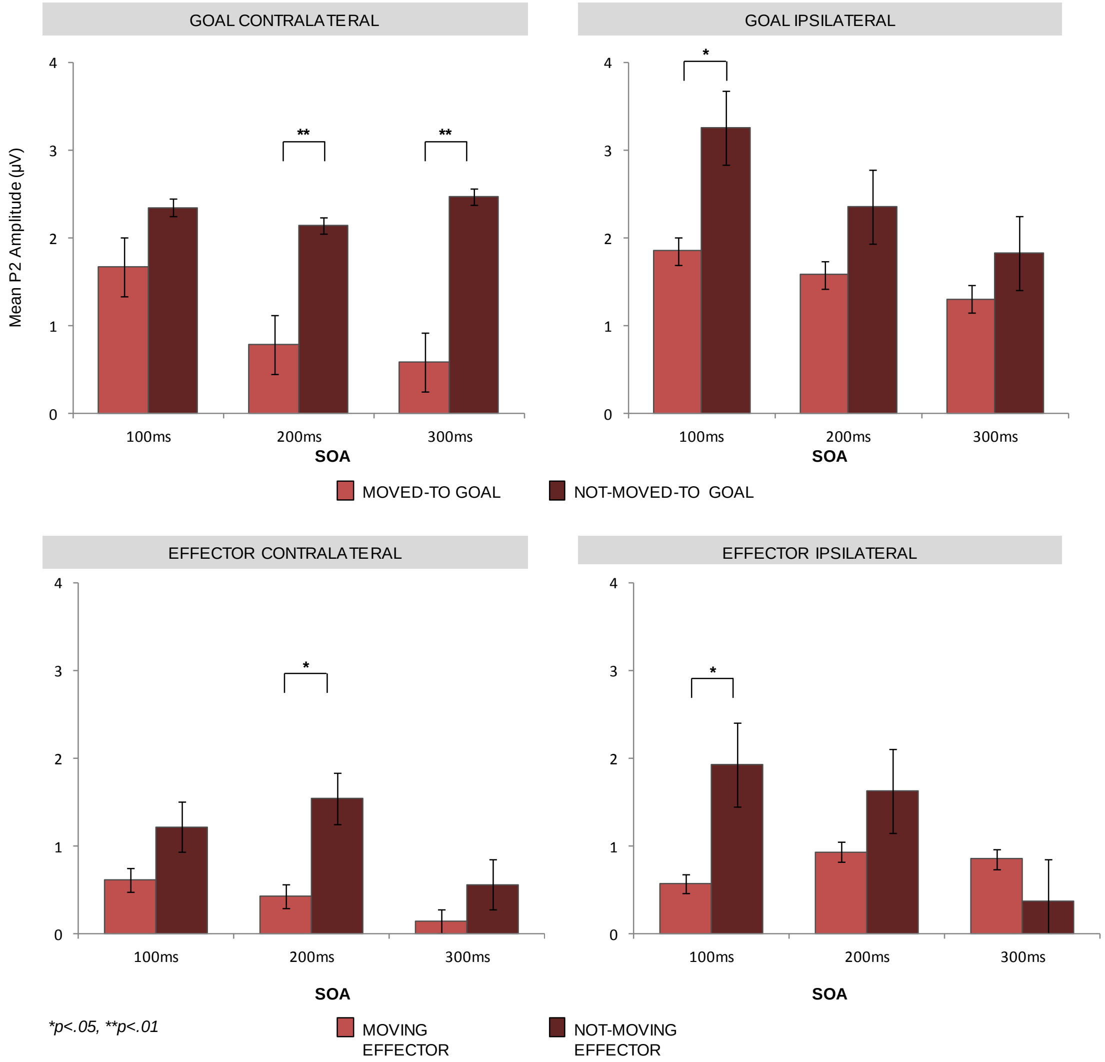


Figure 31. The selection of electrodes at which the P2 component was maximal, broken down by SOA, hemisphere, and probe location (light red lines indicate a goal or effector location involved in an upcoming movement, dark red lines a location *not* involved in an upcoming movement).

Probe location interacted with *hemisphere* and *SOA*, for ERPs elicited by probes presented at the goal, F(2,24)=14.494, p<.001, and at the effector, F(2,24)=7.604, p=.003.



**p<.05, **p<.01*

Figure 32. The interaction between *hemisphere, SOA,* and *probe location,* for electrodes F1/2, FC1/2 and C1/2, shown separately for ERPs elicited by probes presented at the goal (top row) and the effector (bottom row).

ERPs elicited by probes on the effector that was not about to move were larger than those elicited by probes on the effector that was about to move at the 200ms SOA, t(12)=2.295, p=.041 over the contralateral hemisphere, and at the 100ms SOA, t(12)=2.678, p=.020, over the ipsilateral hemisphere.

The main effect of *hemisphere* was significant for ERPs elicited by probes presented at the goal, F(1,12)=22.953, p<.001, and at the effector, F(1,12)=8.623, p=.012. In both cases, P2 amplitudes were larger in the ipsilateral hemisphere.

For probes presented at the goal location, the variables *hemisphere* and *SOA* interacted, F(2,24)=4.595, p=.020. Given the nature of the procedure, in which cue-elicited auditory

ERPs overlap to a greater or lesser degree depending upon the SOA, and due to the overlap between the N1 and P2 waves and the absence of an interaction with *probe location* – which is the variable of primary interest to these experiments – this interaction is not considered meaningful and was not followed up.

Discussion

The aims of this experiment were twofold: 1) to investigate whether visual processing was biased in favour of the goal, the effector, or both; and 2) to ascertain whether, and to what extent, the effects on visual processing of motor preparation change over the time-course of motor preparation.

Participants were cued to make a forward reaching movement, with either their left or right hand, from a starting position in near space to a target button directly in front of them. Visual processing was measured by presenting a task-irrelevant probe stimulus at one of four locations: the target location that was the goal of an upcoming movement, or the target location that was not; or the location of the effector that was about to be used in an upcoming movement, or the location of the effector that was not. These probes were presented at three different SOAs in the time-course of movement preparation, 100, 200 or 300ms after the onset of the cue.

The effects of motor preparation on visual processing

The amplitudes of the visual P1, N1 and P2 components elicited by these probe stimuli were measured, and comparisons made – separately for goal and effector, and for each SOA – for locations that were involved in an upcoming movement and those that were not. The following discussion will focus first on the pattern of modulation of the N1, since this is the component that has most often and most reliably been used as an index of visual processing.

Movement preparation and visual processing at goal and effector locations

Motor preparation affected visual processing at the location of the goal in precisely the way predicted by the Premotor Theory (Rizzolatti et al., 1994), and the Visual Attention Model (Schneider, 1995): target locations that were the goal of an upcoming movement showed enhanced visual processing, as compared to targets that were not involved in movement. The simplest and most parsimonious explanation for this data alone is in terms of selection-for-action: two possible target locations existed within the parameters of this movement paradigm, and the participant selected the appropriate one, based upon information provided by the cue. The neural representation of this target was then facilitated and/or the neural representation of the competing target, inhibited (cf. Duncan, Humphreys, & Ward, 1997). So far, this finding is completely in line with behavioural measures of movement-induced shifts of attention at the goal of a movement (e.g. Deubel, Schneider, & Paprotta, 1998).

A similar pattern of results was also observed at the location of the effector. This is the first time that enhanced processing has been shown simultaneously at both the goal and effector; previous work has shown enhancement at the goal (e.g. Deubel et al., 1998) *or* at the effector (e.g. Forster & Eimer, 2007). This suggests that, at the very least, selection-for-action is not a serial process that first selects one component of movement (e.g. the goal), then deselects it and selects the next component (e.g. the effector). Rather like the work that has shown that, during sequences of manual movements, multiple goal locations are selected in parallel (Baldauf & Deubel, 2008a; Baldauf et al., 2006), the results from the present experiment are more compatible with the idea that motor preparation sets up an attentional field, comprised of patterns of facilitation and perhaps inhibition, that serves the purpose of selecting goals and effectors (see the next experimental chapter for more evidence on this).

A difference between the pattern of data measured at goal and effector locations was in how the effect developed over time. The effect of motor preparation on the effector was only observed at the middle (200ms) SOA, unlike at goal locations where the biasing of perception to movement related locations was consistent across all three SOAs. A bias towards the goal seems to occur, in terms of enhanced processing being more sustained across time at its location, compared to the effector.

A very simple interpretation in terms of selection-for-action would be that the visual system is rapidly selecting a representation of the goal object or location in order to make its spatial coordinates – which derive from vision – available to the motor system in order to plan a movement. Here attention is operating much like the operator of a computer, who clicks on and selects one object out of many on which to perform further computation. A pattern of results in which probes on the moved-to goal showed enhanced processing at one SOA, and on the moving effector at another, would be compatible with this form of serial selection. The present results, in which the bias toward the goal remains constant and the bias toward the effector comes and goes over time, is not.

Task instructions

Of course the goal and effector are not equivalent components of movement in this paradigm. Firstly, the participant has to interpret the meaning of the cue, and to select the goal location amongst two possible targets simply in order for the instruction to have been said to be understood – before anything to do with movement occurs. The instructions given to the participant were, after all, to press a particular *button* (goal), not to move a particular *hand* (effector). Gherri, Van Velzen, & Eimer (2009) have shown that task instructions can, by emphasising one component of movement over the other, bias processing to either the goal or the effector, and it is quite possible that something similar is occurring here. However, the simultaneous enhancement of processing at both the goal and effector locations when measured at the middle SOA suggests that the influence of task instructions can only go so far to explain these results: if instructions shift the balance of processing between goal and effector, it does not seem likely that they can be invoked in order to explain enhanced processing at both at the same time.

Greater functional significance of the goal

It could be argued that there is something special about goal locations, from the point of view of the participant. If one is performing a movement that requires accuracy, such as threading a needle, it feels necessary to *concentrate* on the goal of the movement (the eye of the needle), as compared to the position of the hand that is holding the thread. The potential for distraction by an irrelevant *effector* in such a situation is presumably much smaller, given that we have only two hands, but a potentially limitless number of goal/distracter objects to take into account. Perhaps some form of effortful concentration on the goal sets up and maintains an attentional state that becomes apparent in this experiment by enhanced goal processing across all three SOAs, but no such broad effect at the effector? This is highly speculative, and difficult to investigate experimentally, since it is hard to think of a way of manipulating the functional significance of a goal location. If the goal receives enhanced processing over other components of movement such as the effector – merely by virtue of *being* the goal of the movement – then the temporal bias observed here may be explained.

The (supra?)modality of attention-induced changes in perceptual processing

It is important to consider the fact that participants could not see their hands during this experiment, whereas the goal remained visible throughout (even times when the hand would, in everyday life, obscure the goal). Is it plausible to explain the observed temporal goal bias in terms of the participants having visual access to the goal, but not to the effector?

We do not generally find it necessary to glance at our hands before reaching out to grasp something, and the behavioural performance in this task suggests that a lack of visual access to the effector is no barrier to efficient movement. It cannot be argued that a *visual* probe is an inappropriate measure of the perceptual processing of the *proprioceptively* guided effector, since at the middle SOA the visual probe was quite able to measure such processing: either the effects of action on perception are purely visual, in which case the effector should be essentially invisible to the visual probes used in this experiment, or they are not, in which case we are no closer to an adequate explanation for the temporal goal bias.

Another possibility is that movement is functionally broken down into two phases, a period of motor preparation, which requires information relating to the position of both the goal and the effector in order to set up the motor programme, and a period of execution, in which the effector is guided towards the goal by proprioceptive feedback. This account of motor control would explain the brief bias toward the effector at the middle SOA as belonging to the planning phase, whereas the broader bias to the goal, at all SOAs, would be argued to occur as a consequence of the execution phase needing to focus on an ongoing target toward which to make constant corrections to the trajectory of the effector based upon proprioception.

The suitability of this explanation to the present results depends largely in which perceptual modality motor preparation occurs. Guidance to the goal during such a hypothetical execution phase would originate in vision, since this is how the participant detects the goal in the first place. If guidance of the effector occurs by proprioception alone, then perhaps the visual representation of the effector is not activated, and so this experiment – using, as it does, visual probes to measure attention - cannot get a ‘read’ of whether or not the effector is still being ‘taken into account’ at later stages of movement.

The visual representation of the effector is clearly being activated in the planning phase, however, since this experiment can successfully measure – via a visual probe – enhanced processing on the effector at the middle SOA. The only explanation for how participants located their hand at the start of each trial was via proprioception in the planning phase, and yet the effector showed up when probed, so positing an execution phase in which proprioception guides the effector to the goal *without* it showing up to this experiment begs more questions than it answers.

In fact, these results are a confirmation that the effects of action on perception are not limited to one sensory modality, but occur at a supramodal level of processing. Previous accounts of these effects have shown that visual probes are just as suitable for measuring action-induced changes in perception during purely visual tasks like saccades as they are at the effector for proprioceptive tasks such as lifting a finger (Eimer et al., 2006), or making a reaching movement (Gherri et al., 2009; Van Velzen et al., 2006). An argument *against* supramodal (as opposed to purely visual) effects of action could be mounted that emphasises that participants in these studies could see their hands, thus bringing them into the visual domain. Work in monkeys contradicts this; Graziano (1999) demonstrated the existence of multimodal neurons in the animals' premotor cortex that respond both in the visual modality to the sight of the limb, and in the tactile modality to touches on the limb, or to both. This finding, along with the results of the present experiment, suggest that motor processes do indeed operate at a supramodal level of representation.

The use of starting positions

Participants started the experiment with their hands on two starting positions, were cued to reach to one goal or another, and then returned their hands to the starting position in readiness for the next trial. Visual processing at the goal was measured by probes presented at goal locations, and at the effector by probes presented at the starting position.

Although participants were explicitly instructed to plan and execute a movement to one of the two goal locations, implicitly they knew that they must then return their hand to the starting position, in order for the next trial to begin. This can be viewed as a two stage sequence of movements, from the starting position, to the goal, and back again. Previous work has shown that, in sequences of movements to multiple goals, enhanced processing can be measured at each goal in parallel before the first stage of the sequence has been executed (Baldauf & Deubel, 2008b; Baldauf et al., 2006). In this light, the movement task in this experiment can re-framed as a sequential movement involving two goals, the target location that is reached towards, and the starting position that the hand is returned to.

The present experiment is not able to conclusively rule out this possibility (it is addressed methodologically in the next chapter). The studies referred to above did not probe the time course of visual processing during motor preparation, whereas the present experiment did. The starting position in this experiment showed enhanced processing only at the middle, 200ms, SOA, in contrast to the goal location that was enhanced at all three probe timings. This is evidence for a functional difference between the effector and goal locations, which is not conducive with the suggestion that the starting position was treated as another goal location in a sequential movement.

The P1 and P2 components

The P1 and P2 components showed a pattern of results that is, on the surface, quite puzzling. The effect is elicited by attentional tasks employing attended, unattended and, importantly, neutral conditions. The N1 component to probes presented in the neutral condition is smaller compared to probes presented at attended locations; the N1 can thus be said to reflect the ‘benefits’ or attention. The P1, on the other hand, is no larger to probes presented at attended locations than it is to probes presented in neutral conditions. Instead, the P1 is smaller in the unattended condition. This inhibition relative to neutral conditions can this be said to reflect the ‘costs’ of inattention (Di Russo et al., 2003; Hillyard et al., 1994). The pattern observed in the present experiment was that P1 amplitudes were smaller for probes presented on goals or effectors *not* involved in movement. This suggests that participants were suppressing action-relevant stimuli during the very early stages of visual processing as indexed by the P1. It is possible to mount an argument that some process involved in selection-for-action briefly ‘scans’ action-irrelevant first, but this is highly speculative.

The pattern of the P2 ERP calls this argument further into question, since this component was also smaller for probe stimuli presented at action-irrelevant goals and effectors. Less is known about the processing reflected by the P2 component, but it has previously been shown to be modulated by target features of visual stimuli during attention tasks (Luck & Hillyard, 1994). Clearly, in this experiment, there is no such feature detection taking place, since the probes were task irrelevant, and visually identical.

Rather than attempting to fit interpretations to this puzzling pattern of data, it is possible to explain them with a simpler, yet less interesting, explanation: that the negativity associated with the N1 component spread to the P1 and P2 range, acting as a negative baseline shift against which the positive peaks of the P1 and P2 were measured.

ERP latencies

The latencies of the ERP components differed somewhat depending upon whether they were elicited by probes presented at the goal or the effector location. Di Russo, Martinez, Sereno, Pitzalis, & Hillyard (2002) presented stimuli in the upper and lower parts of their participants’ visual fields, and found a latency shift of the elicited ERP component that was in line with that observed here. Whilst it is possible that the differing functional relevance to motor preparation of the goal and effector locations caused these latency shifts (reflecting some underlying difference in processing), probes on the effector fell in the participants’ lower visual fields and probes on the goal in the upper visual fields, suggesting that these latency differences are caused by a more mundane field effect. Of course this does not preclude an effect on latency related to motor preparation, operating in addition to the field effects reported by Di Russo et al, but this possibility is beyond the explanatory power of the present experiment.

Behavioural results

Movement times did not differ for any variables relating to the presentation of the visual probe stimulus, either in terms of where it was located, or the SOA.

Movement accuracy was affected by the location of the probe, and the SOA between the cue and the probe. Participants were more accurate when reaching toward a target location upon which a probe was presented, than when reaching toward a target location that was not probed, and accuracy increased was higher when probes were presented at the earlier (100, 200ms) SOAs than at the later, 300ms, SOA.

Given that the probes were presented during the planning stage of movement, they may have increased the salience of the target. The effect of SOA may be explained if factors such as saliency impact upon accuracy more at earlier stages of movement preparation.

The sequence of events in this paradigm provides protection for the electrophysiological results, from interference by behavioural results such as these. The probes were presented before the execution of the movement, and the electrophysiological results were measured from the brain’s response to them. Increased accuracy of a movement made subsequently to this measurement being taken cannot plausibly affect the measurement itself[7].

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[7] It could be argued that carry-over effects of alerting or saliency by a probe on a previous trial may yet affect the electrophysiological measurement taken on the current trial. Randomisation of the order of trial presentation precludes this possibility.

CHATPER 5: **SELECTION-FOR-ACTION OF GOAL AND EFFECTOR, AND THE SPATIAL PROFILE OF VISUAL PROCESSING DURING MOTOR PREPARATION**

Abstract

The experiment reported in the previous chapter showed simultaneous enhancement of goal and effector locations during the preparation of a simple reaching movement. A possible explanation for the visual enhancement observed at the effector was that this location also served as the starting point of the movement, and the location to which participants returned their hand at the end of each trial. As such, the starting position could be conceived as the second goal location in a sequential movement, from the starting position, to the movement goal, and back to the starting position again. This experiment aimed to replicate the enhancement observed at the effector location using a paradigm that did not have a fixed starting position. A secondary aim was to increase the number of non-goal locations that were probed, in order to learn more about the spatial profile of action-induced changes in visual perception.

Participants pointed at one target of six arrange in an annular array, and were cued to move their finger in either a clockwise or anti-clockwise direction to point to the next target on the array. Task irrelevant visual probes were presented at one of the six locations on the array on a trial-by-trial basis before movement execution, but after the cue had instructed participants where to move, whilst participants' EEG was recorded.

Results showed simultaneous enhanced processing at both the goal and effector locations, and a preliminary spatial profile that showed a gradual fall-off of processing as distance increased from the goal and effector locations.

Introduction

The previous two chapters both investigated the consequences of action on perception across time. The experiment described in chapter three focused on processing at the goal of a movement, whilst the experiment in chapter four investigated the effect at both the goal and effector. The paradigm used in the present experiment is a departure in two ways: 1) it did not probe the time course of motor preparation, instead concentrating on the spatial profile; and, relatedly, 2) it used a delayed-response (go/no-go) instead of a 'cued movement' paradigm. As such, it continued the investigation of processing at the goal and effector that was established in the previous chapter, using a slightly different paradigm. There are several reasons to switch to such a paradigm for this experiment:

1) Whilst previous behavioural work has used an immediate response paradigm (e.g. (e.g. Deubel & Schneider, 1996), most (if not all) electrophysiological work has used a delayed response paradigm (e.g. Van Velzen et al., 2006). By using both paradigms, this thesis will be able to compare the results from both, thus linking the two different methodologies.
2) In a delayed response paradigm, the auditory cue and the probe are temporally quite distance (often ~800ms), and so the ERPs that each stimulus elicits do not overlap in the EEG. This is not the case for immediate response paradigms, where the cue and probe ERPs overlap, making a full analysis of ERP components at different latencies and different regions of the scalp more difficult.

Previous work has cued participants to plan a sequence of movements to two distinct goals, which are then executed one after the other. Both behavioural (Baldauf et al., 2006) and electrophysiological (Baldauf & Deubel, 2008a) approaches have shown that each goal location receives enhanced processing in parallel, before the movement to either has been executed. The experiment reported in the previous chapter used a reaching task in which participants began at a starting position, were cued to move to a goal, before returning their hands to the starting position in readiness for the next trial, and the results showed enhanced processing at goal and effector locations simultaneously. It could be argued that this was due to the effector location (the starting position) being treated as the second goal of a sequential movement by the motor system, causing enhanced processing because it was being *returned to*, rather than because the effector was located there. The objective of this present experiment is to investigate processing at the goal and effector without the potentially confounding effect of a starting position.

A secondary aim of this experiment is to investigate the spatial profile of action-induced changes in perception. Models of spatial attention make different assumptions about the shape of attentional focus, such as a spotlight (Posner, 1980; Posner et al., 1980), a zoom lens model, in which the visual cortex's ability to resolve details is traded off against the area of the visual field that is selected (C. Eriksen & St. James, 1986), a gradient (LaBerge & Brown, 1989) or a Mexican hat, in which information in the centre of the focus of attention is enhanced, but is surrounded by a ring of suppression which gradually falls of (Müller et al., 2005). Given the similarities between spatial attention and movement, behaviourally (e.g. Rizzolatti et al., 1987), electrophysiologically (e.g. Eimer, Van Velzen, Gherri, & Press, 2006; cf. Mangun & Buck, 1998), functionally (e.g. Corbetta et al., 1998) and neuropsychologically (e.g. Craighero, Carta, & Fadiga, 2001), it is possible that action-induced changes in perception will show a similar pattern.

Much previous research has either only used a relatively small number of possible movement targets, for example two goal locations (e.g. Gherri et al., 2009, and previous chapter of this thesis), or has used more locations but collapsed them before analysis (e.g. Deubel et al., 1998). The design of this present experiment is such that probes are presented at one of six different possible movement locations, either nearer or further from the goal and from the effector. By considering a broader movement landscape, the shape and function of the effect of action can more accurately be described.

The stimuli used in this experiment were six targets arranged in an annular array. This layout has several advantages:

1) Since each of the individual target locations was equidistant from its immediate neighbour in a clockwise or anticlockwise direction, all movements were of the same distance, and direction was balanced out across all trials.
2) All targets were equidistant from a central fixation cross, and thus were equidistant from the fovea.
3) A starting position was randomly selected from the six target locations at the start of each block (or after an error), but was not returned to after each trial. Instead a new goal was cued at the start of each trial.

Given that targets were equidistant from each other, any perceptual enhancement at the goal location could be anticipated to spread to the neighbouring targets on the array. If processing is probed at goal and effector locations in this circumstance, an erroneous measurement of enhanced processing at the effector may be obtained, which in fact merely reflects the influence of the goal on perception. In order to avoid this potential confound, effector locations (which were always one target *before* the goal, in terms of the direction of movement) were compared with the target that was located *after* the goal in the direction of movement. This ‘adjacent to goal’ location, being located as far from the goal in one direction as the effector was in the other, was equally vulnerable to contamination from enhanced processing spreading from the goal, and so functioned - in terms of measuring visual perception - as a control location.

Method

Participants

A sample of 22 participants (16 females) took part in the experiment after giving informed consent. Some were paid in cash, and some received course credit as payment for participation. Participants ranged in age from 19 to 33 (mean age was 21.7 years), all were right handed, had normal or corrected-to-normal vision and none had been diagnosed with any movement disorders. 5 participants were excluded from ERP analyses due to poor control over saccades and blinks, leaving a total of 17 participants.

Stimuli and apparatus

Participants carried out the movement task sitting in front of the mirror system, described fully in the chapter titled *Experimental Methods*. The surface of the mirror system was configured at an angle of 72°, such that participants were presented with a sloping surface similar to a draughtsman's table.

The mirror system served two purposes: 1) to prevent the participant from seeing his or her hand during the movement task; and 2) to allow visual stimuli to be overlaid on top of the movement surface and the participant's hand. This was achieved by configuring the distances between the surface, the mirror, and the monitor such that the participant perceived the image reflected in the mirror to be at the same apparent depth as the surface. As such, any stimuli displayed on the monitor appeared to be projected directly on top of the surface.

Visual stimuli that were presented were:

1) A fixation cross presented in the middle of the movement surface (0.48º x 0.48º).
2) A annular array of six 'target' locations. These were evenly spaced, and their sizes were randomised on each trial, varying from a diameter of between 70 pixels (2.51° x 2.61º) and 200 pixels. The colour of the target circles was grey (RGB: 125,125,125).
3) On each trial, a 'dot probe' (0.88º x 0.87º) was briefly presented on top of one of the target circles (see section below for more details).

Movement data was recorded a touch sensitive panel, placed on the movement surface of the mirror system and measuring 490mm x 315mm with a thickness of 3mm. The panel responded to a participant's finger making contact with or lifting off from its surface. Movement data was recorded in the form of a 'press' or 'release', located by *x* and *y* coordinates in pixels and tagged with a time label in milliseconds, from which movement distances and times were derived.

The panel was made of clear plastic and covered with a piece of black card so as to prevent reflections. It communicated with the stimulus presentation computer via the Universal Serial Bus (USB) interface. In order to reduce ‘jitter’ in the recorded position of the participant’s finger, the software driver was configured to ignore movements of less than 20 pixels.

Cue and ‘go’ stimulus

A symbolic auditory cue of 100 ms duration was employed, consisting of either a high (1000Hz) or a low (400Hz) tone lasting for 100 ms. The meaning of the cue was counterbalanced across participants: for half a high tone instructed them to prepare a movement from the current position of their index finger to the next target in a clockwise direction, and a low tone to prepare to move to the next target in an anticlockwise direction; for the other half this mapping was reversed. The ‘go’ stimulus was a recording of a female voice saying either “stop” or “go”. Both auditory stimuliwere presented from a speaker that was out of sight of the participant and centred so as not to bias attention to one side or another during the cueing period.

Probe

The dot-probe paradigm used in this experiment is described in detail in the chapter titled ‘Experimental Methods’. The probe took the form of a white circle displayed for 100ms on one of the circles in the annular array. This probe was only presented on one target per trial, and the EEG was marked to indicate at which location the probe appeared on a particular trial.

Procedure

Participants sat in front of the mirror system and console in a darkened room whilst their EEG was recorded. Instructions were presented on the surface of the mirror relating to the meaning of the auditory cue. Participants were also instructed to keep their eyes on the fixation cross for the duration of the experiment, and to ignore the visual dot probe stimuli. Participants were instructed to use either their left or right hand on a block by basis. The hand that was used to begin the very first block was counterbalanced across participants.

The sequence of events is illustrated in Figure 35, and a schematic representation of the display that the participant saw and responded to is provided in Figure 36. Each block started with a blank screen, after which a starting location was randomly chosen from the six fixed locations on the annulus. A circle was presented at just this location, and the participant pressed on the movement surface with the tip of their index finger. This signalled that the participant was ready to start the block.

The screen was blanked at the start of each trial for 1000ms, after which circles were drawn at the six locations on the annulus. The size of each circle was randomly varied on each trial so as to prevent movements becoming overly automatic. At the same time as the annular array was presented, an auditory cue sounded. This consisted of either a high or low tone of a duration of 100ms. Depending upon the counterbalancing condition, the cue instructed participants to prepare to move in either a clockwise or an anticlockwise direction.

After the offset of the cue, participants waited 1000ms for an auditory ‘stop/go’ signal, which consisted of a recording of a voice saying “stop” or “go”. On ‘stop’ trials participants did not move, but instead kept their finger pressed on the starting location. On ‘go’ trials participants immediately released their finger from the starting position, and move it to the goal location, which was the next circular target in the array. They placed their finger on the goal position, and held it there.

In the period between the cue but before the execution, the visual probe stimulus was presented. After an inter-stimulus interval of 700ms post cue offset, a small white disc was presented on one of the grey circles in the array, for a duration of 100ms. Participants had been instructed to completely ignore these stimuli.

If participants moved their hand on a ‘stop’ trial, moved to the wrong location on a ‘go’ trial, or missed the circular target on a ‘go’ trial, then the trial was marked as containing a movement error and an auditory feedback was given in the form of a buzzer sound. The screen was then blanked, and a new starting position displayed on screen. The sequence of events then continued from this point in the way described above.

For trials on which a correct movement had been made the EEG was marked with a code representing the movement condition and the location of the probe. Movement data such as the movement time, the absolute distance between starting position and goal, and accuracy (in terms of the distance from the centre of the goal location and the location of the participant’s finger).

At the end of each trial, the participant kept their finger pressed to the location of the goal (‘go’ trials) or the starting position (‘stop’ trials). The screen was then blanked for 1000ms before the targets were drawn, and the sequence of events started again for the next trial.

Participants took part in one practice block and ten experimental blocks. Practice trials differed from experimental only in the proportion of ‘go’ to ‘stop’ trials, which was 50/50 in the practice block and 128/12 on the experimental trials.

Data Analysis

Behavioural Analysis

Movement time and accuracy was recorded on a trial by trial basis, and separate averages were computed for each participant at each *probe location* (*goal, effector, adjacent goal*). These were analysed with repeated measures ANOVA.

EEG recording and data analysis

The EEG was filtered at a rate of 0.1 – 40 Hz using a band-pass filter, and segmented into 700ms epochs, running from 100ms before the presentation of the visual dot probe stimulus to 600ms after. Epochs were averaged relative to a baseline period 100ms before the onset of the probe. Trials with eye blinks or movements (voltage in HEOG channels exceeding +/- 30 µV) or muscle artefacts (voltage at any other electrode site exceeding +/- 80 µV) were discarded.

ERPs were analysed within 40ms latency windows centred on the peak of each component and mean amplitudes were then computed for each of the separate conditions summarised in Table 6, and entered into a repeated measures ANOVA. All results were corrected for violations of sphericity using the Greenhouse-Geisser method where appropriate.

Visual evoked brain responses are generally fairly strongly lateralised at the opposite hemisphere to the side of presentation: brain responses to probes presented in the left visual field are larger at scalp locations on the right hemisphere, and vice-versa. For the sake of brevity and simplicity, information regarding the absolute side of presentation and the hemisphere at which the associated brain response was recorded were collapsed to one variable, *hemisphere,* with two levels, *ipsilateral* (the brain response measured on the same side as presentation) and *contralateral* (the brain response measured on the opposite side). As such, individual electrodes are referred to as ‘P1/2 contralateral’ or ‘P1/2 ipsilateral’.

Table 6. Separate averages were computed for the following variables:

Probe location *(goal/effector/adjacent goal)*	Probes were presented at one of three possible locations on each trial. Probes presented at the location of the hand (the starting position) were coded as being at the *effector*. Probes presented at the goal location of the prepared movement were coded as the *goal*. Probes presented at the location adjacent to the goal, but not involved in the movement, were coded as being at the *adjacent goal* location. These locations are shown in Figure 33.
Scalp region *(anterior, central, central-parietal, parietal, parietal-occiptal, occipital)*	The region of the scalp at which the measurement was taken.
Hemisphere *(contralateral / ipsilatral)*	Recorded whether the measurement of the visual evoked brain response was taken at a scalp location contralateral or ipsilateral to the visual field of presentation. A measure of the degree of lateralisation of the visual response.

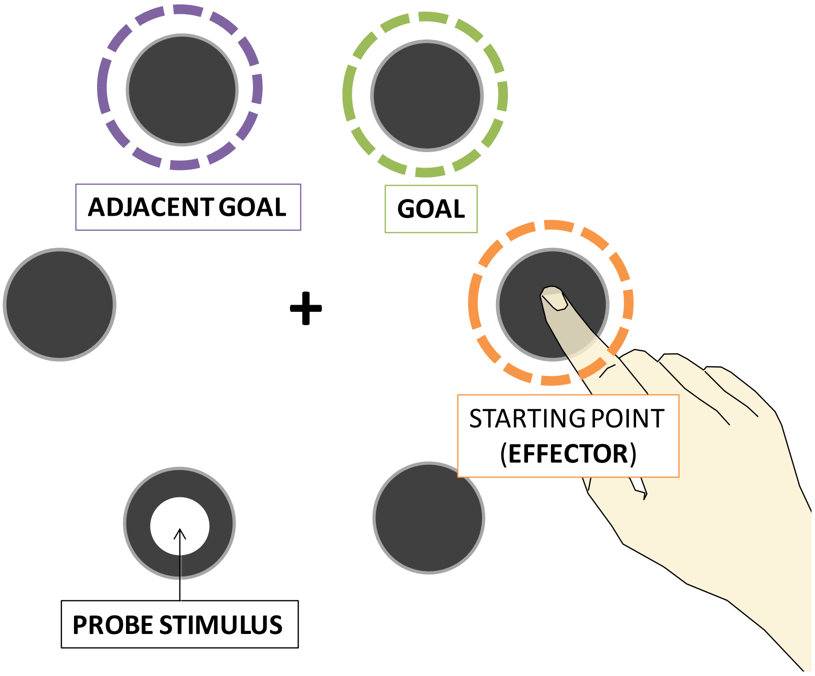


Figure 33. The three movement related locations at which visual probe stimuli were presented. The dashed circles indicate the meaning of three locations for an anticlockwise movement. The hand is shown at the starting position, coded here as *effector* (purple circle). The movement goal is coded *goal* (green circle). The distance between the *goal* and the *effector* is

equal to the distance between the *goal* and the *adjacent goal* (orange circle). The visual probe stimulus is shown here at one of the locations not involved in the movement; in actuality the probes were presented with equal probability at each of the six locations on the array.

Identification of ERPs

Three early visual ERPs, elicited in response to probe stimuli, were observed: a P1, N1 and P2 wave. The latencies of these components are summarised by scalp region in **Error! Reference source not found.**. The P1 was reliably elicited at between 120 and 127ms at all electrode sites except for anterior (AF, F and FC electrodes). The latency of the N1 and P2 components varied across the scalp, showing a general pattern of shorter latency at more anterior sites, and a longer latency and parietal sites. These components are known to result from the summation of more than one individual sub-components originating from separate parts of visual cortex and thought to reflect different aspects of visual processing (Clark et al., 1995; Di Russo et al., 2002).

Table 7. A summary of event related potentials observed in response to visual probe stimuli, organised by electrode site and showing peak latencies of each component. These components were identified from pooled grand average ERPs across the electrode sites listed in the first column.

Scalp region	***Observed peak latency (m.s.)***		
	P1	*N1*	*P2*
Anterior (AF, F, FC)	Not observed	150	205
Central (C)	Not observed	150	213
Central-Parietal (CP)	Not observed	158	213
Parietal 1 (P1, P2)	121	160	221
Parietal 2 (P3-P9)	121	180	225
Parietal-occipital (PO)	127	180	225
Occipital	125	190	225

As such the negative components with the earlier latencies were identified as an anterior N1 (N155), and the components with later latencies as posterior N1 (N180) (see **Error! Reference source not found.** for ERPs, and Figure 39 for scalp maps). In general this pattern held across groups of electrodes, except for the parietal electrodes. At electrodes P1 and P2, the anterior N1 component was observed, whereas at electrodes P3-P10, the posterior N1 component was observed.

The P2 component was observed at different latencies at different electrode sites. The P2 is difficult to identify as it tends to sum with other components of the visual evoked potential, and in this paradigm was in the time range of the very early components of the auditory evoked potential elicited by the ‘go’ signal. As Figure 39 shows, the distribution of the P2 component was broad and fronto-central, and as such the peak latency of the component was taken from F, FC and C electrodes, resulting in the measurement of a P2 component with a peak latency of 213 ms.

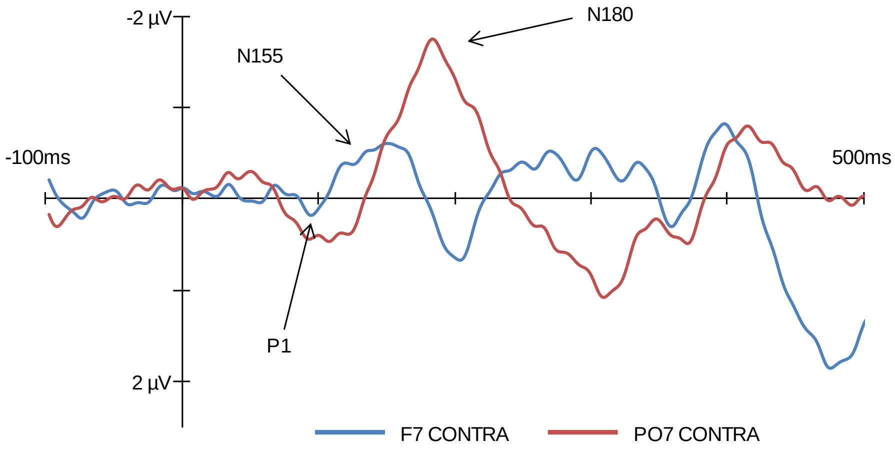


Figure 34. Two N1 subcomponents were observed with different latencies and scalp distributions. An earlier fronto-central N155 component (shown here at electrode F7/8 contralateral, blue line) and a posterior N1 (shown here at electrode PO7/8 contralateral, red line).

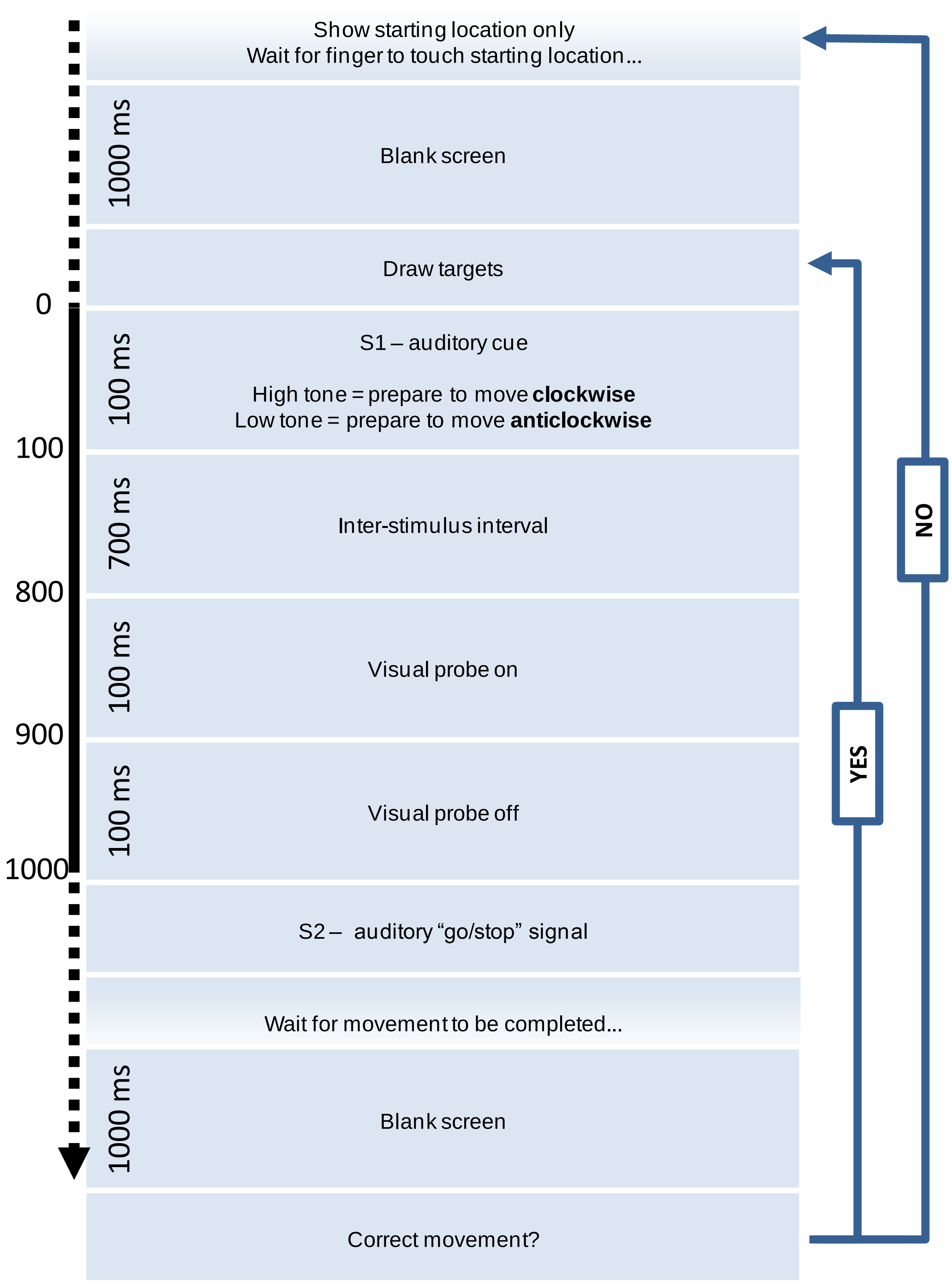
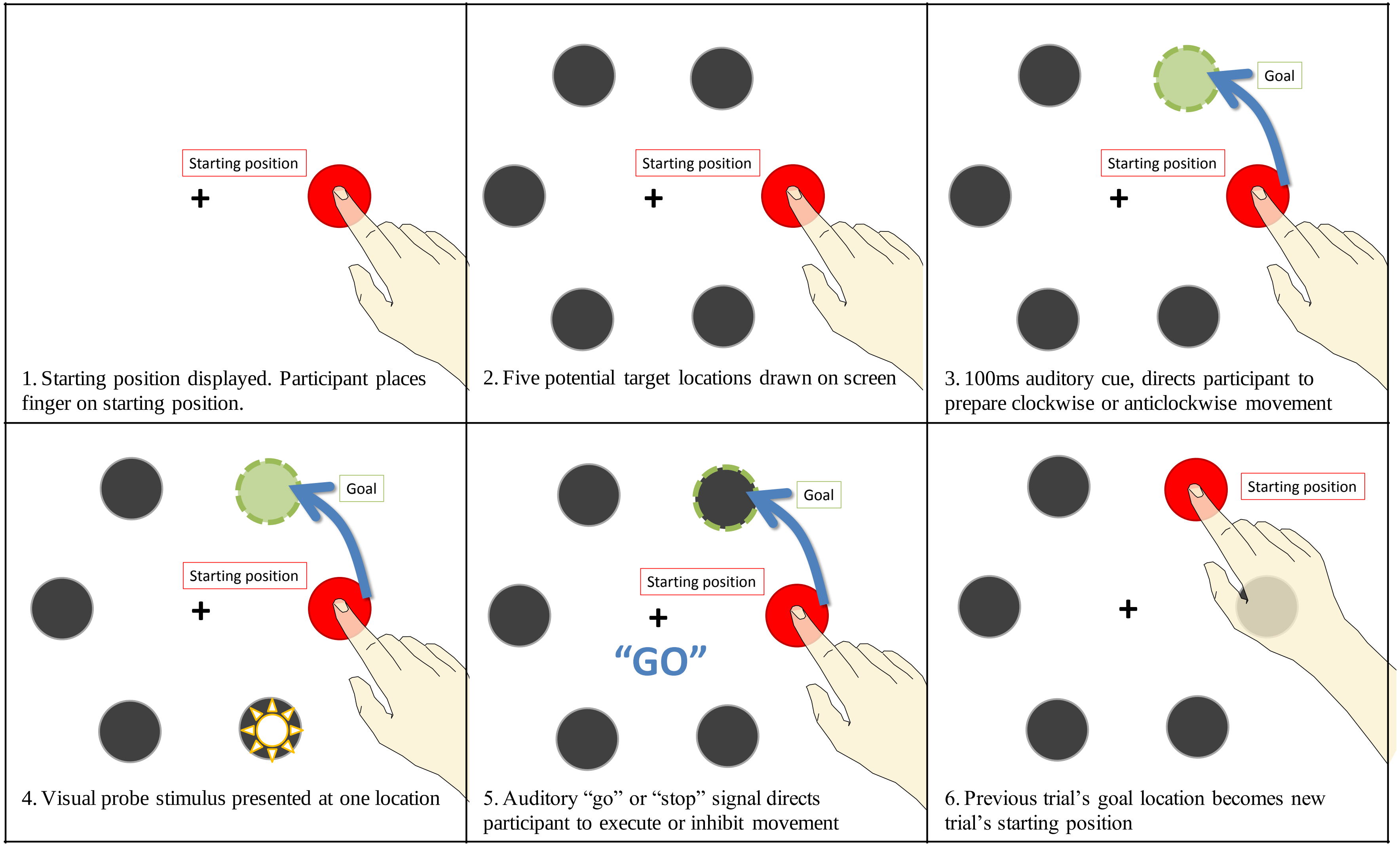


Figure 35. A graphic illustration of the sequence of events in one trial.



1. Starting position displayed. Participant places finger on starting position.

2. Five potential target locations drawn on screen

3. 100ms auditory cue, directs participant to prepare clockwise or anticlockwise movement

4. Visual probe stimulus presented at one location

5. Auditory "go" or "stop" signal directs participant to execute or inhibit movement

6. Previous trial's goal location becomes new trial's starting position

Figure 36. A graphic representation of the procedure.

Results

Behavioural results

Summary of behavioural results

Behavioural data was analysed in order to ascertain whether *probe location* (*goal, effector, adjacent goal*) affected movement speed and accuracy.

No effect of *probe location* was found on movement accuracy.

Movements where the probe fell on the goal were faster than those where the probe fell on the effector or adjacent goal.

Behavioural measures of reaction time, movement time and reaching accuracy were recorded. Any trials with movement times above 2500ms were discarded prior to analysis.

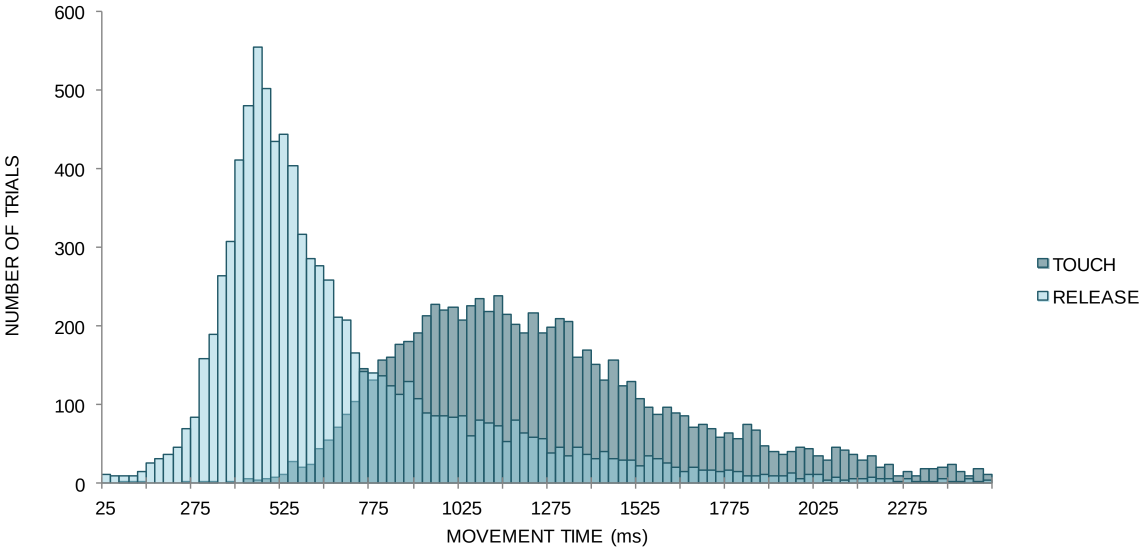


Figure 37. The distribution of movements times, shown separately for releases (start of movement, light blue) and touches (end of movement, dark blue).

Each dependent variable was analysed with repeated measures ANOVA, using the factor *probe location* (*goal, effector, adjacent goal*). The main effect of *probe location* on accuracy was not significant, F(2,32)=.467, p=.631, but on movement times was significant, F(2,32)=10.294, p<001. This result was followed up with post-hoc paired samples t-tests. When the probe was presented at the location of the goal, movement times were faster than when it was presented at the adjacent goal, t(16)=4.561, p<.001, or at the effector, t(16)=2.719, p=.015. This effect is illustrated in Figure 38.

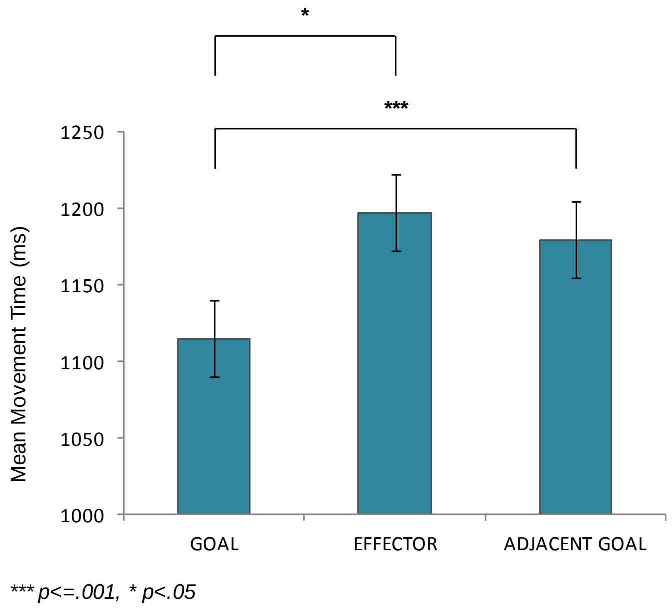
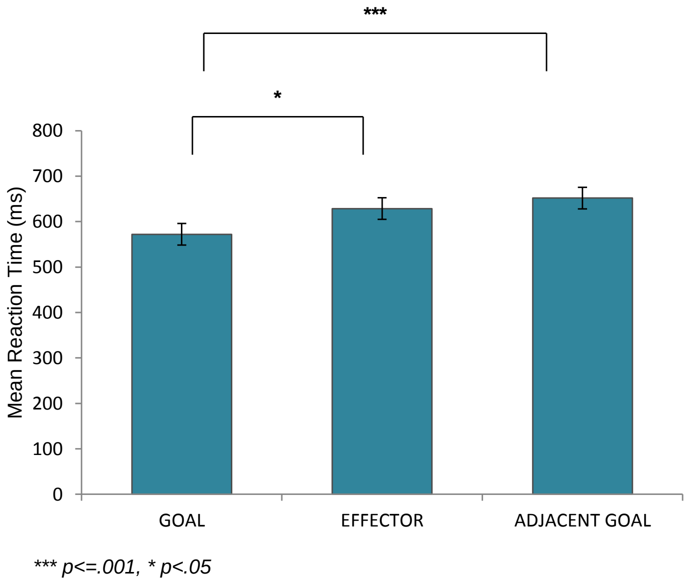


Figure 38. The effect of *probe location* on movement times.

The main effect of *probe location* was also significant for reaction times, F(2,32)=10.294, p<.001. Follow up tests revealed that RTs were faster when probes were presented on the goal as compared to the effector, t(16)=2.719, p=.015, and as compared to the adjacent goal, t(16)=4.561, p<.001. No difference was found between RTs when probes were presented on the effector or the adjacent goal, t(16)=1.431, p=.172.



ERPs elicited in response to visual probe stimuli

Summary of ERP results

A P1, anterior N1 (N155), posterior N1 (N180) and P2 ERP component was elicited by task irrelevant visual probe stimuli.

Anterior N1: showed a weak effect with larger amplitudes at goal locations in the contralateral hemisphere.

Posterior N1: showed enhanced processing at the goal and effector locations, but not at the adjacent goal. This effect interacted with hemisphere, reflecting the lateralised nature of the component.

P1: was larger for probes on the effector and adjacent goal than the goal

P2: showed no significant effects.

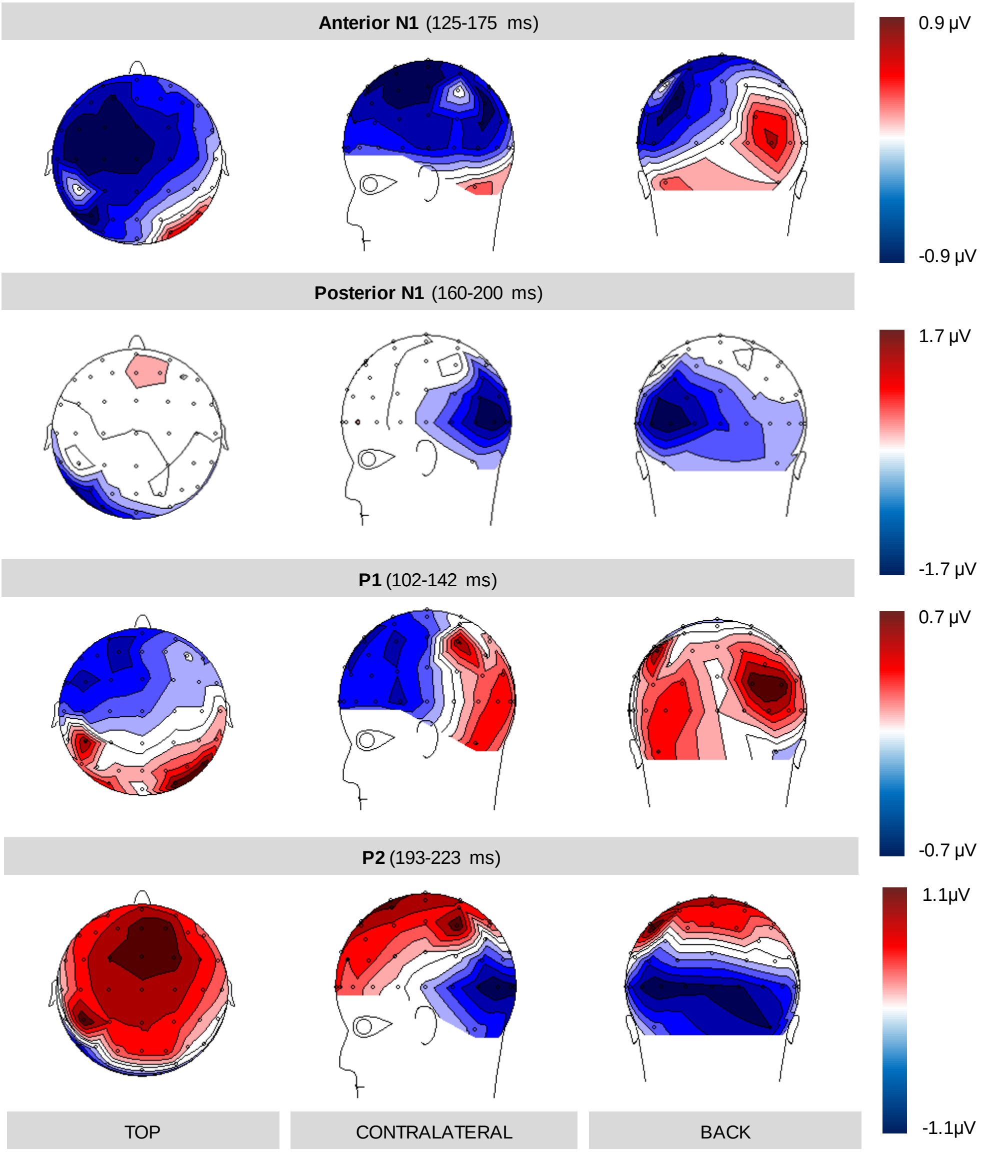


Figure 39. Scalp maps showing the distribution of the anterior N1, posterior N1, P1 and P2 components**.**

Visual processing at goal, effector and adjacent goal locations

1. The anterior N1 component

The anterior N1 component showed a diffused, fronto-central, lateralised scalp distribution, and was maximal at C1/2, C3/4, C5/6, T7/8, FC1/2, FC3/4, FC5/6, FT7/8, F1/2, F3/4, F5/6, F7/8. AF3/4 and AF7/8 contralateral electrodes (Figure 39). Figure 40 shows a selection of ERPs from the identified region, with separate lines plotted for ERPs elicited by probes presented at the goal, effector and adjacent goal.

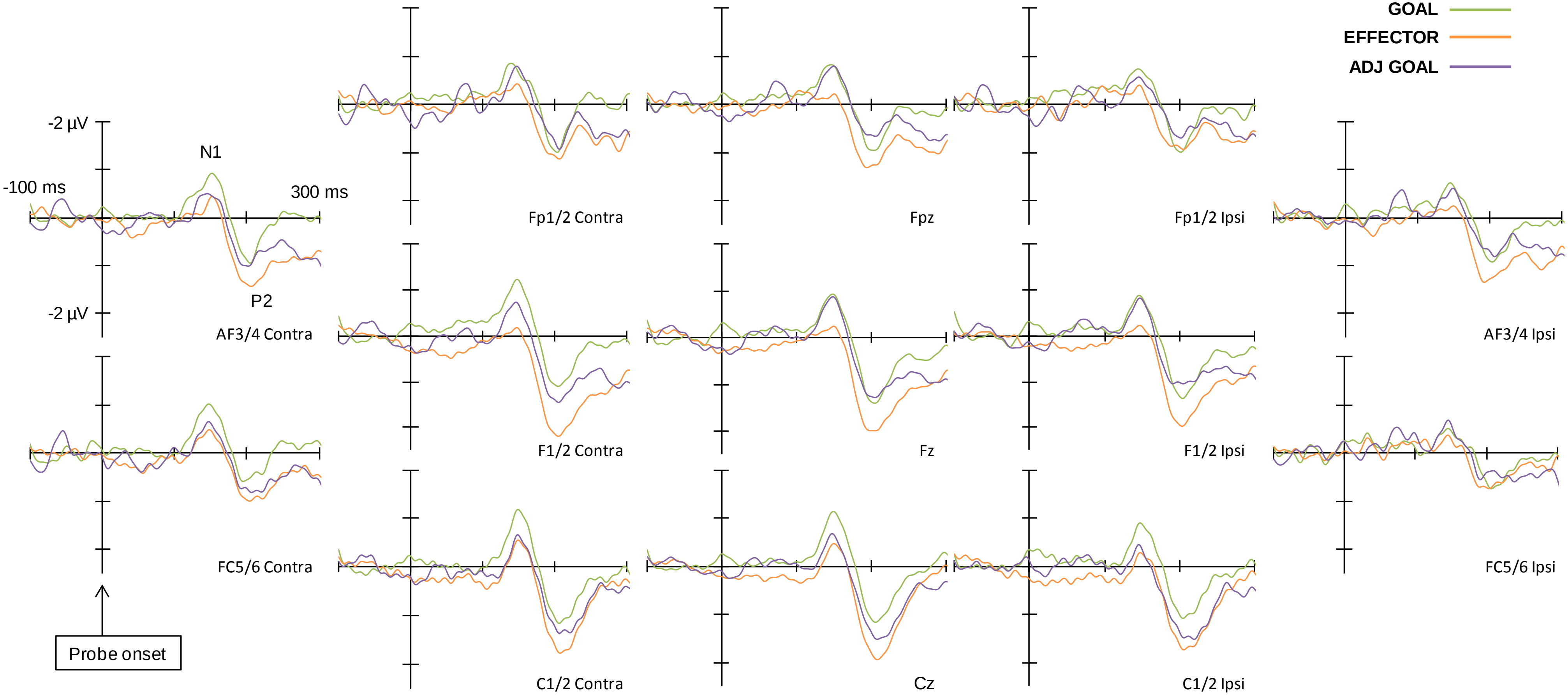


Figure 40. A selection of ERPs from the scalp region at which the anterior N1 component was observed. Separate lines show ERPs elicited by visual probe stimuli presented at the location of the goal (green lines), the effector (purple lines) and the adjacent goal (orange lines).

A general pattern of similar sized brain responses to probes at effector and adjacent goal locations was observed for central and lateral electrodes, with smaller responses to probes at the location of the effector for the most anterior sites. These observations were followed up with repeated measures ANOVA, with factors *probe location*, *region* (*anterior*, *central* and *temporal*) and *hemisphere*. The main effect of *probe location* and *region* were not significant, all F's(2,32) < .974, all p's > .427. The main effect of *hemisphere* was significant, F(1,16)=11.490, p=.004, confirming the lateralised nature of the anterior N1 component.

The interaction between *probe location* and *region* was marginally significant, F(4,62)=2.101, p=.091, whilst the three way interaction between *probe location*, *region* and *hemisphere* was not significant, F(4,64)=1.508, p=.210.

Probe location interacted with *hemisphere*, F(2,32)=3.404, p=.046. This interaction is summarised in Figure 41, and shows a stable ERP response to probes presented at the adjacent goal across hemispheres, whilst ERP responses to probes presented at the goal and the effector are larger when measured over the contralateral hemisphere.

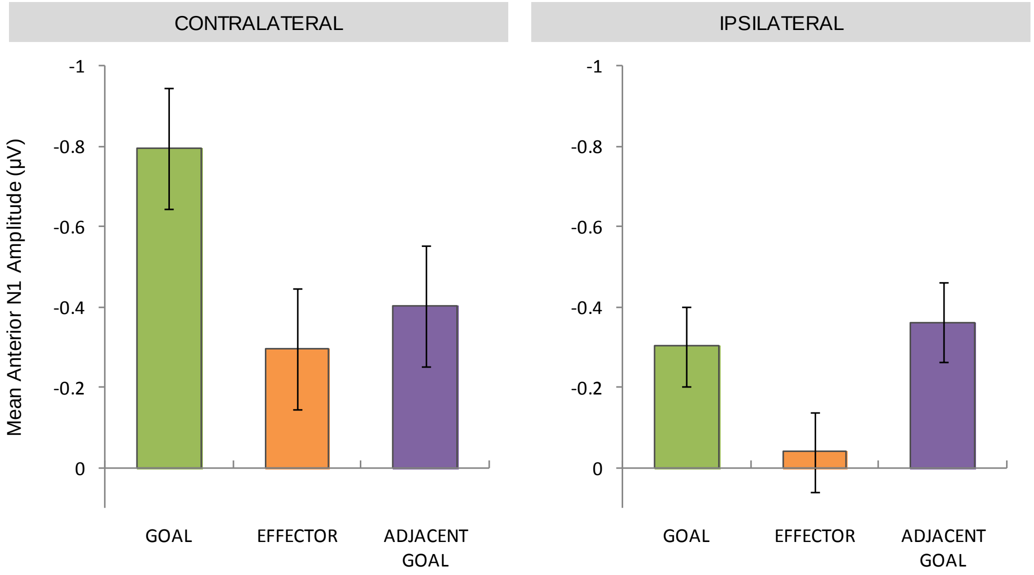


Figure 41. The effect of *probe location* and *hemisphere* and the amplitude of the anterior N1 component, for electrodes AF3-8, F1-8, FC1-6, FT7/8, C1-6, T7/8..

This observation was investigated with paired sample t-tests. Amplitudes of the anterior N1 component were larger when elicited by probes presented at the goal location over contralateral versus ipsilateral electrode sites, t(16)=4.371, p<.003, but the same was only marginally significant when probes were presented at the effector, t(16)=2.054, p=.171, and not significant for adjacent goal locations, t(16)=.293, p>1 (corrected for multiple comparisons).

T-tests were also performed comparing amplitudes of the anterior N1 component to probes presented at the goal vs the adjacent goal, goal vs effector, and effector vs adjacent goal, separately for each hemisphere. None of these comparisons was significant, all t's(16)<+/-1.502, all p's>.152.

2. The posterior N1 component

The posterior N1 component showed a relatively focused, lateralised, parietal distribution and was maximal at electrodes sites CP3/4, CP5/6, P1/2, P3/4, P5/6, P7/8, PO3/4 and PO7/8 contralateral. A selection of ERPs from this region is presented in Figure 43, with separate lines plotted for ERPs elicited by probes presented at the goal, effector and adjacent goal. Whilst the components measured over the ipsilateral side of the scalp appear smaller than those at contralateral sites, a general pattern was observed of larger amplitudes of ERPs elicited by probes presented at the goal than the adjacent goal, with ERPs elicited by probes presented at the effector falling somewhere in between. Since the scalp maps in Figure 39 show a strongly lateralised component, only electrodes contralateral to the side of probe presentation were analysed.

The main effect of *probe location* was significant, F(2,32)=5.680, p=.08. Follow up tests showed that the amplitudes of the posterior N1 component elicited by probes presented at the location of the goal were larger than those presented at the adjacent goal, t(16)=3.141, p=.006, but not different to those presented at the effector, t(16)=1.358, p=.193. The amplitude of the posterior N1 elicited by probes presented at the effector was, in turn, larger than for those presented at the adjacent goal, t(16)=2.408, p=.028.

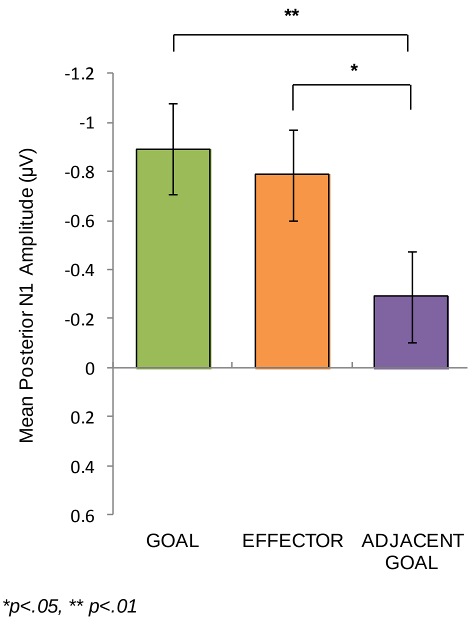


Figure 42. The effect of *probe location* and *hemisphere* on posterior N1 amplitudes at electrodes CP3-6, P1-8, PO3-8. The results of post-hoc tests on pairs of *probe location* levels are shown for contralateral electrodes only.

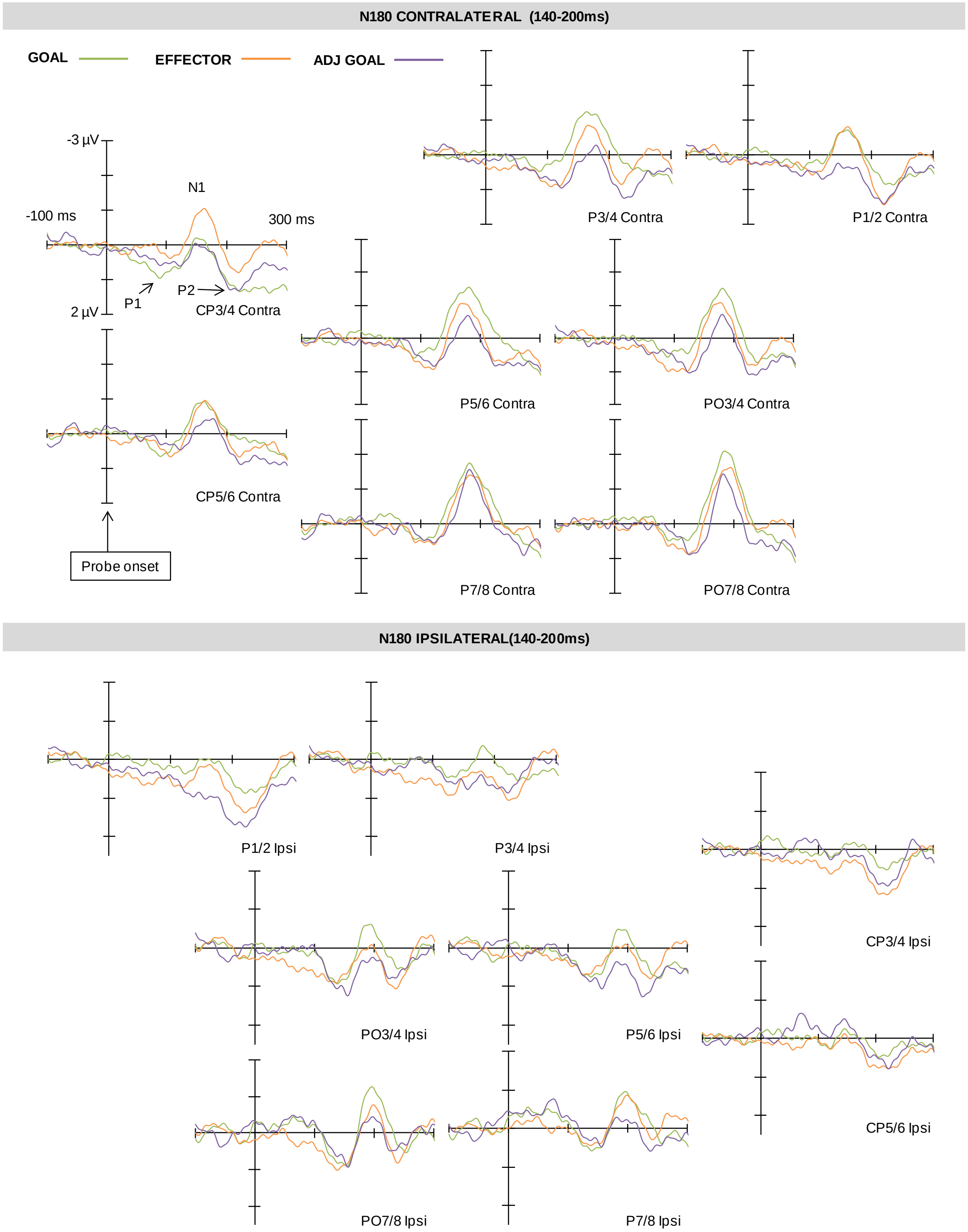


Figure 43. A selection of ERPs from the scalp region at which the posterior N1 component was observed. Separate lines show ERPs elicited by visual probe stimuli presented at the location of the goal (green lines), the effector (purple lines) and the adjacent goal (orange lines).

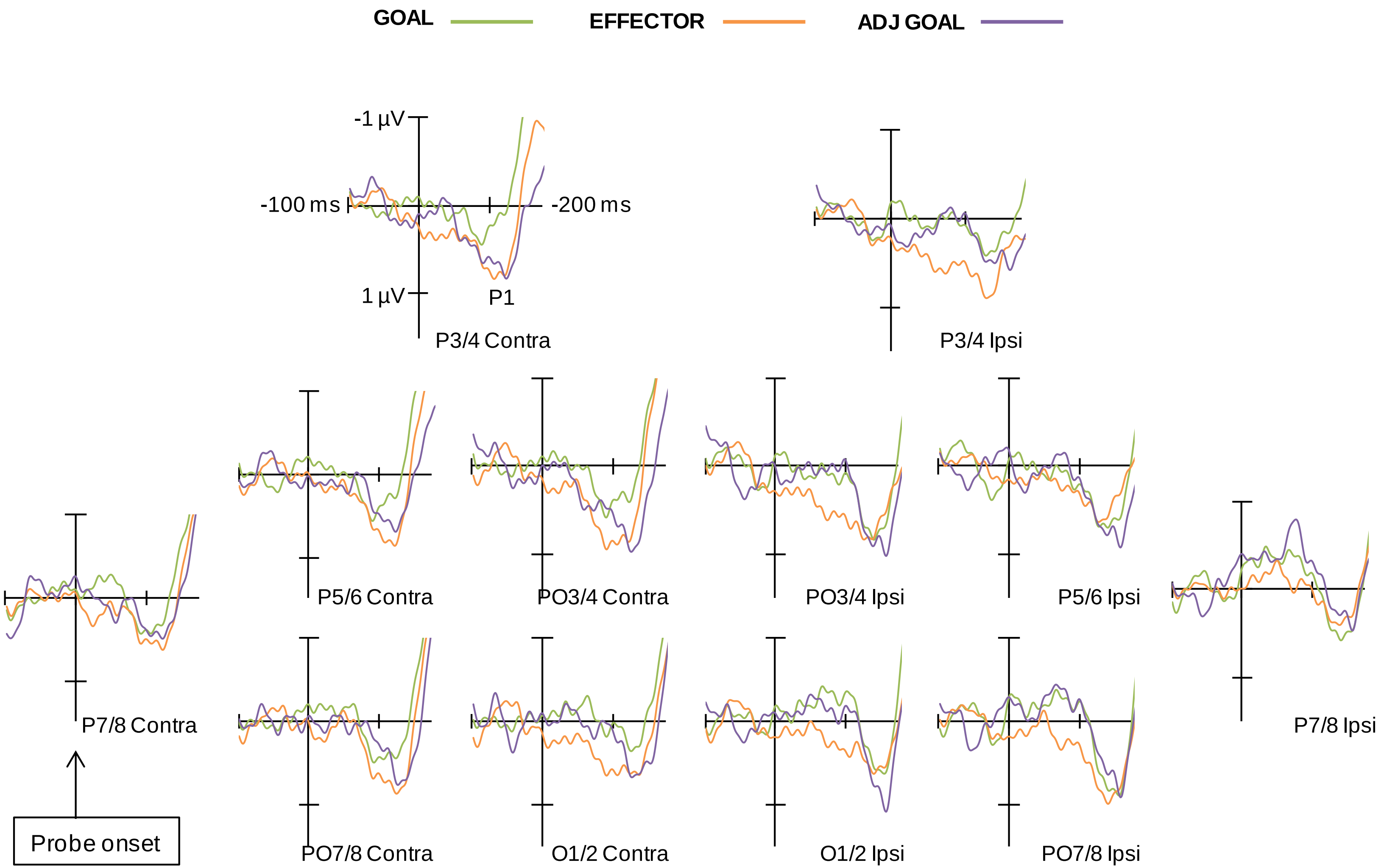


Figure 44. A selection of ERPs from the scalp region at which the P1 component was observed. Separate lines show ERPs elicited by visual probe stimuli presented at the location of the goal (green lines), the effector (purple lines) and the adjacent goal (orange lines).

3. The P1 component

The P1 component showed a broadly parietal distribution, more focused over the ipsilateral hemisphere and more distributed over the contralateral hemisphere. The component was maximal at electrode sites P3/4, P5/6, P7/8, PO3/4, PO7/8 and O1/2, and was observed to be smaller for probes presented at the goal as compared to other locations. These observations were investigated further by performing ANOVA on the data, using the variables *probe location* (*goal, effector, adjacent goal*) and *hemisphere*. Since the scalp distribution of this component was confined to parietal and occipital electrodes, no variable coding for region as included. The main effect of *probe location* was significant, F(2,32)=4.984, p=.013, and is illustrated in Figure 45. This was followed up by post-hoc paired samples t-tests which showed that P1 amplitudes were larger for components elicited by probes presented at the goal compared to the effector, t(16)=1.984, p=.065, but not different for probes presented at the goal compared to the adjacent goal, t(16)=1.007, p=.329, nor at the effector compared to the adjacent goal, t(16)=1.211, p=.244.

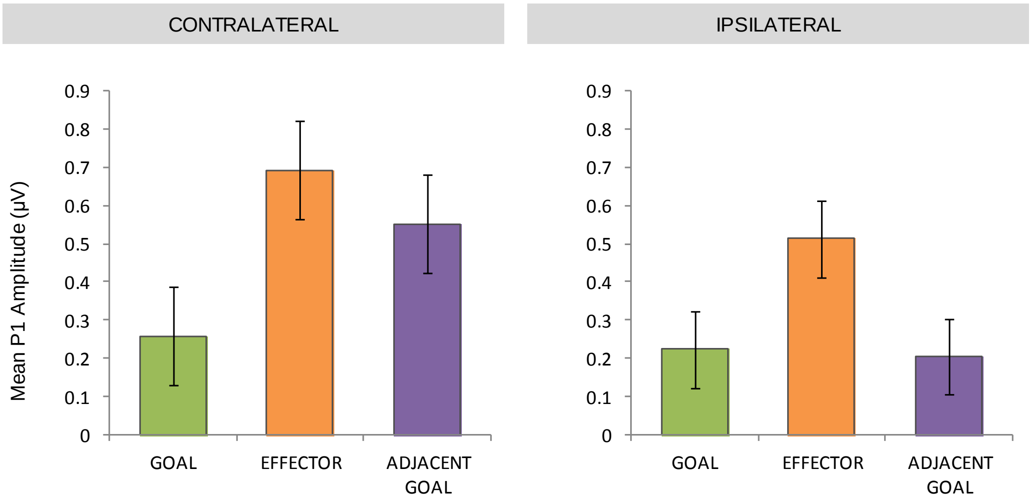


Figure 45. The effect of *probe location* and *hemisphere* on the amplitude of the P1 component, for electrodes P3-8, PO3-8, O1/2.

The main effect of *hemisphere* was not significant, F(1,16)=.878, p=.363, nor was the interaction between *probe location* and *hemisphere*, F(2,32)=.920, p=.409.

4. The P2 component

The P2 component showed a broad positivity across fronto-central areas of the scalp, and did not appear to be lateralised. Given the large area of activation (see Figure 39), a sample of electrodes was taken from the region of scalp at which the component was maximal: F1, F2, FC1, FC2, C1, C2.

The amplitudes of the P2 component at these electrodes was entered into an ANOVA with the factors *probe location* (*goal*, *effector*, *adjacent goal*) and *hemisphere*. Neither the main effect of *probe location*, nor the interaction with *hemisphere* was significant, all F's(2,32)<2.367, all p's>.110. The same was true for the main effect of *hemisphere*, F(1,16)=.746, p=.401.

Visual processing at outer locations on the array

All of the analyses reported so far have been concerned with the functional components of movement: the goal, effector and the adjacent goal, which functions as a control for the influence of the goal. Probes were, however, also presented at other locations not involved in the cued movement. These are referred to in terms of the direction of the movement cued on a particular trial, and are labelled *pre* for the location before the effector, *post* for the location after the *adjacent goal*, and *pre/post* for the location directly opposite the goal, which can equally well be considered as located at the start or the end of the movement trajectory. These locations are shown graphically in Figure 46.

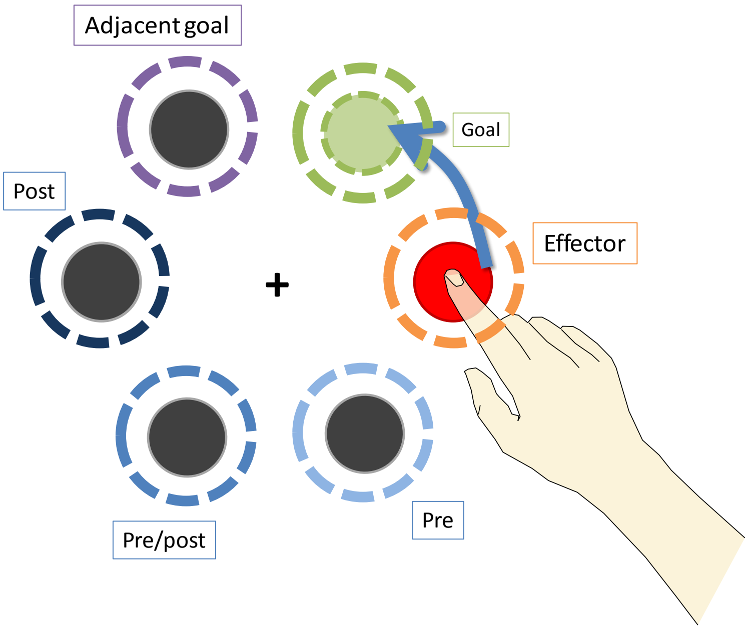
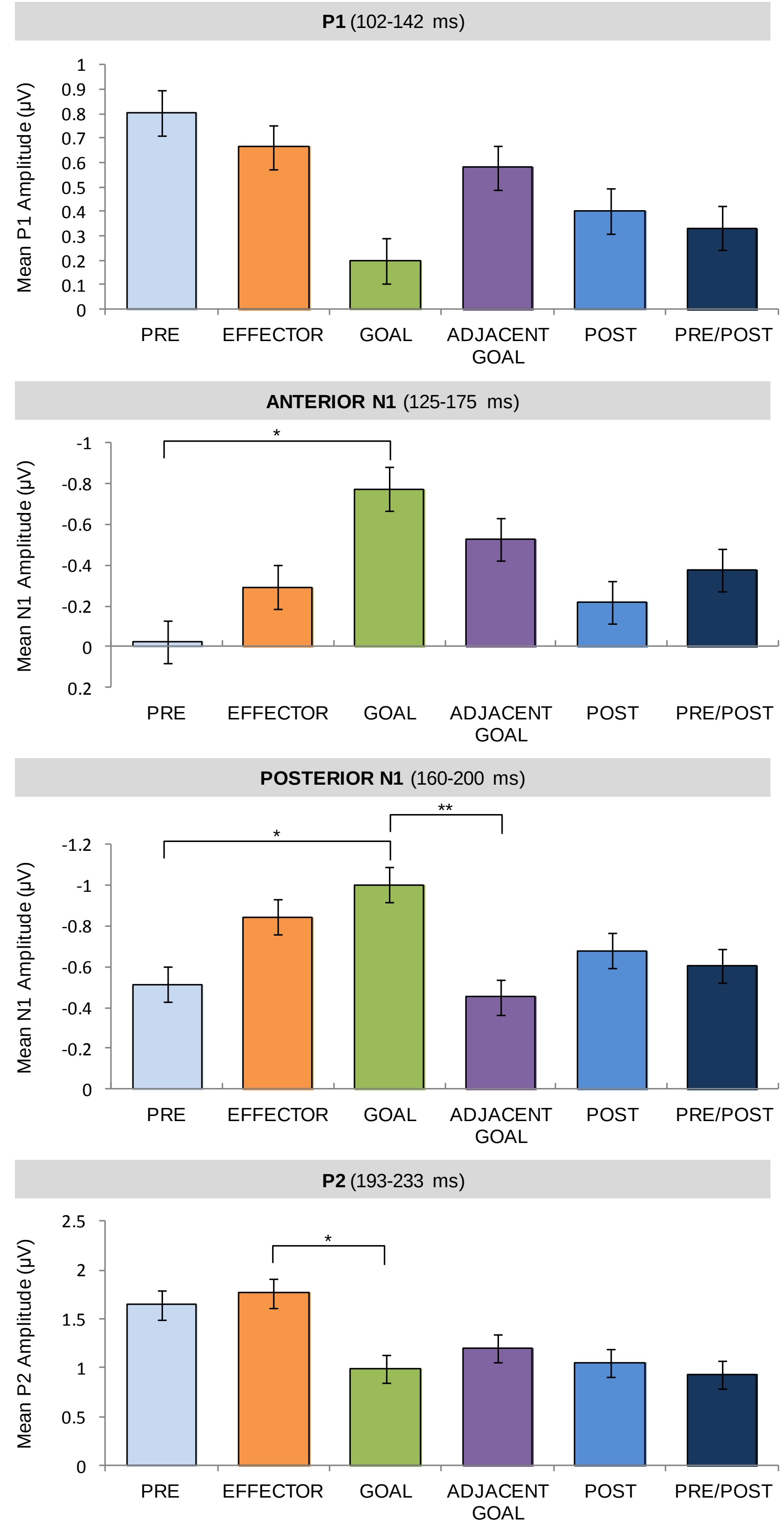


Figure 46. The locations outside of the movement trajectory were labelled *pre*, *post*, and *pre/post*.

Figure 47 shows bar graphs, organised by ERP component, of these outer locations for contralateral electrodes. These data are fairly dense when presented as bar graphs, so are re-plotted as line graphs in Figure 48, to give a better idea of the spatial profile of the effect. A separate ANOVA was performed on the anterior N1, posterior N1, P1 and P2 component, with the factor *probe location* (*goal, effector, adjacent goal, pre, post, pre/post*). The main effect was not significant for any of the components, all Fs(5,85)<1.585, all ps>.174, however a comparison of the sort of patterns found in these data is somewhat problematic for an ANOVA; since each proble location is compared against the average of all other locations, the tendency is for a rising and falling pattern not to be picked out when several levels of the independent variable are entered. Since these analyses are exploratory without a strict hypothesis, t-tests were run for each component, comparing each probe location against the goal. The logic behind this strategy is that the goal is known from an abundance of previous research to receive enhanced processing during motor preparation, whereas the spatial profile of visual processing at other locations during movement tasks is uncertain. By comparing each location with the goal, each can be tested for being enhanced (as defined by being affected by movement) or not enhanced.

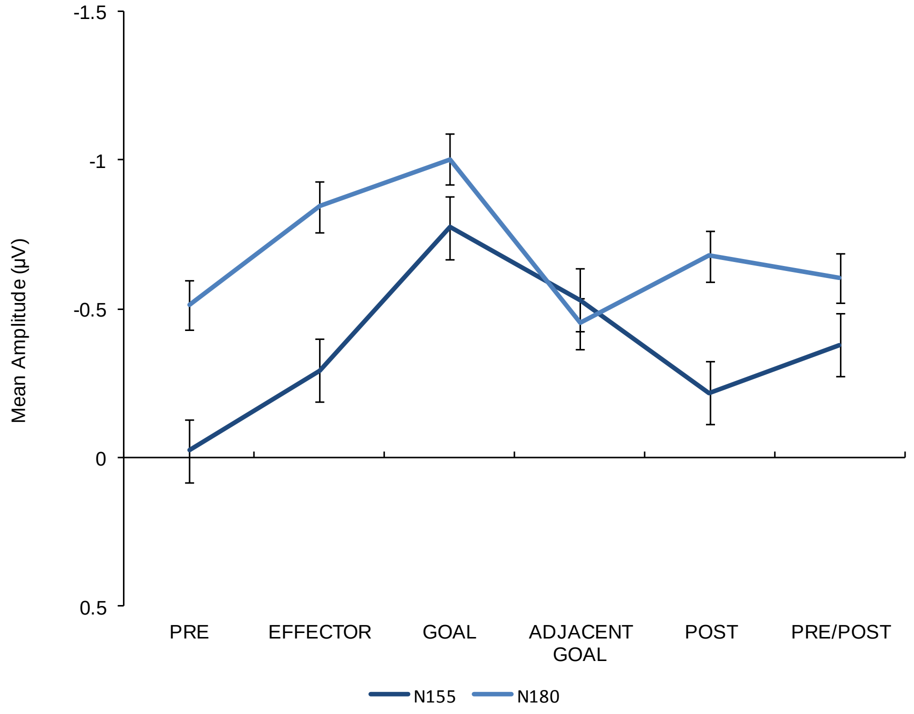
Table 8. Results of post-hoc t-tests, run separately for each component, comparing the goal location with all other locations.

ERP component	***Comparison: goal vs ...***	***t***	***df***	***p***
N155	Adjacent goal	-1.268	16	0.223
	Effector	-1.303	16	0.211
	Post	-1.347	16	0.197
	Pre	-2.705	16	**0.016**
	Pre/Post	-0.869	16	0.398
N180	Adjacent goal	-3.021	16	**0.008**
	Effector	-0.885	16	0.389
	Post	-1.076	16	0.298
	Pre	-2.260	16	**0.038**
	Pre/Post	-1.123	16	0.278
P122	Adjacent goal	-1.934	16	0.071
	Effector	-2.076	16	0.054
	Post	-0.752	16	0.463
	Pre	-1.820	16	0.088
	Pre/Post	-0.549	16	0.590
P213	Adjacent goal	-1.025	16	0.320
	Effector	-1.816	16	0.088
	Post	-0.284	16	0.780
	Pre	-2.519	16	**0.023**
	Pre/Post	0.096	16	0.925



**p<.05, ** p<.01*

Figure 47. The main effect of probe location, including the outer locations not involved with movement, organised by ERP component. Only data from electrodes contralateral to the side of probe presentation is shown. [P1: P3-8, PO3-8, O1/2; anterior N1: AF3-8, F1-8, FT7/8, FC1-6, T7/8, C1-6; posterior N1: CP3-6, P1-8, PO3-8; P2: F1/2, FC1/2, C1/2]



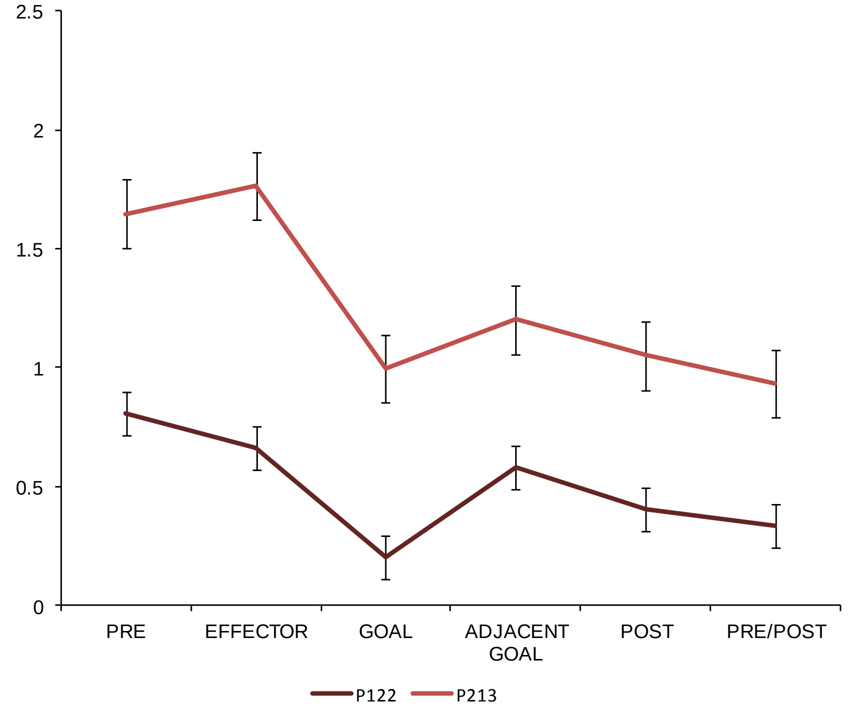


Figure 48. The main effect of probe location, including outer locations not involved with movement, organised by ERP component. Only data from electrodes contralateral to the side of probe presentation are shown. The top graph shows the negative going components (anterior N1, posterior N1), and the lower graph the positive going components (P1, P2). [P1: P3-8, PO3-8, O1/2; anterior N1: AF3-8, F1-8, FT7/8, FC1-6, T7/8, C1-6; posterior N1: CP3-6, P1-8, PO3-8; P2: F1/2, FC1/2, C1/2]

Discussion

The aim of this experiment was to measure visual processing at the goal, the effector, and at other nearby locations, during a simple pointing movement. The experiment reported in the previous chapter made use of an effector starting position, which, it could be argued, may have been treated as a second movement goal in a multi-stage sequential movement (from starting position, to goal, and back again), in which case any enhanced processing measured there may by virtue of it being a secondary goal, rather than being the location of the effector. This experiment dispensed with a starting position, thus ruling out that interpretation.

Participants were cued to make a pointing movement to the next target on an annular array in either a clockwise or anticlockwise direction. In the interval between the cue and the onset of the movement, a visual probe stimulus was presented at one of the six locations on the array; this elicited an ERP, the amplitude of which was compared across movement conditions.

Electrophysiological results

Four components of the visual evoked potential were elicited by task-irrelevant visual probes presented at one of the six possible target locations, a positive going parietal-occipital P1 (P122), followed by two negative going sub-components of the N1 complex, an anterior (N155) and posterior (N180) N1, and finally a positive going P2 (P2) component over fronto-central areas.

Simultaneous selection-for-action of goal and effector locations

The most straightforward result to interpret is what is referred to in this thesis as the "posterior N1", since it is this component at a latency that is often referred to as 'the visual N1', and has the best coverage in the literature. Previous work has shown enhanced processing, in the form of a larger N1 component, at the location of an action goal, both for saccades (Eimer et al., 2006) and for manual movements (Baldauf & Deubel, 2008a; Eimer & Van Velzen, 2006)[8]. This perceptual enhancement is highly similar to that observed as a consequence of spatial attention (e.g. Mangun & Buck, 1998). The results of the present experiment show enhanced processing at both the goal and the effector location simultaneously. If this enhancement is taken to reflect the selection-for-action (Allport, 1987;

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[8] Whilst these cited papers report modulation of visual processing at anterior, central and posterior sites, this was at a latency that corresponds to the posterior N1 component in the present experiment. The results from the present experiment showed an anterior N1 with a shorter latency to the posterior component, and as such it was analysed separately. It is difficult to compare the results of previous work that has either not observed a latency shift (in which case it may not have observed an anterior N1), or has not adjusted the time window at which the anterior component was measured (in which case the anterior N1 was not measured).

Neumann, 1987) of the functional components of movement, such as effector and goal, then these results show that both are selected in parallel. It is tempting to infer from the posterior N1 data that the goal and effector are functionally equivalent, but the P1 and anterior N1 results suggest that this is not the case. As with the experiment reported in the previous chapter, there appears - particularly in the data from these latter two components - that there is something fundamentally different about the goal location.

A specific pattern of results has frequently been observed in spatial attention paradigms involving the posterior and anterior N1, and the P1, components: the posterior N1 is larger for attended stimuli, but unchanged for neutral, suggesting that it operates by facilitating stimuli at task-relevant locations. In contrast, the P1 component is reduced for unattended stimuli and unchanged for neutral, suggesting suppression of stimuli at task-irrelevant locations. The anterior N1 sits functionally between the two, being enlarged for stimuli at relevant locations and reduced for stimuli at irrelevant locations (Di Russo, Martínez, & Hillyard, 2003; Hillyard & Anllo-Vento, 1998).

In the present experiment, P1 amplitudes were reduced when elicited by probes at the goal location, and unchanged for those at the effector and the adjacent goal. Here we see a dissociation between the goal and effector locations between processing reflected by the P1 and posterior N1 components, suggesting a functional difference between the goal and effector. The pattern of anterior N1 amplitudes was weaker, but the component was larger when measured over the hemisphere contralateral to the side of presentation when probes were presented on the goal, but not at other locations, suggesting that goal locations alone were subject to enhanced processing.

It is possible that the P1 component (peaking at 122ms) and the anterior N1 overlapped to some extent. The smaller P1 and larger anterior N1 both register a relative negativity in response to probes at the goal, suggesting that an ongoing negativity across both time points may have been affecting the modulation of both, although it should be noted that the selection of electrodes used in the analysis was guided by scalp maps and ERP plots which clearly showed separate positive and negative deflections.

Regardless of the degree of overlap or the precise functional significance of the modulation observed at the two components, the P1 and anterior N1 show the goal location undergoing a change in visual processing, whilst the effect and adjacent goal locations do not. The posterior N1, on the other hand, does not differ at goal and effector, suggesting that something different is happening at these two locations over the time course of visual processing, and ruling out a complete equivalence between them.

Perhaps the most parsimonious interpretation of this data is to consider the P1 as reflecting inhibition of the goal location during earlier visual processing, followed by enhancement of the goal and effector by the time that the posterior N1 is elicited. This may reflect some form of serial process in which effector locations are more relevant in early stages of processing, whilst goal locations become equally important later on. Di Russo et al. suggest, based upon a combination of source localisation of ERPs and event-related fMRI data, recorded during spatial attention tasks, that the earliest modulation of visual processing, reflected by the P1, takes place in retinotopically organised extrastriate cortex, followed by the later stages of the P1 and N1 time range, which reflect modulation in ventral areas specialised for pattern and object recognition. This hints at the possibility that early retinotopic processing does more work on the effector location whilst suppressing the goal, whilst non-retinotopic ventral processing that is reflected by the N1has equal priority access to representations of both the goal and effector. This may be an artefact of the mirror system that prevented participants from having visual access to their hand. Graziano (1999) showed that monkey premotor cortex contains multimodal neurons that respond both to tactile stimulation of an unseen arm, and to seeing either the monkey's own arm, or a false arm in the correct position. It is interesting to speculate that the greater activation of the (unseen) effector location in retinotopic coordinates hinted at by the P1 data may be due to the visual and motor systems attempting to locate the arm visually, in order to match the proprioceptively felt location of it.

The spatial 'profile' of action-induced enhanced visual processing

The strongest data recorded from this experiment concerned the goal and effector locations. Other locations outside of those involved in movement were also probed, and their results reported in the previous section. Whilst analysis of variance did not show a significant main effect of the various ERP amplitudes across all six locations, post-hoc t-tests and graphs showed some effects. These must be interpreted with caution, and inferences cannot as justifiably be made from these data in the absence of more robust statistical testing as from the goal and effector data discussed above. However, if taken in an exploratory sense, there are some interesting interpretations of this spatial 'profile' of action induced visual processing.

The ‘shape’ or ‘profile’ of visual processing has been addressed at various times in the context of spatial attention (C. Eriksen & St. James, 1986; LaBerge & Brown, 1989; Müller et al., 2005; Posner, 1980; Posner et al., 1980), and various evidence suggests that action planning causes very similar, if not identical, effects on visual processing as cueing attention (Corbetta et al., 1998; Craighero et al., 2001; Eimer et al., 2006; Rizzolatti et al., 1987). Therefore, it is instructional to consider whether similar processes are at work in the present experiment, as have been reported in the attention literature.

The most obvious conclusion from the plots presented in Figure 48 is that the enhancement of visual processing falls off with distance from the goal and effector locations. This is not surprising or contentious, since if the purpose of this change in processing is to select a particular area of space then they must be spatially selective!

A gradient account of processing implies a fall-off with distance that goes only one direction: less processing with distance. A Mexican hat account is similar, but suggests a spotlight of facilitation surrounded by a ring of inhibition (“surround inhibiton”, Müller et al., 2005, p. 1129), followed by either an area of facilitation or, at least, a release from inhibition, at greater distances. The data reported here is, to some extent, compatible with both accounts. If processing is tracked across space from the goal *backwards* to the locations that exist *before* the effector, then the fall of appears to resemble half of a spotlight: anterior and posterior N1 amplitudes decrease with distance and do not rise again. In the other direction, that is to say *forward* in the direction of movement, past the goal location, the pattern resembles half of a Mexican hat. The posterior N1 bottoms out at the location of the adjacent goal, before rising again, whereas the lowest point of the anterior N1 profile is one target beyond the adjacent goal, but again with a relative facilitation past this point.

Paired t-tests on the posterior N1 data (the component that showed the biggest effects), using the goal location as a baseline for comparison, show a significant difference at the location of the adjacent goal – the lowest point of the profile – but no difference at the two next outward-most points (labelled ‘post’ and ‘pre/post’ - Figure 48). This suggests that the ring of inhibition observed at the forward end of the movement space is evident at the adjacent goal, but then decreases after this point.

That this surround inhibition was only evident at locations in the forward direction of movement, but not at the directions preceding the starting position, is at odds with the symmetrical pattern of spatial attention that has been observed. Whilst this effect has been accounted for in terms of the receptive fields of striate and extrastriate neurons (Müller & Kleinschmidt, 2004), the size of the Mexican hat is affected by perceptual and cognitive load in attention tasks (Caparos & Linnell, 2010), suggesting that the presence or absence of the effect in a movement task as a consequence of the direction of movement may reflect the modification of the focus of visual processing according to task requirements.

There are many possible explanations for the presence of surround inhibition in the forward direction of movement only. One is that, whatever the purpose of surround inhibition, it is only necessary, or only implemented, around the goal, but not the effector. Here, the presence or absence of the effect is described in terms of the functional components of movement either eliciting or not eliciting it.

Alternatively, the direction of movement itself may be causing the presence of the effect in the forward direction, but not the reverse. If this is the case, then it is further evidence that the balance of processing priorities around movement are strongly affected by the particular task in hand. Perhaps the surround inhibition - which heightens the distinction between selected, and nearby-but-not-selected, objects and locations – serves to prevent actions being planned toward more distant distracters, and overshooting the target. Why, in this case, should there be no surround inhibition in the reverse direction? One explanation is that there is no danger of "going beyond" this location during motor preparation, since it is only taken into account as the starting point of a movement, whereas the goal is located on the trajectory of the movement, and so more susceptible to the hand physically overshooting it.

Given that enhanced processing was observed at both the goal and effector locations, it is possible that the profiles observed here represent the summation of two Mexican hats, one centred on the goal, and the other centred on the effector. If this is the case, then the point at which surround inhibition would be expected to be evident may differ between the two (goal/effector) profiles. This in itself may account for the lack of surround inhibition in the reverse direction.

One interesting inference that it is possible to draw from these results speaks to a broader issue of how spatial attention should be studied. Accounts of how visual processing is manifest during attention tasks fail to take into account that we rarely engage in such tasks on a day to day basis. The shape of the attentional profile may indeed be a perfect spotlight, gradient or Mexican hat when measured in the absence of any other task, but be fundamentally different when attention is employed as constituent part of something such as action. In this case, is it not more accurate to describe the shape of attention in terms of how it is elicited by action, rather than how it is elicited in the lab? It may be that perceptual-motor tasks such as this one are a more appropriate venue in which to examine phenomena such as spatial attention.

Behavioural results

Movement times were faster when the probe was presented on the goal than when it was presented elsewhere. It is most likely that the appearance of the probe attracted participants' attention to the target location that it was presented on, and caused interference with the cued movement when the probe did not fall on the goal, and facilitated the movement when it did. The difference was statistically significant, and the effect size not trivial (~100ms).

The sequence of events on each trial, however, precluded the possibility that these probe-induced changes in behavioural performance interfered with the ERP data. The probes were presented before the execution of the movement, and the electrophysiological results were measured from the brain's response to them. Speeded movements made subsequently to this measurement being taken cannot plausibly affect the measurement itself.

CHAPTER 6: **GENERAL DISCUSSION**

The experiments reported in the preceding chapters are concerned with the detail of how action affects perception, specifically in terms of the changes that visual perception undergoes during motor preparation. Much recent work, underpinned by the Premotor Theory of Attention (Rizzolatti et al., 1994, 1987) and the Visual Attention Model (Schneider, 1995), concentrated on how motor preparation affects perception at the goal location of an action. One of the major aims of this thesis is to develop the conception of these processes, and to expand the theoretical scope to include perceptual changes at the location of the effector, an aim that was met in chapters four and five. The functional significance of this finding, and its relevance to our understanding of perceptual-motor processing is discussed below.

Chapters three and four reported experiments that aimed to investigate the time course of the action-induced changes to visual processing, using two different classes of manual movement: grasping and reaching. By measuring visual attention at differing time points during motor preparation it was possible to describe how perceptual enhancement of action-relevant stimuli develops over time. Chapter four also described how this temporal pattern applied to the location of the effector, in addition to the goal, and showed differences in how the two components of movement are processed across time.

Chapter five described an experiment using a different ‘go/no-go’ paradigm, and a third class of movement: pointing. The movement task in this experiment allowed visual processing to be measured at more distant locations to those actively involved in the cued movement on any particular trial. This allowed the effect of action-induced changes on perception to be described in terms of its spatial profile, and provided a confirmation of the results concerning the processing of effector locations that were described in chapter four.

Together these experiments add to the existing knowledge about how action affects perception in terms of time and space, and in terms of the functional components of movement, such as effectors and goals. In a broader sense they provide hints of how cognitive mechanisms give rise to the selectivity that supports other, higher level, cognitive processes.

This chapter will summarise and discuss the findings of these experiments in detail, as well as draw more general conclusions from them. Before that, some of the theoretical accounts that were introduced in chapter one will be considered again in light of the experimental findings.

Selection-for-action

Chapter one introduced the concept of selection-for-action (Allport, 1987; Neumann, 1987), the principle that a vital part of motor preparation is the selection of various object representations that are involved in the movement currently being planned. This conception of action planning has been referred to repeatedly throughout this thesis, as it provides a basis for understanding the purpose of the perceptual consequences of action upon which have been investigated herein. A central issue is that of goal and effector selection.

A potential link between overt (in which the eyes fall upon an attended area), and covert (the movement of the 'mind's eye') attention was noticed long before the Premotor Theory of Attention provided an explanatory framework around it (e.g. Crovitz & Daves, 1962). The hypothesis that similar neural mechanisms may be responsible for both the tendency for us to fixate upon salient stimuli, and for the ability to selectively attend to such stimuli in the *absence* of eye movements, is a relatively obvious one, particularly given the predominant role of vision in human and non human primates in guiding everyday behaviour. As such, the very earliest work on perception and action was exclusively concerned with saccades (e.g. Posner, 1980; Rizzolatti et al., 1987), in which case selection-for-action can refer only to goal selection, since the effector involved in a saccade does not occupy an area of space (at least retinotopically) in the same way as a hand or a finger does. Likewise, there is no requirement to select an effector whilst planning a saccade, whereas unimanually reaching out to grasp an object requires at least the specification of which hand, of a choice of two, is going to be used.

Nevertheless, experimental paradigms that were developed to study saccades (e.g. Schneider & Deubel, 1995) were soon extended and applied to manual movements (Deubel et al., 1998) with very similar results. If the enhanced processing that is characteristic of the preparation of both saccades and manual movements is taken to reflect, at least in part, selection-for-action, then goal selection appears to be a cognitive function that operates supramodally, in the sense that it applies to multiple classes of action.

A central question of this thesis is whether this 'supramodal' characterisation of selection-for-action between different classes of movement can also be applied *within* the functional components of each individual movement. Is selection-for-action exclusively a goal-directed phenomenon, specifying and making available for processing the end point of an action in a totally rigid sense? Or could selection-for-action be a more general process that can be applied to goals during saccade preparation, and to goals and effectors during the preparation of manual movements? More broadly, does the data reported in the experimental chapters even justify an account of action-induced perceptual processing in terms of selection-for-action?

The experiment reported in chapter five, in which participants were cued to point to locations on an annular array, clearly shows that the goal *and* effector locations receive enhanced processing during motor preparation, at least in terms of the pattern of the posterior N1 component. Within the confines of that particular movement task the effector and goal were indistinguishable in terms of how action planning causes them to be processed. This was not the case, however, when the time course of motor preparation was taken into account in the reaching experiment described in chapter four; here, goal and effector locations were similar but not equivalent. In terms of the visuo-spatial selection-for-action account, the goal was selected throughout this time period, whereas the effector was only selected in the middle (200 ms) of three points in time at which probes were presented. Taking the very simplest form of selection-for-action as a starting point, in which enhanced processing during motor preparation is considered to fulfil the purpose of selecting the location of one movement component amongst many in binary (selected or not-selected) fashion[9], is not adequate for the following reasons:

1) If selection occurs because a requirement for the successful planning of action is to specify one goal, or one effector location, to pass to motor processes, then the goal location should not remain ‘selected’ at the same time as the effector location. Either a high degree of specificity is needed, or it is not: if it is acceptable to have more than one component location selected at the same time, why bother selecting in the first place?
2) If all that action-induced changes to perception represent are selection processes, and if these processes are supramodal in the sense of being able to select goals or effectors, then the enhancement at the effector location should be identical to that at

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[9] It should be noted here that Allport (1987) and Neumann’s (1987) accounts of selection-for-action are not limited to the simplest version described here. They are deliberately general, and emphasise the requirement for some form of action-selection occurring during movement planning, rather than specifying exactly how. On the other hand, VAM comes close: “*...selection functions are performed by one common visual attention mechanism which selects one object at a time for processing with high priority*” (Schneider & Deubel, 2002, p. 610); the heavily simplified characterisation of selection-for-action under discussion is not, therefore, entirely fanciful in its simplicity.

the goal location. The fact that the pattern of enhancement across time is not suggests a difference in how these two components of movement are processed.

Of course this is only the most basic conception of how selection-for-action may occur, and is to some extent an argument against a simplistic caricature of the process. Observing a pattern of results that is difficult to explain purely in terms of simple selectivity, such as those from the reaching experiment in chapter four, doesn’t rule out selectivity occurring, but may reflect more than one process being active during motor preparation. It would mean going beyond the data from these experiments to decisively suggest what these other processes may be, but one example of many possibilities is that the 200ms probe timing (that showed enhancement at the effector) represents effector selection, whereas one of either the earlier or later probe timing (showing enhancement at the goal) represents a selection of the goal. Some other process, acting upon only the goal in addition to selection-for-action, may then be causing the broader goal-enhancement measured at the other probe timings.

A broader question is whether it is justifiable to use the selection-for-action account to try to understand these results. The results of the pointing experiment in chapter five show enhancement at effector and goal locations. Here, however - as distinct from the reaching experiment of chapter four - the same hand is used for an entire block. Selection, at least in terms of how it has been described above, is a binary concept: a hand is either used in a movement, or it is not. But what was probed in these present experiments was not actually an effector, but a location in space that was occupied by an effector. And what was observed was an *enhancement* of processing at this location, not a black and white pattern of processing at action-relevant locations and no processing elsewhere. The consequences of action are not binary, but a matter of degrees. As already mentioned, part of the contribution to the observed enhancement may be a selection process that *is* binary, but other processes may also be at work, enhancing motor preparation in order to make action more efficient.

The Premotor Theory of Attention

The Premotor Theory (Rizzolatti et al., 1994, 1987) characterises the neural representation of space as emerging online from transformations of multiple effector-specific neural maps of space. These maps are responsible for both the perception of space and the planning of goal directed action, and are activated in a similar way during cued shifts of attention, and motor preparation. According to this view, saccades and shifts of spatial attention are similar because preparing a saccade involves facilitating the goal location of that saccade. This facilitation, applying as it does to perceptual areas, is the enhanced processing associated with attentional benefits, and as such it is also seen when preparing a motor programme. As expected, this goal enhancement was found in all three of the experiments reported herein.

The Visual Attention Model (VAM)

VAM (Schneider & Deubel, 1995) makes similar predictions to the Premotor Theory, predicting that motor preparation activates the neural representation of the goal object in the dorsal processing stream (cf. Goodale & Milner, 1992) in order to make its spatial properties available for incorporation into an action plan. This, in turn, leads to activation of the same object's perceptual representation in the ventral stream, which causes the observed enhanced processing at that location. VAM makes no predictions about effector selection, but it is not difficult to imagine the dorsal representation of an effector also being activated in the same way as the goal, with the same perceptual consequences once activation has spread to the matching ventral representation.

One problem for this interpretation is that VAM specifically predicts that only one object may be activated at a time. This is not compatible with the temporal pattern of results observed in the reaching experiment of chapter four, in which the goal and effect showed enhanced processing at the middle, 200 ms, time point. Of course, as with the discussion of selection-for-action, this assumes that the perceptual enhancement observed is *only* a consequence of processes predicted by VAM, whereas simply positing an unknown additive processes that has the effect of biasing processing at the goal, would clear up the difficulty. Even so, the uncertainty of what this processes or processes may be, and VAM's inability to explicitly predict the pattern of results observed here, is a weakness.

Possible two-process explanations for a temporal bias at the goal

Interpreting the results of the reaching experiment in chapter four in terms of selection-for-action, the Premotor Theory, or VAM, presents problems relating to the time course of the observed goal and effector enhancement. Putting aside worries concerning whether a goal *and* effector should be simultaneously selected-for-action (regardless of the mechanism by which this occurs), there is still the issue of why goal enhancement is seen across the time course of preparation, whereas effector enhancement appears transitory. It has been tentatively suggested that the 'extra' enhancement at the goal, on top of what would be predicted by theories that emphasise selection, may be the result of an additional process which is biased toward the effector, the time course of which is broader. It may be helpful, then, to postulate two processes at work during the preparation of manual movements:

1) *Goal selection*: something akin to the goal selection that occurs during saccades: retinotopic representations of space are weighted according to the location in the visual field of the goal. This may reflect the planning of a saccade to that location, albeit a saccade that is not executed due to participants being instructed to maintain central fixation (we do normally look at goal objects of action, after all). During delayed saccades, attention has been shown to linger on the goal until execution (Deubel & Schneider, 2003). If this first process is assumed to represent a planned saccade to the goal, then the temporal profile – given that the saccade is never executed – would be expected to be flat.
2) *Enhancement of the functional components of action*: in order to maximise the efficiency of action, the action programme requires the most exquisite and detailed information possible regarding the location and orientation of any action-relevant components, such as goals and effectors. As the behavioural consequences of the visual probe stimuli seem to suggest, the more processing that goes on at these locations during movement planning, the faster and more accurate action is. This process may not reflect anything so binary as outright selection, but more of a graded facilitation of relevant locations, perhaps reflecting the total processing capacity of the perceptual-motor system being divided amongst locations. The expected time course of this effect is uncertain, but the behavioural consequences of the probes in the reaching experiment shows a much greater effect on both speed and accuracy at the early, vs the middle and late time probe timings. Confusingly, the simultaneous enhancement of effect and goal is observed in the middle SOA. However, positing this hypothetical second process as being relatively rapid and occurring at a discrete point in time does at least marry in terms of the behavioural and electrophysiological results reported here.

To begin positing multiple processes initiated by motor preparation, the perceptual effect of which is additive, is an open ended exercise. If two processes are possible, then why not three, or five, or twenty? However, there are two reasons why it may be justified to make these predictions: firstly, the pattern of data does not fit neatly with any existing single-process account; and secondly, it would be a rare cognitive process that operates in complete isolation. Whilst it may be unavoidable to describe cognitive processes in a unitary fashion in order to understand them, this is a deliberate simplification, and it is likely to be very unrealistic to assume that this is what is really happening on a functional level. The suggestions made above are best considered as starting points for further research.

In a paradigm in which the effects on perception of preparing to saccade were compared with those of preparing to make a manual movement, then subtracting the pattern of results in the movement condition from that in the saccade condition would remove the effects of processing that are general to both saccades and manual movements. It may be that the only difference is evidence of effector selection in the manual condition, but it may also be that processing at the goal differs between the two. If saccade planning is the second of two additive processes, and goal/effector selection the first, then this design will be capable of eliciting the difference in visual processing between the two.

The effect of required accuracy on perception during grasping movements

The experiment reported in chapter three, in which the degree of accuracy needed to successfully grasp a part of an object was manipulated, did not show such promising results. Whilst the data hinted toward an effect of required accuracy, it was not strong, particularly in comparison to the effect of grasping or not grasping per se, which showed the expected visual modulation of goal locations. The failure to show a clear effect of accuracy may, of course, be attributed to an incorrect hypothesis: perhaps the degree of accuracy simply doesn’t figure in the processing that happens during motor preparation.

On the other hand, the perceptual enhancement and two process accounts described above do have some relevance to the hypothesis:

1) *Perceptual enhancement*: If the simplest form of binary selection-for-action is to be discarded in favour of a graded enhancement of processing at action-relevant locations, as is argued for above, then location that requires a high degree of accuracy would be expected be processed at a higher priority than one requiring less. If maximising the efficiency of the resulting movement, once executed, is the reason for the changes in perceptual processing that are brought about by motor preparation, then required accuracy would be expected to play a part.
2) *Two process account*: That the results of this experiment showed the expected modulation between grasped an ungrasped conditions, but did not sure a strong effect of required accuracy, can be accounted for by positing two processes involved in motor preparation. If the first process is akin to what occurs during saccade planning,

> and causes enhancement of goal location, then this would explain the modulation between grasped and ungrasped conditions. If the modulation according to required accuracy is accounted for by the second process – the same process that was invoked in the passages above to explain the temporal pattern of modulation at the effector in the reaching experiment – then a differential weighting of the contribution of each of the two process may explain the relatively weak results relating to the accuracy manipulation.

If the combination of graded perceptual enhancement *and* a two process account are taken into consideration, then the relative lack of differences between blunt and sharp ends of the object may be due to the required accuracy between the two ends not being great enough. Perhaps the second process of a two process account *was* modulating sharp over blunt ends of the object, but just enough to ensure an accurate grasping movement. Perhaps this degree of modulation was ‘swamped’ in the final analysis by the first process, that biases perception toward goal locations. An accuracy manipulation with a greater difference between less accurate (blunt) and more accurate (sharp) stimuli may cause greater modulation of perception between them.

Additionally, it is possible that a grasping movement is not the most appropriate choice to study this accuracy manipulation, since visual processing is possibly being divided between two goal locations, and perhaps the two finger tips, leaving the paradigm with less ability to discern an difference caused by accuracy alone. Perhaps a task in which the accuracy manipulation is more extreme, with fewer additional factors to distract from it as a primary variable, will resurrect this hypothesis in future.

Movements such as reaching and pointing are implemented by distinct neural circuits as compared to grasping movements. The effects reported in this thesis suggest either that a) the aspects of motor preparation studied here operate independently but in a similar way, or b) are both served by the same systems. It may be that much divergence occurs later in the processing pathway from a motor intention to execution of a subsequent action, but that earlier stages of processing, in which the representation of the goal of action is passed to a motor plan, are the same. Regardless of the exact mechanism, the similarity in terms of the effects on perception of motor preparation across grasping and reaching movements shows that different classes of movement share at least some similarities.

The spatial profile of action-induced changes in perception

The spatial profile of visual attention has been described variously as a hard-edged spotlight (Posner, 1980), in which areas within the spot are attended, and those outside are not; as a gradient (LaBerge & Brown, 1989) of the focus of attention are soft and fall off gradually; and as a Mexican hat (Müller et al., 2005), essentially a spotlight with an area of surround inhibition at its edge (see Figure 1, chapter 1, for a visual illustration of these three possibilities).

The results of the pointing experiment were able to shed some light on how these distinctions apply not only to spatial attention, but also to the spatial profile of the similar effects that are seen in response to motor preparation. The model of a hard-edged spotlight was not supported: as the profiles in Figure 48 show, perceptual enhancement fell of gradually, far more in the style of a gradient model than a spotlight.

The issue of whether surround inhibition was observed is difficult to resolve, since statistical analysis of the different data points did not reveal a strong effect. Some differences were observed by conducting paired-samples t-test that took the level of enhancement at the goal as a baseline and compared it to each other data point. According to these results, enhancement fell off at locations past the adjacent goal location before rising again at more distant locations. This was only observed in the same direction of movement; in other words, *if* this was surround inhibition then it only applied to those locations past the goal, not to those preceding the effector.

Since the differences between data points were often not statistically significant, it is not possible to be definitive about this pattern of results. It can be concluded that the shape of action-induced perceptual enhancement is very similar to that of spatial attention and, whilst it is spatially selective, it is not as specific as could be conceived, since the fall-off with distance is relatively gradual. This specificity may, in line with the zoom lens model of attention (C. Eriksen & St. James, 1986) turn out to vary with task difficulty, or some other measure of cognitive or perceptual load, rather than being a fixed size in any task.

Comparison of perceptual enhancement between experimental tasks

The experiments reported in this thesis used three very different movement tasks: grasping, reaching and pointing. Overall the similarities in the observed effects of movement vastly outweighed the differences, a fact that in itself is informative about the processes underlying motor preparation.

In the experiment that involved reaching movements, the auditory cue instructed participants both where to move, and when to execute the movement (they moved as soon as they heard the cue – “cued movement”). The pointing experiment in chapter five adopted a paradigm in which a separate auditory cue instructed participants where to move, and a second auditory “go” signal instructed them to execute the movement (delayed response, or “go/no-go” paradigm). In the cued movement task, probes were presented shortly after the cue, in a period in which the transition from planning to execution was inherently fuzzy. In the go/no-go task, the planning phase was temporally separate from the execution phase; probes were presented during the former, and never during the latter. Using these two different approaches in the experiments reported here, and showing that the immediate-response paradigm that is typical of behavioural work is comparable to the delayed response paradigm more usually seen in electrophysiological work, goes some way to bridging the gap between the two methodologies. Despite such different approaches to the mechanics of measuring visual processing, the results were very similar.

The cued movement task used probes presented at different times after the onset of the cue/go signal, unlike the go/no-go task, in which the planning phase is artificially lengthened whilst participants wait for the “go” signal[10]. The results of the cued movement task showed enhanced processing of the effector only at the middle time period, but not at earlier and later times. Whilst the statistical analysis of goal and effector locations in the delayed response pointing experiment showed no difference between the two, the bar graph in Figure 43, and the ERPs shown in Figure 40 suggest that the degree of effector enhancement is less than that at the goal: falling midway between goal and adjacent goal. If the results from chapter four chapter were averaged across all three probe timings, this is the pattern of results that would be expected: the effector would show enhancement, but not as much as the goal, by virtue of the more sustained pattern of enhancement over time for that location. Again, it appears that the results from both tasks are in agreement.

The ecological validity of the grasping and reaching experiments is greater than for the pointing experiment. Rarely in life do we prepare to act upon an object or location, and then

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[10] Whilst it would certainly be possible to employ differing probe timings in a delayed-response task, the artificial gap between the cue and the ‘go’ signal makes it difficult to know what this would show. In a immediate response task, it is safe to assume that the participants executed the movement as soon as they could, in which case the time period preceding execution should reflect motor planning. In a delayed-response task, there is not requirement to plan quickly, as there is a large gap (relatively speaking) between planning and execution. As such, the delayed response paradigm does not lend itself to multiple probe timings, at least in terms of providing results that would be easily interpreted.

wait in anticipation of a ‘go’ signal to execute the movement. The comparison of results across the two paradigms suggests that the relative artificiality of the go/no-go paradigm is no barrier to its experimental use, since the results do not appear to differ to those reported in the cued movement task. It is also an indication of how robust the effects reported here are, particularly in terms of enhanced processing at the effector. A result such as this might be expected to disappear as tasks change, but was consistent across two different paradigms, using two different classes of movement, involving the selection of a different number of effectors.

A further difference between the reaching and pointing experiments concerns the use of a starting position. This is a common aspect of movement tasks that measure perceptual processing at the location of the effector (e.g. Forster & Eimer, 2007; Gherri et al., 2009; Van Velzen et al., 2006) since it helps to ensure consistent movement characteristics across trials. Evidence from sequential reaching movements, however, has shown that planning a sequence of movements to multiple goal locations leads to enhanced processing of each goal location in parallel (Baldauf & Deubel, 2008a; Baldauf et al., 2006). If a movement task involves moving from a starting position to a goal and back again, then even though the return leg of the movement is not explicitly cued, it must still be planned. If perceptual processing at the location of the effector is measured by probing the hand at the start location during motor preparation, then any enhancement may be the result of the starting position being the second goal in a sequential movement, rather than a consequence of the effector’s location per se.

The pointing experiment reported in chapter five used a starting location that was only nominated at the beginning of each block, not the beginning of each trial. Instead, participants kept their hand at the end location of the previous trial, and continued the next trial from there. It might be expected that removing the confounding influence of the starting position being a secondary goal would have eliminated the effect of enhanced processing at the effector location, but it did not.

The influence, and relevance, of task instructions

Much of the work concerning perceptual enhancement at the goal and effector during action planning has shown strong effects of task instructions (Gherri et al., 2009; Van Velzen et al., 2006). The experiments reported here did not manipulate task instructions, but chapter one speculated that, whilst task instructions certainly influence outcomes, they are not likely to be the strongest influence. In light of the results described in previous chapters, two points arise that may help to put these studies in context:

1) Enhancement was found at both the effector and the goal simultaneously, in two different experimental tasks, each with slightly different instructions (reflecting the nature of the two tasks) given to participants. The experimental carried out by Gherri et al showed enhancement at either goal *or* effector locations, depending upon which was emphasised in the instructions. It is suggested that task instructions are one factor of many that determine the allocation of enhanced processing. The experiments in this thesis are not able to estimate the relative contribution of task instructions to perceptual outcomes, but do show that it is possible for both goal and effector to be enhanced in parallel.
2) The experiments reported by Van Velzen et al. and Gherri et al both used the same delayed response ('go/no-go') paradigm as the pointing experiment in chapter five. The reaching experiment in chapter four did not, and as such was able to use a more temporally sensitive design and to measure how perception is biased over the time course of motor preparation. Whilst the goal location was enhanced throughout, the effector location only showed enhancement in the middle of the time course but not at early and late probe timings.

   It is difficult to say how the stages of motor preparation compare between in a task in which participants execute a movement immediately and a delayed response task, but it seems reasonable to assume that those studies that show large effects of task instructions may not have been able to probe the same range of stages of preparation as the reaching experiment did. If this is the case, it may be that task instructions altered the temporal sequence of perceptual enhancement, perhaps speeding or delaying it being allocated to goal or effector, or even reordering the sequence, such that only the effector *or* the goal appeared to receive enhanced processing, when in fact the probes were taking a snapshot in time of a particular perceptual state.

Of course task instructions have reliably been shown to affect changes in perception, and it would be interesting to manipulate them using the reaching paradigm, in order to determine how they affect perception over time. It would also be valuable to study how the influence of task instructions affects the time course of the experiment itself: as participants become accustomed to the task in hand over many trials, does the relative influence of the instructions given at the outset decrease?

Multisensory perceptual-motor processing

In all of the experiments reported in chapters three, four and five, participants carried out each movement task without being able to see their hand or finger. This means that they located the starting location of the effector, and then guided the effector to the goal, using only proprioception. The probes used to measure perceptual processing were visual, as was the goal location that formed the movement target. These visual probes showed enhanced processing not just at the visual goal - which, after all, had been located visually - but also at the effector. It suggests that the location of the effector in space, as registered by proprioceptive input[11], updates a supramodal representation of the environment, such that when a visual probe is presented at the same location in allocentric space and perceived in retinotopic space, it must be translated to an allocentric frame of reference in order for the location of the effector to be matched to the location of the probe. This suggests that the effects of action on perception operate in a supramodal fashion, not limited to just vision, or just proprioception. This conclusion lends further weight to the contention that the effects on perception of action are very similar to the effects of spatial attention, which have been shown to operate in both visual and tactile modalities (Eimer & Van Velzen, 2002).

Sensory gain control

Chapter one discussed the neural mechanisms that may underlie spatial attention and, by extension, the modulation of perceptual processing that occurs as a consequence of motor preparation. Much evidence supports the ‘sensory gain’ account of attention, in which the firing rate of neural populations that process perception is increased by top down control (Hillyard & Anllo-Vento, 1998). These areas may be specialised for processing a particular sense modality, a particular feature such as motion or colour, or organised retinotopically and responsible for the perception of a particular area of the visual field.

This process is reflected in the scalp maps that can be calculated from EEG data in spatial attention tasks. If participants are cued to a particular area of space, and subsequently a visual probe stimulus is presented in the attended area, then the scalp distribution of the resulting N1 can be compared with a condition in which the probe was presented in the unattended area. If the gain control account is correct, then the difference between the scalp distribution of the visual N1 ERP across the two conditions will be a matter of amplitude only, that is, the same

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[11] Although this experiment cannot rule out that the location of the effector was stored visually, since the starting position was visible throughout the experiment, even though the hand itself was not.

brain region will be activated, just less so. Spatial attention does not, according to the gain control account, activate any additional neural populations in order to modulate perception.

The same logic can be applied to the results from the experiments reported here. Scalp maps can be calculated from two different classes of brain activity: 1) the distribution of the N1 ERP elicited by the probe stimuli; and 2) the *difference* between the distribution of the N1 elicited in response to a probe on a goal or effector that was involved in a cued movement, and one that was not. This second scalp map is calculated by subtracting the neural activity during the not-moving probe condition from the moving probe condition, and represents the scalp distribution of the action-induced effect itself.

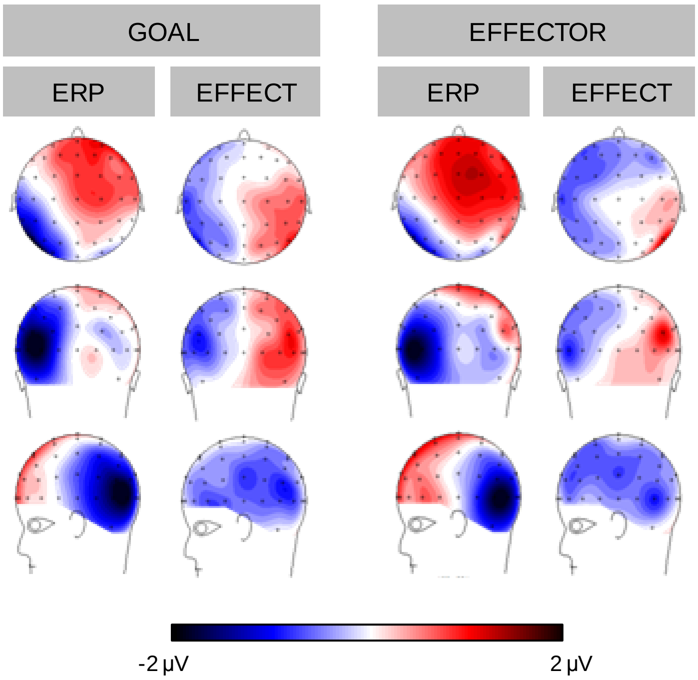

Figure 49. A comparison of scalp distributions of the visual N1 ERP elicited in response to a probe stimulus in the movement condition (left hand column, labelled ‘ERP’) and the scalp distribution of the effect of motor preparation (right hand column, labelled ‘EFFECT’), calculated by subtracting the not-moving condition from the moving condition. Shown separately for probes presented on the goal (left hand side) and the effector (right hand side). Data has been collapsed across hemisphere, such that the left hand side of these maps shows activity contralateral to the side of probe presentation. These maps are taken from the reaching experiment reported in chapter four, and show the mean amplitude of the N1 component in the 40ms measurement window centred on the peak of the ERP, elicited by probes presented at 200ms post cue offset.

Figure 49 shows a comparison of these two scalp maps. If the only neural mechanism responsible for the perceptual enhancement associated with motor preparation, then the maps should show the same distribution (although the amplitude may differ). It can clearly be seen that this is not the case. Parietal areas show a similar distribution, although the distribution of the effect appears to be slightly more anterior than that of the ERP. Fronto-central areas show more of a difference, being relatively positive in the ERP conditions, but noticeable negative in the effect condition. This suggest that, at the time of the visual N1 component, it is not just neural activity in visual cortex that differs.

In the absence of an attention-only manipulation it is not possible to say that this frontal negativity is definitely related to motor preparation; it may simple be that some idiosyncrasy of the task caused these differences. However this pattern of scalp distributions is not compatible with a pure gain control account.

It is perhaps not surprising that it is frontal regions that appear to be driving the differences between how moved-to and not-moved-to areas of space are processed. The putative fronto-parietal attentional network (Corbetta & Shulman, 2002; Gitelman et al., 1999), discussed in chapter one, and often described in terms of the ADAN and LDAP ERP components observed in attentional (e.g. Eimer & Van Velzen, 2002; Hopf & Mangun, 2000; Nobre et al., 2000) and motor tasks (e.g. Eimer et al., 2007; Gherri, Van Velzen, & Eimer, 2007), is hypothesised to reflect attentional control signals, originating in frontal areas and having their effect in visual cortex. Likewise direct electrical stimulation of the FEF in monkeys (Moore & Fallah, 2004; Schiller & Tehovnik, 2001), and TMS stimulation of the putative homologue in humans (Gutteling et al., 2010; Neggers et al., 2007; Van Ettinger-Veenstra et al., 2009) cause the kind of perceptual enhancement in visual areas that is associated with both shifts of spatial attention and the consequences of motor preparation.

Enhanced processing, enhanced action?

The behavioural measures reported in each experimental chapter were not designed to directly address the aims of these experiments, but rather to describe how the manipulations and measurements of action and perception affected the movements themselves. However, they provide indirect evidence for the role that perceptual enhancement may play in motor preparation.

A general pattern across all experiments was that when the visual probe stimuli fell upon the goal of an action, or the effector that was about to be used, then the subsequent movements were more accurate and faster than if they did not. In the reaching experiment described in chapter four, the three probe timings allowed a further insight into this process, in that the probes had a greater facilitative effect on action when they were presented earlier rather than later during motor preparation.

Clearly flashes of light on a relatively dark display, in a darkened room, capture our attention. This does not have consequences on electrophysiological measures of visual processing, since the measurement tool is the probe itself, and by the time it has exerted an effect on movement the measurement has already been taken. However, by analysing the behavioural measures of movement speed and accuracy, it is clear that attracting visual attention to a component involved in a current movement facilitates that movement (or, equally likely, that attracting attention to an irrelevant component causes interference and *harms* the efficiency of the resulting movement, in a similar manner to the irrelevant distracters in Tipper et al., 1992). If exogenous facilitation of goals and effector locations enhance action, then does the endogenous facilitation that occurs as a result of motor preparation reflect a top-down enhancement of these same goals and effectors? If selection is binary, then this process is more akin to a graded gain control, in which the balance between the strength of action-relevant and irrelevant locations in the brain is weighted by the intention to act.

Interpreting these findings in the light of this ‘enhancement’ view of motor preparation makes better sense than doing so in light of the (binary) selection-for-action view, on a number of levels:

1) The reaching and pointing experiments of chapters four and five, respectively, showed a very similar pattern of results. Yet, as discussed above, only the reaching experiment had a clear requirement to select one effector out of two on a trial-by-trial basis. *If* the pointing experiment had less of a requirement for effector selection[12], then the enhancement seen at the effector location can be understood in light of motor preparation enhancing it in order to pass the most complete and detailed perceptual information into the movement plan. This process, unlike effector selection, would be just as much of a requirement on a trial-by-trial basis, regardless of the number of potential effectors to be selected amongst.
2) The broad temporal bias toward the goal in the reaching experiment described in chapter four, not seen at the effector, may also result from a non-equivalence between the two classes of movement component. If perceptual information about the goal location is, for whatever reason, move important to action planning than is information about the location of the effector, then this would explain the relatively

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[12] This is speculative, but does fit with a similar principle established during delayed manual reaching tasks, in which the reach can be ‘pre-planned’ and the motor programme held until executed (Deubel & Schneider, 2003).

longer enhancement at the effector. A binary (selected vs not selected) explanation struggles with these data.

As a postscript, it should be noted that both the endogenous biasing of perception toward the action-relevant as consequence of motor preparation, and the exogenous biasing of perception indicated by the enhanced behavioural performance in response to the visual probes, is entirely compatible with the Integrated Competition Hypothesis (Duncan et al., 1997). In this view, attention serves to modulate neural processing of relevant stimuli at an early stage of cognition, and this early bias then causes a 'cascading ascendency' through later, higher-level stages of cognitive processing. Either endogenous or exogenous biasing of perception of action relevant locations would succeed in 'tagging' their representations early on, with concomitant effects on the movement when it is eventually executed. Whether this tagging originates from top-down processes arising from deliberate motor planning, or as an unintended consequence of exogenous attractors of attention flashing away in the visual field, is unimportant: the attentional state of the individual has been biased one way or another, and tends not to be reset after the fact.

Conclusions

Broadly speaking, the experiments in this thesis confirm what is known about how motor preparation affects perception. Chapter one began by describing these links as "what you *do*, affects what you *see*", and all of the experimental results confirm this statement. These experiments cast action-induced perceptual changes as being highly flexible. Preparing to grasp, reach to, or point at a location in space causes enhanced processing at that location, and at the effector that is executing the movement[13].

The novel finding of simultaneous goal and effector enhancement is important because it clarifies how perception is altered during motor preparation. The existing literature on these effects is mixed, sometimes showing enhancement at the effector, and sometime at the goal – although most frequently at the goal, presumably because the nature of the work in this area was confirmatory rather than exploratory. This has led to an implicit preoccupation with goal locations, and an interpretation of the Premotor Theory and VAM as describing a process that ultimately operates on goal locations.

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[13] At least in the case of reaching and pointing movements; this was not tested in the case of grasping movements, but given the pattern of other results, it is a fair assumption that it would.

Whilst the goal of an action must surely inhabit a privileged position in motor processing, being the end point of the eventual movement, elevating it to the status of being so important that motor preparation is effectively viewed as being specialised with it in mind seems too strong. Assuming an extremely even handed position, however, and assuming that the goal is just one component of movement out of many – the others being effectors, and perhaps obstacles – is to be too strong in the opposite direction. The ease with which empirical evidence has supported a theoretical pre-eminence of goal locations, and the data reported here, suggest that goal locations really are processed at a high priority during movement: just not at the total expense of all others.

The robustness of the findings of enhancement of effector locations across two very different experimental tasks suggests that the prominence given to effectors as a functional component of movement, by the interpretations of these findings, is not unwarranted. Previous studies have shown fleeting effects of processing at effector locations that are liable to vanish completely when the task at hand is merely described goal-centric terms. Taken together, the results from chapters four and five suggest a healthy degree of reliability of these effects.

The fact that perception was enhanced at both goal and effector locations in parallel provides a powerful basis for thinking about motor preparation. A study that showed enhancement at only one location or another can only speak to the fact that, in certain specific situations, *either* goal *or* effector locations seem to be the most prioritised during motor preparation. *Simultaneous* enhancement, on the other hand, demonstrates in principle that both locations are prioritised in tandem. Viewed in light of this conclusion, any movement tasks that do not elicit simultaneous enhancement of both locations are not reporting the full picture. There can be many practical and conceptual reasons for this happening, from how perception is measured, to task instructions, lack of statistical power, or the demands of the task itself. Most often in the existing literature, the reason for not finding effector enhancement is that nobody was looking for it. Whatever reasons, however, the experiments reported here suggest that, if the aim is to elucidate the processes that underlie motor preparation, a lack of enhancement at the effector is a sign that something important may have been missed.

Care has been taken through this thesis to refer to ‘enhanced processing’ as opposed to ‘spatial attention’, despite the clear similarities between the effects reported within it and the effects of cueing attention. The issue at hand here is semantic: what do we mean by the term ‘attention’? It is tempting to constrain the definition by tying it to specific cognitive tasks, such as visual search, or a Posner paradigm, but these are merely demonstrations of particular ways in which attention manifests itself. According to the Integrated Competition Hypothesis, attention is an emergent property of large scale neural networks, changing firing rates according to some criterion relating to relevance or salience at a particular point in time, with a particular cognitive goal in mind. In that case, then when the cognitive goal is to execute a movement, the effects on perception of motor preparation *are* attentional.

This view frames attention as a flexible tool that is directly used by – and indirectly supports – cognitive processing itself. One question that the experiments reported here cannot address is why the effects on perception, caused by action, should even occur. Given the importance of action to animals and humans, it is interesting to speculate whether attention, in all its manifestations, arose from action in the first place, and has since been ‘retooled’ by natural selection to support operations such as visual search, object recognition, and working memory.

The fact that the experiments described here show selection of the components of movement occurring in a dynamic and flexible, but ultimately very reliable, way, suggests that the patterns of inhibition and facilitation that achieve it are always available: always enhancing perception, and recasting our experience of the environment according the requirements of the task at hand.

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